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A probable Pleistocene pangolin (Order: Pholidota) trackway from South Africa's Cape south coast

A fossil trackway, attributed to a probable pangolin trackmaker, has been identified on a Pleistocene aeolianite surface of the Waenhuiskrans Formation in the Bosbokfontein Private Nature Reserve on South Africa's Cape south coast. The trackway consists of eight tracks and two probable tail traces. This appears to be the first description of a pangolin trackway in the global fossil record. The trackway was probably registered during Marine Isotope Stage 6 or 5. Trackway assessment and interpretation involved the integration of indigenous African and Western-based ichnological approaches, leading to a reasonably confident conclusion on the probable trackmaker's identity. Alternative trackmakers (felids, viverrids and canids) were considered, but excluded or regarded as less likely candidates. There are three Cenozoic body fossil records of pangolins from the southwestern Cape, which have been assigned to the giant pangolin (*Smutsia gigantea*). Only Temminck's pangolin (*Smutsia temminckii*) currently occurs in southern Africa. All eight extant pangolin species are considered to be threatened with extinction according to the IUCN Red List of Threatened Species.

Significance:

- A Pleistocene probable pangolin trackway has been identified east of Still Bay, Western Cape Province, South Africa.
- The identification involved integrating indigenous African and Western-based ichnological approaches.
- This appears to be the first known fossilised pangolin trackway.
- The trackway consists of eight tracks and two probable tail traces.
- This discovery could draw attention to the plight of pangolins.

Introduction

Through the Cape south coast ichnology project, over 350 Pleistocene vertebrate ichnosites have been documented along a 350 km stretch of South African coastline. The majority (80%) represent mammal tracks and traces.[1] Until now, no pangolin ichnofossils have been identified, either on the Cape south coast or, to the best of our knowledge, anywhere in the world. Here we describe a trackway on an aeolianite (cemented dune) palaeosurface in the Bosbokfontein Private Nature Reserve, east of Still Bay on the Cape south coast. The lines of evidence converge on a pangolin as the probable trackmaker.

The order Pholidota contains a single family, Manidae, with eight recognised, extant pangolin species from sub-Saharan Africa to India, southern China, southeast Asia and the Philippines.[2] A cryptic ninth Asian species was detected in 2023[3], and awaits formal description. Four of these species occur in Africa – two are arboreal and two (Temminck's pangolin and the giant pangolin) are ground-dwelling. Temminck's pangolin (*Smutsia temminckii*, previously *Manis temminckii*) is also known as the ground pangolin, the Cape pangolin, or the scaly anteater, and is the only pangolin species to currently occur in southern Africa.[2] In the Ju/'hoan language, Temminck's pangolin is known as *n‡hòqò*, and in Afrikaans as the *ietermagog*. The latter is probably of Bantu or Tswana derivation.[4]

All species of extant pangolin are threatened by poaching and habitat loss, and all are classified as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List of Threatened Species.[5] Pangolin meat is regarded as a delicacy, and pangolin scales are used in traditional medicines.[6] There is evidence that pangolins are among the most trafficked wild animals on earth, and 400 000 African pangolins are estimated to be hunted for their meat annually.[7]

The tracks described here were initially identified in 2018 by Renée Rust and family. The tracks are evident on the surface of a large fallen aeolianite block. The putative trackmaker remained enigmatic until our joint analysis in 2023. Two of us (#.D., /.N.) are Indigenous Ju'/hoansi San Master Trackers, and had an immediate, strong sense of what was being examined. This presented the opportunity for Indigenous and modern scientific tracking exponents to engage in a productive exchange of ideas, combining culturally honed and experientially grounded intuitions with modern assessment techniques. This collaborative, interdisciplinary approach has allowed us to arrive at a shared conclusion on the identify of the probable trackmaker.

The purpose of this article is to describe the trackway, discuss the probable trackmaker, consider alternative trackmakers, and discuss the relevance of this discovery. We also reflect on the value of integrating Indigenous African and Western-based ichnological approaches.

Geological context

Pleistocene carbonate aeolianites of the Waenhuiskrans Formation[8], part of the Neogene Bredasdorp Group[9], are exposed along portions of the Cape south coast of South Africa, and have provided evidence for palaeo-shorelines

10 REDUCED INEQUALITIES

and palaeocoastal dune activity[10]. Carbonate aeolianites are consolidated coastal rock formations consisting of at least partially lithified calcareous wind-blown sand. The trackway described here would have been registered on an unconsolidated dune surface, which is now consolidated and cemented into aeolianite. Globally, aeolianites are fairly common in mid-latitude coastal regions between 20° and 40°.[11] Throughout the Pleistocene, global sea-level change meant that the Cape south coast landscape was dynamic. Vertebrate ichnosites encountered on these palaeosurfaces would have been situated at the margin of the Paleo-Agulhas Plain, most of which is presently submerged, but at times sea-level oscillations would have exposed the entire plain.[12] In contrast, sea level was 6–8 metres higher than at present at the height of the Marine Isotope Stage (MIS) 5e marine transgression at ~126 ka.[13]

