

The *South African Journal of Science* follows a double-anonymous peer review model but encourages Reviewers and Authors to publish their anonymised review reports and response letters, respectively, as supplementary files after manuscript review and acceptance. For more information, see [Publishing peer review reports](#).

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 *Smutsia*, with only the four Asian pangolin species belonging to the genus *Manis*. This is also important because later in the manuscript you quote an article that recorded a *Phataginus* fossil from the Cape south coast, while if you use "*Manis temminckii*" then you will need to refer to this fossil as "*Manis* (*Phataginus*)" (i.e., subgenus *Phataginus*).

[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-Agulhas 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 "i"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](#).

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.](#)

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

Figures inserted at the bottom of document.

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.

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

Introduction

34
35
36 Through the Cape south coast ichnology project over 350 Pleistocene vertebrate ichnosites
37 have been documented along a 350 km stretch of South African coastline. The majority (80%)
38 represent mammal tracks and traces.¹ Until now, no pangolin ichnofossils have been identified,
39 either on the Cape south coast or, to the best of our knowledge, anywhere in the world. Here we
40 describe a trackway on an aeolianite (cemented dune) palaeosurface in the Bosbokfontein
41 Nature Reserve, east of Still Bay on the Cape south coast. The lines of evidence converge on a
42 pangolin as the probable trackmaker.

43
44 The order Pholidota contains a single family, Manidae, with eight ~~established~~ recognised, extant
45 pangolin species from sub-Saharan Africa, India, southern China and southeast Asia to the
46 Philippines.² A cryptic ninth Asian species was ~~added~~ detected in 2023,³ and awaits formal
47 ~~description~~. Four of these species occur in Africa - two are arboreal, and two (~~the~~
48 ~~ground~~ Temminck's pangolin and the giant pangolin) are ground-dwelling. ~~The~~
49 ~~ground~~ Temminck's pangolin (~~Manis-Smutsia~~ *temminckii*, ~~previously -or Smutsia~~ *Manis*
50 *temminckii*) is also known as ~~the ground~~ Temminck's pangolin, the Cape pangolin, or the scaly
51 anteater, and is the only pangolin species to currently occur in southern Africa.² In the Ju/'hoan
52 language ~~the ground~~ Temminck's pangolin is known as 'n#hòqò', and in Afrikaans as the
53 'ietermagog'. The latter is probably of Bantu or Tswana derivation.⁴

54
55 All species of extant pangolin are threatened by poaching and habitat loss, and all are classified
56 as ~~v~~ Vulnerable, ~~e~~ Endangered, or ~~e~~ Critically ~~e~~ Endangered on the IUCN Red List of Threatened
57 Species.⁵ Pangolin meat is regarded as a delicacy, and pangolin scales are used in traditional
58 medicines.⁶ There is evidence that pangolins are among the most trafficked wild animals on
59 Earth, and 400,000 African pangolins are estimated to be hunted for their meat annually.⁷

60
61 The tracks described here were initially identified in 2018 by Renée Rust and family. The tracks
62 are evident on the surface of a large fallen aeolianite block. The putative trackmaker remained
63 enigmatic until our joint analysis in 2023. Two of us (anonymised) are indigenous Ju'/hoansi
64 San Master Trackers, and had an immediate, strong sense of what was being examined. This
65 presented the opportunity for indigenous and modern scientific tracking exponents to engage in
66 a productive exchange of ideas, combining culturally honed and experientially grounded

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.

67 intuitions with modern assessment techniques. This collaborative, inter-disciplinary approach
68 has allowed us to arrive at a shared conclusion on probable trackmaker identity.

69
70 The purpose of this article is to describe the trackway, discuss the probable trackmaker,
71 consider alternative trackmakers, and discuss the relevance of this discovery. We also reflect on
72 the value of integrating indigenous African and western-based ichnological approaches.

