Peer review history for:

Helm CW, Carr AS, Cawthra HC, Daqm #, De Vynck JC, Gräbe P-J. A probable Pleistocene pangolin (Order: Pholidota) trackway from South Africa's Cape south coast. S Afr J Sci. 2025;121(3/4), Art. #18687. https://doi.org/10.17159/sajs.2025/18687

HOW TO CITE:
A probable Pleistocene pangolin (Order: Pholidota) trackway from South Africa's Cape south coast [peer review history]. S Afr J Sci. 2025;121(3/4), Art. #18687.
https://doi.org/10.17159/sajs.2025/18687/peerreview

Reviewer 1: Round 1
Date completed:15 October 2024
Recommendation: Accept / **Revisions required** / Resubmit for review / Resubmit elsewhere / Decline / See comments
Conflicts of interest: None

Does the review fall within the scope of SAJS?
Yes/No
Is the review written in a style suitable for a non-specialist and is it of wider than only specialist interest?
Yes/No
Do the Title and Abstract clearly and accurately reflect the content of the review?
Yes/No
Does the review provide a significantly novel perspective or significant recent advances in the field?
Yes/No
Is the objective of the review concisely stated?
Yes/No
Is appropriate and adequate reference made to other work in the field?
Yes/No
Do current debates and points of contention receive appropriate coverage?
Yes/No/**Not applicable**
Are gaps in the literature adequately identified?
Yes/No/Not applicable
Does the review provide direction for future research?*
Yes/No/**Not applicable**
Are the methodology and statistical treatment appropriate?
Not applicable/**Yes**/No/Partly/Not qualified to judge
Are the interpretations and recommendations aligned with the objective?
Yes/Partly/No
Please rate the manuscript on overall contribution to the field
Excellent/**Good**/Average/Below average/Poor
Please rate the manuscript on language, grammar and tone
Excellent/**Good**/Average/Below average/Poor
Is the manuscript concise and free of repetition and redundancies?
Yes/No
Is the supplementary material relevant and separated appropriately from the main document?
Yes/No/**Not applicable**
Please rate the manuscript on overall quality
Excellent/**Good**/Average/Below average/Poor

If accepted, would you recommend that the article receives priority publication?

Yes/**No**

Are you willing to review a revision of this manuscript?

Yes/No

With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.

Yes/No

Comments to the Author:

This is a very interesting manuscript and is also the first record that I know of a probable pangolin trackway from anywhere in the world. The manuscript is well written overall, although I have made some suggested edits in the attached manuscript for you to consider.

My biggest comment is that the most widely accepted common name (and the name accepted by the IUCN Species Survival Commission Pangolin Specialist Group) for the species is Temminck's pangolin, and I recommend that you use that name rather than the older "ground pangolin". Similarly, the most recent taxonomy indicates that both Temminck's and Giant pangolin belong to the genus <i>Smutsia</i>, with only the four Asian pangolin species belonging to the genus <i>Manis</i>. This is also important because later in the manuscript you quote an article that recorded a <i>Phataginus</i> fossil from the Cape south coast, while if you use "<i>Manis temminckii</i>" then you will need to refer to this fossil as "<i>Manis</i> (<i>Phataginus</i>)" (i.e., subgenus <i>Phataginus</i>).

[See Appendix 1 for Reviewer 1's comments made directly on the manuscript]

Author response to Reviewer 1: Round 1

We were able to incorporate all of Reviewer 1's suggestions, many of which dealt with the issue of correct nomenclature.

Reviewer 2: Round 1

Date completed: 11 October 2024

Recommendation: Accept / Revisions required / Resubmit for review / Resubmit elsewhere / Decline / See comments

Conflicts of interest: None

Does the review fall within the scope of SAJS?

Yes/No

Is the review written in a style suitable for a non-specialist and is it of wider than only specialist interest?

Yes/No

Do the Title and Abstract clearly and accurately reflect the content of the review?

Yes/No

Does the review provide a significantly novel perspective or significant recent advances in the field?

Yes/No

Is the objective of the review concisely stated?

Yes/No

Is appropriate and adequate reference made to other work in the field?

Yes/No

Do current debates and points of contention receive appropriate coverage?

Yes/No/**Not applicable**

Are gaps in the literature adequately identified?

Yes/No/Not applicable

Does the review provide direction for future research?*

Yes/No/Not applicable

Are the methodology and statistical treatment appropriate?	
Not applicable/**Yes**/No/Partly/Not qualified to judge	
Are the interpretations and recommendations aligned with the objective?	
Yes/Partly/No	
Please rate the manuscript on overall contribution to the field	
Excellent/Good/Average/Below average/Poor	
Please rate the manuscript on language, grammar and tone	
Excellent/Good/Average/Below average/Poor	
Is the manuscript concise and free of repetition and redundancies?	
Yes/No	
Is the supplementary material relevant and separated appropriately from the main document?	
Yes/No/**Not applicable**	
Please rate the manuscript on overall quality	
Excellent/Good/Average/Below average/Poor	
If accepted, would you recommend that the article receives priority publication?	
Yes/No	
Are you willing to review a revision of this manuscript?	
Yes/No	
With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.	
Yes/No	

Comments to the Author:

TITLE: A PROBABLE PLEISTOCENE PANGOLIN TRACKWAY FROM SOUTH AFRICA'S CAPE SOUTH COAST
Recommended edit to title: include "Order Pholidota" in parenthesis after the word pangolin
General comments and recommendations

This was a fascinating manuscript to review, thank you for the opportunity.

Having the privilege of working very closely with Smutsia temminckii over the past 15 years, I have very little doubt that these are the tracks made from that species over the dunes of the Palaeo-Augulhas plain during the Pleistocene. I took the liberty of sending the image of the tracks to two other colleagues that have (and are still) working with the species for many years on a day-to-day basis (under strict confidentiality of this peer review process). They both agreed with your interpretation.

Many of my comments below further support your study, there are also a few editorial suggestions provided. I recommend the manuscript be published in its current form following very minor grammatical edits.

Specific comments

Line 40: check spelling "Pholidota" not "Phiolidota"
Line 42: reference to a 9th species has not been established nor accepted by the IUCN
Line 43: the accepted common name by the IUCN for Smutsia temminckii is Temminck's pangolin not ground pangolin. Smutsia is the accepted genus that differentiates the arboreal tree pangolins from the ground pangolins
Lines 202-206: Just a comment: Klein et al (2007) were very likely incorrect in assigning the fossilized remains of pangolin to the genus Phataginus, it was very likely that of Smutsia as tropical forests did not occur in the western Cape at that time. Hence, providing more evidence of Smutsia in the Cape supporting your findings. However, he supported this in an early study anyway (Line 209: Klein, 1972)
Line 211: check spelling temminckii with two "ii"s
Line 258: I do not agree with Liebenberg (2000), the claws of the hindfeet are not evident in the tracks of Temminck's, these nail-like claws are rudimentary and do not offer dorsal protection or traction but rather lateral, much like those of an elephant. Interestingly, your study indicates a type of "pigeon-toed track"

shape with the tracks curved inward somewhat – this is diagnostic of the bipedal gait of a Temminck's pangolin. The tail acts as a counter-balance and the tip does occasionally touch the surface, just as indicated in your study tracks
Line 276: Temminck's pangolin in the only species of pangolin that is bipedal
Line 280: I too do not agree with Stuart & Stuart, the Temminck's tracks are singular in lineage, one hind foot in front of another, as depicted in your study
Line 344: pace length you indicate (18-20 cm) is correct for an adult Temminck's pangolin stride when not foraging
Line 355-356: phrase repeated here

Author response to Reviewer 2: Round 1

Likewise, we incorporated Reviewer 2's suggestions. We have a minor point of disagreement with Reviewer 2's comment: "I do not agree with Liebenberg (2000), the claws of the hindfeet are not evident in the tracks of Temminck's, these nail-like claws are rudimentary and do not offer dorsal protection or traction but rather lateral, much like those of an elephant." In this case, we concur with Liebenberg (2000), and point to the illustration on page 199 of Van den Heever et al. (2024) as further evidence of hindfoot claw impressions.

Reviewer 3: Round 1
Date completed: 25 October 2024
Recommendation: Accept / **Revisions required** / Resubmit for review / Resubmit elsewhere / Decline / See comments
Conflicts of interest: None

Does the review fall within the scope of SAJS?
Yes/No
Is the review written in a style suitable for a non-specialist and is it of wider than only specialist interest?
Yes/No
Do the Title and Abstract clearly and accurately reflect the content of the review?
Yes/No
Does the review provide a significantly novel perspective or significant recent advances in the field?
Yes/No
Is the objective of the review concisely stated?
Yes/No
Is appropriate and adequate reference made to other work in the field?
Yes/No
Do current debates and points of contention receive appropriate coverage?
Yes/No/**Not applicable**
Are gaps in the literature adequately identified?
Yes/No/**Not applicable**
Does the review provide direction for future research?*
Yes/No/Not applicable
Are the methodology and statistical treatment appropriate?
Not applicable/Yes/No/Partly/Not qualified to judge
Are the interpretations and recommendations aligned with the objective?
Yes/Partly/No
Please rate the manuscript on overall contribution to the field
Excellent/Good/**Average**/Below average/Poor
Please rate the manuscript on language, grammar and tone
Excellent/**Good**/Average/Below average/Poor
Is the manuscript concise and free of repetition and redundancies?

Yes/No

Is the supplementary material relevant and separated appropriately from the main document?

