

Holocene Footprints in Namibia: The Influence of Substrate on Footprint Variability

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ABSTRACT We report a Holocene human and animal footprint site from the Namib Sand Sea, south of Walvis Bay, Namibia. Using these data, we explore intratrail footprint variability associated with small variations in substrate properties using a “whole foot” analytical technique developed for the studies in human ichnology. We demonstrate high levels of intratrail variability as a result of variations in grain size, depositional moisture content, and the degree of sediment disturbance, all of which determine the bearing capacity of the substrate. The two principal trails were examined, which had consistent stride and step lengths, and as such variations in print typology were primarily controlled by substrate rather than locomotor mechanics. Footprint typology varies with bearing capacity such that firm substrates show limited impressions associated

with areas of peak plantar pressure, whereas softer substrates are associated with deep prints with narrow heels and reduced medial longitudinal arches. Substrates of medium bearing capacity give displacement rims and proximal movement of sediment, which obscures the true form of the medial longitudinal arch. A simple conceptual model is offered which summarizes these conclusions and is presented as a basis for further investigation into the control of substrate on footprint typology. The method, model, and results presented here are essential in the interpretation of any sites of greater paleoanthropological significance, such as recently reported from Ileret (1.5 Ma, Kenya; Bennett et al.: *Science* 323 (2009) 1197–1201). *Am J Phys Anthropol* 000:000–000, 2013. © 2013 Wiley Periodicals, Inc.

Since the discovery of the 3.66 Ma Laetoli footprints in the late 1970s (Leakey and Hay, 1979; Leakey and Harris, 1987; Deino, 2011), footprints have held a place in the paleoanthropological record. With each new discovery, the body of human footprint evidence has grown (Behrensmeier and Laporte, 1981; Mietto et al., 2003; Avanzini et al., 2008; Bennett et al., 2009), but until recently the tools with which to objectively interpret this evidence have been limited. Fossil footprints, regardless of age, provide information about hominin presence and behavior, the evolution of bipedalism, and modern locomotion (Lockley et al., 2008; Kim et al., 2008a,b; Bennett et al., 2009). Here, we use a new “whole-foot” analytical tool which attempts to remove some of the subjectivities which have hitherto hindered the interpretation of ancient footprint sites (Crompton et al., 2012). In doing so, we hope to move the discipline away from simple site description adopted at many sites to date (Brown, 1947; Aldhouse-Green et al., 1992; Roberts et al., 1996a; Webb et al., 2006; Aramayo and Manera de Bianco, 2013; Kim et al., 2009; Schmincke et al., 1979) to a more forensic approach to unlock the true paleoanthropological potential of human trace fossils (Allen, 1997; Tuttle, 2008). There are number of critical questions that need to be addressed to decipher the biomechanical signature within footprints not of least of which is the relationship between footprint depth and peak or duration of plantar pressure (D’Aout et al., 2010; Hatala et al., 2013; Richmond et al., 2012). However, here we focus on the role of the substrate.

Before biomechanical inferences can be made from a footprint site animal or human, two key issues must be addressed. First, the control of substrate on print morphology (Laporte and Behrensmeier 1980; Scrivner and Bottjer, 1986; Cohen et al., 1991, 1993; Allen, 1997; Bromley, 2001; Melchor et al., 2002, 2006; Manning, 2004; Milàn, 2006; Jackson et al., 2009; Marty et al., 2009) which affects the degree to which variation in sedimentology may obscure the anatomical and biomechanical signature of the print maker. This is vital both when comparing prints from different sedimentological environments, as well as prints from within a single environment (Milàn, 2006; Scott et al., 2007, 2008; Milàn and

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Bromley, 2008; Marty et al., 2009). Second, the level of variability of print typology within a single trail has yet to be addressed in a statistical manner. A comprehensive understanding of both is critical in making inferences from older paleoanthropological sites. The number of hominin footprint sites predating *Homo sapiens* is limited, as is the number of individual prints at these sites and therefore comparisons of small samples between sites with different sedimentological and paleoenvironmental contexts are required (Bennett et al., 2009; Meldrum et al., 2011). As a consequence, the effects of substrate and intratrail variability must be understood and accounted for. The stakes are particularly high where wholesale interpretations of the biomechanical characteristics of human species and interspecies differences are being examined (Charteris et al., 1981, 1982; White and Suwa, 1987; Tuttle et al., 1990; Meldrum, 2004; Raichlen et al., 2010; Crompton et al., 2012). This is not just about the macroscale differences between two sedimentary environments, but also the microscale differences within one environment caused by such things as variations in moisture content or grain size. It is these microscale variations, for example, which pose the greatest challenge in interpreting the 1.5 Ma Ileret prints in northern Kenya (Bennett et al., 2009). In this study, we use a Holocene footprint site from Namibia to examine the influence of microscale variations in substrate on footprint typology through the application a series of new analytical tools which, we believe, have the potential to revolutionize approaches to human ichnology. Although vertebrate ichnology, in general, has a head start on these factors owing to the great number of known dinosaur footprint sites (Gatesy et al., 1999; Diedrich, 2002; Fornós et al., 2002; Melchor et al., 2002, 2006), this is the first attempt to understand which type of substrate has to do with the formation of human prints. As our understanding of substrate influence on footprint typology improves, our ability to interpret the biomechanical signals left by our ancestors should be enhanced.

HOLOCENE FOOTPRINTS OF THE NAMIB SAND SEA

Geological and archaeological context

The Kuiseb¹ River is located in south of Walvis Bay in Namibia and flows northwest, defining the northern boundary of the Namib Sand Sea (Fig. 1). Coastal reworking of sediment supplied by the northward migration of the dune field (>10 m/year; Ward and Von Brunn, 1985), along with periodic sediment discharge via the Kuiseb River during flood episodes, has led to the creation of an extensive sand spit backed by salt flats (Stengel, 1964; Ward, 1987; Smith et al., 1993; Miyamoto, 2010). To the east, there is a complex network of mudflats and sand-/silt-filled interdune channels associated with flood drainage from the Kuiseb River referred to as the Kuiseb Delta (Vogel 1982, 1989; Ward, 1987; Smith et al., 1993; Kinahan, 1996, 2001; Miyamoto, 2010).

The area has a rich archaeological record, with Holocene inhabitants traveling between the sources of seasonal inland animal grazing and the coast where they exploited resources and engaged in trade (Kinahan, 2001). Extensive shell middens and transitory settlements within the Kuiseb delta contain the remaining of a

¹The spelling of Kuiseb used here is the most common usage in scientific literature; however, the spelling “!Khuseb” is also commonly used locally.

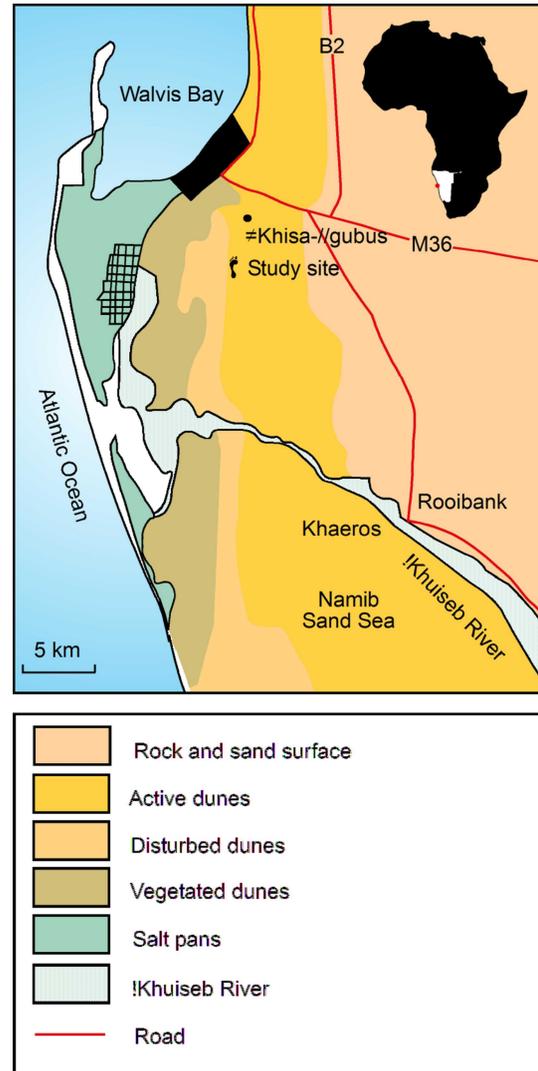


Fig. 1. Location map showing the main site discussed in the text. The study site is located at: 23° 00' 25" S; 14° 29' 26" E. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

wide range of marine and terrestrial food sources (including domestic animals), pottery, and a variety of indigenous and exotic trade goods (Kinahan, 2001). Animal tracks including a range of domestic animals (e.g., cattle, sheep, and goats) as well as giraffe, elephant, and a variety of birds can be found (Sandelowsky et al., 1976; Kinahan et al., 1991; Kinahan, 1996). Although there are numerous footprint surfaces within the delta, one locality was chosen for particular study owing to the quality and quantity of human prints present (Fig. 1).