74 75 **Geological context**

76
77 Pleistocene aeolianites (cemented dunes) of the Waenhuiskrans Formation⁸, part of the
78 Neogene Bredasdorp Group⁹, are exposed along portions of the Cape south coast of South
79 Africa, and have provided evidence for palaeo-shorelines and palaeo-coastal dune activity.¹⁰
80 Globally, aeolianites are fairly common in mid-latitude coastal regions between 20° and 40°.¹¹
81 Aeolianite surfaces preserve a record of the passage of trackmakers when they comprised
82 unconsolidated sand. Throughout the Pleistocene, global sea-level change meant that the Cape
83 south coast landscape was dynamic. Vertebrate ichnosites encountered on these
84 palaeosurfaces would have been situated at the margin of the Paleo-Agulhas Plain, most of
85 which is presently submerged, but at times sea-level oscillations would have exposed the entire
86 Plain.¹² In contrast, sea level was 6–8 ~~metres~~ [meters](#) higher than at present at the height of the
87 Marine Isotope Stage (MIS) 5e marine transgression at ~126 ka.¹³

88
89 Optically Stimulated Luminescence (OSL) dating of onshore aeolianites has shown that most
90 date to MIS 5 and late MIS 6.¹³⁻¹⁶ MIS 11 deposits¹⁷ and MIS 3 deposits¹⁸ have also been
91 identified, with a resulting age range of dated deposits presently spanning ~400–35 ka. Roberts
92 and Cole provided an explanation for the profusion of ichnosites, postulating a combination of a
93 cohesive moulding agent (moist sand), rapid track burial (facilitated by high sedimentation
94 rates), rapid lithification (via partial solution and re-precipitation of bioclasts), and finally re-
95 exposure of track-bearing surfaces through shoreline erosion.¹⁹

96
97 In general, the grain size of the substrate inversely influences the preservation quality of fossil
98 tracks. In Cape south coast Pleistocene deposits, tracks made on moderately coarse-grained
99 dune surfaces tend to show poor to intermediate preservation quality, certainly inferior to that
100 seen elsewhere in the world, particularly clay or mud substrates on cave floors. Belvedere and

101 Farlow introduced a four-point preservation scale, in which 0 represents an unidentifiable track,
102 and 3 represents a track of exceptional quality.²⁰ It is unusual for tracks within the Cape south
103 coast deposits to rise above 2 on this scale.

104
105 Active shoreline erosion causes coastal cliffs to fragment or collapse, sometimes exposing new
106 ichnosites, while known sites deteriorate in quality or loose blocks slump into the ocean.
107 Ichnosites are thus ephemeral. The taphonomic erosive effects of wind and water, either pre-
108 burial or post re-exposure, can result in loss of track preservation quality. In the latter case, even
109 if the tracks displayed anatomical fidelity at the time of re-exposure, over time their quality can
110 deteriorate.¹ The causes of relatively poor preservation (moderately large grain size, pre-burial
111 erosion and post-exposure erosion) may be difficult to distinguish, especially if it is not known
112 for how long the surface has been exposed.^{21,22}

113
114 The Bosbokfontein tracksite is located in a remote section of coastline (Figure 1), characterised
115 by aeolianite cliffs as high as 30 m. High tides and storm surges cause cliff sections to collapse,
116 whereupon loose blocks come to rest on unstable slopes or near the high-tide mark at the cliff
117 base.

118
119 One section in this region, situated ~8 km east of the Bosbokfontein site, had been dated prior
120 to our studies.¹³ Ages obtained through OSL dating produced a range of 140 ± 8 ka to 91 ± 5
121 ka. Our subsequent work has yielded several results of relevance here (in each case a five-digit
122 number is preceded by "Leic"). The closest of these lies 4.5 km east of the Bosbokfontein site,
123 where an age of 126 ± 9 ka was obtained (Leic21005).²³ Other results from sites located slightly
124 further east include 161 ± 12 ka (Leic20033), 139 ± 10 ka (Leic20031), 134 ± 9 ka (Leic21008),
125 and 109 ± 9 ka (Leic20024).²³⁻²⁵ It therefore seems likely that the Bosbokfontein track-bearing
126 surface occurs in deposits within the age range of ~161–91 ka, from MIS 6 or MIS 5.

127
128

129 **Methods**

130
131 Track measurements (in cm) included length, width, depth, pace length, and stride length.
132 External trackway width was measured in cm, representing "the distance between the footfall of
133 left and right feet, measured between the outside extremities of the tracks".²⁶ Global Positioning
134 System locality readings were taken using a hand-held Garmin 60 device. Locality data were

135 stored with the African Centre for Coastal Palaeoscience at Nelson Mandela University, to be
136 made available to researchers upon request.