Optically stimulated luminescence (OSL) dating of onshore aeolianites has shown that most date to MIS 5 and late MIS 6.[13-16] MIS 11 deposits[17] and MIS 3 deposits[18] have also been identified, with a resulting age range of dated deposits presently spanning ~400–35 ka. Roberts and Cole provided an explanation for the profusion of ichnosites, postulating a combination of a cohesive moulding agent (moist sand), rapid track burial (facilitated by high sedimentation rates), rapid lithification (via partial solution and re-precipitation of bioclasts), and finally re-exposure of track-bearing surfaces through shoreline erosion.[19]

In general, the grain size of the substrate inversely influences the preservation quality of fossil tracks. In Cape south coast Pleistocene deposits, tracks made on moderately coarse-grained dune surfaces tend to show poor to intermediate preservation quality, certainly inferior to that seen elsewhere in the world, for example in clay or mud substrates on cave floors. Belvedere and Farlow introduced a four-point preservation scale, in which 0 represents an unidentifiable track, and 3 represents a track of exceptional quality.[20] It is unusual for tracks within the Cape south coast deposits to rise above 2 on this scale.

Active shoreline erosion causes coastal cliffs to fragment or collapse, sometimes exposing new ichnosites, while known sites deteriorate in quality or loose blocks slump into the ocean. Ichnosites are thus ephemeral. The taphonomic erosive effects of wind and water, either pre-burial or post-re-exposure, can result in loss of track preservation quality. In the latter case, even if the tracks displayed anatomical fidelity at the time of re-exposure, over time their quality can deteriorate.[1] The causes of relatively poor preservation, such as moderately large grain size (in this case medium-grained sand), pre-burial erosion and post-exposure erosion, may be difficult to distinguish, especially if it is not known for how long the surface has been exposed.[21,22]

The Bosbokfontein tracksite is located in a remote section of coastline (Figure 1), characterised by aeolianite cliffs as high as 30 m. High tides and storm surges cause cliff sections to collapse, whereupon loose blocks come to rest on unstable slopes or near the high-tide mark at the cliff base.

One section in this region, situated ~8 km east of the Bosbokfontein site, had been dated prior to our studies.[13] Ages obtained through OSL dating produced a range of 140 ± 8 ka to 91 ± 5 ka. Our subsequent work has yielded several results of relevance here (in each case a five-digit number is preceded by 'Leic'). The closest of these lies 4.5 km east of the Bosbokfontein site, where an age of 126 ± 9 ka was obtained (Leic21005).[23] Other results from sites located slightly further east include 161 ± 12 ka (Leic20033), 139 ± 10 ka (Leic20031), 134 ± 9 ka (Leic21008), and 109 ± 9 ka (Leic20024).[23-25] Although direct stratigraphic correlation between these sites is not feasible, due to an absence of laterally persistent layers or marker beds, it nonetheless seems likely that the Bosbokfontein track-bearing surface occurs in deposits within the age range of ~161–91 ka, from MIS 6 or MIS 5.

Methods

Track measurements (in cm) included length, width, depth, pace length, and stride length. External trackway width was measured in cm, representing "the distance between the footfall of left and right feet, measured between the outside extremities of the tracks".[26] Global Positioning System locality readings were taken using a handheld Garmin 60 device. Locality data were stored with the African Centre for Coastal Palaeoscience at Nelson Mandela University, to be made available to researchers upon request.

The tracksite was photographed, and photogrammetric analysis was performed.[27,28] 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 μm). The final images were rendered using CloudCompare (v.2.10-beta). The tracks could be assessed by climbing to the top of the block and examining the surface, but for optimal recording, including photogrammetry studies, access via a portable ladder proved useful. A DJI Mini 2 drone with an inbuilt DJI camera/video was used to obtain further photographs.