Yes/No/**Not applicable**

Please rate the manuscript on overall quality

Excellent/**Good**/Average/Below average/Poor

If accepted, would you recommend that the article receives priority publication?

Yes/**No**

Are you willing to review a revision of this manuscript?

Yes/**No**

With regard to our policy on 'Publishing peer review reports', do you give us permission to publish your anonymised peer review report alongside the authors' response, as a supplementary file to the published article? Publication is voluntary and only with permission from both yourself and the author.

Yes/No

Comments to the Author:

The manuscript is well-written and concise, and interprets a poorly preserved fossil trackway as produced by relatives of the extant pangolin. To my knowledge, it is true that there is no ichnological record of pangolins and this is a good reason to communicate the finding. I think that the authors seize adequately the meager available evidence. I suggest acceptance after minor revision; however, I would like that the authors consider the following aspects (see also the attached file):

1) A more precise sedimentologic description of the block containing the footprints, especially because it is a fallen block. Dune fields are not only composed by cross-bedded dune deposits but other low-angle facies also occur.
2) A more descriptive and technical language is desirable in several passages.
3) I am not familiar with pangolins, however the reason for producing a bipedal trackway with such a high pace angulation are not explained. The pangolin trackway of Fig. 5b also display a difference related to the presence of pairs that are not seen in the fossil example.
4) Alternative producers for the trackway include only quadrupedal mammals, why not a bipedal producer like a running bird for example?

[See Appendix 2 for Reviewer 3's comments made directly on the manuscript]

Author response to Reviewer 3: Round 1

We incorporated almost all of Reviewer 3's suggestions. An exception involves the Marchetti et al. (2019) reference which Reviewer 3 kindly provided. We have chosen not to include it, as we already have a reference by Falkingham and Gatesy (2020) which discusses the paper that Reviewer 3 suggested (and it is in the same journal, Earth-Science Reviews). We thought that including both references would be redundant. The Falkingham and Gatesy paper is titled: "Discussion: defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al."

Several of Reviewer 3's comments related to the double-blind anonymised nature of the review, and were therefore not addressed. We have kept our manuscript 'blinded'', as required.

Author response: Other additions

All changes have been highlighted in yellow, with explanatory comments wherever appropriate in the right margin. One reference has been updated, one new reference has been added, and one reference has gone from 'under review' to 'in press', and publication is apparently imminent.

[See Appendix 3 for the Author response to reviewers made directly on the revised manuscript]

Appendix 1: Reviewer 1's comments on manuscript (round 1)

A PROBABLE PLEISTOCENE PANGOLIN TRACKWAY FROM SOUTH AFRICA'S CAPE SOUTH COAST

Abstract

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 comprises 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 probable trackmaker 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 ~~the ground~~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™~~or endangered~~.

Commented [A1]: The accepted common name according to the IUCN Pangolin Specialist Group is Temminck's pangolin

Commented [A2]: "Endangered" is a sub-category of "threatened". The categories "Vulnerable", "Endangered" and "Critically Endangered" are all considered to be "Threatened" categories according to the IUCN Red List, and the eight pangolin species span all three these categories.

Significance of the main findings

- 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 comprises eight tracks and two probable tail traces.
- This discovery could draw attention to the plight of pangolins.

Commented [A3]: How?
I think the mere fact that you found a fossilized pangolin trackway is amazing in its own right.

KEYWORDS: pangolin, fossil tracks, aeolianites, Cape south coast, Pleistocene

Figures inserted at the bottom of document.

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

Commented [A4]: Although these authors named this ninth taxon, it was not described as per the rules of the International Code of Zoological Nomenclature, and their 'description' does not represent a valid taxonomic act. Their proposed scientific name is therefore a *nomen nudem*, and is not valid. In short, although we know that there is a ninth extant species, it has not been formally described yet.

All species of extant pangolin are threatened by poaching and habitat loss, and all are classified as ~~v~~Vulnerable, ~~e~~Endangered, or ~~c~~Critically ~~e~~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 (anonymised) 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, inter-disciplinary approach has allowed us to arrive at a shared conclusion on probable trackmaker identity.

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 aeolianites (cemented dunes) 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 and palaeo-coastal dune activity.[10] Globally, aeolianites are fairly common in mid-latitude coastal regions between 20° and 40°.[11] Aeolianite surfaces preserve a record of the passage of trackmakers when they comprised unconsolidated sand. 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~~meters 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, particularly 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 (moderately large grain size, 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] It therefore 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 hand-held 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 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 µum). 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.

Having viewed the tracksite in detail together, and examined 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 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 occurred since identification in 2018, but assessment and interpretation of tracks and trackway morphology remained feasible.

The block has come 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. Trackmaker direction is inferred to be upslope with respect to the current orientation, and the trackway is interpreted here with the viewer facing landwards and northwest, i.e., as if the trackmaker was progressing upslope. The tracks are preserved in convex 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 longitudinal ‘smudges’, 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 distal portions. Pace length in tracks 3 through 7 is relatively constant (18–20 cm). Track depth varies from 1.0 to 1.5 cm, with the distal portions of the tracks slightly deeper than the proximal portions. The external trackway width appears narrow, 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 ~~P~~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 (~~*Manis*~~ *Smutsia gigantea*). It was suggested that it may have used its forelimbs more than *~~M~~S. temminckii.* The specimen was assigned to *~~M~~S. gigantea*, making it the oldest known representative of that species.[29]

Commented [A5]: According to the South African constitution the province name is “Western Cape”. “Province”therefore doesn’t form part of the pronoun, and as such shouldn’t be capitalised.

Klein et al. described a pangolin assigned to the genus *Phataginus* from the Elandsfontein Main site in the Western Cape ~~P~~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. *temmincki*”.[34]

The southern African Holocene and historic record is more extensive for ~~the ground~~Temminck’s pangolin. Possible sources include historical accounts, ethnographic records, rock art and place names. Möller noted that ~~the ground~~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 ~~P~~province), and that this probably constituted the southernmost record for the species (~32°~~º~~ 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 type specimen is from 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, ~1,500 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 a site in Limpopo ~~P~~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 lies ~~under eight~~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~~the ground~~ 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 in having five tracking manuals to refer to.[26,39,42-44] Each describes Temminck's~~ground~~ pangolin tracks, reviewed here in order of publication date. Figure 4b depicts the forefeet and hindfeet of a Temminck's~~ground~~ 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 is evident 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 ~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~~the ground~~ 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, /N) examined the surface unprimed by any hypotheses on trackmaker identity. Once they 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 included 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). 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.[45]

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 but 4.5 cm[44], and the hind foot even smaller,

Whereas Temminck’s~~ground~~ 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 due to a soft, non-cohesive substrate at the time 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~~ground~~ pangolin and serval might appear round, without further morphological details. In such a situation, trackmaker identity would depend more on trackway morphology than of individual tracks. In the Bosbokfontein trackway, however, there is a hint of a triangular track morphology, or at least of some tracks appearing wider distally.

Commented [A6]: Proximally?

The inference of trackmaker direction is based on some tracks appearing slightly wider in their distal portions, the overall indentation pattern, and the orientation of the 'smudges'. These impressions at the ~~proximal~~ distal 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.

Commented [A7]: Proximal? Pangolin tracks are wider in front than at the back.

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, as in the Bosbokfontein trackway and in Figure 6a.

Another potential distinguishing factor involves the relative lightness of the gait. A serval, like all cats, walks or runs lightly. A Temminck's~~ground~~ 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, suggests a pangolin trackmaker.

Opinions from expert southern African trackers were most helpful. ~~We approached Opinions from expert southern African trackers were most helpful.~~ We approached [anonymised], [anonymised], [anonymised], [anonymised], [anonymised], and [anonymised].

Their feedback was measuredly supportive. None thought the tracks were inconsistent with those of a pangolin. [anonymised] 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.*"

[anonymised] 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.

[anonymised] 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."*

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 ~~P~~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~~ground~~ pangolin trackmaker, distinctly more than a serval or any other candidate species. The Pleistocene distribution range of Temminck's~~the ground~~ 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.[46]

Conclusions

A Temminck's~~ground~~ 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.[47] The title of a book by Liebenberg specified that the art of tracking was “the origin of science”.[48] In our experience, the outcomes and conclusions that result are richer for integrating ancient and modern science.

Acknowledgements

We thank Linda Helm, Louis Liebenberg, Christina Mars, Richard McKibbin, Andrew Paterson, Wendy Panaino, Renée and Niekie Rust, Chris and Mathilde Stuart, Alex Van den Heever, and Richard Webb for their assistance.

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

References

1. AUTHOR

2. Gaudin T. Pholidota. In: Werdelin L, Sanders WJ, editors. Cenozoic Mammals of Africa. Berkeley: University of California Press; 2010. p. 599–602.

3. Gu T-T, Wu H, Yang F, Gaubert P, Heighton SP, Fu Y, et al. Genomic analysis reveals a cryptic pangolin species. Proc Natl Acad Sci USA. 2023;120(40):e2304096120. https://doi.org/10.1073/pnas.2304096120

4. Möller LA. Of the Same Breath: Indigenous Animal and Place Names. Sun Media Bloemfontein (Pty) Ltd.: Bloemfontein; 2017. https://doi.org/10.18820/9781928424031

5. IUCN Red List of Threatened Species. 2023. https://www.iucnredlist.org/search?query=Pangolins&searchType=species

6. D'Cruze N, Assou D, Coulthard E, Norrey J, Megson D, Macdonald DW, et al. Snake oil and pangolin scales: insights into wild animal use at "Marché des Fétiches" traditional medicine market, Togo. Nat Conserv. 2020;39:45–71. https://doi.org/10.3897/natureconservation.39.47879

7. Ingram DJ. 400,000 African pangolins are hunted for meat every year – why it's time to act. The Conversation Africa 2019. https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540

8. Malan JA. Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group) – South African Committee for Stratigraphy Lithostratigraphic Series 8. Pretoria: Department of Mineral and Energy Affairs;1989.