137
138 The tracksite was photographed, and photogrammetric analysis performed.^{27,28} 3D models were
139 generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal
140 length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 μm). The final images were
141 rendered using CloudCompare (v.2.10-beta). The tracks could be assessed by climbing to the
142 top of the block and examining the surface, but for optimal recording, including photogrammetry
143 studies, access via a portable ladder proved useful. A DJI Mini 2 drone with an inbuilt DJI
144 camera/video was used to obtain further photographs.

145
146 Having viewed the tracksite in detail together, and examined photographs and photogrammetry
147 models, we reviewed our findings and opinions. This permitted further integration of the
148 perspectives and interpretations of Master Trackers and western-trained ichnologists.
149 Furthermore, we engaged with some of southern Africa's tracking (neoichnology) experts,
150 asking for their opinions on trackmaker identity based on photographic and photogrammetric
151 images.

152

153

154

Results

155

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

164

165 The block has come to rest at an angle, and the track-bearing surface faces seaward and
166 skywards, in a southeasterly direction. The trackway, which is ~160 cm in length, is thus aligned
167 in a southeast-northeast direction as the loose block is currently orientated, but this may be
168 subject to change following storm surges. Viewed in cross section, the block exhibits laminar

169 bedding, mostly parallel but with slight distortion in places and faint cross-bedding. Trackmaker
170 direction is inferred to be upslope with respect to the current orientation, and the trackway is
171 interpreted here with the viewer facing landwards and northwest, i.e., as if the trackmaker was
172 progressing upslope. The tracks are preserved in convex epirelief.

173
174 Eight tracks are evident (Figure 3), but the distal track occurs at the edge of the surface and is
175 partial, and the two proximal tracks are partially obscured by two longitudinal 'smudges', aligned
176 in approximately the same direction as the trackway. These are approximately 10.0–12.5 cm
177 long and 4.5–6.0 cm wide. Tracks 3 through 7 therefore offer the best potential for analysis. The
178 trackway curves gently to the left, such that its distal end is orientated ~30° leftward of that of its
179 proximal end. Faint displacement rims partially encircle some of the tracks, suggesting that the
180 tracks were registered on a slightly sloping surface.

181
182 Track lengths (5.5–6.0 cm) and track widths (5.0–5.5 cm) are relatively constant. Tracks 6 and
183 7 appear slightly wider in their distal portions. Pace length in tracks 3 through 7 is relatively
184 constant (18–20 cm). Track depth varies from 1.0 to 1.5 cm, with the distal portions of the tracks
185 slightly deeper than the proximal portions. The external trackway width appears narrow,
186 approximately 7.5 cm.

187

188

189 Discussion

190

191 **The prehistoric and historic distribution of southern African** 192 **pangolins**

193

194 The global record of pangolins extends back to the Oligocene Epoch²⁹, as reviewed by Gaudin
195 et al.³⁰ The prehistoric distribution of pangolins in southern Africa in the palaeontological record
196 is meagre for the southern Cape and western Cape: there are only three reported Cenozoic
197 fossils of pangolins from these regions.³¹ These all represent skeletal evidence, and we are not
198 aware of trace fossil records of pangolins in the global ichnology record. The three reported
199 southwestern Cape fossil records are now summarised.

200

201 Hendey reported an unstudied early Pliocene pangolin from the 'E' Quarry at Langebaanweg in
202 the Western Cape Province near the South African west coast.³² Botha and Gaudin²⁹ formally
203 described this specimen as probably ground dwelling, and possibly having engaged in a
204 quadrupedal gait similar to that of the extant giant pangolin (*Manis Smutsia gigantea*). It was
205 suggested that it may have used its forelimbs more than *MS. temminckii*. The specimen was
206 assigned to *MS. gigantea*, making it the oldest known representative of that species.²⁹

207
208 Klein et al. described a pangolin assigned to the genus *Phataginus* from the Elandsfontein Main
209 site in the Western Cape Province on South Africa's west coast, ~350 km WNW of the
210 tracksite reported on here.³³ It was described as an "extralimetary species" that contributed to
211 the exceptional faunal diversity of the site. The age of the faunal assemblage was estimated to
212 be in the range of 1.0–0.6 Ma.³³