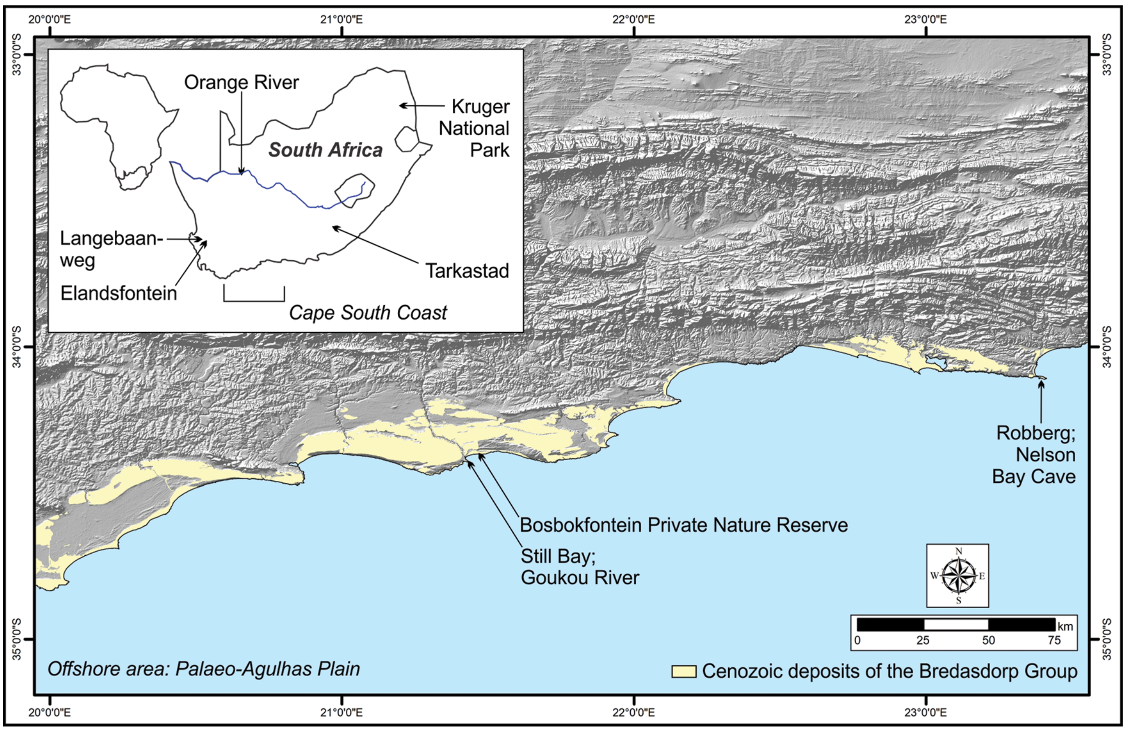


Figure 1: Map of South Africa's coast, indicating the Bosbokfontein site, the extent of Pleistocene deposits, and sites mentioned in the text.

After viewing the tracksite in detail together, and examining photographs and photogrammetry models, we reviewed our findings and opinions. This permitted further integration of the perspectives and interpretations of Master Trackers and Western-trained ichnologists. Furthermore, we engaged with some of southern Africa's tracking (neoichnology) experts, asking for their opinions on trackmaker identity based on photographic and photogrammetric images.

Results

The tracksite is located within the Bosbokfontein Private Nature Reserve, approximately 6.5 km east of the mouth of the Goukou River and the community of Still Bay. It occurs on the upper surface of a large ex-situ block, which has tumbled down the vegetated slopes from cliffs above and has come to rest above the high-tide mark (Figure 2). The maximum length of the block is ~7 m, with a maximum thickness of 4.5 m. However, the approximately triangular-shaped track-bearing surface is smaller, with maximum dimensions of ~200 x 180 cm. Slight deterioration in the preservation quality of the tracks and trackway has occurred since identification in 2018, but assessment and interpretation of tracks and trackway morphology remained feasible.

The block came to rest at an angle, and the track-bearing surface faces seaward and skywards, in a southeasterly direction. The trackway, which is ~160 cm in length, is thus aligned in a southeast-northeast direction as the loose block is currently orientated, but this may be subject to change following storm surges. Viewed in cross-section, the block exhibits laminar bedding, mostly parallel but with slight distortion in places and faint cross-bedding. The relative absence of cross-bedding suggests that the tracks might have been registered on a more level interdune area. The trackway is interpreted here with the viewer facing landwards and northwest, as if the trackmaker was progressing up the current slope of the loose block. The tracks are preserved in concave epirelief.

Eight tracks are evident (Figure 3), but the distal track occurs at the edge of the surface and is partial, and the two proximal tracks are partially obscured by two elongated depressions, aligned in approximately the same direction as the trackway. These are approximately 10.0–12.5 cm long and 4.5–6.0 cm wide. Tracks 3 through 7 therefore offer the best potential for analysis. The trackway curves gently to the left, such that its distal end is orientated ~30° leftward of that of its proximal end. Faint displacement rims partially encircle some of the tracks, suggesting that the tracks were registered on a slightly sloping surface.

Track lengths (5.5–6.0 cm) and track widths (5.0–5.5 cm) are relatively constant. Tracks 6 and 7 appear slightly wider in their anterior portions. Pace length in tracks 3 through 7 is relatively constant (18–20 cm). Track depth varies from 1.0 cm to 1.5 cm, with the anterior portions of the tracks slightly deeper than the posterior portions. The external trackway width appears narrow, at approximately 7.5 cm.

Discussion

The prehistoric and historic distribution of southern African pangolins

The global record of pangolins extends back to the Oligocene Epoch[29], as reviewed by Gaudin et al.[30] The prehistoric distribution of pangolins in southern Africa in the palaeontological record is meagre for the southern Cape and western Cape: there are only three reported Cenozoic fossils of pangolins from these regions.[31] These all represent skeletal evidence, and we are not aware of trace fossil records of pangolins in the global ichnology record. The three reported southwestern Cape fossil records are now summarised.

