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The search for Pleistocene lion tracks with Indigenous San trackers on South Africa's coast

The African record of fossil large felid tracks is sparse. Three Pleistocene sites (one previously reported and two described here for the first time) add to this record, and provide the only reported fossilised probable lion tracksites in southern Africa. All three sites are preserved on aeolianite surfaces on South Africa's Cape south coast. Trackmaker and trackway identification and interpretation were made as a collaboration between Western-trained scientists and Ju/'hoansi San Master Trackers from Namibia. The value of the integration of Western science and Indigenous knowledge and expertise has thus been demonstrated, and has led to a deeper understanding of the trackmakers and their behaviours.

Significance:

- Three African large felid (probable lion) fossil tracksites have been identified on South Africa's Cape south coast.
- All three sites date to the Pleistocene epoch.
- These tracksites add to a sparse African record of fossilised large felid footprints.
- Trackmaker identifications and interpretations were made as a collaboration between Western scientists and Ju/'hoansi San Master Trackers from northeastern Namibia, which led to refined identifications and behavioural interpretations.

Introduction

Since the inception of the Cape South Coast Ichnology Project in 2008, almost 400 Pleistocene vertebrate tracksites have been identified along a 350-km stretch of coastline on South Africa's Cape coast[1], and numerous peer-reviewed scientific articles have resulted to date. The project is based out of the African Centre for Coastal Palaeoscience at the Nelson Mandela University. Consequently, the global understanding of Quaternary ichnology (the study of tracks and traces) has been enhanced.[2,3]

The purpose of this article is to describe three Cape south coast tracksites attributed to the African lion, *Panthera leo* (Figure 1). While the three sites may have a common Pleistocene trackmaker species, their interpretation differed in salient aspects, leading to different types of collaborative approaches between the Western-trained scientists and the Ju/'hoansi Indigenous Master Trackers in our research team. The findings described here build on the foundation established through previous publications on hyena footprints and a probable pangolin trackway.[4,5] The compelling benefits that have accrued through the fusion of two perspectives, whereby traditional scientific knowledge is blended with modern scientific approaches, have been extolled. Moreover, the remarkable skills of Indigenous Master Trackers, inculcated from an early age, have been summarised.[6]

All three sites are located on aeolianite (cemented dune) surfaces of the Waenhuiskrans Formation[7], which forms part of the Bredasdorp Group[8]. The footprints would have been registered on dune surfaces or interdune areas when they comprised unconsolidated sand. All three sites are thought to be within the range of Marine Isotope Stage (MIS) 6 to MIS 4 (~156–65 ka), given the consistency of the age results for Cape south coastal Waenhuiskrans Formation deposits.[9] Only Site 1 has been directly dated using optically stimulated luminescence, which yielded an age of 70 ± 4 ka (sample code Leic20003).[10]

The African record of fossilised lion (or large felid) footprints is relatively sparse. Other than the sites described here, the only African record is from the Pliocene at Laetoli, Tanzania.[11] In Europe, a large trackmaker assemblage from Bottrop-Welheim in northern Germany contained, inter alia, footprints of the cave lion.[12,13] A trackway attributed to the extinct European cave lion (*Panthera leo spelaea*), dated to 42–35 ka, was also recovered from Bottrop.[14,15] In Western Australia, thousands of Pleistocene claw scratch marks on the walls of Tight Entrance Cave have been attributed to the marsupial lion (*Thylacoleo carnifex*), the largest-known marsupial carnivore (which, despite its name, belongs to the order Diprotodontia, rather than Carnivora).[16]

Multiple reports exist of medium-sized or large felid footprints from the Americas, North America in particular. For example, footprints of the extinct *Panthera atrox* were reported from Cat Track Cave in Missouri, from the North American Pleistocene.[17] Large felid footprints reported from Chilly Bowl Cave in Arkansas were also attributed to *Panthera atrox*.[18] Also in Missouri, footprints in the Berome Moore Cave[17] have been attributed to either a jaguar (*Panthera onca*) or *Smilodon*, both of which were present in the regional fossil record[19]. Smaller footprints attributed to jaguars (*Panthera onca*) have been reported from several sites, for example, Jaguar Cave in Tennessee.[20] From South America, medium-sized footprints have been reported from the Late Pleistocene Pehuen Co site in Argentina.[21] Also from Argentina, two large felid footprints (with a manus length of 19.2 cm) were reported from near the city of Miramar.[22] The Cape south coast sites described here thus make a significant contribution to the global record.