Methods and new approaches

Owing to the abundance of animal and human prints, it was not possible to select all prints for excavation and recording. Consequently, human footprint trails were identified via a random walk process and included within the study on the basis of trail length. Human and animal prints were typically infilled by windblown sand and encrusted with salt, making excavation with dental picks and small brushes necessary to reach the plantar



Fig. 2. **A:** Study site, typical of the broad interdune areas in which the sediment surfaces containing animal and human prints are found (Type One Surface). **B:** Typical combination of human and animal prints within a less densely printed area at Locality One, note the displacement rims around the prints and the smooth undisturbed surface showing primary bedding with rain pits, typical of the “firm surface.” **C:** Trail One crossing the runnel. Note the elephant prints crosscutting the trail. **D:** Human print is filled with salt-cemented wind-blown sand prior to excavation. **E:** Excavated prints with displacement rims forming part of Trail One on the “firm surface.” **F:** Shallow print of right foot showing both proximal slippage under the toes and forward drag of the toes, most notably the third toe. **G:** Plantar skin texture preserved beneath a protective veneer of salt cemented silt removed by the application of water. **H:** A typical human footprint before excavation. It has been filled with sediment and capped with a salt crust, so that it appears inverted. **I:** Typical print at the site showing trapezoidal-shaped toes owing to forward drag and transverse midfoot ridge caused by the proximal movement of sediment below the plantar surface of the foot during rotation of the longitudinal rotation of the ball. **J:** Left foot showing evidence of proximal movement of sediment on the medial side, giving the ball area a rectangular shape in plan form. **K:** Left foot showing proximal movement of sediment in the proximal part of the midfoot adjacent to the longitudinal medial arch. **L:** Trail of large hyena prints. **M:** Large bird print, identified by a local guide as being a type of buzzard.

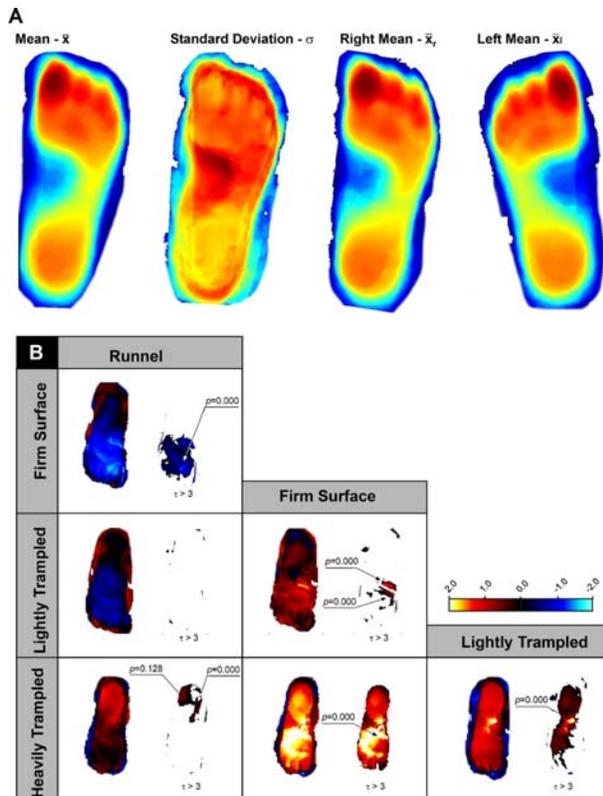


Fig. 6. **A:** Summary data for Trail One. **B:** Pair-wise *t*-tests between the mean print for each section of Trail One. The left-hand side plot shows the statistical parametric map (*t*-values) for the two means being compared; warm colors indicate a positive difference and cool colors a negative difference between the two means. The right-hand side plot shows the image with a $t > 3$ threshold applied and significance values appended.

surface (Fig. 2D). Excavated prints were mapped using a Leica differential GPS (± 20 mm), photographed, described, and scanned using a Konica Minolta VI900 optical laser scanner (± 0.09 mm; Bennett et al., 2009). Scans were postprocessed in Rapidform-2006 and output as XYZ files. Further processing was undertaken in Foot Processor, a piece of software written by Marcin Budka (Bournemouth University). This program allows rapid visual editing of XYZ data files to: 1) rectify prints to the orthogonal plane, 2) rotate prints into a consistent longitudinal orientation, 3) mirror left into right prints to allow comparison of all prints within a trail for selected analyze, 4) crop extraneous material from the margins of a print, and 5) contour plot, place landmarks, and measure interlandmark distances. Sedimentary properties for key samples were determined from field samples back in the laboratory using a combination of dry and wet sieving with clay fractions determined by sedimentation. Salt content was determined by mass loss during wet sieving.

Multiple prints from single trails were analyzed using Pedobarographic Statistical Parametric Mapping (pSPM) run in Matlab, a method developed originally for the analysis of foot pressure data to compute the measures of central tendency for multiple pressure records, but applied here to footprints substituting depth for pressure. More information on pSPM methods and uses has been provided in the previously published literature (Pataky and Goulermas, 2008b; Pataky et al., 2008a,c; Crompton and Pataky, 2009; Patkay et al., 2011). However, a step in processing prints in pSPM has been changed for this article. Rather than using a vertical height threshold to remove extraneous material from around the print, here we use Foot Processor to crop the printout of the surface, following a polygonal line within 10 mm of the print edge. This is important to ensure that interprint registration is based on the typology of the print rather than the surrounding surface.

Footprint typology and substrate

Site description. The site consists of a broad interdune area approximately 350 m long by 250 m wide oriented along a south-west to north-east axis surrounded by large (>10 m high) active sand dunes ($23^{\circ} 00' 25''$ S; $14^{\circ} 29' 26''$ E; Figs. 1 and 2). Much of the original sediment surface within the interdune area is actively deflating; however, to the west there is an undisturbed area forming a raised terrace (85 m wide by 151 m long). This terrace is consistent with a bar top, drained by a shallow runnel (<50 mm deep; 2–5 m wide; 116 m long) running from the northeast to the southwest. The terrace surface is imprinted with numerous animal footprints dominated by bovid prints predominantly of goats/sheep, cattle, potentially buffalo, and less commonly giraffe, elephant, birds, and dog/hyena (Fig. 2B,E,L) the density of which increases to the north. We recognize two distinct human footprint populations on the basis of foot length at the site (Fig. 3 and Table 1); a limited number of larger prints (ca. 230 mm in length) associated with a few prominent trails crosscutting the site, and numerous smaller prints in randomly oriented short trails (ca. 195 mm; Fig. 3). Using the foot length to height empirical relationships of Webb et al. (2006), this gives potential subject height inferences of 1.26 ± 0.1 and 1.53 ± 0.11 m tall (Table 1). The trails containing the larger prints trend in a south to north direction and

appear to postdate much of the animal trampling, whereas the smaller prints and trails have a more random orientation and appear to be penecontemporaneous with animal trampling.