9. Malan JA. 1990. The stratigraphy and sedimentology of the Bredasdorp Group, Southern Cape Province, South Africa. MSc thesis. Cape Town: University of Cape Town; 1990.

10. Roberts DL, Cawthra HC, Musekiwa C. Dynamics of late Cenozoic aeolian deposition along the South African coast: a record of evolving climate and ecosystems. In: Martini IP, Wanless HR, editors. Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences. Special Publication of the Geological Society of London 2013:388. p. 353–387 http://dx.doi.org/10.1144/SP388.11

11. Brooke B. The distribution of carbonate eolianite. Earth-Sci Rev. 2001:55;135–164. https://doi.org/10.1016/S0012-8252(01)00054-X

12. Marean CW, Cowling RC, Franklin J. The Palaeo-Agulhas Plain: temporal and spatial variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic Region. In: Cleghorn N, Potts AJ, Cawthra HC, editors. The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235:106161. https://doi.org/10.1016/j.quascirev.2019.106161

13. Carr AS, Bateman MD, Roberts DL, Murray-Wallace CV, Jacobs Z, Holmes PJ. The last interglacial sea-level high stand on the southern Cape coastline of South Africa. Quat Res. 2010;73:351–363. https://doi.org/10.1016/j.yqres.2009.08.006

14. Roberts DL, Bateman MD, Murray-Wallace CV, Carr AS, Holmes PJ. Last Interglacial fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South Africa. Palaeogeogr Palaeoclimatol Palaeoecol. 2008;257(3):261–279. https://doi.org/10.1016/j.palaeo.2007.08.005

15. Bateman MD, Carr AS, Dunajko AC, Holmes PJ, Roberts DL, Mclaren SJ, et al. The evolution of coastal barrier systems: a case study of the Middle-Late Pleistocene Wilderness barriers, South Africa. Quat Sci Rev. 2011;30:63–81. https://doi.org/10.1016/j.quascirev.2010.10.003

16. Cawthra HC, Jacobs Z, Compton JS, Fisher EC, Karkanas P, Marean CW. Depositional and sea-level history from MIS 6 (Termination II) to MIS 3 on the southern continental shelf of South Africa. Quat Sci Rev. 2018;181:156–172. https://doi.org/10.1016/j.quascirev.2017.12.002

17. Roberts DL, Karkanas P, Jacobs Z, Marean CW, Roberts RG. Melting ice sheets 400,000 yr ago raised sea level by 13 m: past analogue for future trends. Earth Planet Sci Lett. 2012;357–358:226–237. https://doi.org/10.1016/j.epsl.2012.09.006

18. Carr AS, Bateman MD, Cawthra HC, Sealy J. First evidence for onshore marine isotope stage 3 aeolianite formation on the southern Cape coastline of South Africa. Mar Geol. 2019;407:1–15. https://doi.org/10.1016/j.margeo.2018.10.003

19. Roberts D, Cole K. Vertebrate trackways in Late Cenozoic coastal eolianites, South Africa. Geological Society of America Abstracts with Programs, XVI INQUA Congress. 2003:70(3);196.

20. Belvedere M, Farlow JO. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur tracks: the next steps. Bloomington and Indianapolis: Indiana University Press; 2016. p. 92–99.

21. Falkingham PL, Gatesy SM. Discussion: defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al. Earth-Sci Rev. 2020;208:103320. https://doi.org/10.1016/j. earscirev.2020.103320

22. Gatesy SM, Falkingham PL. Neither bones nor feet: track morphological variation and ‘preservation quality’. J. Vertebr. Paleontol. 2017;37:e1314298. https://doi.org/10.1080/0 2724634.2017.1314298

23. AUTHOR ET AL.

24. AUTHOR ET AL.

25. AUTHOR ET AL.

26. Van den Heever A, Mhlongo R, Benadie K. Tracker Manual – a Practical Guide to Animal Tracking in Southern Africa. Struik Nature: Cape Town; 2017.

27. Matthews NA, Noble TA, Breithaupt BH. Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur Tracks: The Next Steps. Bloomington: Indiana University Press; 2016. p. 28–55.

28. Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, et al. 2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology, 2018;61(4):469-480. https://doi.org/10.1111/pala.12373

29. Botha J, Gaudin T. An Early Pliocene pangolin (Mammalia; Pholidota) from Langebaanweg, South Africa. J Vertebr Paleontol. 2007;27:484–491.

30. Gaudin TJ, Emry RJ, Wible JR. The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: a morphology based analysis. J. Mammal. 2009;16:235–305.

31. Avery DM. A Fossil History of Southern African Land Mammals. Cambridge University Press: Cambridge; 2019. https://doi.org/10.1017/9781108647243

32. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. Ann S Afr Mus. 1981;84(1):1–104.

33. Klein RG, Avery G, Cruz-Uribe K, Steele TE. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. J Hum Evol. 2007;52:164–186. https://doi.org/10.1016/j.jhevol.2006.08.006

34. Klein RG. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. Quat Res. 1972;2:135–142.

35. Skead CJ. Historical Mammal incidence in the Cape Province Vol. I. Western Cape and Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei. Chief Directorate, Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope: Cape Town; 1987.

36. Layard EL. Catalogue of the specimens in the collection of the South African Museum. Part 1. The Mammalia. Saul Solomon and Co.: Cape Town; 1861.

37. Shortridge GC. Field notes on the first and second expeditions of the Cape Museum's mammal survey of the Cape Province; and descriptions of some new subgenera and subspecies. Ann S Afr Mus. 1942;36:27–99.

38. Lichtenstein WHC. Travels in Southern Africa, in the years 1803, 1804, 1805 and 1806. Vol. 2 (Translation by Anne Plumtre). Van Riebeeck Society No. 11: Cape Town; 1815.

39. Burchell WJ. Travels in the Interior of Southern Africa. Vol. 2. Longman, Hurst, Rees, Orme, Brown, and Green: London; 1824.

40. Stuart C, Stuart T. 2019. A Field Guide to the Tracks and Signs of Southern and East African Wildlife. Struik Nature: Cape Town; 2019.

41. AUTHOR ET AL.

42. Liebenberg L. 2000. A Photographic Guide to Tracks and Tracking in Southern Africa. Struik Publishers: Cape Town; 2000.

43. Walker C. Signs of the Wild – A Field Guide to the Spoor & Signs of the Mammals of Southern Africa. Struik Nature: Cape Town; 2018.

44. Gutteridge L, Liebenberg L. Mammals of Southern Africa and their Tracks and Signs. Jacana Media (Pty) Limited: Auckland Park; 2021.

45. Klein RG. Carnivore size and Quaternary climatic change in Southern Africa. Quat Res. 1986;26:153–170.

46. Cowling RM, Potts AJ, Franklin J, Midgley GF, Engelbrecht F, Marean CW. Describing a drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the Palaeo-Agulhas Plain. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235;105866. https://doi.org/10.1016/j.quascirev.2019.105866

47. AUTHOR ET AL.

48. Liebenberg L. The Art of Tracking – the Origin of Science. David Phillip: Claremont, South Africa; 1990.

Figures captions

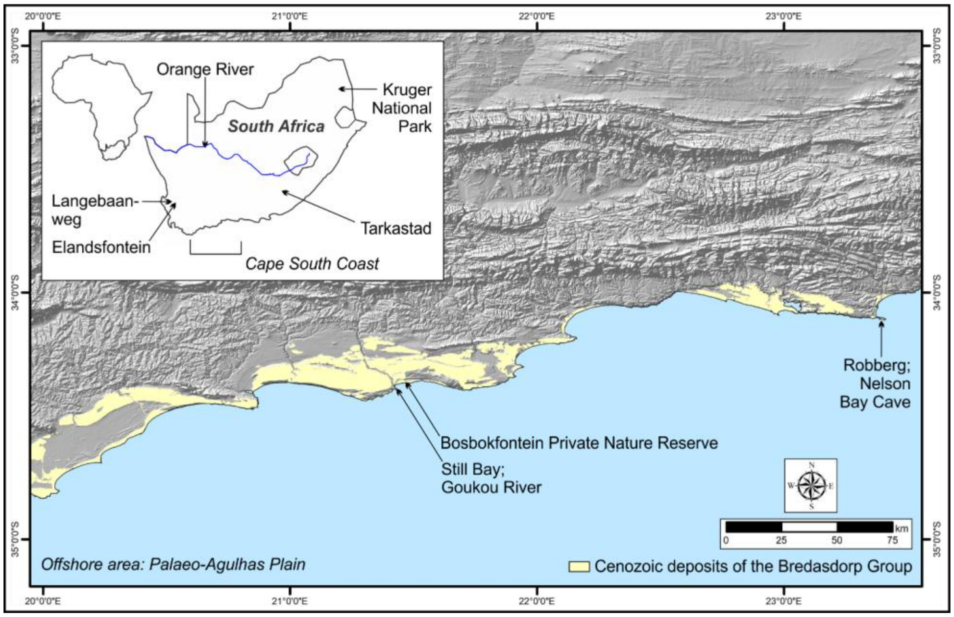

Figure 1: Map of South Africa's coast, indicating the Bosbokfontein site, the extent of Pleistocene deposits, and sites mentioned in the text.

