

## Research Article

# A Pleistocene hyenid trackway from the Cape south coast of South Africa

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## Abstract

The global record of fossil hyenid tracks is sparse—the only formal reports that can be considered reliable are of trackways from Tanzania and a single track from Greece. However, trackway and track patterns of the four extant members of the Hyaenidae are distinctive among the tracks of carnivorans. A Pleistocene trackway comprising five manus–pes pairs has been identified on an aeolianite surface on the Cape south coast of South Africa, and is attributed to a hyena, most likely the brown hyena (*Parahyaena brunnea*). The diagnostic approach followed involves a combination of the knowledge of Indigenous Master Trackers and the methods of modern ichnology.

**Keywords:** Hyenid, Cape south coast, Aeolianites, Marine Isotope Stage 11, Pleistocene

## Introduction

The purpose of this article is to report a circa 400-ka trackway from the Cape south coast of South Africa at Dana Bay, which is interpreted as having probably been made by a brown hyena, *Parahyaena brunnea*. While the preservation quality of the tracks is not optimal, a distinctive gait pattern is evident. Two authors (#D, /N) are indigenous Ju'hoansi San Master Trackers, allowing for ancient and modern track identification skills to be productively combined.

Hyenas (order Carnivora, family Hyaenidae) have an evolutionary lineage that extends from the Early Miocene (ca. 22 Ma) to the present (Mills, 1982; Macdonald, 1993). There are four extant species: the striped hyena (*Hyaena hyaena*), the brown hyena (*Parahyaena brunnea*), the spotted hyena (*Crocuta crocuta*), and the aardwolf (*Proteles cristata*). The brown hyena, with a temporal range in southern Africa from Pliocene to present (Mills, 1982; Avery, 2019), is sometimes assigned to the genus *Hyaena*, and is the rarest of the four species, being limited to southern Africa (Mills, 1982; Stuart and Stuart, 2019). It is also known as the strandwolf or strandjutfwolf, Afrikaans terms that respectively mean 'beach wolf' or 'beach-scavenger wolf' (Möller, 2017). In the Ju'hoan language it is known as !'hau. Its conservation status is 'near threatened', with an estimated population in 2015 of 4000–10,000 individuals (Wiesel, 2015).

Through the Cape south coast ichnology project, conducted through the African Centre for Coastal Palaeoscience, more than 350 Pleistocene vertebrate ichnosites have been identified along a

350-km stretch of coastline since 2008. Out of a total of 260 mammalian ichnosites, 30 were attributed to carnivorans (Helm, 2023). In most cases, these could not be identified to family, genus, or species level, consequent to the suboptimal level of morphological detail that characterizes many such tracks in the region. For example, subtle features such as claw impressions, which may help to distinguish among felid, canid, hyenid, and herpestid tracks, may only be apparent briefly after the fossil tracks are exposed before track quality deteriorates as a result of erosion. Therefore, an identification simply of 'carnivoran tracks' often has to suffice, where overall size is a major factor in the identification process. The trackway reported here is an exception and this is related in part to the unique gait pattern exhibited by hyenas.

## Geological context

The majority of the Cape south coast Pleistocene tracksites occur in aeolianites (cemented dune deposits) of the Waenhuiskrans Formation (Malan, 1989). A minority occur in Pleistocene foreshore and lagoonal deposits of the Klein Brak Formation (Malan, 1991). These two formations comprise part of the Cenozoic Bredasdorp Group (Malan, 1990).

Optically stimulated luminescence (OSL) dating indicates that the deposits range in age from Marine Isotope Stage (MIS) 11 at approximately 400 ka (Roberts et al., 2012) to MIS 3 at approximately 36 ka (Carr et al., 2019). Most of the sites date to MIS 5 (Roberts et al., 2008, 2012; Bateman et al., 2011; Cawthra et al., 2018; Helm et al., 2023a). Figure 1 shows the extent of Cenozoic deposits on the Cape south coast and depicts the location of the Dana Bay site described herein.

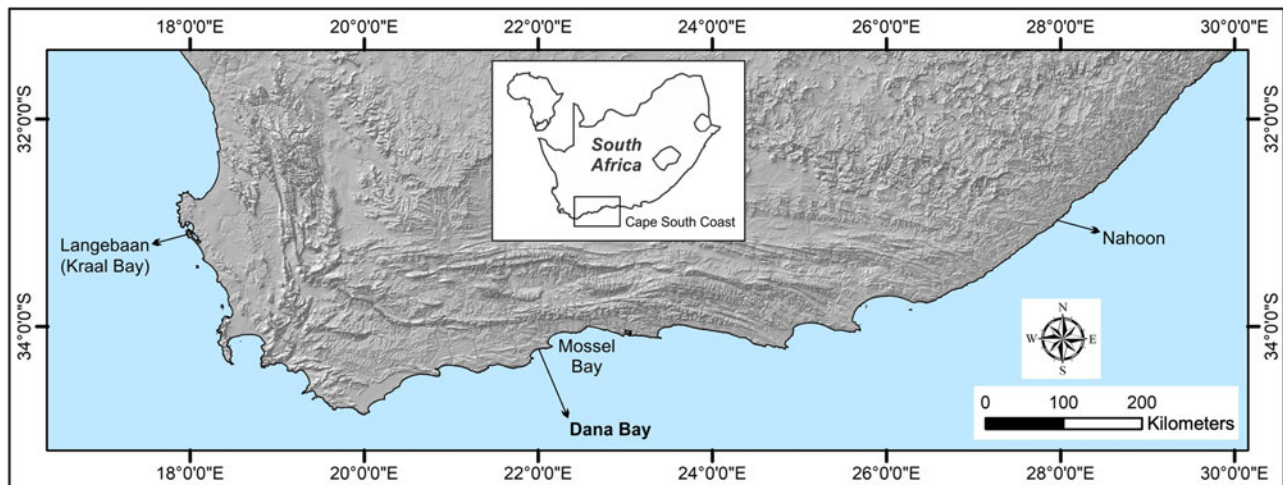
At Dana Bay, MIS 5 aeolianite deposits are draped in places over underlying MIS 11 aeolianite deposits. A laterally persistent

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**Cite this article:** Helm C, Cawthra H, Daqm #oma, De Vynck J, N#amce /uce, Thompson C (2025). A Pleistocene hyenid trackway from the Cape south coast of South Africa. *Quaternary Research* 123, 59–69. <https://doi.org/10.1017/qua.2024.31>

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**Figure 1.** Map of the Cape south coast, showing the location of the Dana Bay tracksite.

transgressive lag deposit containing a rip-up clast layer occurs towards the upper part of the MIS 11 sequence (Roberts et al., 2012). In-situ tracksites that occur below this marker horizon can safely be assumed to date to MIS 11.