Five geotrenches, each 1 m wide, were dug around the margins of the terrace to a maximum depth of 3 m. The sedimentary succession in each is similar, consisting of a series of unlithified fining upward cycles from medium/coarse sand to fine sand and silt. Ripples, crosslamina-tions, and small scours (<20 cm) are common in finer units that overlie thicker (ca. 0.5 m) massive or horizontally stratified sands with occasional low-angle cross-sets. The prints are found on the upper most surfaces of the fining upward successions within fine sand, silt, and clay partially cement by salt. Within one of the geotrenches, a prominent organic-rich horizon (35 mm below the surface) was sampled for radiocarbon assay. A bulk sample of the organics yielded a date of 530 ± 40 BP with a calibrated calendar age at two standard deviations of either AD 1320–1350 or AD 1390–1440. At one standard deviation, this range falls to AD 1400–1430. Within this sample, the fragments of charcoal gave an age of 320 ± 40 BP and a potential calendar age at two standard deviations of AD 1460–1660. Samples from three of the geotrenches were also submitted for OSL dating yielding dates of: 411 ± 40 , 415 ± 30 , and 426 ± 30 BP, respectively (Evans, personal communication). Taken together, these dates suggest an age of between 400 and 500 years ago during which time the area is known to have been occupied by an indigenous population exploiting coastal resources and grazing livestock (Kinahan, 2001).

To explore the influence of substrate and the degree of intratrail print variability, attention is focused on a total of 12 trails with particular emphasis on the two longest trails (Trails One and Two) at the site.

Trail One

Trail One is the longest trail ($N = 77$ prints) with a length of 54 m starting at a shallow runnel in the south and continuing due north until the trail becomes indistinct in an area containing a high density of animal prints. There is a uniform step (0.65 ± 0.03 m) and stride length (1.38 ± 0.02 m) throughout the trail and no deviation or evidence of pause, suggesting that the individual was moving consistently and at a steady pace. Many of the prints in the trail have well-developed rim structures (Prints #21, 25, and 36, Fig. 4), showing the evidence of longitudinal slippage (Prints #49 and 58, Fig. 4) and internal and external rotation (Prints #25 and 36, Fig. 4) consistent with the individuals' feet failing to gain the traction necessary to maintain forward motion before and during the midstance stage and during plantar-flexion in the later stages of stance. At the northern end of the trail, the surrounding areas show an increase in animal print density which predates it, and the human prints within the trail become progressively deeper and more trapezoidal in shape (Print #77, Fig. 4).

This typological variability causes basic print dimensions to vary (Fig. 5). Print length, defined as the distance from the heel to the tip of the second toe, varies by ± 60 mm (Table 1) associated primarily with: 1) extension of the toes owing to forward drag, 2) internal and external rotation of the foot as the individual effectively lost traction and "skated" on the mud, and 3) compression owing to proximal slippage in the later part of

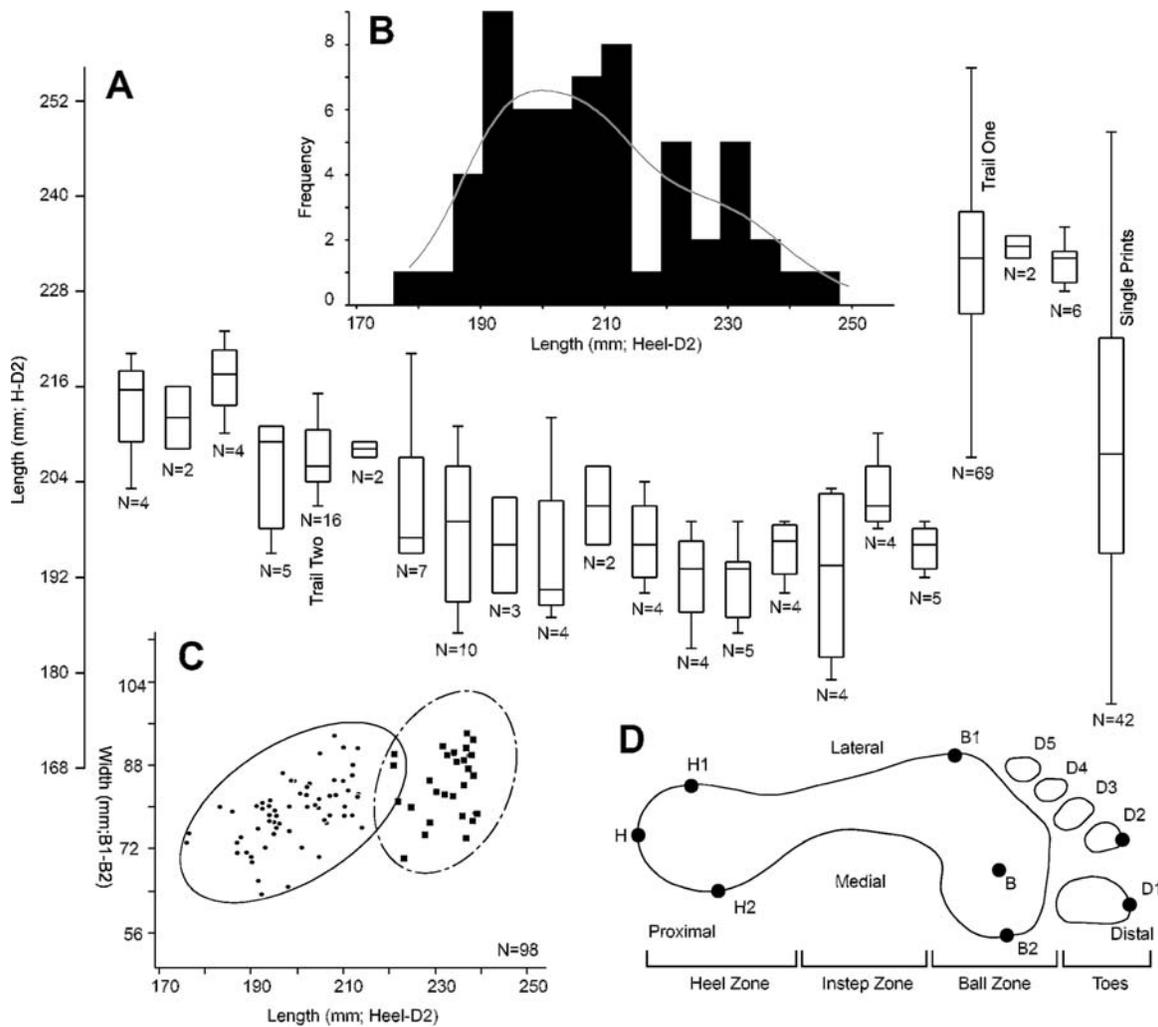


Fig. 3. Basic biometric data for the prints at the study site. **A:** Box plot showing mean, one standard deviation, and range for all the trails within this study. **B and C:** Length (Heel to D2) and Width (B1–B2) plots showing the crude bimodal size distribution present. This is based on 150 individual prints each from different trails. **D:** Landmarks used to collect the biometric data.

TABLE 1. Data for the key trails T1 to T21^a

	Trail One	Trail Two	Singles																			
N	69	16	4	2	4	5	2	7	10	3	4	2	4	4	5	4	4	4	5	2	6	42
Min	207	201	203	208	210	195	207	195	185	190	187	196	190	183	185	190	179	198	192	232	228	176
Max	267	223	220	216	223	211	209	220	211	202	212	206	204	199	199	199	203	210	199	235	236	248
Mean	232	208	214	212	217	205	208	202	199	196	195	201	197	192	192	196	192	203	196	234	232	210
Std. Error	1.5	1.5	3.7	4.0	2.7	3.4	1.0	3.5	3.0	3.5	5.7	5.0	3.0	3.3	2.5	2.0	6.0	2.6	1.4	1.5	1.2	2.7
Stand. Deviation	12.1	5.9	7.3	5.7	5.4	7.7	1.4	9.3	9.4	6.0	11.5	7.1	6.0	6.7	5.6	4.0	12.1	5.3	3.0	2.1	2.9	17.3
Median	232	206	216	212	218	209	208	197	199	196	191	201	196	193	193	197	194	201	196	234	232	208

^a All measurements are given in millimeter and are derived digitally from laser scans of the prints. Height estimates are based on the method described in Webb et al. (2006).

stance. Both heel and ball width show less variability although both decrease as print depth increases at the northern end of the trail (Fig. 5).