Hendey reported an unstudied early Pliocene pangolin from the 'E' Quarry at Langebaanweg in the Western Cape Province near the South African west coast.[32] Botha and Gaudin[29] formally described this specimen as probably ground dwelling, and possibly having engaged in a quadrupedal gait similar to that of the extant giant pangolin (*Smutsia gigantea*). It was suggested that it may have used its forelimbs more than *S. temminckii.* The specimen was assigned to *S. gigantea*, making it the oldest known representative of that species.[29]

Klein et al. described a pangolin assigned to the genus *Phataginus* from the Elandsfontein Main site in the Western Cape Province on South Africa's west coast, ~350 km WNW of the tracksite reported on here.[33] It was described as an "extralimitary species" that contributed to the exceptional faunal diversity of the site. The age of the faunal assemblage was estimated to be in the range of 1.0–0.6 Ma.[33]

The closest pangolin body fossil site to the Bosbokfontein site, temporally and spatially, was reported by Klein from Nelson Bay Cave near Robberg, 180 km east of Bosbokfontein.[34] It was located in Late Pleistocene deposits dating to 18–16 ka. It was described as the "Cape pangolin, *Manis* cf. *temminckii*"[34].

The southern African Holocene and historical record is more extensive for Temminck's pangolin. Possible sources include historical accounts, ethnographic records, rock art and place names. Möller noted that Temminck's pangolin had a wide distribution and occurred all over southern Africa, and that the lack of early reports might be attributable to its nocturnal habits.[4] Skead[35] reported that a probable pangolin had been recorded in 1825 from the Tarkastad or Queenstown area (in the current Eastern Cape Province), and that this probably constituted the southernmost record for the species (~32° S). Skead[35] quoted Layard[36] that the pangolin was "not now" found in the Cape Colony (i.e. south of the Orange River), perhaps implying that it had occurred previously within it. Shortridge[37] reported that it was absent from "Little Namaqualand" but noted a pangolin skin from the Upington area and records south of the Orange River from Prieska and Colesberg. The 1865 holotype is from

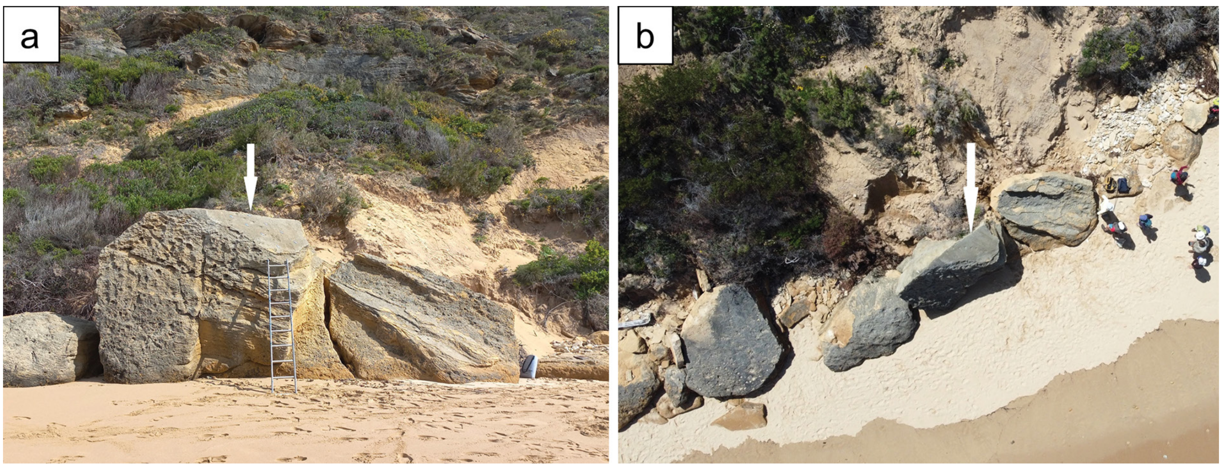


Figure 2: (a) The large loose block containing the purported pangolin trackway on its upper surface; the ladder length is 410 cm. (b) The track-bearing block, viewed from above using a drone; adult human figures for scale. Arrows point to the track-bearing surface.

Litakun (Latakou), ~250 km north of the Orange River, and north of present-day Kuruman.[30] Lichtenstein[38] and Burchell[39] also reported the occurrence of the pangolin in the Litakun area.

Möller provided two place names, Ietermagô and Khwaru, that refer to pangolins.[4] Both are in the Kruger National Park in South Africa's Limpopo Province, ~1500 km northeast of the Bosbokfontein site. They are therefore unhelpful regarding a potential southern Cape distribution range.

Rock art can provide information on prehistoric pangolin distribution, although it only implies the artist's awareness that the species existed, not its occurrence in that precise locality. Despite consultation with rock art experts, we are not aware of rock art depicting pangolins in southern Africa, other than at a site in the Limpopo Province (Figure 4a), where a frieze of engraved animal tracks of eight species contains an engraving of a possible pangolin hindfoot track.[40] 'Fragile Images', a YouTube video, includes footage of the engraving at 12 minutes and 10 seconds: https://www.youtube.com/watch?v=Ra12BKeH7Js.