213
214 The closest pangolin body fossil site to the Bosbokfontein site, temporally and spatially, was
215 reported by Klein from Nelson Bay Cave near Robberg, 180 km east of Bosbokfontein.³⁴ It was
216 located in Late Pleistocene deposits dating to 18–16 ka. It was described as the "Cape
217 pangolin, *Manis cf. temminckii*".³⁴

218
219 The southern African Holocene and historic record is more extensive for the ground Temminck's
220 pangolin. Possible sources include historical accounts, ethnographic records, rock art and place
221 names. Möller noted that the ground Temminck's pangolin had a wide distribution and occurred
222 all over southern Africa, and that the lack of early reports might be attributable to its nocturnal
223 habits.⁴ Skead³⁵ reported that a probable pangolin had been recorded in 1825 from the
224 Tarkastad or Queenstown area (in the current Eastern Cape Province), and that this probably
225 constituted the southernmost record for the species (~32° S). Skead³⁵ quoted Layard³⁶ that the
226 pangolin was "not now" found in the Cape Colony (i.e., south of the Orange River), perhaps
227 implying that it had occurred previously within it. Shortridge³⁷ reported that it was absent from
228 "Little Namaqualand" but noted a pangolin skin from the Upington area and records south of the
229 Orange River from Prieska and Colesberg. The 1865 type specimen is from Litakun (Latakou),
230 ~250 km north of the Orange River, and north of present-day Kuruman.³⁰ Lichtenstein³⁸ and
231 Burchell³⁹ also reported the occurrence of the pangolin in the Litakun area.

232
233 Möller provided two place names, Ietermagô and Khwaru, that refer to pangolins.⁴ Both are in
234 the Kruger National Park in South Africa's Limpopo Province, ~1,500 km northeast of the

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.

235 Bosbokfontein site. They are therefore unhelpful regarding a potential southern Cape
236 distribution range.

237
238 Rock art can provide information on prehistoric pangolin distribution, although it only implies the
239 artist's awareness that the species existed, not its occurrence in that precise locality. Despite
240 consultation with rock art experts, we are not aware of rock art depicting pangolins in southern
241 Africa other than a site in Limpopo Province (Figure 4a), where a frieze of engraved animal
242 tracks of eight species contains an engraving of a possible pangolin hindfoot track.⁴⁰ 'Fragile
243 Images', a YouTube video, includes footage of the engraving at 12 minutes and 10 seconds:
244 <https://www.youtube.com/watch?v=Ra12BKeH7Js->.

245
246 In summary, the body fossil record demonstrates the presence of pangolins in the southwestern
247 Cape region of South Africa during the Pliocene and Pleistocene. The situation is perhaps
248 analogous to that of the giraffe (*Giraffa camelopardalis*), for which there is no body-fossil
249 evidence from the Pleistocene in the southwestern Cape, but a trace fossil record confirms its
250 presence.⁴¹ The giraffe tracksite lies ~~under eight~~ less than 8 km east of the Bosbokfontein
251 tracksite. The presence of giraffe tracks implies the presence of trees and a probable savanna
252 palaeoenvironment.⁴¹ This may have been suitable for ~~Temminck's~~ the ground pangolin, with a
253 preferred habitat of savanna woodland. The record from Nelson Bay Cave³⁴ lies just within the
254 last glacial period, when aspects of this habitat might still have been present. Historical records,
255 place names and rock art do not contribute to an understanding of pangolin distribution in the
256 southwestern Cape.

257 258 **Pangolin track morphology**

259
260 Southern African neoichnologists are fortunate in having five tracking manuals to refer to.^{26,39,42-}

261 ⁴⁴ Each describes ~~Temminck's~~ ground pangolin tracks, reviewed here in order of publication
262 date. Figure 4b depicts the forefeet and hindfeet of a ~~Temminck's~~ ground pangolin.