Aeolianites occur predominantly between latitudes 20° and 40° in both hemispheres (Brooke, 2001). The Cape south coast aeolianites comprise medium- to fine-grained sand with a high carbonate content derived from marine shell fragments. Cementation results from downward percolation of mildly acidic rainwater in the meteoric diagenetic zone in which the dissolved carbonate shell component is re-deposited as interstitial cement within the sandstone matrix (Flügel, 2004). Tectonic activity is not considered to be a significant factor in the region (Fleming et al., 1998). It can therefore be assumed that in-situ bedding planes lie close to their original angulation. Horizontally bedded deposits suggest interdune areas, whereas many sedimentary beds lie close to the angle of repose of wind-blown sand.

Ichnosites in these deposits tend to be ephemeral. After they become exposed through cliff-collapse events, they are subjected to wind and water erosion, or they may slump into the ocean. Many are submerged twice daily at high tide, or are often covered by meters of beach sand. Vigilance is therefore required to rapidly

identify transiently exposed tracksites. In-situ hyporelief exposures often preserve relatively superior track quality, partly because erosive forces tend to have less effect on them than on epirelief surfaces, and partly because they may occur at a slightly higher elevation above sea level.

The preservation quality of fossil tracks is inversely related to the grain size of the substrate. Regrettably, the relatively coarse grain size of dune sand often leads to relatively poor preservational fidelity of tracks and traces, compared with tracks in finer-grained sediments such as clay or mud deposits in caves. Belvedere and Farlow (2016) developed a four-point preservation scale (0-1-2-3), in which '0' represents a virtually unidentifiable track, and '3' represents a track of exceptional quality. On the relatively coarse-grained Cape south coast aeolianite surfaces, encountering tracks that score 2 or more on this scale is unusual.

## Morphology of hyaenid tracks

### Neoichnology

Three extant species, the brown hyena, spotted hyena, and aardwolf, occur in southern Africa. The striped hyena occurs in northern and eastern Africa, the Middle East, and parts of Asia. Southern African neoichnology is fortunate in being able to refer to five thorough book sources on tracking (Liebenberg, 1999; Van den Heever et al., 2017; Walker, 2018; Stuart and Stuart, 2019; Gutteridge and Liebenberg, 2021).

Van den Heever et al. (2017, p. 75) noted that: "The gait is unique to the hyaena family... and completely different from that of the cats. This is probably caused by the design and movement of the hip: the hind leg swings across the line of movement..., and steps next to the opposite side's front foot. For example, the right hind track will register just behind the left front track. The hind foot registers either behind, next to or slightly on top of the front foot, depending on the speed at which the animal is travelling." Gutteridge and Liebenberg (2021, p. 234) concurred that the left pes impression is recorded behind the right manus impression (and vice versa) and commented that the toes of each foot point "outwards, away from its side of the body".

All five sources remark on the difference in size between the larger front feet and the smaller back feet, and, with the exception



**Figure 2.** One brown hyena trackway approaches the viewer on the left, and three brown hyena trackways extend away from the viewer. Reproduced with permission from the Desert Lion Trust.

of Walker (2018), noted that this difference is more pronounced in the brown hyena than the spotted hyena. Mills (1982) made a similar observation. Walker (2018) commented that the tracks of both are ‘dog-like’. Gutteridge and Liebenberg (2021, p. 224) used an exclamation mark with respect to tracks of the brown hyena: “The hind- and forefeet are very different in size with the front nearly an additional half a size bigger than the hind!”

All five sources are agreed that the tracks of the spotted hyena are larger than those of the brown hyena: a length of 106 mm for manus tracks and 100 mm for pes tracks (Van den Heever et al., 2017) for the spotted hyena, versus a mean manus track length of 97 mm and a mean pes track length of 78 mm for the brown hyena. Stuart and Stuart (2019) recorded respective track lengths for the brown hyena of 85 mm and 66 mm, excluding claw impressions. Figure 2 illustrates several brown hyena trackways in the Namib Desert, and Figure 3 illustrates two examples of brown hyena tracks.

The metapodial pad is large and its posterior edge is angled and asymmetrical (more so in the spotted hyena than the brown hyena); the large digit pads lie in close proximity to the metapodial pad and are grouped tightly together in what Van den Heever et al. (2017, p. 75) referred to as “almost jigsaw puzzle-like”. Gutteridge and Liebenberg (2021, p. 234) reported similar findings: “the toes fit tightly together”. The outer digit impressions are kidney shaped. Blunt, thick claws are characteristic and leave large impressions.

A potentially useful distinguishing feature of brown hyena tracks (compared with those of the other hyena species) is related to a thick mat of hair around the foot. This may leave traces in and around the track, especially in soft substrates, and may partially obscure claw impressions.

Only Stuart and Stuart (2019) depicted tracks of the striped hyena: they appear similar to those of the brown hyena. Tracks of the aardwolf shown a broadly similar pattern (perhaps rather more like a canid) but are substantially smaller—Van den Heever et al. (2017) reported a length of 54 mm for the manus track, and 45 mm for the pes track, with both measurements including claw impressions.

### Paleoichnology

Melchor et al. (2019) performed a thorough taxonomic review of the Canipeda and Felipeda. This included a review of ‘canid-like footprints’, meaning tracks with similar morphologies to those of modern canids, including fossil tracks assigned to hyenids and creodonts. Factors used to distinguish among the tracks of canids, felids, hyenids, and other carnivorans included the number of digital pads, the position of the foot, the presence or absence of claw impressions, and the relative difference between the manus and pes tracks.