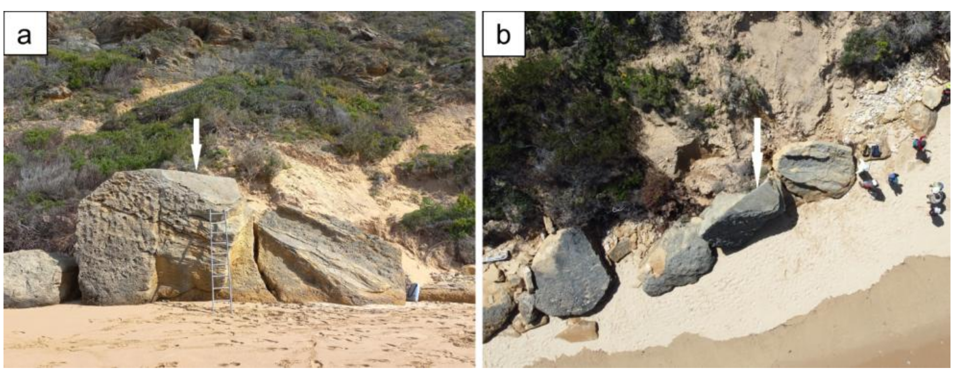

Figure 2: (a) The large loose block containing the purported pangolin trackway on its upper surface; the ladder length is 410 cm. (b) The track-bearing block, viewed from above using a drone; adult human figures for scale. Arrows point to the track-bearing surface.

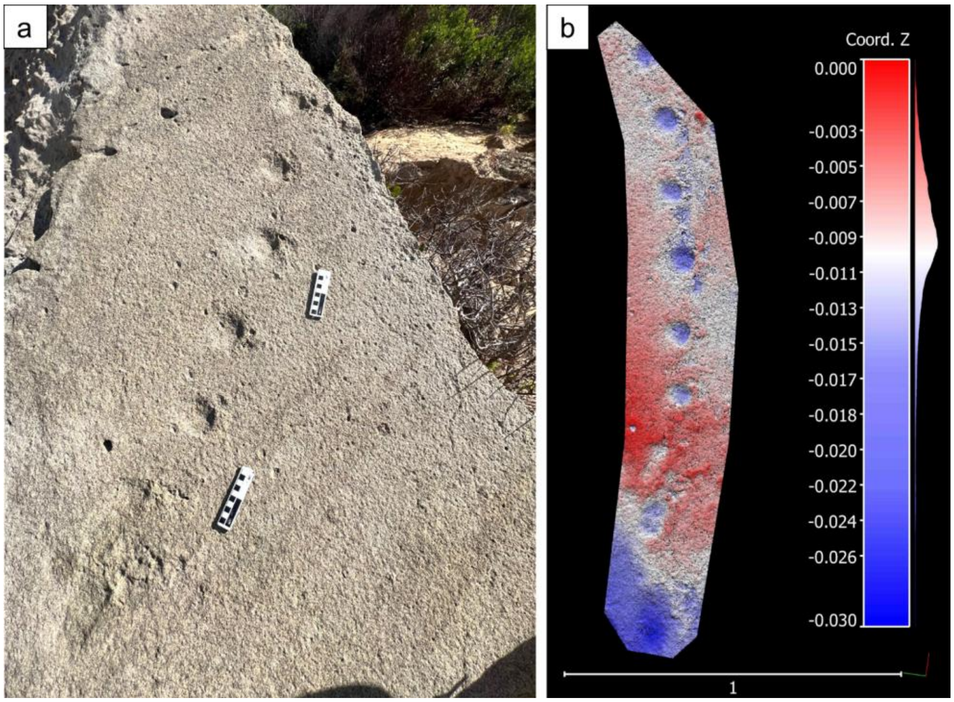

Figure 3: (a) The purported pangolin trackway; scale bars = 10 cm. (b) Photogrammetry colour mesh of the trackway; vertical and horizontal scales are in ~~metres~~meters.

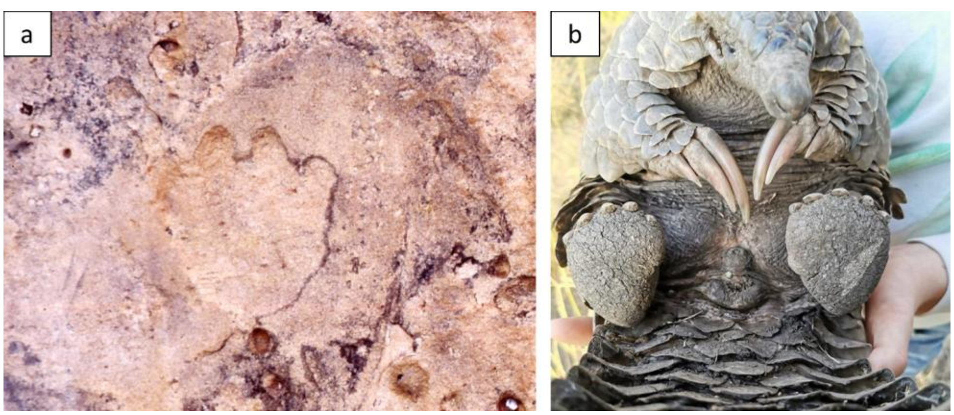

Figure 4: (a) ~~A r~~Rock engraving of a probable pangolin track in Limpopo ~~P~~province, South Africa; reproduced with permission from Chris and Mathilde Stuart. (b) The forefeet and hindfeet of a ~~ground~~ Temminck's pangolin, viewed from below; reproduced with permission from [anonymised].

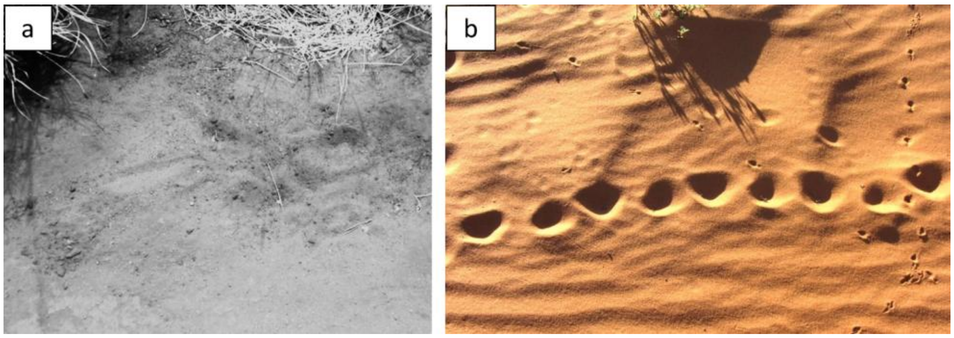

Figure 5: (a) Scuff marks registered by the tail of a ~~ground~~ Temminck's pangolin; reproduced with permission from Bruno Nebe. (b) ~~A t~~Trackway of a Temminck's~~ground~~ pangolin, showing (in this case) a short pace length; reproduced with permission from [anonymised].

Figure 6: A Temminck's~~ground~~ pangolin walking with a longer pace length; reproduced with permission from [anonymised]**.**

Appendix 2: Reviewer 3's comments on manuscript (round 1)

A PROBABLE PLEISTOCENE PANGOLIN TRACKWAY FROM SOUTH AFRICA'S CAPE SOUTH COAST

Commented [A1]: Authors?

Abstract

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 comprises 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 probable trackmaker 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. Only the ground pangolin currently occurs in southern Africa. All pangolin species are threatened or endangered.

Significance of the main findings

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

KEYWORDS: pangolin, fossil tracks, aeolianites, Cape south coast, Pleistocene

Figures inserted at the bottom of document.

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 Nature Reserve, east of Still Bay on the Cape south coast. The lines of evidence converge on a pangolin as the probable trackmaker.

Commented [A2]: I would omit this here

The order Phiolidota contains a single family, Manidae, with eight established, extant pangolin species from sub-Saharan Africa, India, southern China and southeast Asia to the Philippines.[2] A cryptic ninth Asian species was added in 2023.[3] Four of these species occur in Africa - two are arboreal, and two (the ground pangolin and the giant pangolin) are ground-dwelling. The ground pangolin (*Manis temminckii* or *Smutsia temminckii*) is also known as Temminck's 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 the ground 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.[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 (anonymised) 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, inter-disciplinary approach has allowed us to arrive at a shared conclusion on probable trackmaker identity.

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 ~~(cemented dunes)~~ 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 and palaeo-coastal dune activity.[10] Carbonate aeolianites are consolidated coastal rock formation consisting of at least partially lithified calcareous wind-blown sand. Globally, aeolianites are fairly common in mid-latitude coastal regions between 20° and 40°.[11] Aeolianite surfaces preserve a record of the passage of trackmakers when they comprised unconsolidated sand. 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, particularly clay or mud substrates on cave floors. Belvedere and Farlow introduced a four-point preservation scale, in which 0 represents an unidentifiable track,

Commented [A3]: I suggest adding this sentence or something similar that is more specific that “cemented dune”

Commented [A4]: Lower case

Commented [A5]: Why only in cave floors? Fine grained substrates exposed aerially can also produce high quality footprints

Commented [A6]: Refined by Marchetti et al. 2019 Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melchor, R.N., Farlow, J.O., 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. Earth-Science Reviews 193, 109–145. 10.1016/j.earscirev.2019.04.008

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 (moderately large grain size, 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]

Commented [A7]: Can you give an idea of the size range? For example, medium to coarse grained sand?