Using Pedobarographic Statistical Parametric Mapping (pSPM), a series of means were calculated for 49 out of the 77 prints in Trail One (Fig. 6). A total of 28 prints were excluded from this analysis being either

partial prints (lacking either a forefoot or a heel) or containing significant taphonomic disturbance caused by animal overprinting. Initially, means were determined for right and left prints separately (Fig. 6) and *t*-values in a Statistical Parametric Map (SPM) image were calculated (SPM(*t*)), which revealed no significant differences (*t* > 1) with the exception of a localized difference in the

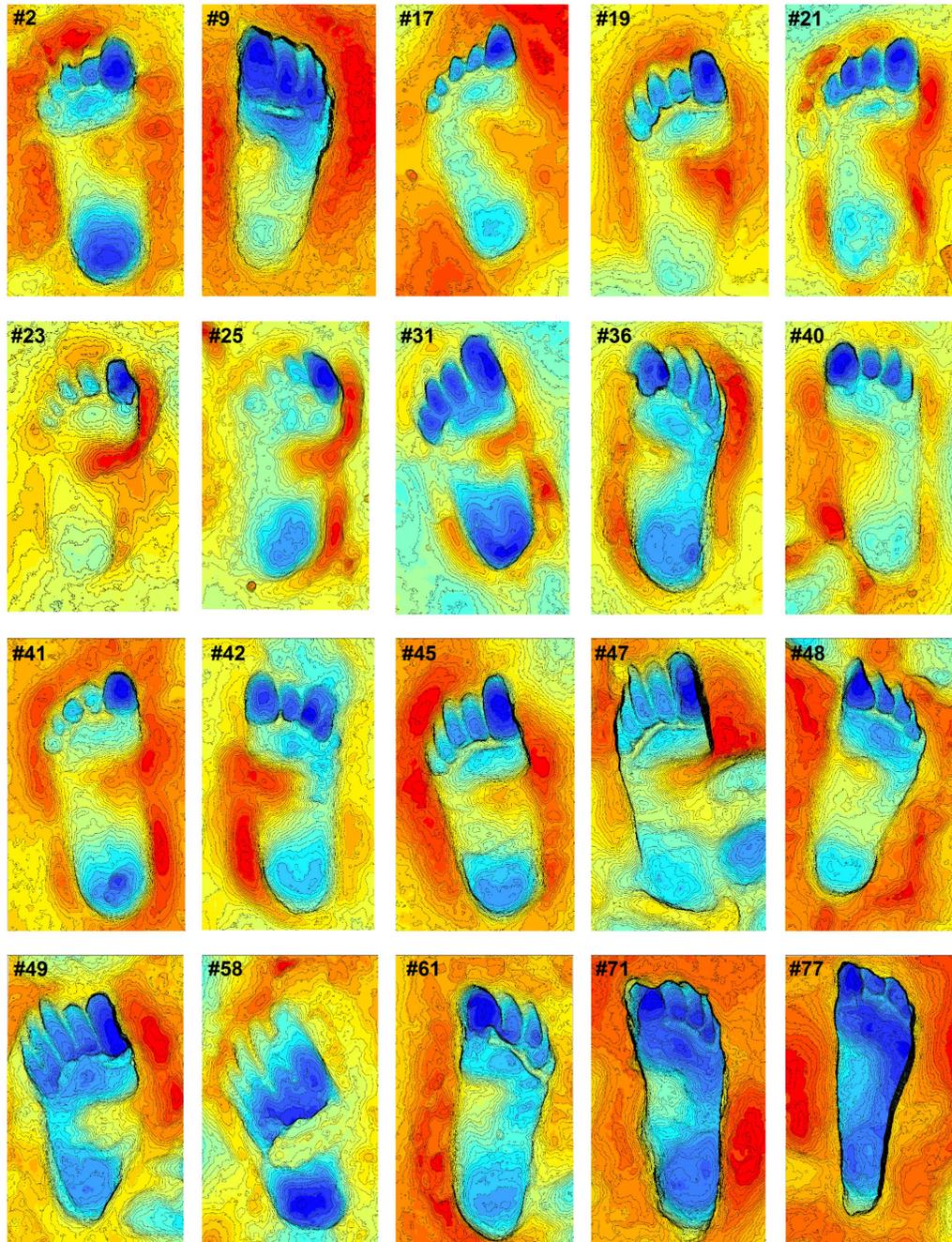


Fig. 4. A selection of prints from Trail One. The color rendered contours at 1-mm intervals; warm colors indicated elevated areas. All squares are of equal size approximately 250 mm long. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

heel outline, with the left print, showing a slightly less rounded outline on the proximal medial quarter than the right print (Fig. 6). Although not statistically significant, other minor differences between left and right prints are worth noting. In the left print, means of all five toes are visible, in contrast to the right print where the fifth toe is frequently obscured. The ball area is more restricted laterally on the left foot than on the right foot consistent with a tendency observed in the trail for the print maker's feet to rotate slightly in unison, in an anti-clock wise direction during the latter half of stance. This rotation was facilitated by the lack of compressibility

within the substrate and near-surface shear, but the actual cause is uncertain and could be linked to any or all of the following: 1) direction of eye gaze, 2) the print-maker carrying something although there is no difference in depth between right and left prints, 3) right versus left foot dominance, and 4) pathology or simply something distinctive about the individual's gait.

Given the absence of statistical significant differences between the right and left prints, all the prints in the trail were combined to give a single global average (Fig. 6) which reveals: 1) a print with a well-defined heel with maximum depth on the medial side, 2) a prominent