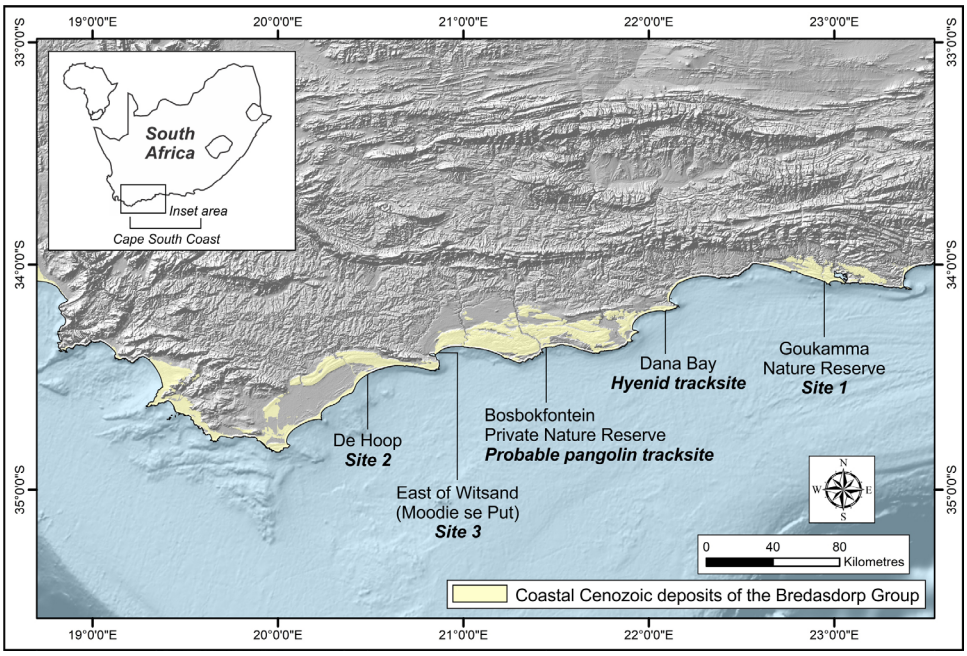


Figure 1: Map of South Africa's Cape south coast, showing the extent of Cenozoic deposits and sites mentioned in the text.

Methods

Tracksites were assessed and documented through measuring footprint length, footprint width, footprint depth, pace length, stride length and trackway width, following the methods of Leonardi[23]. The sites were interpreted in the context of the local stratigraphy. Where appropriate, strike and dip readings of the strata were taken, the degree of weathering was determined, and primary bedding was described geologically. Global Positioning System coordinates were obtained, using a handheld Garmin Etrex 10 device. Locality data were stored in the African Centre for Coastal Palaeoscience at Nelson Mandela University.

Photographs were taken, including for photogrammetric analysis.[24,25] 3D models were generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 um). The final images were rendered using CloudCompare (v.2.10-beta).

At each of the three tracksites, independent assessments were undertaken by the Ju/'hoansi trackers and the team members trained in the application of the Western scientific method, ahead of discussion regarding interpretation, so as to avoid cognitive bias in either direction. The Ju/'hoansi team members would examine, confer at length in Ju/'hoan, and reach a conclusion. Interpretations would then be shared, along with 3D photogrammetry data where applicable. We would aim to reach consensus through our respective but complementary perspectives.