While Melchor et al. (2019) provided this global summary of felid and canid tracksites, and suggested useful criteria through which tracks of these two groups could be distinguished, it required neoichnological observations in order to comment meaningfully on hyenid tracks. This reflects the paucity of the hyenid paleoichnological record.

Finally, the size of Pleistocene carnivoran tracks should be interpreted with caution. Carnivoran body size in southern Africa has been shown to vary according to Pleistocene climate conditions, with size being greater during glacial phases than interglacial phases (Klein, 1986). For example, Pleistocene brown hyena tracks from a glacial phase might be larger than

modern tracks of the same species, and the possibility that tracks represent a hitherto undocumented extinct species or subspecies cannot be excluded.

### Methods

Track measurements included length, width, depth, pace length and stride length (cm), and the angulation of the track in degrees relative to the axis of the trackway. Global Positioning System locality readings were taken of the tracksite using a hand-held Garmin 60 device. Locality data were stored with the African Centre for Coastal Palaeoscience at Nelson Mandela University, to be made available upon request.

The tracksite was photographed, including for photogrammetric analysis (Matthews et al., 2016; Falkingham et al., 2018). Three-dimensional models were generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal length 4.5 mm; resolution 4000 × 3000; pixel size 1.56 × 1.56 µm). The final images were rendered using CloudCompare (v.2.10-beta).

Sand cover was removed from the tracksite in order to enable trackway analysis (Fig. 4). This was followed by a review of photographs and photogrammetry models. In combination, this approach permitted a fusion of the perspectives and interpretations of traditional Indigenous Master Trackers and western-trained ichnologists.

### Results

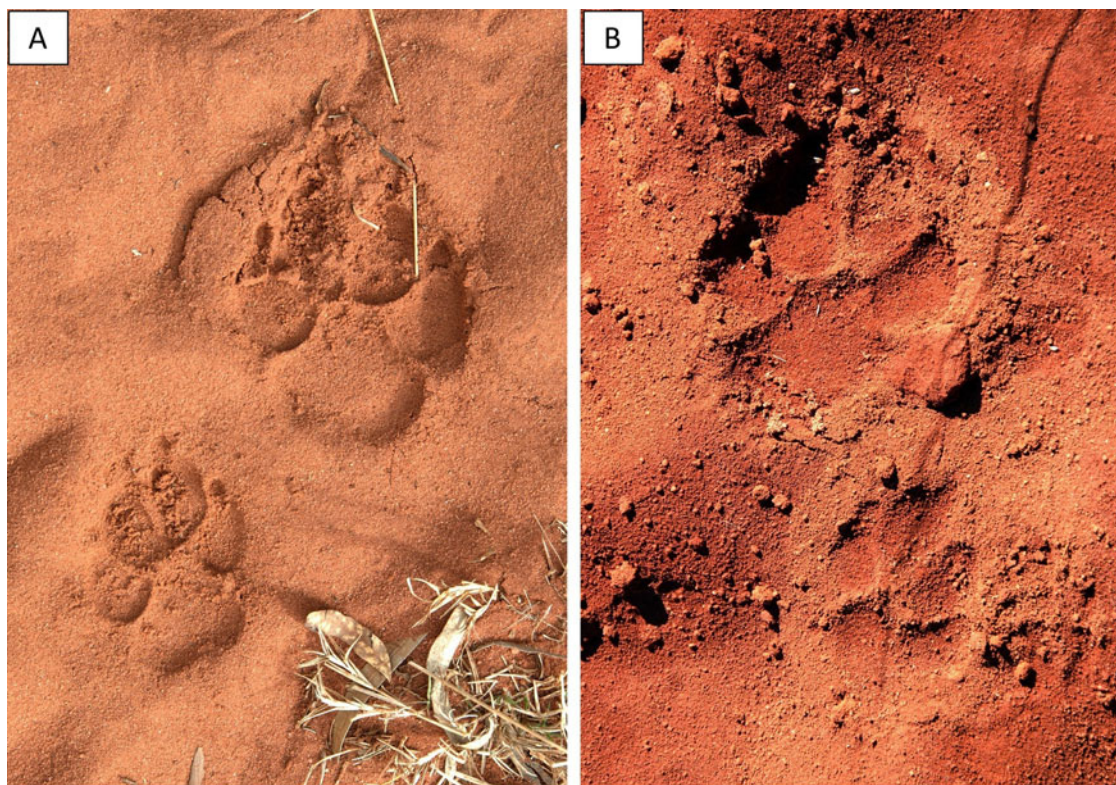
The community of Dana Bay is situated approximately 9 km west-southwest of the town of Mossel Bay on South Africa’s Cape south coast. Here, aeolianites crop out intermittently along a 2.5-km stretch of coastline, alternating with expanses of unconsolidated beach sand. At the eastern end of the beach there is an unconformity with Paleozoic deposits of the Cape Supergroup.

The Dana Bay tracksite was identified by Ilona and Aleck Birch, two citizen scientists who for years have kept a close watch for Pleistocene vertebrate ichnosites at Dana Bay, in particular with respect to transient exposures as a result of substantial sand movements. In 2020, they noted that a large in-situ aeolianite track-bearing surface had become exposed on the coast 30 m below their home. It had not been visible previously.

The Dana Bay tracksite lies well below the transgressive-lag marker horizon, and the tracks were therefore registered during MIS 11 (ca. 400 ka). The nearest dated sample from the MIS 11 deposits was obtained 250 m to the east and was dated to 382 ka ± 28 ka (Roberts et al., 2012).

The tracks were shallow, and thus best viewed and photographed under angled lighting conditions close to sunset (Fig. 5). The Birches obtained photographs that yielded adequate photogrammetry models (Figs. 6 and 7). Within days, the track-bearing surface was again covered by sand, and remained so until we visited the site in 2023. Fortunately, a small, raised corner of the outcrop could be identified. Sand removal was necessary to expose the track-bearing surface and allow track interpretation.