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] It therefore 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.

Commented [A8]: Can you explain what is the stratigraphic relationship of the sites where these samples were obtained. Are they part of the same transgressive dune system?

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 hand-held Garmin 60 device. Locality data were

Commented [A9]: repeated

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 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 um). 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.

Having viewed the tracksite in detail together, and examined 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 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 occurred since identification in 2018, but assessment and interpretation of tracks and trackway morphology remained feasible.

The block has come 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. Trackmaker direction is inferred to be upslope with respect to the current orientation, and the trackway is interpreted here with the viewer facing landwards and northwest, i.e., as if the trackmaker was progressing upslope. The tracks are preserved in convex 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 longitudinal 'smudges', 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 distal portions. Pace length in tracks 3 through 7 is relatively constant (18–20 cm). Track depth varies from 1.0 to 1.5 cm, with the distal portions of the tracks slightly deeper than the proximal portions. The external trackway width appears narrow, approximately 7.5 cm.

Commented [A10]: This sedimentologic description is not acceptable since a detailed evaluation of the sedimentary structures should be included. How do you know that the interval containing the footprints is cross-bedded? I suggest including an illustration depicting the sedimentary structures of the block. What is the objective evidence that the trackmaker travelled upslope? This should be discussed. I can see a marginal ridge that is lateral to the prints thus suggesting progression on an inclined surface but parallel to strike direction. Dune systems can contain also low angle bedding that belongs to interdunes.

Commented [A11]: After the illustrations it is concave epirelief, unless you changed the scale of the elevation model.

Commented [A12]: Please, use a descriptive an objective term and indicate this on the figures. You are referring to elongated depressions, isn't it?

Commented [A13]: Please, add numbers to Fig. 3b

Commented [A14]: I think that they are lateral.

Commented [A15]: Please, describe the shape of the tracks

Commented [A16]: You mean anterior? How do you established the sense of movement?

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 (*Manis gigantea*). It was suggested that it may have used its forelimbs more than *M. temminckii.* The specimen was assigned to *M. 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. *temmincki*”.[34]

The southern African Holocene and historic record is more extensive for the ground pangolin. Possible sources include historical accounts, ethnographic records, rock art and place names. Möller noted that the ground 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°0 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 type specimen is from 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.

Commented [A17]: Please indicate, the type of?

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, ~1,500 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 a site in 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 lies under eight 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 the ground 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 in having five tracking manuals to refer to.[26,39,42-44] Each describes ground pangolin tracks, reviewed here in order of publication date. Figure 4b depicts the forefeet and hindfeet of a ground 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 is evident 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 ~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 the ground 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 be 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, /N) examined the surface unprimed by any hypotheses on trackmaker identity. Once they 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 included felids such as serval (*Leptailurus serval*), caracal (*Caracal caracal*) and African wild cat (*Felils 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). 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.[45]

Commented [A18]: Felis

Commented [A19]: I cannot understand why you are proposing only quadrupedal mammals. The trackway is probably more compatible with a bipedal producer.

The tracks, 5-6 cm in size, are consistent with those of both extant 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 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 but 4.5 cm[44], and the hind foot even smaller,

Whereas ground 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 due to a soft, non-cohesive substrate at the time the tracks were registered, the effects of grain size, or pre-burial or post-re-exposure erosion.[1] Consequently, the tracks of both ground pangolin and serval might appear round, without further morphological details. In such a situation, trackmaker identity would depend more on trackway morphology than of individual tracks. In the Bosbokfontein trackway, however, there is a hint of a triangular track morphology, or at least of some tracks appearing wider distally.

The inference of trackmaker direction is based on some tracks appearing slightly wider in their distal portions, the overall indentation pattern, and the orientation of the 'smudges'. 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.

Commented [A20]: Please, use a more descriptive term

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, as in the Bosbokfontein trackway and in Figure 6a.

Commented [A21]: The figure have only one image

Another potential distinguishing factor involves the relative lightness of the gait. A serval, like all cats, walks or runs lightly. A ground 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, suggests a pangolin trackmaker.

Commented [A22]: I do not know what is a light gait, I suggest using technical terms. Are you referring to footprint depth? In a loose substrate like dry and sloping carbonate sand , 1-1.5 cm in depth is not deep enough, and the depth can be changed by grain flows triggered by the passage of the animal.

Commented [A23]: Unconvincing

Opinions from expert southern African trackers were most helpful. We approached Opinions from expert southern African trackers were most helpful. We approached [anonymised], [anonymised], [anonymised], [anonymised], [anonymised], [anonymised], and [anonymised].

Commented [A24]: lc

Commented [A25]: what is this?

Their feedback was measuredly supportive. None thought the tracks were inconsistent with those of a pangolin. [anonymised] 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.*"

[anonymised] 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.

[anonymised] 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."*

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 ground pangolin trackmaker, distinctly more than a serval or any other candidate species. The Pleistocene distribution range of the ground 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.[46]

Conclusions

A ground pangolin probably walked across a soft, sandy dune surface near the margin of the Palaeo-Agulhas Plain, most likely during MIS6 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.[47] The title of a book by Liebenberg specified that the art of tracking was "the origin of science".[48] In our experience, the outcomes and conclusions that result are richer for integrating ancient and modern science.

Acknowledgements

We thank Linda Helm, Louis Liebenberg, Christina Mars, Richard McKibbin, Andrew Paterson, Wendy Panaino, Renée and Niekie Rust, Chris and Mathilde Stuart, Alex Van den Heever, and Richard Webb for their assistance.

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

References

Commented [A26]: There are many missing references

1. AUTHOR

2. Gaudin T. Pholidota. In: Werdelin L, Sanders WJ, editors. Cenozoic Mammals of Africa. Berkeley: University of California Press; 2010. p. 599–602.

3. Gu T-T, Wu H, Yang F, Gaubert P, Heighton SP, Fu Y, et al. Genomic analysis reveals a cryptic pangolin species. Proc Natl Acad Sci USA. 2023;120(40):e2304096120. https://doi.org/10.1073/pnas.2304096120

4. Möller LA. Of the Same Breath: Indigenous Animal and Place Names. Sun Media Bloemfontein (Pty) Ltd.: Bloemfontein; 2017. https://doi.org/10.18820/9781928424031

5. IUCN Red List of Threatened Species. 2023. https://www.iucnredlist.org/search?query=Pangolins&searchType=species

6. D'Cruze N, Assou D, Coulthard E, Norrey J, Megson D, Macdonald DW, et al. Snake oil and pangolin scales: insights into wild animal use at "Marché des Fétiches" traditional medicine market, Togo. Nat Conserv. 2020;39:45–71. https://doi.org/10.3897/natureconservation.39.47879

7. Ingram DJ. 400,000 African pangolins are hunted for meat every year – why it's time to act. The Conversation Africa 2019. https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540

8. Malan JA. Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group) – South African Committee for Stratigraphy Lithostratigraphic Series 8. Pretoria: Department of Mineral and Energy Affairs;1989.

9. Malan JA. 1990. The stratigraphy and sedimentology of the Bredasdorp Group, Southern Cape Province, South Africa. MSc thesis. Cape Town: University of Cape Town; 1990.

10. Roberts DL, Cawthra HC, Musekiwa C. Dynamics of late Cenozoic aeolian deposition along the South African coast: a record of evolving climate and ecosystems. In: Martini IP, Wanless HR, editors. Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences. Special Publication of the Geological Society of London 2013:388. p. 353–387 http://dx.doi.org/10.1144/SP388.11

11. Brooke B. The distribution of carbonate eolianite. Earth-Sci Rev. 2001:55;135–164. https://doi.org/10.1016/S0012-8252(01)00054-X

12. Marean CW, Cowling RC, Franklin J. The Palaeo-Agulhas Plain: temporal and spatial variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic Region. In: Cleghorn N, Potts AJ, Cawthra HC, editors. The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235:106161. https://doi.org/10.1016/j.quascirev.2019.106161

13. Carr AS, Bateman MD, Roberts DL, Murray-Wallace CV, Jacobs Z, Holmes PJ. The last interglacial sea-level high stand on the southern Cape coastline of South Africa. Quat Res. 2010;73:351–363. https://doi.org/10.1016/j.yqres.2009.08.006

14. Roberts DL, Bateman MD, Murray-Wallace CV, Carr AS, Holmes PJ. Last Interglacial fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South Africa. Palaeogeogr Palaeoclimatol Palaeoecol. 2008;257(3):261–279. https://doi.org/10.1016/j.palaeo.2007.08.005

15. Bateman MD, Carr AS, Dunajko AC, Holmes PJ, Roberts DL, Mclaren SJ, et al. The evolution of coastal barrier systems: a case study of the Middle-Late Pleistocene Wilderness barriers, South Africa. Quat Sci Rev. 2011;30:63–81. https://doi.org/10.1016/j.quascirev.2010.10.003

16. Cawthra HC, Jacobs Z, Compton JS, Fisher EC, Karkanas P, Marean CW. Depositional and sea-level history from MIS 6 (Termination II) to MIS 3 on the southern continental shelf of South Africa. Quat Sci Rev. 2018;181:156–172. https://doi.org/10.1016/j.quascirev.2017.12.002

17. Roberts DL, Karkanas P, Jacobs Z, Marean CW, Roberts RG. Melting ice sheets 400,000 yr ago raised sea level by 13 m: past analogue for future trends. Earth Planet Sci Lett. 2012;357–358:226–237. https://doi.org/10.1016/j.epsl.2012.09.006

18. Carr AS, Bateman MD, Cawthra HC, Sealy J. First evidence for onshore marine isotope stage 3 aeolianite formation on the southern Cape coastline of South Africa. Mar Geol. 2019;407:1–15. https://doi.org/10.1016/j.margeo.2018.10.003

19. Roberts D, Cole K. Vertebrate trackways in Late Cenozoic coastal eolianites, South Africa. Geological Society of America Abstracts with Programs, XVI INQUA Congress. 2003:70(3);196.