Results and interpretation

Site 1 – Goukamma

The Goukamma tracksite (Figure 2), located on the coast in the Goukamma Nature Reserve, was reported by Helm et al. in 2018[26], and is briefly summarised here. The site has been dated to 70 ± 4 ka (sample code Leic 20003).[10] Two large carnivoran prints, each clearly containing a main pad and four digit pads, form the most obvious feature of a short trackway (Figure 2A–D). The footprints occur on a fallen aeolianite block, and are preserved in concave epirelief (Figure 2E). Claw impressions are absent. The highest level of anatomical fidelity is present in the second footprint.

The first footprint measured 15 cm in maximum length, 13 cm in maximum width and 3.0 cm in maximum depth. The second footprint measured 17 cm in maximum length, 14 cm in maximum width and 4.0 cm in maximum depth. Ahead of it were fainter impressions which probably represented an indirect register. A pace length of 76 cm was measured. Indistinct indentations anterior to each footprint were present.

On the same surface, exhibiting less relief but nonetheless clearly evident when angled early-morning lighting was present, another short trackway segment was evident, aligned in the same direction as the first. In this case, the two footprints took the form of crescentic depressions, interpreted as large footprints that had been almost completely filled in by sand, presumably deposited by wind. These features were situated 65 cm from the main trackway (to the left of the main trackway when viewed from the direction of travel of the main trackmaker). The trackmaker responsible for the infilled footprints could not be identified from the appearance of these two crescents alone, but in the same axis the footprint-bearing surface ended, and an underlying layer situated 1.5 cm below it was exposed. Distal to these two crescentic shapes, and on this underlying layer, two footprints were present, each with maximum length and width of 12 cm. Overall morphology was similar to that of the two main footprints described above, other than the smaller size. The likelihood of this being a four-footprint trackway, with the proximal two footprints largely infilled and the distal two footprints being transmitted tracks (undertracks), was supported by the consistent pace lengths of 60 cm, 61 cm and 61 cm. No displacement rims were evident around the footprints on the main layer, suggesting that the footprints were registered on a fairly level dune surface.

As the best-preserved main footprint was of a high degree of preservation and anatomical fidelity[27], the identification of a large felid (almost certainly lion) trackmaker was not in doubt and a report on the site had already been published. However, when we viewed the site together, these findings were not divulged. After briefly conferring, the Ju/'hoansi team members immediately confirmed the interpretation of a lion trackway, adding the new information that they were interpreting evidence of a male and female pair travelling in the same direction. A juvenile, rather than a female, could potentially be postulated, but we note the subtle differences that exist between male and female lion footprints.[28,29] Further discussion then involved the subtleties of the female lion trackway, with its footprints infilled by windblown sand on the main layer, and transmitted tracks on an underlying layer. The footprints of the (heavier) male lion were better preserved than those of the female, exhibiting deeper indents and sharper margins. The presence of a nearby in situ level surface in the nearby cliffs was noted, and it was agreed that the footprints had probably been registered on this interdune surface.