A single trackway containing 10 tracks was present, preserved in shallow concave epirelief and heading in a shore-parallel, westerly direction. The trackway comprised five manus–pes pairs, with the manus impressions appearing ahead of the pes impressions. The first three manus–pes pairs exhibited the best morphological detail. The most obvious feature was the size difference



**Figure 3.** Examples of brown hyena manus and pes pairs, exhibiting features mentioned in the text. (A) Right manus impression and left pes impression. (B) Left manus impression and right pes impression. Manus impressions are ~8.5 cm in length; pes impressions are ~6.6 cm in length. Reproduced with permission from Chris and Mathilde Stuart.

between the tracks of the manus and pes: the manus impressions are ~11 cm long and ~12 cm wide, whereas pes impressions are ~8 cm long and ~9 cm wide. Manus length may be a slight underestimate, if the pes tracks impinged on the posterior aspects of the manus tracks. Pace length of 51 cm was recorded. The smaller pes tracks, and to a lesser extent the larger manus tracks, point at a lateral angle relative to the longitudinal axis of the trackway (Figs. 6 and 7). Possible claw marks were identified ahead of some tracks (e.g., Fig. 7b). Limited morphological details of pad impressions were present (e.g., Figs. 7a and 7c).



**Figure 4.** Removing sand to re-expose the Dana Bay tracksite in 2023.

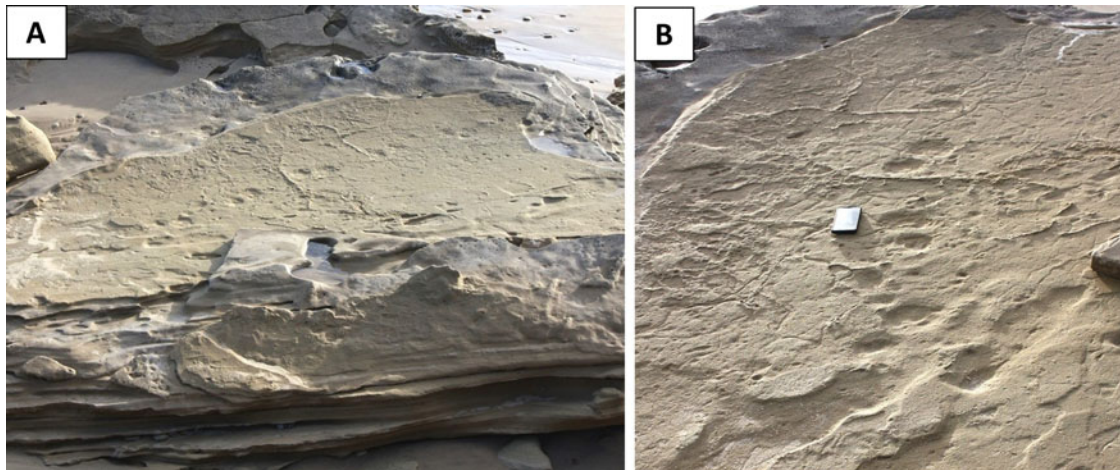
## Discussion

### *The global hyenid ichnology record*

At a global level there are few records of fossil hyenid tracks (McDonald et al., 2007). Iliopoulos et al. (2012) regarded the pre-Pliocene record of hyenid footprints as questionable. The Eurasian record is presented here in chronological order, followed by the record of African sites. Figure 8 illustrates sites from which possible or unequivocal hyenid tracks have been reported (other than the South African sites, which are shown in Figure 1).

Eurasian reports include one Early Miocene site, two Late Miocene sites, and one Pleistocene site. It cannot be assumed that hyenid tracks remained similar from the Early Miocene to the present. For example, Anton et al. (2004) noted that early members of the family still had retractable claws (a capacity that was subsequently lost), potentially creating confusion with felid tracks. Furthermore, Miocene hyenas were often substantially smaller than extant hyenas. Therefore, in considering the Early Miocene tracksite of Salinas de Añana in Spain, Anton et al. (2004) considered a hyenid origin for carnivorous tracks, but did not reach a definitive conclusion and contended that a small felid was equally plausible.

Abbassi (2010, 2022, p. 162, fig. 71 B) and Abbassi and Shakeri (2005, p. 81) reported a Late Miocene tracksite from Mushampa in Iran that contained a manus–pes pair of tracks in epirelief on fine-grained sandstone (Fig. 9), which they assigned to the ichnogenus *Creodontipus* Santamaria et al., 1989–1990, based on the shape and position of the digit impressions. The pes track, which partially overlapped much of the manus track, measured 4 cm in length and 4.9 cm in width. It was suggested that the trackmaker



**Figure 5.** (A, B) Two views of the Dana Bay trackway in 2020 under angled lighting conditions. The manus impressions are ~11 cm long and ~12 cm wide, and the pes impressions are ~8 cm long and ~9 cm wide. Photos courtesy of Aleck and Ilona Birch.

was hyena-like. The manus track does not appear to be larger than the pes track.

Iliopoulos et al. (2012) inferred a probable hyenid origin for a single, large, Late Miocene track, preserved in convex hyporelief at the Platýlakkos site in Crete, Greece. The footprint, which was noted on a sandstone slab that represented a lacustrine environment, comprised a natural cast of a left manus impression, with traces of the metapodial pad, four digital pads, and claw traces indicating non-retracted claws. The maximum print length was measured at ~12.6 cm, including claw traces (excluding the claw traces, length was ~9.8 cm). Maximum print width was 9.5 cm. The digital pad traces were noted to be large and closely spaced, with the outer digital pad traces diverging strongly outwards and a concave anteromedial border to the lateral digital pad trace. The metapodial pad cast was noted to be large, sub-triangular, and asymmetrical in outline, with concave anterolateral and anteromedial borders. It was noted that the morphology of the track resembled that of the tracks of extant hyenids, and that its size happened to be comparable to that of the extant spotted hyena. A new ichnotaxon was not erected, given the presence of just a single track.