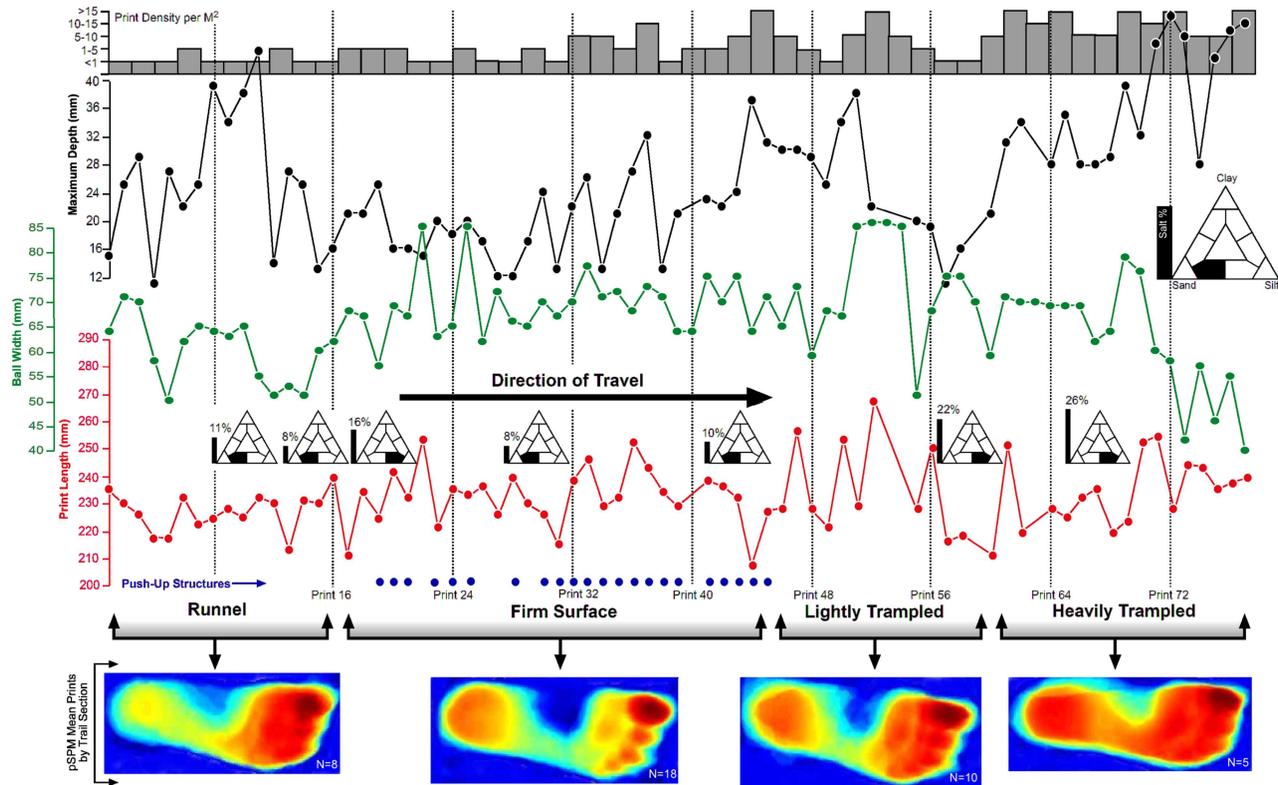


Fig. 5. Compilation of data for Trail One. Grain-size analysis is based on the bulk samples, wet sieving, and sedimentation. The mean prints, calculated using pSPM, are based on both right and left prints for different sections of the trail as described in the text. Print density is based on a simple count of the number of animal/human prints per meter square. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

medial longitudinal arch, 3) a ball area with maximum depth located over the second or third metatarsal head, and 4) well-defined toe pads with minimal abduction of the hallux and with maximum depth associated with toe-off over the first toe. If we examine the SPM of standard deviation for the mean (Fig. 6), the areas of maximum variance correspond to: 1) the proximal edge and width of the heel, 2) maximum variation around the medial longitudinal arch (especially distally) associated with the amount of proximal displacement in this area, and 3) considerable variation around toe impression length linked to slippage or drag of the toes, which also impacts on the variance around the margin of the ball area. As already noted, variation in toe length reflects the degree of both proximally directed slip during toe-off and distally directed drag thereafter. Proximally directed slip of the toes causes the removal or shortening of the ball area in some prints (Print #58, Fig. 4). There is also a much squarer proximal boundary to the ball area in prints with a large amount of slippage often associated with an enhanced displacement rim in the longitudinal arch area. This obscures the scale and development of the longitudinal arch in some prints.

To understand the role that substrate has on the variation in print typology, the trail was divided into four sections (Fig. 5), each representing a different type of substrate condition—grain size and print density—identified in the field on the basis of surface grab samples and field observations. In this instance, print depth provides a proxy for substrate yield strength since stride and step lengths, and therefore plantar force, remained consistent along the length of the trail. This assumption

is reinforced by the association of print depth with the proportion of fines, salt content, and animal trampling (Fig. 5). The more densely trampled areas are likely to have been weaker owing to repeated sediment failure and mixing which would remove primary depositional structures such as bedding and resulting in fine-grained homogeneous sediment. Animal trampling, to any great degree, also leads to surface water retention within the puddled surface, enhancing pore-water content which again leads to a potentially weaker substrate. The increase in salt content (evaporation of retained water) with print density supports this, given that the water table below the surface is (and probably was) at a uniform depth owing to the absence of any significant surface topography. On this basis, there is evidence to support the proposition that the bearing capacity of the sediment at the time of imprinting was slightly lower in the runnel area (owing to water retention) and toward the northern end of the trail where animal trampling was highest (Fig. 5).

Using pSPM, a mean print for each of the four trail sections was calculated, excluding displacement rim structures, and compared statistically via pair-wise SPM(t) (Figs. 5 and 6). The key conclusions are as follows: 1) Runnel versus Firm, the significant difference between these prints is in the ball area, with the prints found in the runnel section having a deeper ball and a ridge of sediment proximal to the ball on the medial side enhancing the height distal part of longitudinal medial arch; 2) Runnel versus Lightly Trampled, there is no statistically significant difference between these prints; 3) Runnel versus Heavily Trampled, the main significant difference is that the prints in the runnel have shallower

heels; 4) Firm versus Lightly Trampled, the main statistically significant difference is associated with a ridge(s) of sediment proximal to the ball on the medial side; 5) Firm versus Heavily Trampled, most of the plantar surface shows a statistically significant difference, reflecting the greater depth of the prints in the heavily trampled section, with the key areas being around the longitudinal medial arch which is much less pronounced in the deeper print and along the lateral side of the foot in the ball region; and 6) Lightly Trampled versus Heavily Trampled, key differences are around the longitudinal medial arch which is flatter in the prints from the heavily trampled section and around the heel and lateral side of the foot where there is greater depth in the print from the heavily trampled section. These observations can be related to the substrate characteristics as follows:

1. **Runnel.** The substrate is likely to have been comparatively weaker. It contains evidence of worm burrows and reed fragments and is likely to have had higher water content as the runnel would have been the last area of the terrace to drain. The prints in this section of the trail show a much higher degree of depth variation than elsewhere. They show strong depth asymmetry (enhanced ball/hallux depths) occurring in sequence with those that do not (Fig. 5). There are no displacement rims, implying that strain was accommodated via compression and there is evidence of the proximal movement of loose sediment behind the ball. In some cases, the substrate seems to have borne the subjects' weight, whereas in others it has compressed preferentially in the ball/toe areas during the latter phases of stance. Longitudinal depth asymmetry is enhanced by the proximal movement of sediment below the foot.
2. **Firm.** Grain size is finer in this section of the trail, with undisturbed primary bedding and a lower salt content indicative of a drier, firmer substrate (Fig. 5). Longitudinal asymmetry in print depth is less pronounced with the deepest points occurring more uniformly in both the heel and the toe/ball region. The medial longitudinal arch is well defined as those are individual's toe pads, and marginal displacement rims are common, suggesting that strain accommodation occurred via both sediment displacement and compression. There is evidence of plantar slippage and foot rotation within the near surface layer which appears to have acted as shallow shear zone between a more stable sublayer and the plantar surface of the foot. Despite this fact, basic print lengths and widths show less variability than other sections of the trail (Fig. 5).
3. **Lightly trampled.** In this area, the trail-maker overprinted animal prints, which increase in number along the trail. The substrate grain size remains fine and the salt content remains high (Fig. 5). The prints are similar to those in the previous section (Firm) from which they grade in typology gradually deepening and developing more defined ball regions. This is owing, in part, to the proximal movement of sediment during print formation on the medial side which enhances the prominence of the medial longitudinal arch. In some cases, it becomes part of well-developed marginal displacement rims. Print length is inconsistent, reflecting the greater variability in print topology and the influence of surrounding animal prints.
4. **Heavily trampled.** Toward the end of the trail, the density of surrounding animal prints increases markedly

as does the salt content of the sediment and print depth (Fig. 5). There is a slight rise in print length and both the ball and the heel width decrease. This is particularly true in the heel which gives some prints a typically trapezoidal shape in plan-form (Print #77, Fig. 4). Length variability reflects increased forward drag as the foot was extracted from a deeper socket and the decrease in width, especially around the heel, is ascribed to side-wall suction as the foot was withdrawn. Overall, print depths increase but there is less apparent variation in depth between heel, ball, and toe areas such that the degree of plantar detail is reduced; for example, less distinction is seen around individual toe pads and the medial longitudinal arch is suppressed. Displacement rims are absent, suggesting that strain is almost totally accommodated by compression.

These observations indicate that small-scale variations in substrate properties, particularly water content and animal trampling, have a control on print typology. Deeper prints are found in softer substrates and appear to have more subdued medial longitudinal arches and narrower heels. Intermediate strength substrates are associated with the movement of sediment to the proximal ball medially, enhancing the medial longitudinal arch. Increased longitudinal depth asymmetry (i.e., deeper ball than heel) is associated with substrates of more variable strength.