20. Belvedere M, Farlow JO. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur tracks: the next steps. Bloomington and Indianapolis: Indiana University Press; 2016. p. 92–99.

21. Falkingham PL, Gatesy SM. Discussion: defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al. Earth-Sci Rev. 2020;208:103320. https://doi.org/10.1016/j. earscirev.2020.103320

22. Gatesy SM, Falkingham PL. Neither bones nor feet: track morphological variation and ‘preservation quality’. J. Vertebr. Paleontol. 2017;37:e1314298. https://doi.org/10.1080/0 2724634.2017.1314298

23. AUTHOR ET AL.

24. AUTHOR ET AL.

25. AUTHOR ET AL.

26. Van den Heever A, Mhlongo R, Benadie K. Tracker Manual – a Practical Guide to Animal Tracking in Southern Africa. Struik Nature: Cape Town; 2017.

27. Matthews NA, Noble TA, Breithaupt BH. Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur Tracks: The Next Steps. Bloomington: Indiana University Press; 2016. p. 28–55.

28. Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, et al. 2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology, 2018;61(4):469-480. https://doi.org/10.1111/pala.12373

29. Botha J, Gaudin T. An Early Pliocene pangolin (Mammalia; Pholidota) from Langebaanweg, South Africa. J Vertebr Paleontol. 2007;27:484–491.

30. Gaudin TJ, Emry RJ, Wible JR. The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: a morphology based analysis. J.Mammal. 2009;16:235–305.

31. Avery DM. A Fossil History of Southern African Land Mammals. Cambridge University Press: Cambridge; 2019. https://doi.org/10.1017/9781108647243

32. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. Ann S Afr Mus. 1981;84(1):1–104.

33. Klein RG, Avery G, Cruz-Uribe K, Steele TE. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. J Hum Evol. 2007;52:164–186. https://doi.org/10.1016/j.jhevol.2006.08.006

34. Klein RG. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. Quat Res. 1972;2:135–142.

35. Skead CJ. Historical Mammal incidence in the Cape Province Vol. I. Western Cape and Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei. Chief Directorate, Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope: Cape Town; 1987.

36. Layard EL. Catalogue of the specimens in the collection of the South African Museum. Part 1. The Mammalia. Saul Solomon and Co.: Cape Town; 1861.

37. Shortridge GC. Field notes on the first and second expeditions of the Cape Museum's mammal survey of the Cape Province; and descriptions of some new subgenera and subspecies. Ann S Afr Mus. 1942;36:27–99.

38. Lichtenstein WHC. Travels in Southern Africa, in the years 1803, 1804, 1805 and 1806. Vol. 2 (Translation by Anne Plumtre). Van Riebeeck Society No. 11: Cape Town; 1815.

39. Burchell WJ. Travels in the Interior of Southern Africa. Vol. 2. Longman, Hurst, Rees, Orme, Brown, and Green: London; 1824.

40. Stuart C, Stuart T. 2019. A Field Guide to the Tracks and Signs of Southern and East African Wildlife. Struik Nature: Cape Town; 2019.

41. AUTHOR ET AL.

42. Liebenberg L. 2000. A Photographic Guide to Tracks and Tracking in Southern Africa. Struik Publishers: Cape Town; 2000.

43. Walker C. Signs of the Wild – A Field Guide to the Spoor & Signs of the Mammals of Southern Africa. Struik Nature: Cape Town; 2018.

44. Gutteridge L, Liebenberg L. Mammals of Southern Africa and their Tracks and Signs. Jacana Media (Pty) Limited: Auckland Park; 2021.

45. Klein RG. Carnivore size and Quaternary climatic change in Southern Africa. Quat Res. 1986;26:153–170.

46. Cowling RM, Potts AJ, Franklin J, Midgley GF, Engelbrecht F, Marean CW. Describing a drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the Palaeo-Agulhas Plain. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235;105866. https://doi.org/10.1016/j.quascirev.2019.105866

47. AUTHOR ET AL.

48. Liebenberg L. The Art of Tracking – the Origin of Science. David Phillip: Claremont, South Africa; 1990.

Commented [A27]: please complete

Commented [A28]: Please complete

Figures captions

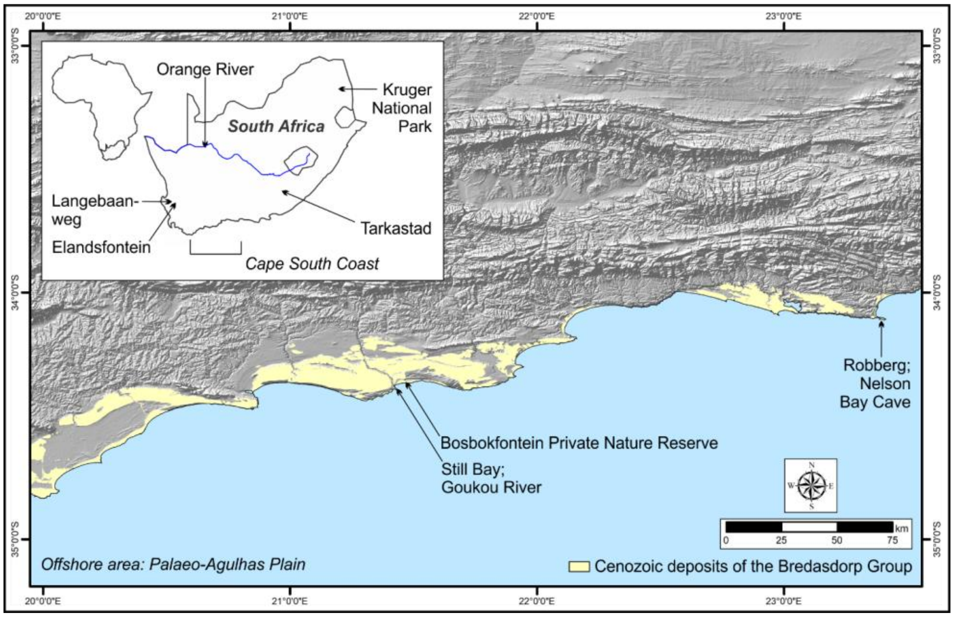

Figure 1: Map of South Africa's coast, indicating the Bosbokfontein site, the extent of Pleistocene deposits, and sites mentioned in the text.

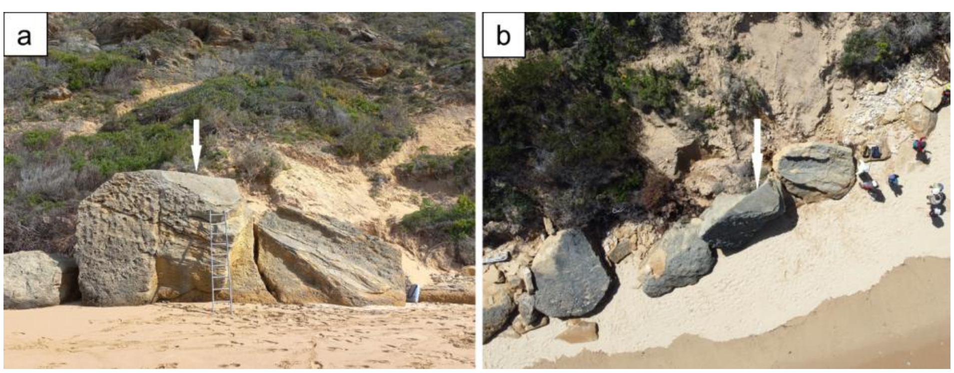

Figure 2: (a) The large loose block containing the purported pangolin trackway on its upper surface; the ladder length is 410 cm. (b) The track-bearing block, viewed from above using a drone; adult human figures for scale. Arrows point to the track-bearing surface.