In summary, the body fossil record demonstrates the presence of pangolins in the southwestern Cape region of South Africa during the Pliocene and Pleistocene. The situation is perhaps analogous to that of the giraffe (*Giraffa camelopardalis*), for which there is no body-fossil evidence from the Pleistocene in the southwestern Cape, but a trace fossil record confirms its presence.[41] The giraffe tracksite

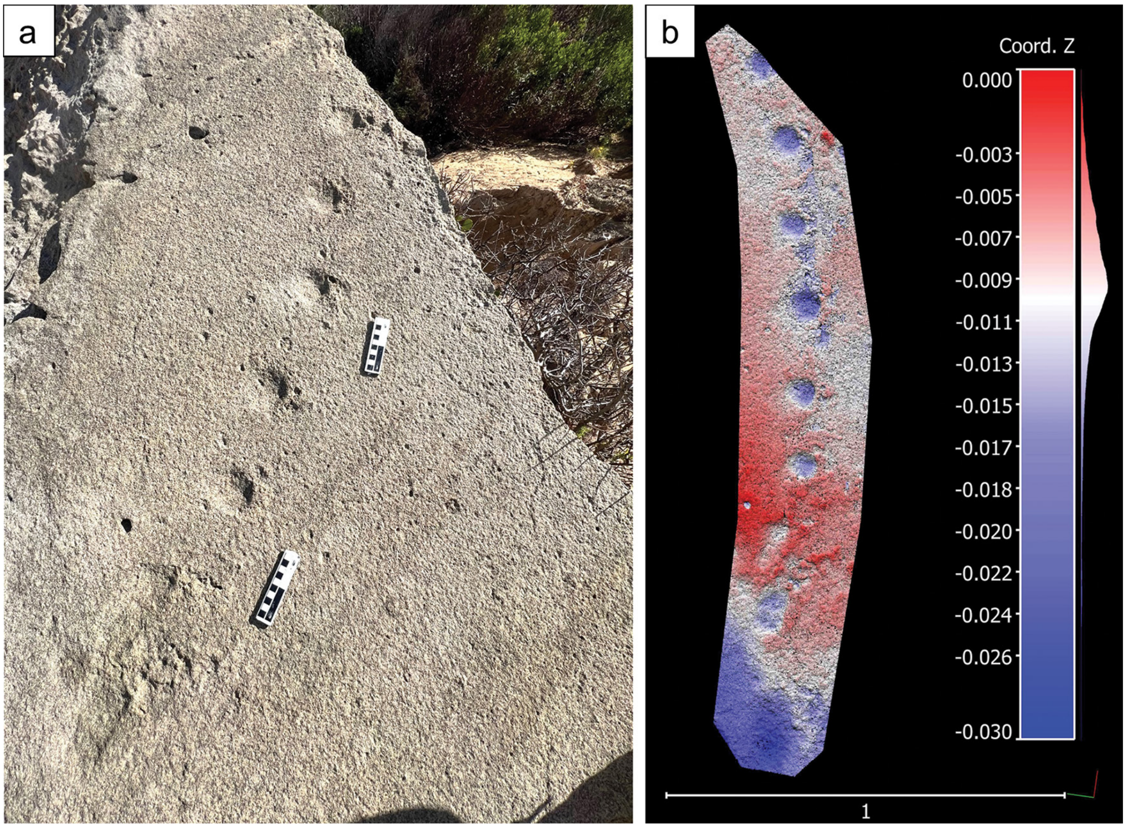
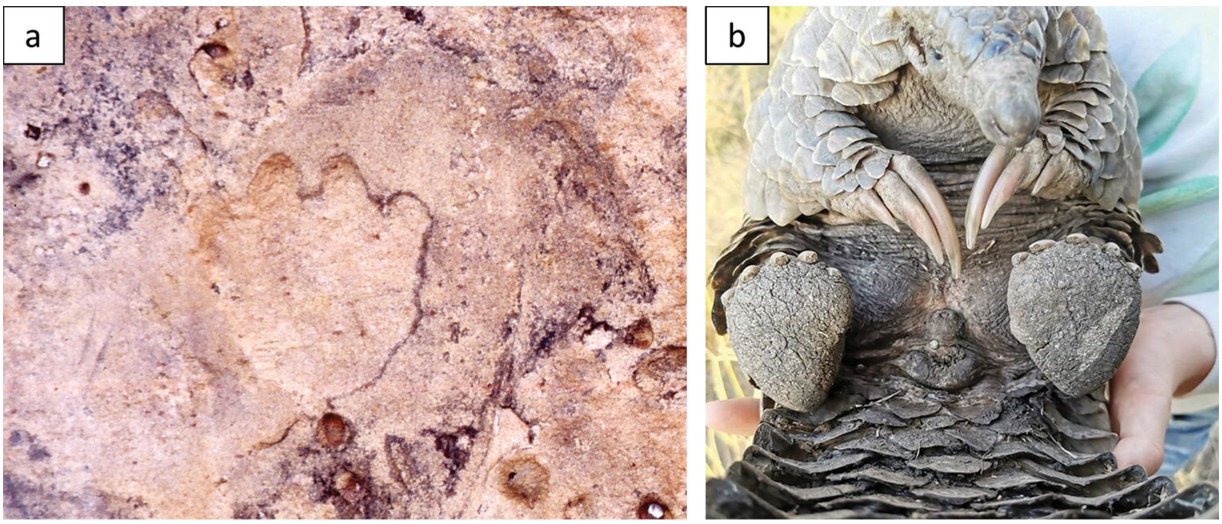