263
264 Liebenberg described five toes on the forefeet (the first with a small nail and the central three
265 with long, strongly curved claws), and five toes on the hindfeet, each with a short nail-like claw
266 that is evident in the tracks.⁴² The body was noted to be balanced on the hindfeet when walking,
267 with the forefeet and tail held off the ground. Tracks were noted to show the rounded pads of
268 the hindfeet with four nails usually touching the ground. The occasional tail scrape and traces

269 made by the front edges of the front claws were also noted. Hindfoot tracks were reported as 6
270 cm in length.⁴²

271
272 Van den Heever et al.²⁶ also noted that both forefeet and hindfeet have five toes, and that the
273 first and fifth toes of the front feet are reduced, leaving three middle toes with long curved claws,
274 well adapted for digging. The forefoot track (when present) was noted to record the upper
275 surfaces of the three middle claws, which curl under the foot. The hindfoot was described as
276 padded and triangular, with five toes, and ~5 cm in length. Movement was described as bipedal,
277 with the forefeet seldom touching the ground. Scuff marks made by dragging the tail were
278 reportedly occasionally present.²⁶

279
280 Walker⁴³ described the pangolin as moving along on its hind legs, occasionally dropping onto all
281 fours or using the tail and forelegs for balance. Claws were noted to be prominent, and claws 2,
282 3 and 4 (presumably on the forefeet) were well-developed and recurved. Pangolins were noted
283 to walk mainly on their hind legs in an upright position. Hindfoot tracks were reportedly ~4.5 cm
284 long and wide.⁴³

285
286 Stuart and Stuart described (questionably in our opinion) a “typical tramline-like trail”, resulting
287 from the fairly wide spacing of the hindfeet, on which ~~Temminck's~~ pangolin normally
288 walks, with the short, heavily clawed forefeet held clear off the ground.⁴⁰ The forefeet were
289 noted to be used mostly for digging. Hindfoot track length of 6 cm was reported, with slight
290 intoeing. An image of a pangolin trackway was not provided.⁴⁰

291
292 Gutteridge and Liebenberg described the “interesting spoor” of the pangolin, which usually
293 moves bipedally on the rounded hindfeet.⁴⁴ These were noted to drag, as the pangolin walks in
294 a kind of shuffle. The unique marking made by the tail was also noted. Hindfoot track length was
295 reported as being 6.5 cm.⁴⁴

296
297 While there are slight differences in the focus of these descriptions, there is substantial
298 agreement, involving a predominantly bipedal gait, with hindfoot tracks 4.5–6.5 cm in size,
299 occasional forefoot traces, and occasional tail drag marks.

300
301 **Interpretation and trackmaker identity**

302

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

312
313 Other plausible trackmaker candidates included felids such as serval (*Leptailurus serval*),
314 caracal (*Caracal caracal*) and African wild cat (*Felis lybica*), the viverrids African civet
315 (*Civettictis civetta*), rusty genet (*Genetta maculata*) and large-spotted genet (*Genetta genetta*),
316 and canids such as jackals and foxes (in a soft, sandy substrate the claw impressions of canids
317 might not be preserved). There is no evidence in the Pleistocene fossil record or among extant
318 southern African species of other animals that could have made these tracks. One caveat is that
319 carnivoran size (hence track size) varied during the Pleistocene, being reportedly larger during
320 glacial phases.⁴⁵

321
322 The tracks, 5–6 cm in size, are consistent with those of both extant [Temminck's](#) pangolin and
323 serval, although a pangolin's hindfoot track length is marginally greater than those of a serval's
324 forefoot and hindfoot. *Contra* Stuart and Stuart⁴⁰, the narrow external trackway width is
325 consistent with the trackways of both [Temminck's](#) pangolin and, on occasion, serval. However,
326 the trackway widths of caracal⁴⁴ and especially civet (our own observations) are distinctly
327 broader. While the African wild cat can also produce a round track, the smaller size of its track
328 and pace length exclude it. Similar considerations exclude both species of genet. Jackal tracks,
329 in the 5 cm range, are relatively slender and more elongated (especially in the case of the
330 smaller hind foot), definitely not “soos ‘n ronde stok wat in die grond ingedruk is”. The same is
331 true of fox tracks (Cape and Bat-eared), with the front foot of the Bat-eared fox (*Octocyon*
332 *megalotis*) measuring but 4.5 cm⁴⁴, and the hind foot even smaller,

333
334 Whereas [Temminck's ground](#) pangolin hindfoot tracks are triangular (with the apex pointing
335 backwards, away from the direction of travel) and well-preserved serval tracks exhibit pad and
336 digit impressions, none of these features might be present in Cape south coast aeolianites. This

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

Commented [A6]: Proximally?