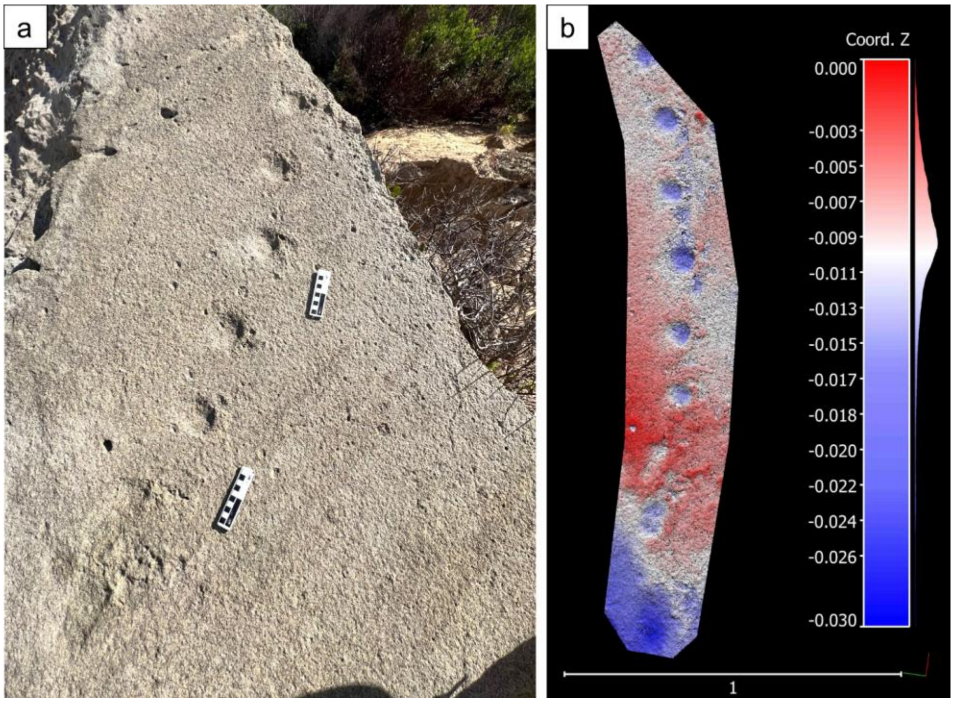

Figure 3: (a) The purported pangolin trackway; scale bars = 10 cm. (b) Photogrammetry colour mesh of the trackway; vertical and horizontal scales are in metres.

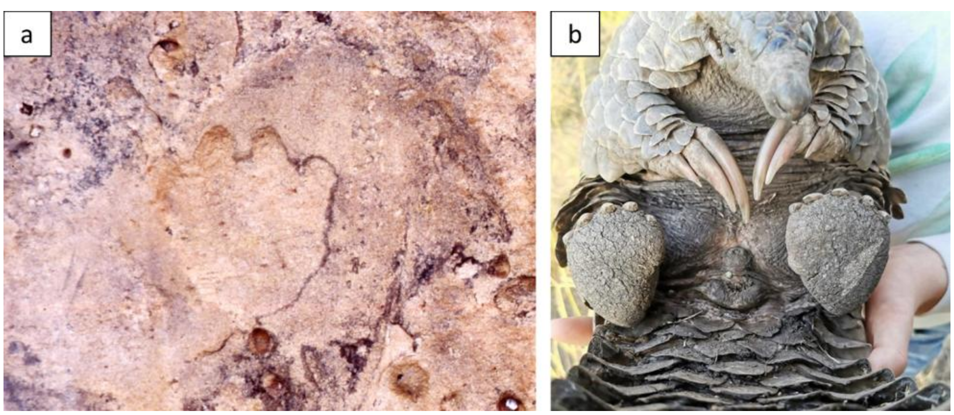

Figure 4: (a) A rock engraving of a probable pangolin track in Limpopo Province; reproduced with permission from Chris and Mathilde Stuart. (b) The forefeet and hindfeet of a ground pangolin, viewed from below; reproduced with permission from [anonymised].

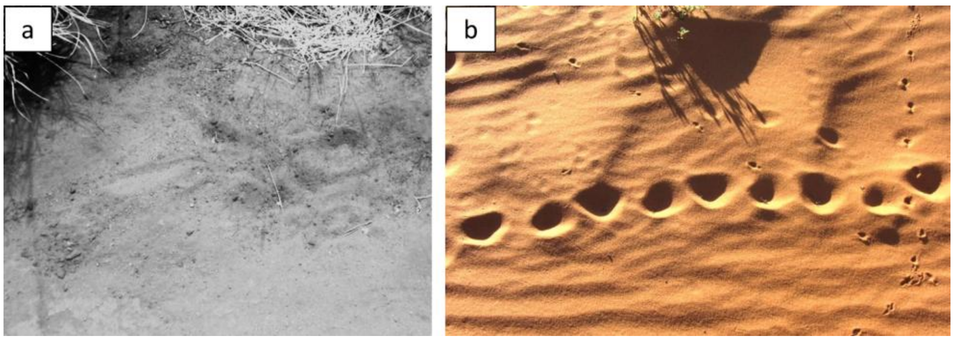

Figure 5: (a) Scuff marks registered by the tail of a ground pangolin; reproduced with permission from Bruno Nebe. (b) A trackway of a ground pangolin, showing (in this case) a short pace length; reproduced with permission from [anonymised].

Commented [A29]: A scale is necessary in both images

Commented [A30]: Please indicate also the footprints, trackway width seem to be larger than in the next photo

Commented [A31]: This trackway displays pairs of tracks that is not evident in the fossil example.

Figure 6: A ground pangolin walking with a longer pace length; reproduced with permission from [anonymised]**.**

Appendix 3: Author response to reviewers on revised manuscript (round 1)

A PROBABLE PLEISTOCENE PANGOLIN (ORDER PHOLIDOTA) TRACKWAY FROM SOUTH AFRICA'S CAPE SOUTH COAST

Commented [A1]: Added upon recommendation of Reviewer 2.

Abstract

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 comprises 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 probable trackmaker 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.

Commented [A2]: All Reviewer 1's suggestions were incorporated into these sentences.

Significance of the main findings

- A Pleistocene probable pangolin trackway has been identified east of Still Bay, Western Cape province, South Africa.

Commented [A3]: Added in response to Reviewer 1 suggestion.

- The identification involved integrating indigenous African and western-based ichnological approaches.
- This appears to be the first known fossilised pangolin trackway.
- The trackway comprises 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 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 recognized, extant pangolin species from sub-Saharan Africa, India, southern China and southeast Asia to 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]

Commented [A4]: Typo correction as pointed out by Reviewer 2.

Commented [A5]: Changed in response to Reviewer 1 suggestion.

Commented [A6]: Changed in response to Reviewer 1 suggestion, which addresses Reviewer 2's comment as well.

Commented [A7]: Nomenclature corrected in this paragraph and elsewhere according to Reviewer 1 and Reviewer 2 suggestions.

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]

Commented [A8]: As per Reviewer 1 suggestion.

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, inter-disciplinary approach has allowed us to arrive at a shared conclusion on probable trackmaker identity.

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 and palaeo-coastal 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]

Commented [A9]: Sentences added for clarification in response to Reviewer 3 suggestions

Commented [A10]: Changed to lower case 'p', in response to Reviewer 3.

Commented [A11]: Reviewer 1 suggested 'meters', but we think 'metres' is consistent with SAJS style.

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

Commented [A12]: Clarified in response to Reviewer 3 comment.

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]

Commented [A13]: Clarified in response to Reviewer 2.

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.

Commented [A14]: Added in response to Reviewer 3 request.

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 hand-held 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 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.

Commented [A15]: Thanks to Reviewer 1 for the correction.

Having viewed the tracksite in detail together, and examined 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 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 occurred since identification in 2018, but assessment and interpretation of tracks and trackway morphology remained feasible.

The block has come 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 to 1.5 cm, with the anterior portions of the tracks slightly deeper than the posterior portions. The external trackway width appears narrow, 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.

Commented [A16]: These sentences have been rephrased for clarification and to avoid the confusion that resulted from our initial sentences, all in response to Reviewer 3's comments.

Commented [A17]: Corrected, as pointed out by Reviewer 3.

Commented [A18]: Changed from 'smudges' to 'elongated depressions' here and elsewhere, as suggested by Reviewer 3.

Commented [A19]: Two reviewers (1 and 3) commented on our use of 'distal' and 'proximal' in relation to track morphology - it is clear that these terms have created confusion. We have addressed this by using 'anterior' or 'posterior' where appropriate.

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 historic 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 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.

Commented [A20]: Decapitalised the P in province throughout, where appropriate, as per Reviewer 1 suggestion..

Commented [A21]: Corrected with thanks to reviewers 1 and 3.

Commented [A22]: Clarification as requested by Reviewer 3.

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, ~1,500 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 a site in 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 lies less than eight 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 in having five tracking manuals to refer to.[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 ~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]

Commented [A23]: Reviewer 1 typo correction.

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, /N) examined the surface unprimed by any hypotheses on trackmaker identity. Once they 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 but 4.5 cm[44], and the hind foot even smaller,

Commented [A24]: Corrected as pointed out by Reviewer 3.

Commented [A25]: Inserted in response to Reviewer 3 comment.

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 due to a soft, non-cohesive substrate at the time 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 of individual tracks. In 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.

Commented [A26]: Two reviewers commented on our use of 'distal' and 'proximal' - it is clear that these terms have created confusion. We have addressed this by using 'anterior' or 'posterior' where appropriate.

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.

Commented [A27]: Added in response to Reviewer 2.

Commented [A28]: Corrected as pointed out by Reviewer 3.

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.

Commented [A29]: Softened the text here in response to Reviewer 3 comment.

Opinions from expert southern African trackers were most helpful. We approached [anonymised], [anonymised], [anonymised], [anonymised], [anonymised], and [anonymised].

Their feedback was measuredly supportive. None thought the tracks were inconsistent with those of a pangolin. [anonymised] 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."*

[anonymised] 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.

[anonymised] 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.

Commented [A30]: Paragraph added in response to Reviewer 2 comments.

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.

Acknowledgements

We thank Linda Helm, Louis Liebenberg, Christina Mars, Richard McKibbin, Andrew Paterson, Wendy Panaino, Renée and Niekie Rust, Chris and Mathilde Stuart, Alex Van den Heever, and Richard Webb for their assistance. We are grateful to the three anonymous reviewers for their thorough and helpful comments, which led to substantial improvements in the manuscript.