Trail Two. Trail Two, located 8 m to the east of Trail One, also shows typological variation with substrate. This trail is shorter, consisting of 18 prints and extending for 9.75 m long, with a consistent stride (0.976 ± 0.09 m) and step length (0.37 ± 0.01 m). The trail is not as long as Trail One as its full length is difficult to trace owing to animal overprinting. Print length is smaller (mean, 208 mm) than that for Trail One, suggesting that the trail maker belonged to the smaller of the two hypothesized size categories at this site (Fig. 3 and Table 1). As shown in Figure 7, the trail also crosses the runnel, with grain size and salt content correlating with runnel depth. The runnel is slightly deeper on its northwest side where the sediment is poorly sorted and has higher clay content. The higher clay content may be owing to greater residence time with respect to standing water in the deeper part of the runnel. This suggests that the substrate was likely to have had higher water content and therefore have been softer at the time of imprinting. There are two distinct print typologies related to depth (Fig. 8). The shallow typology is associated with marginal areas of the runnel and slightly coarser grain sizes. These prints consist of a heel strike or contact zone, poorly defined ball, and prominent hallux. The prints lack displacement rims and in some cases the heel impression is almost absent. Only areas of maximum plantar pressure are recorded in the prints. As the substrate appears to gain strength, this becomes increasingly restricted to the hallux and ball area alone. The deeper print typology has a very well-defined heel, ball, and toe area although even here the prints are not especially deep. Proximal shear beneath the foot along the lateral side is present in some prints, causing deformation of the distal heel outline (Print #36, Fig. 8A). The contrast between the shallow and deep prints along the trail is most visible in the lateral area of the ball as indicated by the SPM of standard deviation (Fig. 8A).

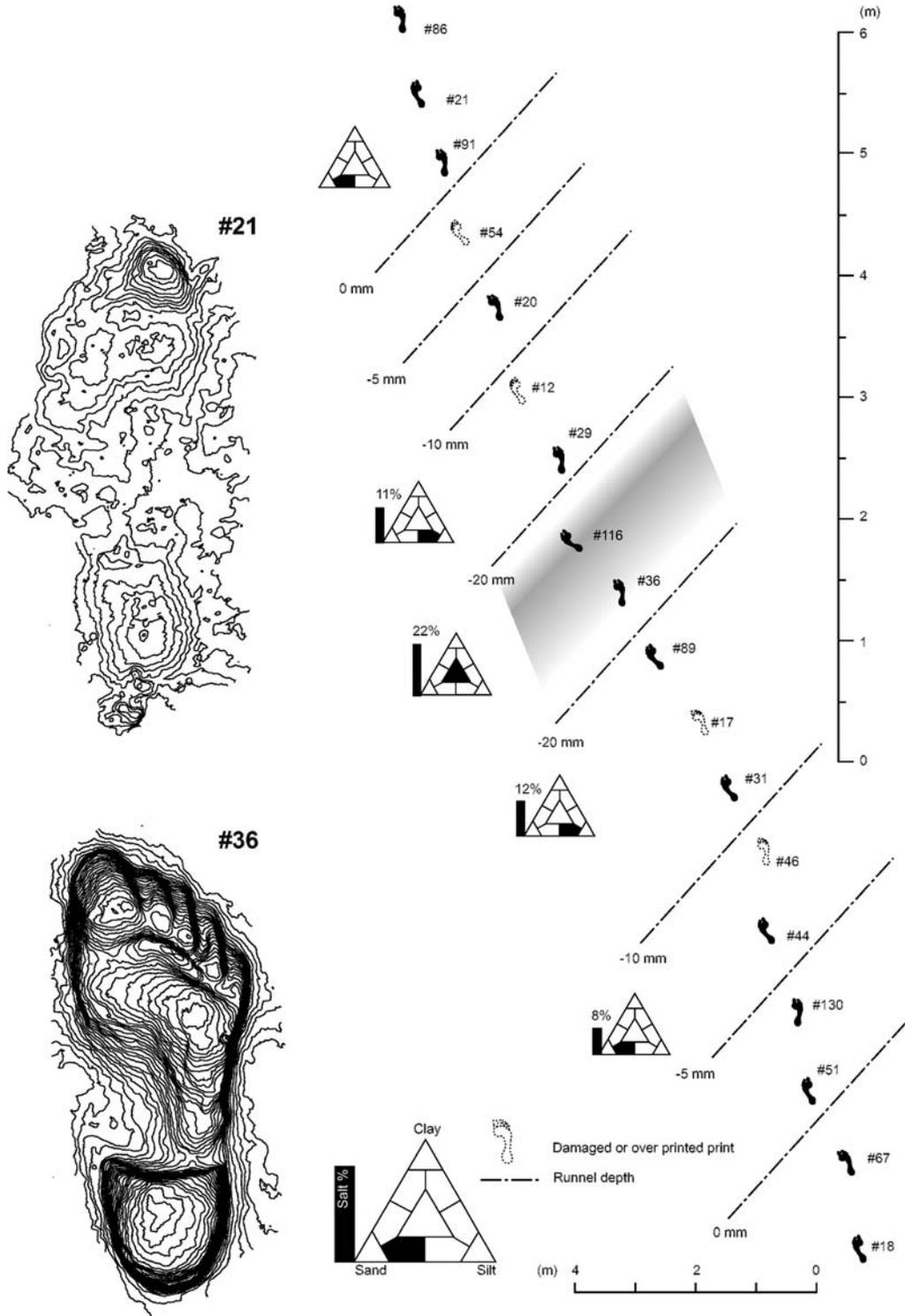


Fig. 7. Map of Trail Two across the runnel. Contour intervals are 1 mm for the prints illustrated and show a typical example of a shallow and deep print from this trail.

Shorter trails. The mean and standard deviation prints for a further seven short trails show similar typological characteristics (Fig. 8B) with the maximum intra-trail variance being associated with: 1) depth and definition within the lateral ball area, as in Trail Two (Fig. 8B); and 2) variability around the degree of longitudinal depth asymmetry, with most prints within a trail,

showing a marked longitudinal asymmetry in depth where there appears to be variability in substrate strength along a trail. It is important to note that variance around the print margins has been largely discounted as in all cases it reflects individual prints with distinct print-marginal taphonomic modification caused by overprinting from adjacent animal prints.