Figure 3: (a) The purported pangolin trackway; scale bars = 10 cm. (b) Photogrammetry colour mesh of the trackway; vertical and horizontal scales are in metres.



Images with permission from Chris and Mathilde Stuart (a) and Simon Naylor (b).

Figure 4: (a) Rock engraving of a probable pangolin track in Limpopo Province. (b) The forefeet and hindfeet of a Temminck's pangolin, viewed from below.

lies less than 8 km east of the Bosbokfontein tracksite. The presence of giraffe tracks implies the presence of trees and a probable savanna palaeoenvironment.[41] This may have been suitable for Temminck's pangolin, with a preferred habitat of savanna woodland. The record from Nelson Bay Cave[34] lies just within the last glacial period, when aspects of this habitat might still have been present. Historical records, place names and rock art do not contribute to an understanding of pangolin distribution in the southwestern Cape.

Pangolin track morphology

Southern African neoichnologists are fortunate to have five tracking manuals to which to refer.[26,39,42-44] Each describes Temminck's pangolin tracks, reviewed here in order of publication date. Figure 4b depicts the forefeet and hindfeet of a Temminck's pangolin.

Liebenberg described five toes on the forefeet (the first with a small nail and the central three with long, strongly curved claws), and five toes on the hindfeet, each with a short nail-like claw that sometimes registers an impression in the tracks.[42] The body was noted to be balanced on the hindfeet when walking, with the forefeet and tail held off the ground. Tracks were noted to show the rounded pads of the hindfeet with four nails usually touching the ground. The occasional tail scrape and traces made by the front edges of the front claws were also noted. Hindfoot tracks were reported as 6 cm in length.[42]

Van den Heever et al.[26] also noted that both forefeet and hindfeet have five toes, and that the first and fifth toes of the front feet are reduced, leaving three middle toes with long curved claws, well adapted for digging. The forefoot track (when present) was noted to record the upper surfaces of the three middle claws, which curl under the foot. The hindfoot was described as padded and triangular with five toes, and as being ~5 cm in length. Movement was described as bipedal, with the forefeet seldom touching the ground. Scuff marks made by dragging the tail were reportedly occasionally present.[26]

Walker[43] described the pangolin as moving along on its hind legs, occasionally dropping onto all fours or using the tail and forelegs for balance. Claws were noted to be prominent, and claws 2, 3 and 4 (presumably on the forefeet) were well developed and recurved. Pangolins were noted to walk mainly on their hind legs in an upright position. Hindfoot tracks were reportedly ~4.5 cm long and wide.[43]

Stuart and Stuart described (questionably in our opinion) a "typical tramline-like trail", resulting from the fairly wide spacing of the hindfeet, on which Temminck's pangolin normally walks, with the short, heavily clawed forefeet held clear off the ground.[40] The forefeet were noted to be used mostly for digging. Hindfoot track length of 6 cm was reported, with slight intoeing. An image of a pangolin trackway was not provided.[40]

Gutteridge and Liebenberg described the "interesting spoor" of the pangolin, which usually moves bipedally on the rounded hindfeet.[44] These were noted to drag, as the pangolin walks in a kind of shuffle. The unique marking made by the tail was also noted. Hindfoot track length was reported as being 6.5 cm.[44]

While there are slight differences in the focus of these descriptions, there is substantial agreement, involving a predominantly bipedal gait, with hindfoot tracks 4.5–6.5 cm in size, occasional forefoot traces, and occasional tail drag marks.

Interpretation and trackmaker identity

During the 2023 visit, the Master Trackers in our team (#.D. and /.N.) examined the surface unprimed by any hypotheses on trackmaker identity. Once they had presented their analysis, the rest of our team provided their own hypotheses and interpretations. The heuristic conclusion of the Master Trackers was of a probable pangolin trackway. They inferred a bipedal gait with tracks "*soos 'n ronde stok wat in die grond ingedruk is*" ("like a round stick poked into the ground") – for them indicative of a pangolin trackmaker. Their reading of the external trackway width and pace length fortified their conclusion. For the rest of us, unfamiliar as we were with such tracks, the proposal of a pangolin was a novelty. When photogrammetry images became available, we jointly re-reviewed the lines of evidence.