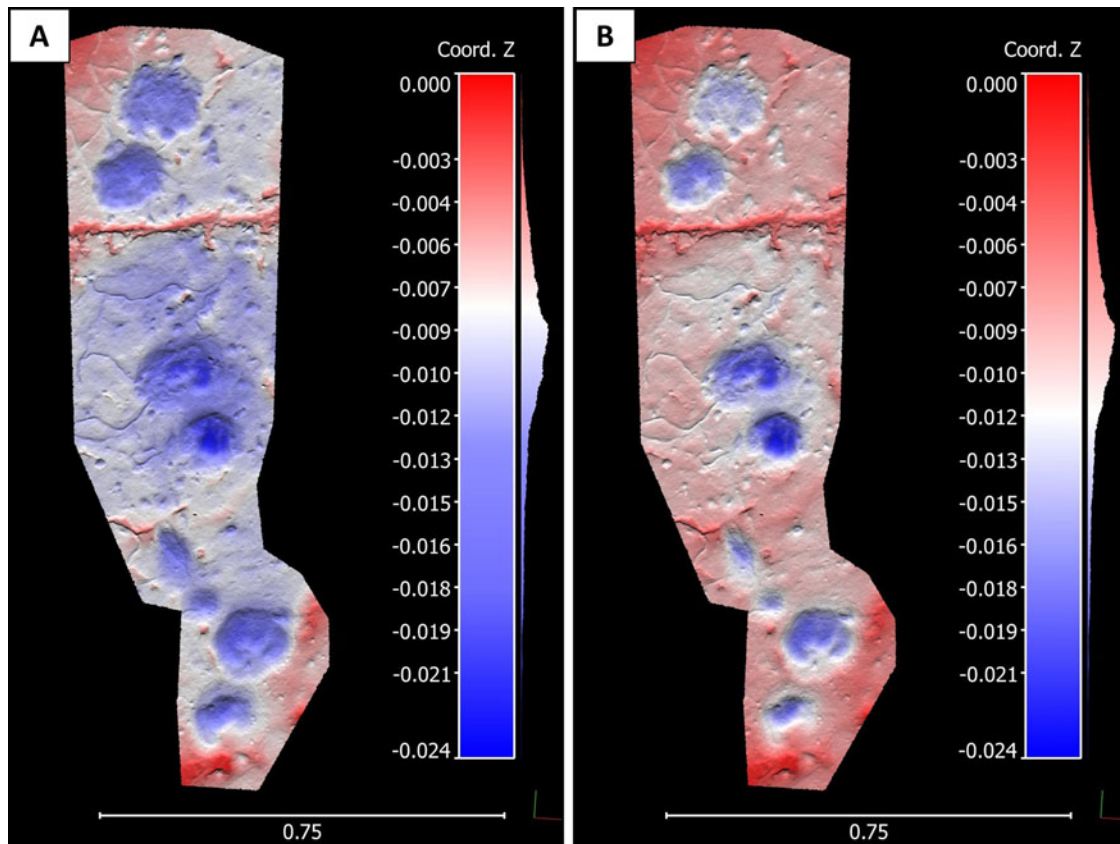
Casteret (1948) described terminal Pleistocene hyena tracks and coprolites from a den in the Aldène Cave in France, along with bear tracks and hominin tracks. At the time, the assemblage was thought to date to 15–20 ka, but the hominin tracks have subsequently been dated to circa 8 ka (Ambert et al., 2000). European hyena populations became extirpated around the end of the Pleistocene, essentially ruling out a Holocene age for the hyena tracks (Varela et al., 2010). The photographs of the well-preserved hyenid tracks (Casteret, 1948, p. 410) show closely packed digit impressions in a jigsaw pattern.

Given the sparse record of unequivocal hyenid tracks from Eurasia, the African examples are essential to considering a dedicated ichnotaxon. Records are presented from north to south. Reports of Pliocene trackways from Laetoli in Tanzania are reviewed, followed by a Pliocene record and a Holocene record from Namibia, and finally three Pleistocene trackways from South Africa that have previously been attributed to possible hyenids. One is from the South African east coast at Nahoon, and the other two are from the west coast in the Langebaan area.

Altamura et al. (2020) reported a cluster of four sub-elliptical depressions (7–12 cm in diameter) from the Gombore II Open Air Museum site in Ethiopia, dated to the Early Pleistocene (1.2–0.85 Ma). It was noted that the best-preserved track of this type might be carnivoran in origin, and that it resembled modern hyena tracks. No formal ichnotaxonomy was presented.

While the Pliocene Laetoli site in Tanzania is best known for its 3.66 Ma australopith trackways (Leakey and Hay, 1979; Deino, 2011), less well known are the almost 9500 vertebrate tracks that have been identified at 18 distinct sites around Laetoli (Leakey, 1987). Leakey (1987) noted that track descriptions and interpretations were provisional and preliminary in nature. In total, 226 tracks at four of the 18 sites were attributed to hyenids. While the possibility of more than one trackmaker species was considered, related to evidence of five species from the region in the body fossil record (Barry, 1987), the tracks in general were reported as being similar to those made by *Crocota crocuta*. More than one gait pattern was inferred. The longest potential hyenid trackway was 11 m in length and contained 43 tracks. Measurements were recorded from a 9-m-long trackway, with size ranging from 13 cm long and 10 cm wide to 10.5 cm long and 9.5 cm wide. It was suspected that these probably represented manus and pes impressions, respectively, but this could not be confidently concluded as a size gradation from smallest to largest (rather than two distinct sizes) was present and a clear pattern of registration was not evident. Formal ichnotaxonomy was not discussed. Musiba et al. (2008) reinvestigated several of the tracksites and reported that in many cases the quality had deteriorated, and that some trackways were no longer identifiable.

Bennett et al. (2010) and Morse et al. (2013) described well-preserved Holocene trackmaker assemblages on dried floodplains of the Kuiseb Delta near Walvis Bay in Namibia, dated to circa 1.7–0.5 ka. The track-bearing surfaces are often covered by migrating dunes. Bennett et al. (2010) simply noted the presence of hyena tracks, whereas Morse et al. (2013, fig. 2L) included a small image of two track pairs attributed to a hyena. It appears that a trackway pattern similar to that seen at Dana Bay is present, and at least one of the probable manus tracks appears larger than the pes track behind it. Impressions registered by the metapodial pad and digit pads are evident. No further descriptions were provided, and no formal ichnotaxonomy was presented.