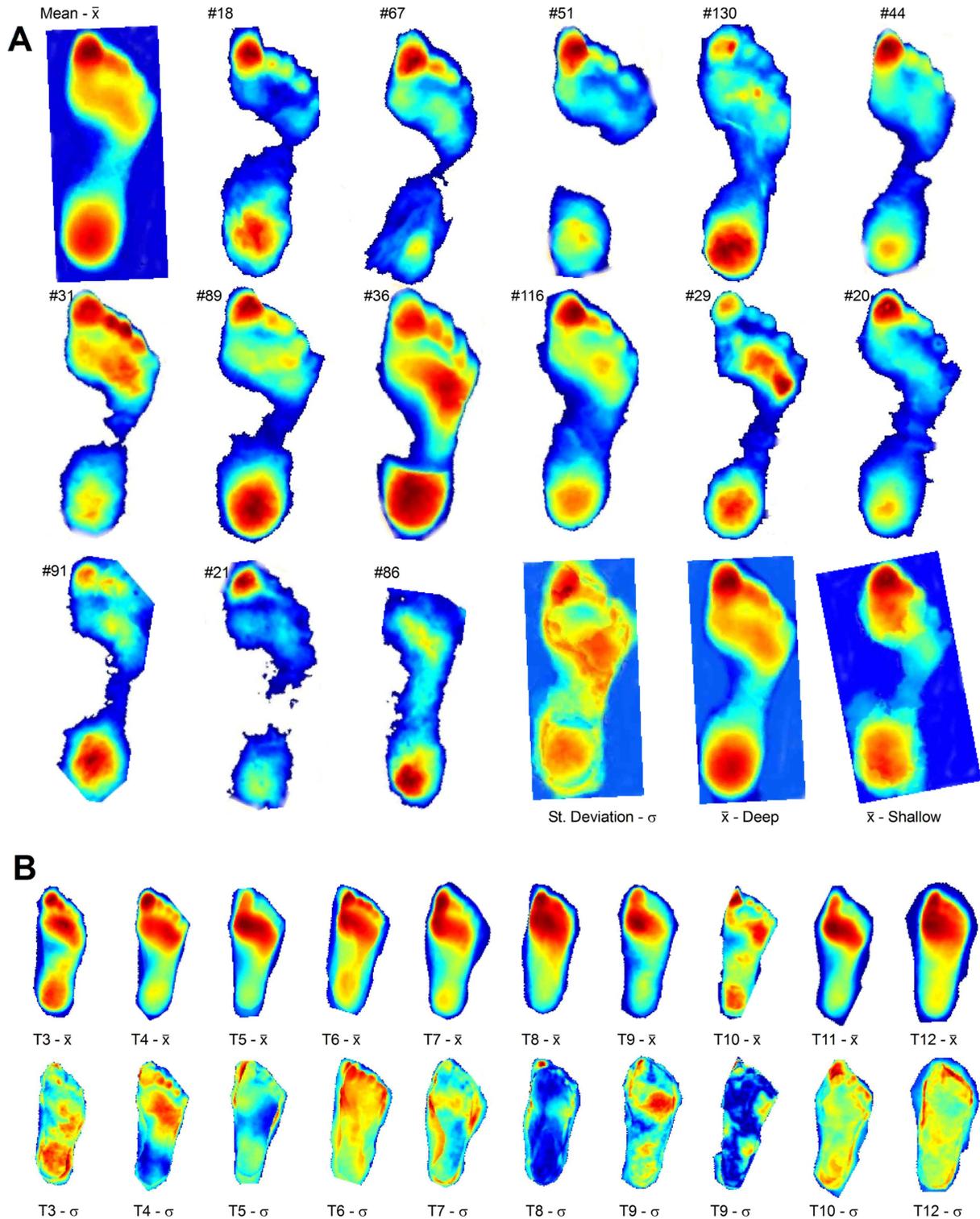


Fig. 8. A: Mean and summary data for Trail Two. B: Mean and standard deviation for other short trails. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

DISCUSSION

A number of issues arise from these analyses, namely: 1) the variation in print typology with substrate and 2) the implications of these observations for other footprint sites of greater paleoanthropological significance.

Model of print typology variance with substrate

Building on the work of Allen (1997) and first sedimentary principles (Leeder, 1999), it is possible to suggest that strain will be accommodated within a substrate in response to the applied stress associated

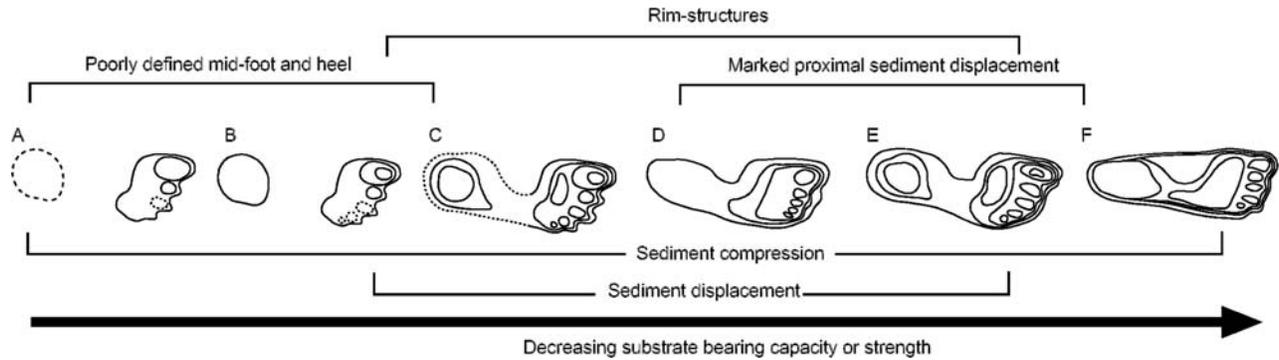


Fig. 9. Conceptual model of variation in print topology with substrate properties.

with footfall to create a footprint in one or more of the following ways: 1) compression and consolidation of the sediment, 2) sediment displacement from areas of high to low stress, and 3) physical excavation of sediment by plantar shear beneath the sole of the foot, block displacement, sediment adhesion to the sole, or by forward drag as the foot is removed. Compression, displacement, and excavation provide three broad footprint-forming processes influenced by substrate properties, none of which are mutually exclusive. As a foot impacts on a dry or slightly damp substrate such as a typical sand it will compress, gaining strength as intergranular friction increases, until it is able to bear the load, at which point strain, and therefore deformation, will slow or stop despite continued application of stress. Then, the sediment beneath the foot will begin to behave as a more rigid solid, transmitting stress to the surrounding area. The degree to which the applied stress can be accommodated by compression is a function of such sedimentary properties as grain size, sorting, grain shape, porosity, packing, consolidation, and pore water content (Allen, 1985; Leeder, 1999). Pore-water content is critical, as is sediment permeability and the rate of stress application (Allen, 1997). Sediment displacement in footprint formation will occur whenever compression alone cannot accommodate strain. This takes place through intergranular interaction in dry coarse sediment, via block displacement in damper sediment (Lockley et al., 2008), or through plastic deformation in fine saturated sediments (Allen, 1997). Vertical and horizontal variability in sediment properties associated with primary depositional structures are also important in determining the bearing capacity of a surface (Collinson and Thompson, 1989; Melchor et al., 2006; Milàn, 2006).

Combining this with the observations described here from Namibia, it is possible to propose a tentative model of how print topology varies with substrate strength at footprint sites dominated by silt and fines sand (Fig. 9). At the site described here, softer substrates at the time of printing occur where the degree of trampling and water content is higher, whereas firmer substrates are associated with undisturbed areas, lower water contents, and primary depositional bedding forming a firm sub-base. This is consistent with modern analogue studies at lake margins (Cohen et al., 1991, 1993; Scott et al., 2008). In firmer substrates, footprints show greater longitudinal symmetry in terms of depth (heel to ball/toes) and shallow impressions that are confined to areas of assumed maximum plantar stress. In the most extreme cases, this is limited to just the hallux and ball areas of

a print, as illustrated in parts of Trail Two (Fig. 8). As the sediment becomes softer, more of the footprint outline and anatomical detail become evident. Lateral displacement of sediment, facilitated by its fine grained nature, high water content, and subsurface incompressibility, leads to well-developed displacement rims (Allen, 1997; Marty et al. 2009; Schmincke et al., 1979). As the substrate softens, further proximal movement of sediment to rear of the ball begins to first exaggerate the medial longitudinal arch and then obscure it beneath excavated/displaced sediment. This is enhanced in certain areas by the fact that the sediment is undisturbed and largely incompressible beneath a thin veneer of surface mud. This incompressibility reflects the presence of coarser subsurface sand units in the undisturbed sediment which, being better drained, are much stronger than the surface mud. The result is a near-surface deformation or shear zone in which the footprint is accommodated. The only way that strain can be accommodated is by displacement to the print margins. This saturated and mobile mud promotes a high level of foot slippage, rotation, and shear-based plantar excavation. As the substrate becomes softer, the prints first become increasingly asymmetrical in terms of longitudinal depth (Fig. 9). This reflects the fact that the substrate bears the weight initially but as the full force of the later stages of stance is brought to bear it tends to fail, leading to deep ball/toe areas and marked proximal sediment displacement. Prints of this sort often have: 1) poorly defined medial longitudinal arches because of the proximal movement of sediment under the rotation of the ball, 2) a more pronounced medial ball area giving the proximal boundary of the ball a much more rectangular appearance rather than tapering toward the lateral side of the foot, and 3) the area of maximum depth in the ball area located more medially and the hallux is often very pronounced. This type of print is very common at the locality studied, as illustrated by the shorter trails, reflecting the key characteristics of much of the heavily disturbed substrate that it is soft enough to allow easy walking, but not yet firm. It is a state which may favor footprint preservation in general; if the substrate is too firm, then the impressions will be very shallow and poorly preserved, but if it is too soft then the deep prints are more likely to suffer post- or syn-imprinting collapse/modification. Consequently, such prints have a greater preservation potential in the geological record, but crucially do not necessarily accurately display the anatomical characteristics or the range of individuals present. As the substrate softens further, the prints deepen and the