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

References

1. AUTHOR

2. Gaudin T. Pholidota. In: Werdelin L, Sanders WJ, editors. Cenozoic Mammals of Africa. Berkeley: University of California Press; 2010. p. 599–602.

3. Gu T-T, Wu H, Yang F, Gaubert P, Heighton SP, Fu Y, et al. Genomic analysis reveals a cryptic pangolin species. Proc Natl Acad Sci USA. 2023;120(40):e2304096120. https://doi.org/10.1073/pnas.2304096120

4. Möller LA. Of the Same Breath: Indigenous Animal and Place Names. Sun Media Bloemfontein (Pty) Ltd.: Bloemfontein; 2017. https://doi.org/10.18820/9781928424031

5. IUCN Red List of Threatened Species. 2023. https://www.iucnredlist.org/search?query=Pangolins&searchType=species

6. D'Cruze N, Assou D, Coulthard E, Norrey J, Megson D, Macdonald DW, et al. Snake oil and pangolin scales: insights into wild animal use at "Marché des Fétiches" traditional medicine market, Togo. Nat Conserv. 2020;39:45–71. https://doi.org/10.3897/natureconservation.39.47879

7. Ingram DJ. 400,000 African pangolins are hunted for meat every year – why it's time to act. The Conversation Africa 2019. https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540

8. Malan JA. Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group) – South African Committee for Stratigraphy Lithostratigraphic Series 8. Pretoria: Department of Mineral and Energy Affairs;1989.

9. Malan JA. 1990. The stratigraphy and sedimentology of the Bredasdorp Group, Southern Cape Province, South Africa. MSc thesis. Cape Town: University of Cape Town; 1990.

10. Roberts DL, Cawthra HC, Musekiwa C. Dynamics of late Cenozoic aeolian deposition along the South African coast: a record of evolving climate and ecosystems. In: Martini IP, Wanless HR, editors. Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences. Special Publication of the Geological Society of London 2013:388. p. 353–387 http://dx.doi.org/10.1144/SP388.11

11. Brooke B. The distribution of carbonate eolianite. Earth-Sci Rev. 2001:55;135–164. https://doi.org/10.1016/S0012-8252(01)00054-X

12. Marean CW, Cowling RC, Franklin J. The Palaeo-Agulhas Plain: temporal and spatial variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic Region. In: Cleghorn N, Potts AJ, Cawthra HC, editors. The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235:106161. https://doi.org/10.1016/j.quascirev.2019.106161

13. Carr AS, Bateman MD, Roberts DL, Murray-Wallace CV, Jacobs Z, Holmes PJ. The last interglacial sea-level high stand on the southern Cape coastline of South Africa. Quat Res. 2010;73:351–363. https://doi.org/10.1016/j.yqres.2009.08.006

14. Roberts DL, Bateman MD, Murray-Wallace CV, Carr AS, Holmes PJ. Last Interglacial fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South Africa. Palaeogeogr Palaeoclimatol Palaeoecol. 2008;257(3):261–279. https://doi.org/10.1016/j.palaeo.2007.08.005

15. Bateman MD, Carr AS, Dunajko AC, Holmes PJ, Roberts DL, Mclaren SJ, et al. The evolution of coastal barrier systems: a case study of the Middle-Late Pleistocene Wilderness barriers, South Africa. Quat Sci Rev. 2011;30:63–81. https://doi.org/10.1016/j.quascirev.2010.10.003

16. Cawthra HC, Jacobs Z, Compton JS, Fisher EC, Karkanas P, Marean CW. Depositional and sea-level history from MIS 6 (Termination II) to MIS 3 on the southern continental shelf of South Africa. Quat Sci Rev. 2018;181:156–172. https://doi.org/10.1016/j.quascirev.2017.12.002

17. Roberts DL, Karkanas P, Jacobs Z, Marean CW, Roberts RG. Melting ice sheets 400,000 yr ago raised sea level by 13 m: past analogue for future trends. Earth Planet Sci Lett. 2012;357–358:226–237. https://doi.org/10.1016/j.epsl.2012.09.006

18. Carr AS, Bateman MD, Cawthra HC, Sealy J. First evidence for onshore marine isotope stage 3 aeolianite formation on the southern Cape coastline of South Africa. Mar Geol. 2019;407:1–15. https://doi.org/10.1016/j.margeo.2018.10.003

19. Roberts D, Cole K. Vertebrate trackways in Late Cenozoic coastal eolianites, South Africa. Geological Society of America Abstracts with Programs, XVI INQUA Congress. 2003:70(3);196.

20. Belvedere M, Farlow JO. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur tracks: the next steps. Bloomington and Indianapolis: Indiana University Press; 2016. p. 92–99.

21. Falkingham PL, Gatesy SM. Discussion: defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al. Earth-Sci Rev. 2020;208:103320. https://doi.org/10.1016/j. earscirev.2020.103320

22. Gatesy SM, Falkingham PL. Neither bones nor feet: track morphological variation and ‘preservation quality’. J. Vertebr. Paleontol. 2017;37:e1314298. https://doi.org/10.1080/0 2724634.2017.1314298

23. AUTHOR ET AL.

24. AUTHOR ET AL.

25. AUTHOR ET AL.

26. Van den Heever A, Mhlongo R, Benadie K, Thomas I. Tracker Manual – a Practical Guide to Animal Tracking in Southern Africa. Struik Nature: Cape Town; 2024.

Commented [A31]: Reference has been updated, now 2024 instead of older 2017 edition.

27. Matthews NA, Noble TA, Breithaupt BH. Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur Tracks: The Next Steps. Bloomington: Indiana University Press; 2016. p. 28–55.

28. Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, et al. 2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology, 2018;61(4):469–480. https://doi.org/10.1111/pala.12373

29. Botha J, Gaudin T. An Early Pliocene pangolin (Mammalia; Pholidota) from Langebaanweg, South Africa. J Vertebr Paleontol. 2007;27:484–491.

30. Gaudin TJ, Emry RJ, Wible JR. The phylogeny of living and extinct pangolins (Mammalia, Pholidota) and associated taxa: a morphology based analysis. J.Mammal. 2009;16:235–305.

31. Avery DM. A Fossil History of Southern African Land Mammals. Cambridge University Press: Cambridge; 2019. https://doi.org/10.1017/9781108647243

32. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. Ann S Afr Mus. 1981;84(1):1–104.

33. Klein RG, Avery G, Cruz-Uribe K, Steele TE. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. J Hum Evol. 2007;52:164–186. https://doi.org/10.1016/j.jhevol.2006.08.006

34. Klein RG. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. Quat Res. 1972;2:135–142.

35. Skead CJ. Historical Mammal incidence in the Cape Province Vol. I. Western Cape and Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei. Chief Directorate, Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope: Cape Town; 1987.

36. Layard EL. Catalogue of the specimens in the collection of the South African Museum. Part 1. The Mammalia. Saul Solomon and Co.: Cape Town; 1861.

37. Shortridge GC. Field notes on the first and second expeditions of the Cape Museum's mammal survey of the Cape Province; and descriptions of some new subgenera and subspecies. Ann S Afr Mus. 1942;36:27–99.

38. Lichtenstein WHC. Travels in Southern Africa, in the years 1803, 1804, 1805 and 1806. Vol. 2 (Translation by Anne Plumtre). Van Riebeeck Society No. 11: Cape Town; 1815.

39. Burchell WJ. Travels in the Interior of Southern Africa. Vol. 2. Longman, Hurst, Rees, Orme, Brown, and Green: London; 1824.

40. Stuart C, Stuart T. 2019. A Field Guide to the Tracks and Signs of Southern and East African Wildlife. Struik Nature: Cape Town; 2019.

41. AUTHOR ET AL.

42. Liebenberg L. 2000. A Photographic Guide to Tracks and Tracking in Southern Africa. Struik Publishers: Cape Town; 2000.

43. Walker C. Signs of the Wild – A Field Guide to the Spoor & Signs of the Mammals of Southern Africa. Struik Nature: Cape Town; 2018.

44. Gutteridge L, Liebenberg L. Mammals of Southern Africa and their Tracks and Signs. Jacana Media (Pty) Limited: Auckland Park; 2021.

45. AUTHOR ET AL.

Commented [A32]: New reference added in response to Reviewer 3 comment.

46. Klein RG. Carnivore size and Quaternary climatic change in Southern Africa. Quat Res. 1986;26:153–170.

47. Cowling RM, Potts AJ, Franklin J, Midgley GF, Engelbrecht F, Marean CW. Describing a drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the Palaeo-Agulhas Plain. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-

Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235;105866. https://doi.org/10.1016/j.quascirev.2019.105866

48. AUTHOR ET AL.

49. Liebenberg L. The Art of Tracking – the Origin of Science. David Phillip: Claremont, South Africa; 1990.

Commented [A33]: This reference is still 'in press', but publication appears to be imminent.

Figure captions

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

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.

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.

Figure 4: (a) Rock engraving of a probable pangolin track in Limpopo Province; reproduced with permission from [anonymised], (b) The forefeet and hindfeet of a Temminck's pangolin, viewed from below; reproduced with permission from [anonymised],

Figure 5: (a) Scuff marks registered by the tail of a Temminck's pangolin; reproduced with permission from [anonymised], (b) A trackway of a Temminck's pangolin, showing (in this case) a short pace length; reproduced with permission from [anonymised],

Figure 6: A Temminck's pangolin walking with a longer pace length; reproduced with permission from [anonymised],