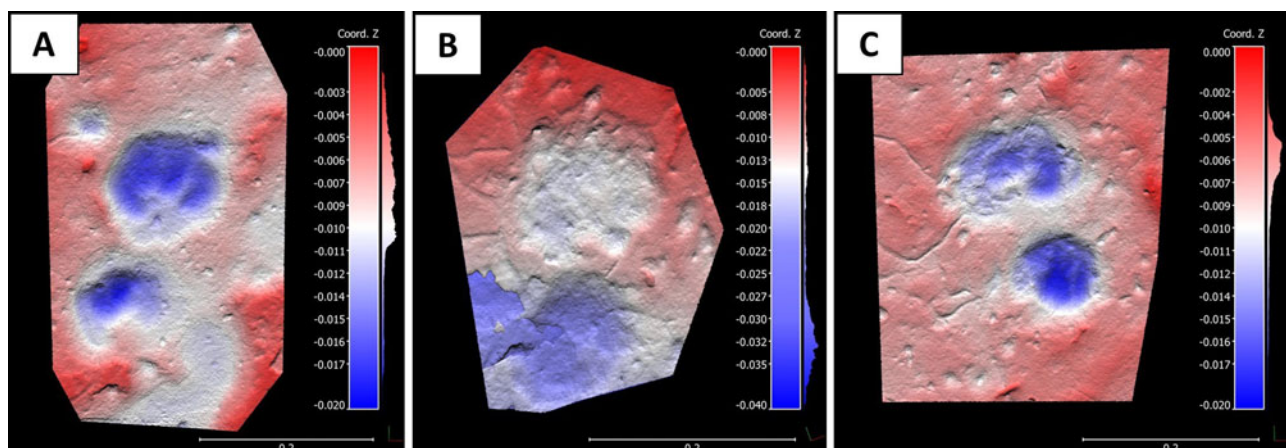


**Figure 6.** Three-dimensional photogrammetry models of the first three manus–pes sets in the trackway, with bluer (A) and redder (B) color variations; horizontal and vertical scales are in meters.

Morales et al. (2011) reported an aeolianite site in the Tsondab Formation at Meob, in the Namib Sand Sea. Here, the lower dentition of an Early Pliocene hyenid, thought to be *Crocota dietrichi*, was found in association with coprolites and carnivoran tracks. It was inferred that the tracks may have been made by a hyena of that species. This inference was made not on the basis of morphological characteristics of the tracks, but on the spatial association with the skeletal material and coprolites (which were characteristic of a hyenid). It

was noted the foreprints and hindprints were of approximately similar size.

Among the three South African reports, the first (Mountain, 1966), from Nahoon, described a surface that contained the first example of open-air hominin tracks in the world, preserved in hyporelief, and subsequently dated through OSL to  $124 \pm 4$  ka (Jacobs and Roberts, 2009). On the same surface were six enigmatic tetrapod tracks. Mountain (1966, p. 106–107, pl. VI) showed these to a colleague, Hendey, who observed faint claw



**Figure 7.** Three-dimensional photogrammetry models of (A) the first manus–pes set, (B) the second manus–pes set, and (C) the third manus–pes set in the trackway; horizontal and vertical scales are in meters.



**Figure 8.** Map showing putative hyenid tracksites in the global ichnology record (other than the South African sites, which are shown in Figure 1).

traces and “suggested that the six footprints might be those of the brown hyena (*Hyaena brunnea*) or strandwolf... he considers further that they were possibly made by two animals.” Roberts (2008, p. 204, figs. 2, 21) noted that the tracks were each ~8 cm in length and ~3–4.5 cm in width, which is too small for an adult brown hyena or spotted hyena, and did not exhibit a difference in size between manus and pes tracks. It was concluded that “the maker of this trackway remains unidentified”.

Tankard (1976, p. 104, 106) described a “series of footprints of a terrestrial mammal, probably the strandwolf (*Hyaena brunnea*)” on an aeolianite surface at Kraal Bay near Langebaan, preserved in epirelief. The site was not directly dated, but subsequent dating of aeolianites in the general area yielded an age of circa 117 ka (Roberts, 2008). An accompanying photograph (Tankard, 1976, fig. 21) indicated a straight trackway of at least six large, round tracks (apparently all of similar size), and the figure caption

drew attention to claw marks within one of the tracks. Track dimensions were not specified, and no rationale for the attribution to the brown hyena was provided. We note that the tracks do not appear to exhibit the distinguishing features of brown hyena tracks described herein or in southern African tracking manuals (Liebenberg, 1999; Van den Heever et al., 2017; Stuart and Stuart, 2019; Gutteridge and Liebenberg 2021). Furthermore, if the claw impressions are indeed located within the tracks, the foot dimensions might be smaller than they initially appeared from the track size. By 1995, Roberts (2008) was unable to re-locate the trackway.

Finally, Roberts (2008, p. 191, fig. 22) noted: “Early in 1995, while exploring aeolianite outcrops at Kraal Bay, I found the trackway of a large carnivore, probably a hyena on a dunerock paleo-surface.” Four tracks were noted, preserved in epirelief, three of which displayed a good quality of preservation. A rear print diameter of 125 mm was noted, and was contrasted with the diameters of the two smaller tracks of 110 mm and 115 mm. Digit impressions and claw impressions were noted in some of the tracks. Based on the large overall dimensions, claw marks, and size differentiation between manus and pes, Roberts (2008, p. 204) suggested that the trackmaker was “a hyena rather than a felid or canid (manus is larger than pes in hyenas), probably the brown hyena *Hyaena brunnea*, still present in the area.” We note, however, that the size difference between manus and pes tracks in this case is less than that reported here from the Dana Bay site, or in the southern African tracking manuals.

Consequently, in all three southern African cases from the second half of the twentieth century, we do not consider the identification of a hyenid trackmaker to be conclusive. Of the three, the trackway identified by Roberts in 1995 (Roberts, 2008) appears the most plausible, while in our view remaining equivocal.