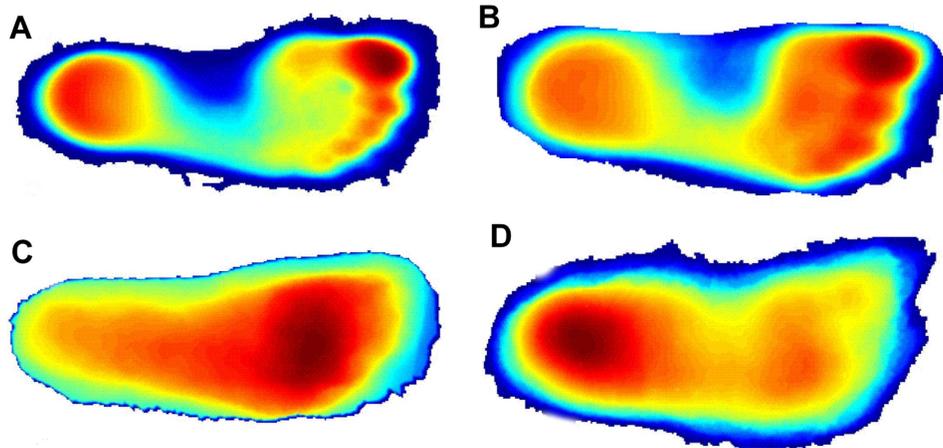


Fig. 10. A–D: Average footprints for modern humans ($N=100$), Walvis Bay (Namibia; $N=49$; c. 0.5 Ka), Ileret (FWJj14E, Kenya; $N=12$; 1.5 Ma), and Laetoli (Tanzania; $N=11$; 3.66 Ma). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

relative depths on the plantar surface tend to decrease such that the medial longitudinal arch is often less well defined. The planform of the prints becomes more trapezoidal with narrow heels owing to interwall suction caused by the withdrawal of the heel from the damp sediment sealed around the foot. These prints often have curved toe pads and show nail drag marks forward of the print. The typological association with substrate strength shown in Figure 9 is consistent across the site described here from Namibia and forms the basis of a model that needs to be tested at other footprint sites and in other depositional environments.

Implications for other footprint sites

Bennett et al. (2009) reported the discovery of a footprint site in northern Kenya (Ileret) dated to approximately 1.5 Ma and tentatively attributed to *H. erectus*. This site has attracted considerable interest as it is the oldest known *Homo* spp. footprint site being slightly older and superior in anatomical detail to that reported from just south of Koobi Fora (Kenya) by Behrensmeier and Laporte (1981). When compared to the footprints at Laetoli which are generally ascribed to *Australopithecus afarensis* (Leakey and Hay, 1979; Charteris et al., 1982; Meldrum et al., 2011), we have the potential to examine biomechanics and foot anatomy across the *Australopithecus–Homo* transition (Bennett et al., 2009; Crompton et al., 2012). This is not without significant challenge as first the two sites are preserved in different substrates, with different sedimentological and paleoenvironmental contexts; Ileret is in fine-grained overbank flood deposits and Laetoli is air fall volcanic ash. Second, Ileret can be classified as a congregation site with the prints densely clustered around a water source characterized largely by standing and short randomly directed trails, whereas Laetoli is a transit site with a clear direction of travel to both the human and the animal trails. Third, syn- and postimprinting modifications of the prints at Ileret (i.e., foot withdrawal, sediment slumping from walls, and animal overprinting) is a significant issue, as there are small case variations in substrate properties and associated variation in print typologies which has an undue impact because of the limited number of prints and trails (Bennett et al., 2009). It is the last point which is perhaps the most challenging as one has to use isolated

prints for comparison and then filter out the site-specific noise. We would argue, however, that the site described here from Namibia provides an excellent analogue to assist with this challenge owing to similar depositional context with that of Ileret. In fact, the model shown in Figure 9 may be of particular help in doing this.

Both sites represent waning sheet flood deposits, delineated by fining upward cycles of sand to silt and clay, and it is the upper surface of these cycles that is imprinted. Bed thicknesses are very similar and while one flood was constrained by sand dunes (Namibia) and the other (Ileret) by flood plain topography in the form of levees and channel distributaries, both form sheet-like deposits. Both were foci for animal watering with a high proportion of bird and bovid prints (Bennett et al., 2009) although in the case of Namibia this clearly involved some domesticated and wild stock as well. The level of trampling at Ileret is of similar intensity to that of in Namibia and subtle variations in moisture content appears to have been a feature of both sites (Bennett et al., 2009).

One of the features of the Ileret site are a series of very deep, elongated prints which narrow slightly toward the heel and have elongated toes (Bennett et al., 2009). This is consistent with the observation made from Namibia that deeper prints are associated with a narrow heel caused by suction against the print walls as the heel is withdrawn. The elongated toe is also a feature of toe drag as the foot is removed from deep pockets. The other feature of the Ileret site is a series of prints in which only the toes and ball are imprinted. In some cases, the heel and mid-foot has been lost owing to animal overprinting. However, in other cases, there is no direct evidence for why the mid-foot and heel are absent. This is again consistent with some of the print typologies associated with slightly firmer sediment or lighter loads.

Figure 10 shows a comparison of four mean prints: 1) a mean of 100 modern habitually shod humans made in fine sand under laboratory conditions, 2) the Trail One mean reported here, 3) a mean of 12 prints from the upper footprint surface at Ileret, and 4) a mean of 11 prints from the G1 Trail at Laetoli. The degree to which the contrasts between the four means can be ascribed to differences in biomechanics versus those of substrate is a vital question for paleoanthropology and the data reported here from Namibia are useful in this respect. The Ileret mean has a narrow heel with a proximal taper, consistent with the

deep print in softer substrates, with a high level of animal trampling from Namibia. The mean Ileret print has also marked longitudinal asymmetry in terms of depth, and a less well-developed longitudinal medial arch than other prints. The toe pads are also less well developed than in the other means. These are all features of prints from Namibia. These similarities might suggest that substrate may be the more dominant influence rather than biomechanical differences and that despite the 3.66 Ma year span represented by the four footprint means in Figure 10 the level of biomechanical difference may be slight. This is something which requires further analysis and discussion.

CONCLUSIONS

Human footprints can be preserved in a range of depositional environments and may be more ubiquitous than previously suggested (Lockley et al., 2008). One of the challenges in ichnology is understanding the influence of different depositional environments and the associated taphonomic processes to allow reliable intersite comparison between regions, depositional environments, time periods, and hominid species. Although macroscale differences, for example, between mud and volcanic ash, are obvious, although not necessarily understood, the microscale variations within a single depositional environment must also be better understood to assess the reliability of the inferences on anatomy and gait made at a single site. These microscale variations reflect variations in sedimentological facies, moisture content, and the paleoenvironmental context. The observations presented here illustrate the influence of these more localized variables on determining print typology and as such represent an important step forward in human ichnology.

The Holocene footprint site from Namibia reported here offers an exceptional opportunity to study human ichnology, given the superior levels of preservation, including skin texture, and the plethora of prints. Using this print laboratory, we have explored intratrail variability in footprint typology as a consequence of subtle variation in sediment moisture content and disturbance. Microscale variations in grain size, moisture content, and sediment trampling result in a very clear print typology which varies with the bearing capacity of the substrate (Fig. 9). The challenge with this model is how it can be used to explore the differences not just within a single depositional facies but between depositional environments. Comparison of four mean prints across a span of 3.66 Ma (Fig. 10) shows a remarkable level of similarity, with some of the strongest differences being within the Ileret prints. The study presented here suggests that a significant proportion of these differences may be ascribed to the influence of substrate rather than to biomechanical differences across the three potential hominin species represented. This might imply that the degree of biomechanical change is small and this is something that requires further investigation, because it carries with it the implication of little biomechanical change over this period.

Lockley et al. (2008) suggested that the study of footprints was coming of age and we agree with this assessment, given the range of new tools now available with which to capture footprint data in the field and allow subsequent objective, landmark-free analyses. We believe it is these tools that will enable the study of human footprints to realize their full potential within paleoanthropology and the degree of variation in biomechanical signatures between our ancestors to be resolved.

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