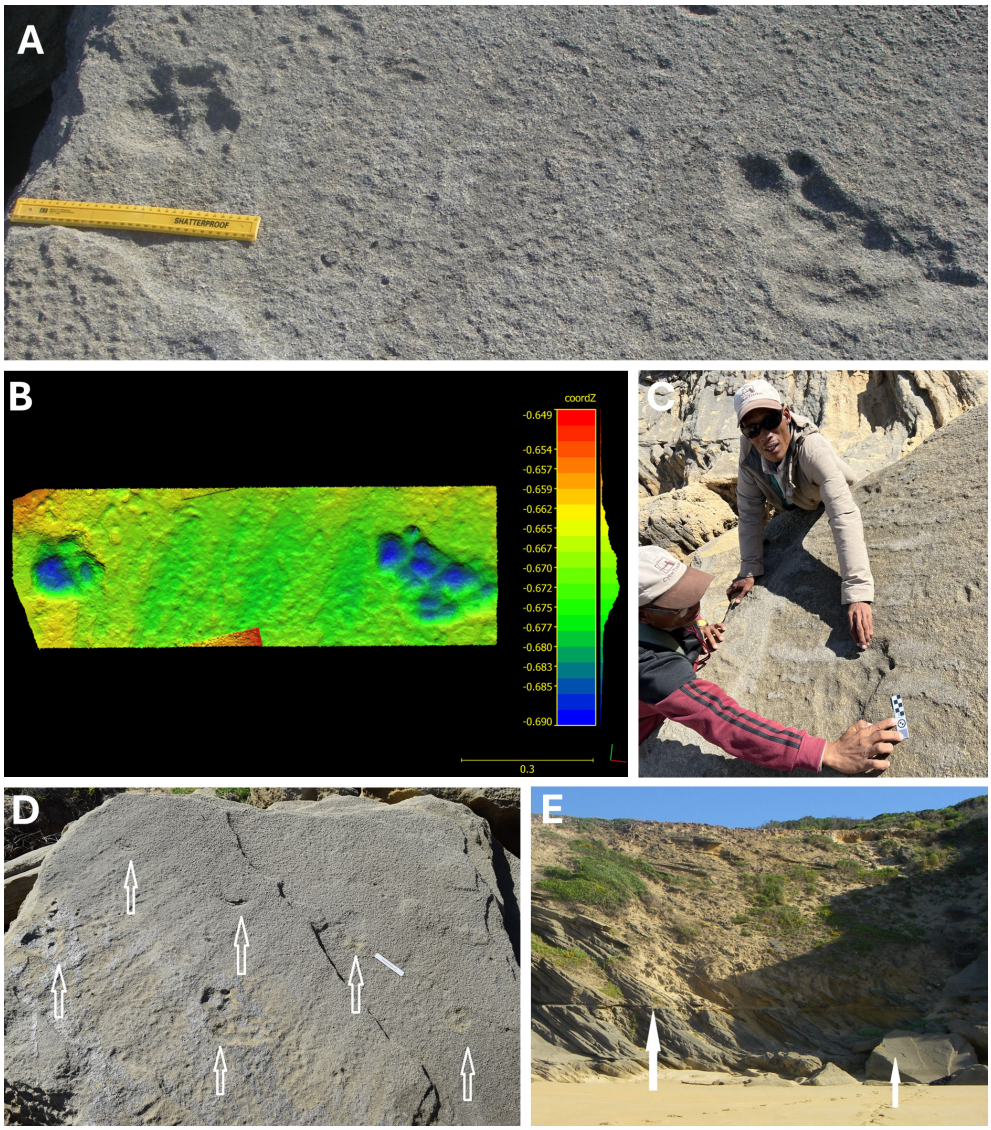


Figure 2: (A) The main trackway at Site 1; ruler = 30 cm. (B) 3D photogrammetry model of the Site 1 trackway; the vertical scale is in metres. (C) Co-authors #.D. and /.N. examine the Site 1 footprints; scale bar = 10 cm. (D) Arrows indicate the Site 1 footprints: the two bottom left arrows indicate the main trackway, the two top left arrows indicate the infilled footprints which now appear as crescents, and the two right arrows indicate the transmitted tracks; scale bar = 16 cm. (E) The context of the loose track-bearing block is apparent; the right arrow indicates the footprints, whereas the left arrow indicates the level bedding plane, representing an interdune area, on which the footprints were probably registered.

Site 2 – De Hoop

In the coastal portion of the De Hoop Nature Reserve, an in situ aeolianite surface surrounded by loose aeolianite blocks contained two adjacent footprints (Figure 3A), preserved in concave epirelief. As viewed in the photogrammetry image in Figure 3B, the left footprint was better defined and contained at least three distinct large digit pad traces. The main pad impression was partially infilled and therefore could not be described further, but the footprint length was 14 cm. The right footprint was less well defined, and mostly comprised two large digit pad impressions. A fainter impression was evident between these two footprints, suggesting that the trackmaker had shifted its foot ~4 cm to the left (the middle impression thus being older than the left impressions).