In summary, the record of a large track from Crete (Iliopoulos et al., 2012) appears morphologically convincing (exhibiting the ‘jigsaw pattern’) but suffers from being a single isolated track. The tracks at the Aldène Cave site (Casteret, 1948) appear convincing, but were not formally described. The other Eurasian sites are intriguing but equivocal. The Ethiopian tracks are highly speculative because a carnivorous origin cannot be confirmed. The



**Figure 9.** Manus–pes pair assigned to the ichnogenus *Creodontipus* by Abbassi and Shakeri (2005); a hyenid origin was considered; scale bar is in cm. Reproduced with kind permission from Nasrollah Abbassi (Abbassi 2022, fig. 71B).

Laetoli sites in Tanzania contain by far the largest number of tracks thus far attributed to hyenids. However, the site and track descriptions were acknowledged to be preliminary, and details of track morphology and rationale for attribution to hyenids were not provided. Among the southern African sites, the evidence from the Namibian Holocene sites is rudimentary, without detailed descriptions, the evidence from the Namibian Pliocene site (Morales et al., 2011) is circumstantial and not based on morphological grounds, and none of the three South African sites (all of which were attributed to the brown hyena) seems conclusive. Only the Langebaan site identified in 1995 (Roberts, 2008) claims to show a heteropodial trackway (with manus track larger than pes tracks), but the typical hyenid trackway pattern does not appear to be present. Moreover, the size difference is less than what is reported in regional tracking manuals, and other causes for the size difference are possible.

The global sparsity of fossil hyenid tracks can be contrasted with the rich record of coprolites (most of which have been attributed to the brown hyena) from scavenger dens (e.g., Carrión et al., 2000; Scott et al., 2003; Rector and Reed, 2010; Badenhorst et al., 2016). However, a discussion on hyena coprolites is beyond the scope of this article.

We note also that Ellenberger (1980) erected the ichnotaxon *Hyaenodontipus praedator* to describe Eocene tracks in France. We mention this only because this taxon may sound like one describing hyenid tracks. However, these clearly predate any members of the Hyaenidae, and describe tracks made by a representative of the Hyaenodontidae family.

### Tracksite review and trackmaker identity

By Cape south coast standards, the Dana Bay tracksite provides a reasonable standard of preservation: the shallow tracks provide interpretable information of track size and trackway morphology. A score of 1 or 1.5 on the scale of Belvedere and Farlow (2016) can be assigned (where 3 represents the highest possible score). By global, standards, however, according to which higher scores are often assigned to tracks registered in fine-grained sediments and not subjected to substantial erosion, the Dana Bay tracksite is suboptimal.

Nonetheless, the track-bearing surface is relatively large, with a single trackway comprising ten tracks (five manus–pes pairs). The relatively consistent pace length and the repeated pattern of one track in each pair being substantially larger than the other are noteworthy. The indications that the smaller (pes) tracks (and, to a lesser extent, the manus tracks) are angled outwards in relation to the direction of movement, along with probable claw impressions, are in accordance with the appearance of hyenid tracks as indicated in modern regional tracking manuals. These gait and track features are also well recognized in modern trackways by Indigenous Master Trackers and other southern African tracking experts. In combination, these features allow us to identify a trackway registered by a large hyenid.

The single purported large hyena track from the Platýlakkos site in Crete presents a notable contrast to the Dana Bay trackway. In one case, excellent preservation quality exists, allowing the identification of a jigsaw pattern and other morphological features that support a hyenid origin, but there is only a single track. In the other case, the trackway is long enough to exhibit a characteristic repeating pattern, but the quality of preservation in individual tracks is poor. The two examples can be viewed as representing

different ends on an ichnological spectrum. Considering them in combination therefore has merit.

Among extant hyenids, the substantial size difference between manus and pes impressions in the Dana Bay tracksite is in keeping with the relative dimensions of brown hyena tracks. A spotted hyena origin cannot be completely excluded, but the manus-to-pes ratio is not as great in this species. The tracks are clearly much too large for an aardwolf to be considered. A striped hyena origin is plausible on morphological grounds, but there is only limited evidence that it has inhabited southern Africa. Turner (1988) attributed a skull to *Hyaena hyaena* from the Swartkrans site in “Lower Pleistocene” deposits, and Kuhn et al. (2017) attributed two teeth at Cooper’s Cave in Early Pleistocene deposits to this species. Both cases are from South Africa’s Gauteng Province. There are thus no fossil records of the striped hyena from the middle Pleistocene or from the Western Cape or Eastern Cape provinces, in contrast to the extensive records of the brown hyena from these regions during the middle Pleistocene (Avery, 2019). The larger than expected size of the tracks can be attributed either to substrate factors (tracks in sand are often larger than their equivalents in more cohesive substrates) and to the notion of Pleistocene carnivore tracks often being larger than those of their extant descendants, or to a combination of these factors. Hyenids were abundant during the Early Pleistocene, while during the middle Pleistocene the hyenid fauna decreased, leaving only those species that have survived to the present (Ewer, 1967; Mills, 1982). In the Western Cape, the brown hyena has been reported in the body fossil record from Pleistocene deposits at several sites on the Cape west coast and southwest coast (Avery, 2019). Fewer Pleistocene body fossil sites have been reported from the Cape south coast: Herold’s Bay Cave (Brink and Deacon, 1982), the Klipdrift Shelter Complex (Henshilwood et al., 2014), the Pinnacle Point Complex (Rector and Reed, 2010), and Nelson Bay Cave (Klein, 1972). These Cape south coast sites are from the late Pleistocene or the later part of the middle Pleistocene. The oldest, at Pinnacle Point, is dated to 151 ka (Rector and Reed, 2010). The presence of brown hyena tracks from deposits dated to circa 400 ka thus represents a substantial temporal extension for the Cape south coast and indicates that hunter-scavengers such as brown hyenas inhabited the region during MIS 11.

### The Quaternary ichnology conundrum

From the substantial corpus of reported Quaternary tracksites from Africa, in only four cases was formal ichnotaxonomy presented (Lockley et al., 2019, 2021; Plint and Magill, 2021; Helm et al., 2023b). In three cases, this involved the erection of new ichnogenera and ichnospecies. It seems that, in Africa at least, researchers do not typically include formal ichnotaxonomy in their descriptions of Quaternary tracks. This may be related to the fact that many of the trackmaker taxa from the Pleistocene and Holocene are extant, in forms that are typically similar to those of their Pleistocene ancestors. Modern tracking manuals are therefore often used to help identify Quaternary tracks and traces. In contrast, such a ‘short-cut’ is inappropriate when considering Pliocene, Miocene, or older tracks and traces.