Other plausible trackmaker candidates include felids such as serval (*Leptailurus serval*), caracal (*Caracal caracal*) and African wild cat (*Felis lybica*), the viverrids African civet (*Civettictis civetta*), rusty genet (*Genetta maculata*) and large-spotted genet (*Genetta genetta*), and canids such as jackals and foxes (in a soft, sandy substrate the claw impressions of canids might not be preserved). Bipedal avian trackmakers would be expected to leave at least some evidence of didactyl, tridactyl or tetradactyl morphology[45], and the two elongated depressions are inconsistent with an avian origin. There is no evidence in the Pleistocene fossil record or among extant southern African species of other animals that could have made these tracks. One caveat is that carnivoran size (hence track size) varied during the Pleistocene, being reportedly larger during glacial phases.[46]

The tracks, 5–6 cm in size, are consistent with those of both extant Temminck's pangolin and serval, although a pangolin's hindfoot track length is marginally greater than those of a serval's forefoot and hindfoot. *Contra* Stuart and Stuart[40], the narrow external trackway width is consistent with the trackways of both Temminck's pangolin and, on occasion, serval. However, the trackway widths of caracal[44] and especially civet (our own observations) are distinctly broader. While the African wild cat can also produce a round track, the smaller size of its track and pace length exclude it. Similar considerations exclude both species of genet. Jackal tracks, in the 5 cm range, are relatively slender and more elongated (especially in the case of the smaller hind foot), definitely not "*soos 'n ronde stok wat in die grond ingedruk is*". The same is true of fox tracks (Cape and bat-eared), with the front foot of the bat-eared fox (*Octocyon megalotis*) measuring only 4.5 cm[44] and the hind foot even less.

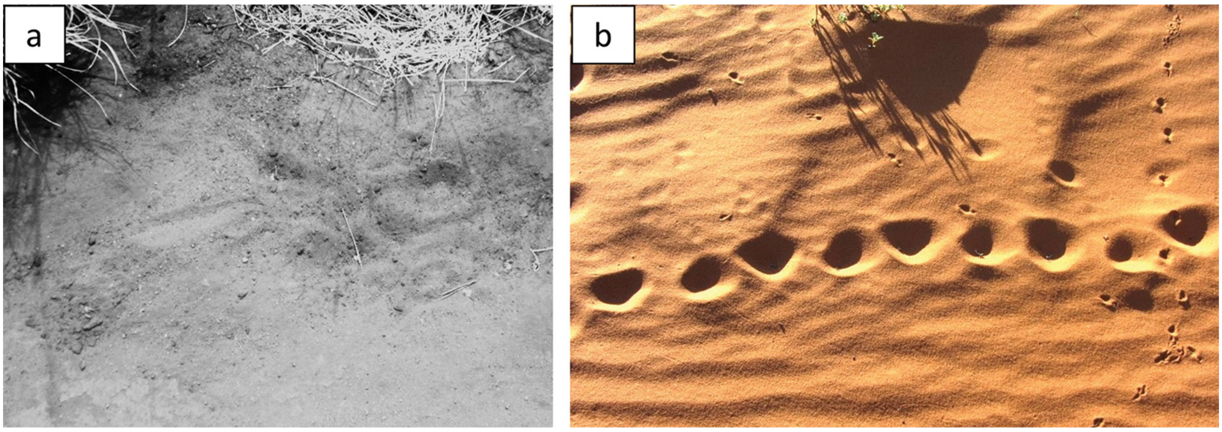
Whereas Temminck's pangolin hindfoot tracks are triangular (with the apex pointing backwards, away from the direction of travel) and well-preserved serval tracks exhibit pad and digit impressions, none of these features might be present in Cape south coast aeolianites. This may either be because of a soft, non-cohesive substrate at the time at which the tracks were registered, the effects of grain size, or pre-burial or post-re-exposure erosion.[1] Consequently, the tracks of both Temminck's pangolin and serval might appear round, without further morphological details. In such a situation, trackmaker identity would depend more on trackway morphology than on individual tracks. With the Bosbokfontein trackway, however, there is a hint of a triangular track morphology, or at least of some tracks appearing wider in their anterior portions.

The inference of trackmaker direction is based on some tracks appearing slightly wider in their anterior portions, the overall indentation pattern, and the orientation of the two elongated depressions. These impressions at the proximal end of the trackway and in line with it are consistent with the scuff-marks made by the pangolin tail (Figure 5a), and less consistent with tail traces made by servals or other potential trackmakers.

Pace length is consistently 18–20 cm, and therefore the distance between tracks is about three times the size of each track. While a pangolin sometimes walks with a shuffle and a relatively short pace length (Figure 5b), it can also walk with a longer pace length when not foraging, as in the Bosbokfontein trackway and in Figure 6.

Another potential distinguishing factor involves the relative lightness of the gait. A serval, like all cats, walks or runs lightly. A Temminck's pangolin, bulky, slower and bipedal, has a more ponderous gait. Therefore, pangolin tracks tend to be deeper than serval tracks. While this is not an absolute criterion, the depth of the tracks in question (1.0–1.5 cm), bolstered by the notion of the round end of a stick poked into the ground, is more consistent with a pangolin trackmaker.