Based on the footprint size and prominent digit pad impressions and morphology, the tentative interpretation by our Western-trained scientists was of probable large felid (most likely lion) footprints, but the confidence to reach a definite conclusion was lacking. The discussion on this occasion took longer, but the conclusion reached by the Ju/'hoansi team members was expressed with confidence: these were lion footprints. Furthermore, a crouching position of a lion that was ready to pounce was suggested – an interpretation that explained the set of two footprints adjacent to one another, pointing in the same direction. Thus, the Ju/'hoansi team members assertively contended that the footprints were from a lion, and they provided additional behavioural interpretations.

Site 3 – East of Witsand

This site was located at the foot of aeolianite cliffs on the coast east of the community of Witsand, close to the old well dug in aeolianites that is known as Moodie se Put. An in situ aeolianite surface dipped at an angle of 30° to the south, and contained an assemblage of footprints preserved in epirelief (Figure 4). The most obvious features were the substantial displacement mounds at the downslope ends of three of the footprints, along with the large size of the generally roundish footprints (Figure 4A,B). Approximate footprint size was 14 cm for the larger footprint and 11 cm for the smaller footprints. Footprint depth is approximately 1.5 cm (not including displacement mounds) and 5 cm (including displacement mounds).

The interpretation of our Western-trained team members was simply of large, unidentifiable trackmakers that had registered footprints on a steep dune slope. In this case, however, animated discussion ensued among our Ju/'hoansi team members, after which an interpretation of a lion tracksite was made, including trackways of male (larger footprints) and female

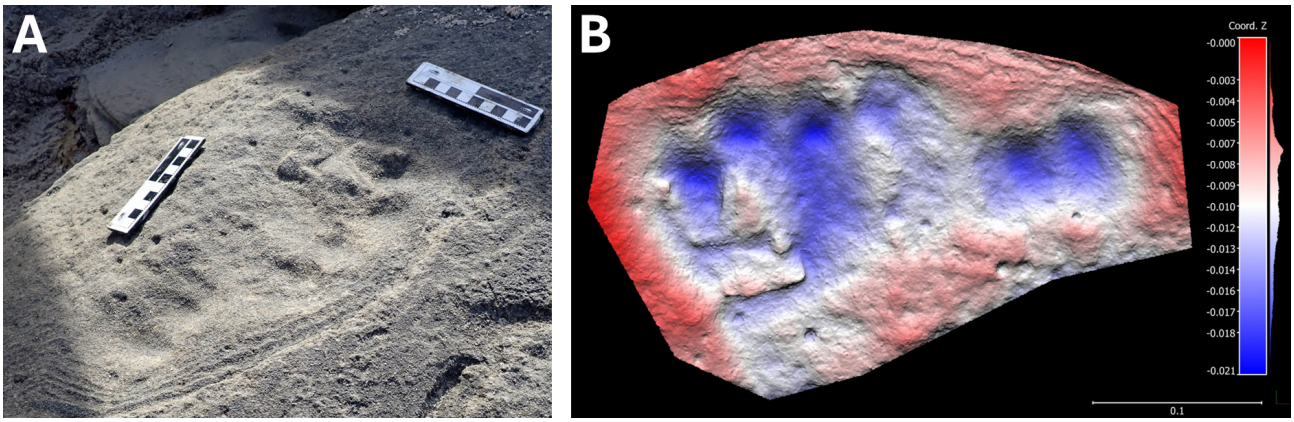


Figure 3: (A) The Site 2 footprints – direction of travel is from left to right; scale bars = 10 cm. (B) 3D photogrammetry model of the Site 2 tracks; horizontal and vertical scales are in metres. The two images display a different orientation: in (A) the direction of travel is down and to the right, while in (B) it is directly upwards; the top right footprint in (A) is therefore on the left in (B).