Lockley and Harris (2010, p. 36–37) addressed a fundamental ichnological maxim: “Older organisms are generally less like extant ones than are younger ones. Therefore, the problems of determining trackmaker affinity increase with the increasing age of the fossil footprints.” In the case of the tracksite described

herein, the southern African tracking manuals have proven invaluable, and there is a minimal paleoichnological record that can be consulted. Nonetheless, we attempted to follow a disciplined approach, whereby tracks, trackways, and traces are first considered on their own merits and described according to their morphology, before speculating on trackmaker identity.

### *Ancient and modern ways of knowing*

There is a strong case for drawing on indigenous knowledge when applying current scientific methods in the field of ichnology. The art of tracking—provocatively but justifiably described by Liebenberg (1990) as ‘the origin of science’—is applied with demonstrable success by the remaining hunter-gatherers of the Kalahari in central southern Africa. The Ju’/hoansi San are socially conditioned from a very early age in field awareness, including how to identify animal tracks and signs in their environment. This prowess has operated as an indispensable survival competency over (at least) tens of thousands of years. It is a skill analogous to learning how to read, and the early uptake at a time of brain plasticity gives these practitioners a lifelong literacy advantage over latecomers to the discipline.

Two authors (#D, /N), Ju’/hoansi San, are certified as Indigenous Master Trackers through the accreditation program developed by CyberTracker, which involves peer recognition within the tracker community. “A distinction is made between the Indigenous Master Tracker and the Master Tracker. The Indigenous Master Tracker was or still is a traditional hunter, using the persistence method and/or traditional poison bow-and-arrow” (<https://cybertracker.org/track/master-trackers/>). The Master Tracker is the highest tracker qualification, and only a handful of indigenous trackers across the Kalahari are currently recognized as Master Trackers.

Precedents exist for the collaborative approach followed here between Indigenous Master Trackers and modern-day scientists. In the Tracking in Caves project, Ju’/hoansi Indigenous Master Trackers assisted scientists in the interpretation of hominin track-sites in French caves (Biese, 2021; Lenssen-Erz and Pastoors, 2021; Pastoors et al., 2021). More recently, Ju’/hoansi Indigenous Master Trackers assisted in the interpretation of prehistoric tracks in the rock art record in Namibia (Lenssen-Erz et al., 2023).

Tracking in the substrates of northeastern Namibia is different in key respects from searching for and examining ichnological patterns on paleosurfaces of the Cape south coast, where, for example, many tracks are preserved in hyporelief on ceilings and in profile in cliff exposures. In addition, some diagnostic tools available to contemporary trackers are not available to paleoichnologists: inspection of the entire area where tracks have been located, feeding and other associated signs, picking up the spoor later (farther away) when the tracks are interrupted, knowledge of the time of day the tracks were registered, the role of dew, and even the ability to track down the actual quarry. In paleoichnology, on the other hand, the evidence is nearly always fragmentary and often imperfectly preserved.

The approach followed was for the paleoichnologists in our team to first provide instruction on regional geology, geomorphology and the varieties of track preservation that might be encountered. Known tracksites of interest were pointed out to the Indigenous Master Tracker team members without any elaboration. With fresh eyes, the latter would discuss between themselves and would then indicate what they had discerned to the rest of the team, from basic species identification through (where applicable) to indications of animal behavior. Then would follow an exchange

in which insights were shared and debated. Typically, a joint conclusion was reached. Within a short space of time the Indigenous Master Trackers had begun identifying newly exposed tracksites for the first time. In the case of the hyena trackway described here, the photogrammetry results were also shared and debated by the research team after the in-situ inspection.

Working as a research team that integrates indigenous and modern expertise, we have demonstrated that such barriers are easily overcome through practical training, allowing for commonalities to be explored and tracksites to be interpreted in a disciplined manner. The prospect exists of permanent cross-skilling, a fusion whereby the traditional neo-ichnologists amongst us learn and adopt contemporary scientific methods, while the paleoichnologists amongst us hone our tracking and animal behavior insights under expert tutelage.

In our experience, the fusion of ancient traditional and modern scientific approaches potentially leads to outcomes and conclusions that are richer for being integrative and holistic. Ideally, as occurred in the case of the Dana Bay tracksite, each of the two groups within the team assesses the tracks independently, without knowing in advance the opinion or conclusion of the other group. The Dana Bay tracksite, where congruence emerged between these two ways of knowing, provides a salient example of this potential.

### **Conclusions**

This research has resulted in identification of the first unequivocal fossil hyenid trackway. The Tanzanian trackways that were attributed to hyenids are more equivocal, given the lack of formal descriptions, the preliminary and provisional nature of the identifications, and the lack of two distinct track sizes. Located in Pleistocene aeolianite deposits at Dana Bay on South Africa’s Cape south coast, the unequivocal fossil hyenid trackway is almost always covered in deep layers of beach sand. The distinctive hyenid trackway morphology is in accordance with findings in modern southern African tracking guides. Combining these findings with the report of a single, highly probable, very well-preserved hyenid track from Crete (Iliopoulos et al., 2012), results in insights into the morphology of fossil hyenid tracks and trackways. Such insights could be enhanced by a re-evaluation of the tracks attributed to hyenids in Tanzania. The Dana Bay trackway, from MIS 11 that was attributed to a brown hyena, complements the regional body fossil record in providing the first evidence of a hyenid on the Cape south coast older than MIS 6. A collaborative approach that synthesizes ancient and modern skills of track identification, as followed here, can result in enhanced, accurate interpretation, and a high level of diagnostic accuracy.

**Acknowledgements.** We appreciate the support of the Blombos Museum of Archaeology, the Discovery Wilderness Trust, the Desert Lion Trust, the Hessekwa Society for Archaeology, Nasrollah Abbassi, Aleck and Ilona Birch, Pieter-Jan Gräbe, Linda Helm, Renée and Niekie Rust, Chris and Mathilde Stuart, and Richard Webb and members of the Still Bay Camera Club.

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