Opinions from expert southern African trackers were most helpful. We approached Louis Liebenberg of CyberTracker, Alex van den Heever of the Tracker Academy, Richard McKibbin (wildlife guide and a moderator of the Facebook group 'Tracks and Signs South Africa'), Steff McWilliam (trail guide associated with the African Pangolin Working Group and the Johannesburg Wildlife Veterinary Hospital), Wendy Panaino (pangolin



Images with permission from Bruno Nebe.

Figure 5: (a) Scuff marks registered by the tail of a Temminck's pangolin. (b) A trackway of a Temminck's pangolin, showing (in this case) a short pace length.

Image with permission from Scott Hurd.

Figure 6: A Temminck's pangolin walking with a longer pace length.

researcher at the Tswalu Foundation's Kalahari Endangered Ecosystem Project), and Nicci Wright (Co-chair of the African Pangolin Working Group).

Their feedback was measuredly supportive. None thought that the tracks were inconsistent with those of a pangolin. Liebenberg provided a confident assessment:

> *I agree with trackers that this is pangolin. Definitely not a cat, since the gait is not that of a four-legged animal, whose footprints would be in pairs (front and hind close together). Pangolin is only bipedal gait with feet this shape and stride length.*

McKibbin cautioned that a serval's faded tracks could also appear very round and could present with a narrow straddle, but, as we have indicated, the track depth tilts towards a pangolin.

Wright provided a detailed comment:

> *To me, the tracks look like those of Temminck's pangolin, bipedalling along. The length between prints would be determined by the animal's overall size. Young pangolins have a much smaller gap between their footprints. The largest adult pangolin I have dealt with was 18.5 kgs, which nowadays is unusual to find. I think that if it had moved, fast-paced, through soft mud or sand, the length between prints would have been around 18–20 cm or even a bit longer, and would be deeper than those of a young pangolin which would weigh less.*

Furthermore, one of the three very knowledgeable anonymous reviewers of this manuscript (under strict confidentiality of the peer review process) sent the image of the fossilised trackway to two colleagues who have worked with Temminck's pangolin for many years on a day-to-day basis.

Both the reviewer and the two colleagues agreed with the interpretation of a pangolin trackway.

In the less likely scenario that the tracks were registered by a serval, a 'direct register' would be inferred whereby the hindfoot was placed precisely on top of the forefoot track. (Stealth hunters often employ this economical, sound-minimising foot-placement pattern.) From a prehistoric distribution perspective, a serval trackmaker is plausible. Avery reported Pliocene serval records from Gauteng Province, and Pleistocene and Holocene records from, inter alia, the southwestern Cape.[31]

Our overall conclusion is that the trackway cannot be attributed with absolute certainty to any trackmaker. However, it is most consistent with a Temminck's pangolin trackmaker, distinctly more than a serval or any other candidate species. The Pleistocene distribution range of the Temminck's pangolin included the southwestern Cape, in a situation that is analogous to that of the giraffe, the preferred habitat of both species being savanna woodland. Such habitat might have been present on the now-submerged Palaeo-Agulhas Plain.[47]

Conclusions

A Temminck's pangolin probably walked across a soft, sandy dune surface near the margin of the Palaeo-Agulhas Plain, most likely during MIS 6 or MIS 5, leaving a trackway. Eight tracks and, suggestively, two tail traces are preserved and amenable to interpretation. For many, fossil trackways are to body fossils what movies are to photographs, and evocative trackways tell a story of something that might have walked by yesterday, or over 100 000 years ago.

While the loose block containing the track-bearing surface is too large to physically recover, the photogrammetry data can be used to make a replica of the trackway, which could be exhibited in the Blombos Museum of Archaeology in Still Bay. What to date is probably the first reported pangolin trackway in the world could thus serve to draw attention to the plight of pangolins worldwide.

In a recent publication, we described the advantages of collaboration between Indigenous Master Trackers and Western-trained ichnologists in interpreting Pleistocene trackways.[48] The title of a book by Liebenberg specified that the art of tracking was "the origin of science"[49]. In our experience, the outcomes and conclusions that result are richer for integrating ancient and modern science.

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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.

Authors' contributions

C.W.H.: Lead author, corresponding author, conceptualisation, field work, project leadership, photogrammetry. A.S.C.: Conceptualisation, OSL dating expertise, data analysis, review of drafts and revisions. H.C.C.: Conceptualisation, data analysis, geological analysis, review of drafts and revisions. #.D.: Conceptualisation, data analysis, field work, review of drafts and revisions. J.C.D.V.: Conceptualisation, data analysis, field work, review of drafts and revisions. P-J.G.: Conceptualisation, data analysis, field work, review of drafts and revisions, photography. /.N.: Conceptualisation, data analysis, field work, review of drafts and revisions. C.R.T.: Conceptualisation, data analysis, geological analysis, field work, review of drafts and revisions. All authors read and approved the final manuscript.

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