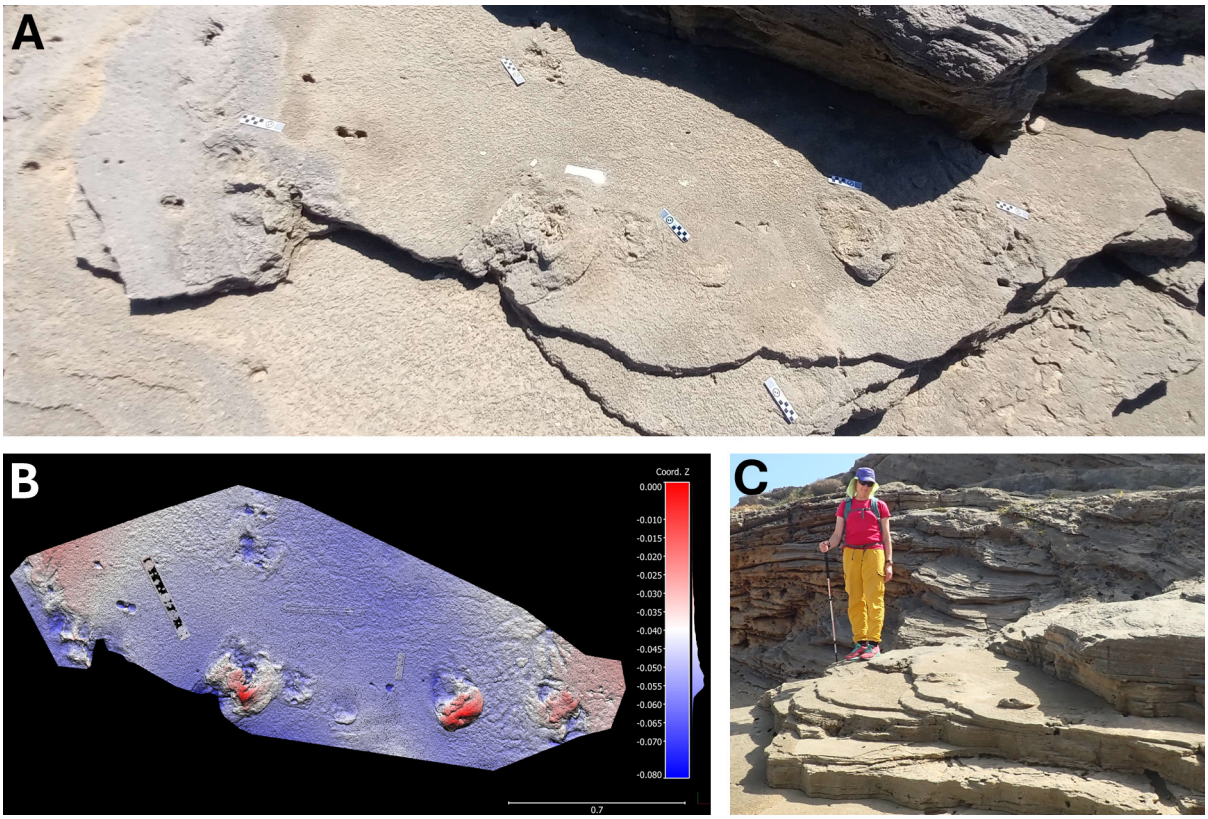


Figure 4: (A) The Site 3 track-bearing surface; scale bars = 10 cm. (B) 3D photogrammetry model of the Site 3 footprints; horizontal and vertical scales are in metres. (C) Adult human figure beside the track-bearing surface, showing the surrounding cliffs; the track-bearing surface is just below the centre of the photograph.

(smaller footprints) lions that crossed each other (the subtle morphological differences between the footprints of male and female lions have been alluded to above). Claw impressions were discussed and attributed to the dune slope the lions were climbing, while the large main pad impression of the male lion and its distinctive posterior margin were noted.

Discussion

Extant African lion footprint morphology

Five comprehensive guides are available for southern African trackers.[28-32] The closeness in time (from a geological perspective) of the Pleistocene to the present implies that they can be used with reasonable confidence when interpreting Pleistocene footprints. Furthermore, vertebrate trackmaker species which are extinct have been well documented through the body fossil record.[33,34]

Liebenberg noted that the male lion's footprints are larger and proportionately broader than those of the female, that the female's toes are more slender than the male's, and that a young male lion's footprint can thus be distinguished from that of the female by the general shape.[28] It was noted that the claws are often extended when a lion is charging and then show in the footprints. The average length of an adult male forefoot is reportedly 14.5 cm, and that of the hindfoot is 15 cm.[28]

Walker described lion footprints as "unmistakable", and as being made by a "large pug".[30] Stuart and Stuart noted that the very large footprints of lions were unlikely to be mistaken for those of other species, and that the

hindfoot footprints were narrower than forefoot footprints.[31] The large toe pads and three lobes of the posterior margin of the main pad were remarked upon.[31]

Gutteridge and Liebenberg noted the large size of the footprints (length of as much as 14 cm for the forefoot footprint), three lobes at the back of the main (metatarsal) pad, and the generally broader footprint of the male.[32] It was noted that while the claw impressions do not usually show in the footprints, exceptions include footprints in soft, muddy substrates or when the animal has slipped. A slight out-toeing gait was also mentioned.[32]

Van den Heever et al. provided the most detailed description of lion footprints and traces, with eight pages of information, including sage advice on modern lion-tracking.[29] In addition to generally concurring with the above-mentioned sources, the authors noted how the main pad is more symmetrical than that of hyenas, observing also that lion claw marks are not usually evident unless the trackmaker is running, making a sudden direction change, stepping in mud or jumping. They then devoted attention to gait patterns: in a slow walking gait, the hindfoot is registered behind the forefoot; with a slight increase in pace, the hindfoot registers on top of the forefoot impression; with further acceleration, the hindfoot lands further and further ahead of the forefoot. Ipsilateral forefoot and hindfoot footprints register on the ipsilateral side of the trackway midline, in a fairly narrow-straddle pattern. During galloping, only claw and toe impressions are registered. Footprint lengths for the male lion were recorded as 13.8 cm for the forefoot and 14.1 cm for the hindfoot, substantially larger than those of the next-largest felid, the leopard (*Panthera pardus*).[29]

Collaborative interpretation

Lion-tracking has developed a mystique, and is often viewed as the peak experience of modern tracking.[35] There is likewise a degree of excitement involved in identifying a fossilised lion trackway, as with minimal imagination it may seem that an imposing lion passed by recently rather than tens or hundreds of thousands of years ago.

Other than *Panthera leo*, there is no extant carnivoran in southern Africa that would have been capable of making footprints of the dimensions noted. Among extinct felids, the only known contender would have been a dirk-toothed (sabre-toothed) cat species, but, from the body fossil record, this subfamily (Smilodontini) of the Felidae appears to have become extinct in southern Africa[36] around 600 ka – an age that is substantially older than that of the Cape south coast aeolianites. Likewise, a more recent reference details a probable extinction date for *Dinofelis* in Kenya during the early Pleistocene.[37]

The relatively large size prompted speculation that the footprints at Site 1 may have been registered by *Panthera leo melanochaitus*, the purported extinct Cape Lion, or "black-maned lion".[38,39] Klein reported that carnivoran body size was sometimes larger during the Pleistocene[40], and footprints registered in soft sand may appear slightly larger than those registered in firmer substrates[29]. Moreover, the existence of this subspecies has been challenged, as genetic analysis has indicated that Cape lions were not substantially genetically distinct from other southern African lions.[41] Figure 5 depicts an artistic rendition of a male Cape Lion.

The three sites, although all attributed to lion trackmakers, differed substantially in how collaboration ensued between Western-trained and Ju/'hoansi team members. At Site 1, the attribution to *Panthera leo* was not in doubt by either group, and discussion revolved around the subtler nuances of ichnological phenomena, such as footprints partially infilled by windblown sand and transmitted tracks. Congruence was quickly achieved, and the passage of a female lion, which had not been asserted by the Western-trained scientists, was added to the interpretation.

At Site 2, a tentative identification of a lion trackmaker had been made by our Western-trained scientists, but it was open to doubt and a confident conclusion was lacking. Input from the Ju/'hoansi team members led to this tentative interpretation being upgraded to 'confirmed', and a more detailed explanation for the pattern of noted features was provided.

At Site 3, no identification had been made by our Western-trained scientists, other than that the footprints were registered by large unidentified trackmakers progressing on a steep dune slope, producing substantial displacement rims. Our Ju/'hoansi team members took the interpretation to a higher level, not only identifying trackmaker species but also providing a rationale for their conclusions and providing behavioural interpretation. The footprints at Site 3 are not considered amenable to detailed morphological appraisal or comparison with examples in the palaeo-ichnological record by our Western-trained scientists.



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Figure 5: Artwork by Maggie Newman-Lambert depicting a male Cape Lion.

The temporal proximity of the Pleistocene to the present, combined with the extensive amount of archaeological and palaeontological research that has been performed along the Cape south coast, makes it extremely unlikely that a hitherto unrecorded large felid may have inhabited the area during the Pleistocene. While such a possibility can never be totally excluded, the footprints described here can in all probability be attributed to *Panthera leo*.

Ichnotaxonomy

The morphofamily Felipedidae Remeika, 2001 was proposed to incorporate footprints with the classic felid morphology, similar to that described above, usually with an absence of claw impressions.[42] The ichnogenus *Felipeda* Panin and Avram, 1962 was proposed to include plantigrade to semi-plantigrade footprints with four digits, each exhibiting a round or oval digit pad. The digit pads have the appearance of a semicircle anterior to the metatarsal pads. The dimensions of the digit pads are typically similar, but may show slight variation. Again, claw impressions may be present, but are typically absent.[43]

The ichnogenus *Pantheraichnus* Diedrich, 2011, was proposed to encompass lion footprints from northern Germany[13], but is regarded as a junior synonym of *Felipeda*[44]. It seems that the footprints described here can be referred to Felipedidae and *Felipeda*.

Conclusions

The three Cape south coast tracksites not only add substantially to the sparse global record of fossilised large felid (almost certainly lion) footprints, but also provide a stark ichnological reminder of the pre-colonial presence of lions in the southern Cape. Whether the Cape Lion deserves to be regarded as a distinct subspecies should not obscure the fact that large lions left their footprints and traces on Pleistocene dune surfaces.

In each case, the San provided more details about the represented footprints, including specific behaviours not originally interpreted by the Western-trained team members. Furthermore, in two cases, the specific taxon (lion) was asserted by the San, although the Western-trained researchers were originally less certain.

While the identification of well-preserved lion and other large felid footprints is relatively straightforward, less obvious cases require considerable expertise. The ability of Ju/'hoansi Indigenous Master Trackers to make the transition from tracking in Kalahari sands to tracking on Cape south coast aeolianite surfaces is both remarkable and welcome. Using their skills and insights, which have been inculcated from an early age, they hold the potential to contribute to further enhancements in the interpretation of the Cape coastal fossil record from the Pleistocene. Through the examination of the three sites described here, the capacity has again been demonstrated for the emergence of results that are richly compelling through the blending of diverse perspectives.

Acknowledgements

Our colleague Steve Kunta passed away in October 2025, shortly before we finalised this article for submission. Had he not passed away, he would have been listed as a coauthor. We acknowledge Steve's wonderful contributions to our research team and to ichnology, and we dedicate this paper to his memory. We also acknowledge the helpful support from Dam Debe of the Nyae Nyae Conservancy in helping to finalise the manuscript. We thank Jack Carrigan and CapeNature staff for their support. We thank the anonymous reviewers for their thoroughness and constructive suggestions.

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Data availability

The data supporting the results of this study are available upon request to the corresponding author.

Declarations

We have no competing interests to declare. We have no AI or LLM use to declare. All authors read and approved the final manuscript.

Contributors' contributions

C.W.H.: Lead author, conceptualisation, formal analysis, investigation, writing – original draft, project administration. H.C.C.: Conceptualisation, formal analysis, investigation, writing – review and editing. #.D.: Formal analysis, investigation, writing – review and editing. J.C.D.V.: Conceptualisation, formal analysis, investigation, writing – review and editing. /.N.: Formal analysis, investigation, writing – review and editing. C.R.T.: Conceptualisation, formal analysis, funding acquisition, investigation, writing – review and editing. S.K.: Track identification and interpretation.

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