343
344 The inference of trackmaker direction is based on some tracks appearing slightly wider in their
345 distal portions, the overall indentation pattern, and the orientation of the 'smudges'. These
346 impressions at the proximal-distal end of the trackway and in line with it are consistent with the
347 scuff-marks made by the pangolin tail (Figure 5a), and less consistent with tail traces made by
348 servals or other potential trackmakers.

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

349
350 Pace length is consistently 18–20 cm, and therefore the distance between tracks is about three
351 times the size of each track. While a pangolin sometimes walks with a shuffle and a relatively
352 short pace length (Figure 5b) it can also walk with a longer pace length, as in the Bosbokfontein
353 trackway and in Figure 6a.

354
355 Another potential distinguishing factor involves the relative lightness of the gait. A serval, like all
356 cats, walks or runs lightly. A [Temminck's ground](#) pangolin, bulky, slower and bipedal, has a more
357 ponderous gait. Therefore pangolin tracks tend to be deeper than serval tracks. While this is not
358 an absolute criterion, the depth of the tracks in question (1.0–1.5 cm), bolstered by the notion
359 of the round end of a stick poked into the ground, suggests a pangolin trackmaker.

360
361 Opinions from expert southern African trackers were most helpful. ~~We approached Opinions~~
362 ~~from expert southern African trackers were most helpful.~~ We approached [anonymised],
363 [anonymised], [anonymised], [anonymised], and [anonymised].

364 Their feedback was measuredly supportive. None thought the tracks were inconsistent with
365 those of a pangolin. [anonymised] provided a confident assessment:

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

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

372 [anonymised] provided a detailed comment:

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

380
381 In the less likely scenario that the tracks were registered by a serval, a 'direct register' would be
382 inferred whereby the hindfoot was placed precisely on top of the forefoot track. (Stealth hunters
383 often employ this economical, sound-minimising foot-placement pattern.) From a prehistoric
384 distribution perspective, a serval trackmaker is plausible. Avery reported Pliocene serval records
385 from Gauteng [Pp](#)rovince, and Pleistocene and Holocene records from, *inter alia*, the
386 southwestern Cape.³¹

387
388 Our overall conclusion is that the trackway cannot be attributed with absolute certainty to any
389 trackmaker. However, it is most consistent with a [Temminck'sground](#) pangolin trackmaker,
390 distinctly more than a serval or any other candidate species. The Pleistocene distribution range
391 of [Temminck'sthe-ground](#) pangolin included the southwestern Cape, in a situation that is
392 analogous to that of the giraffe, the preferred habitat of both species being savanna woodland.
393 Such habitat might have been present on the now-submerged Palaeo-Agulhas Plain.⁴⁶

394
395

396 Conclusions

397
398 A [Temminck'sground](#) pangolin probably walked across a soft, sandy dune surface near the
399 margin of the Palaeo-Agulhas Plain, most likely during MIS_6 or MIS 5, leaving a trackway. Eight
400 tracks and, suggestively, two tail traces are preserved and amenable to interpretation. For
401 many, fossil trackways are to body fossils what movies are to photographs, and evocative

402 trackways tell a story of something that might have walked by yesterday, or over 100,000 years
403 ago.

404
405 While the loose block containing the track-bearing surface is too large to physically recover, the
406 photogrammetry data can be used to make a replica of the trackway, which could be exhibited
407 in the Blombos Museum of Archaeology in Still Bay. What to date is probably the first reported
408 pangolin trackway in the world could thus serve to draw attention to the plight of pangolins
409 worldwide.

410
411 In a recent publication we described the advantages of collaboration between indigenous
412 Master Trackers and western-trained ichnologists in interpreting Pleistocene trackways.⁴⁷ The
413 title of a book by Liebenberg specified that the art of tracking was “the origin of science”.⁴⁸ In our
414 experience, the outcomes and conclusions that result are richer for integrating ancient and
415 modern science.

416
417

418 **Acknowledgements**

419
420 We thank Linda Helm, Louis Liebenberg, Christina Mars, Richard McKibbin, Andrew Paterson,
421 Wendy Panaino, Renée and Niekie Rust, Chris and Mathilde Stuart, Alex Van den Heever, and
422 Richard Webb for their assistance.

423
424 The data supporting the results of this study are available upon request to the corresponding
425 author.

426
427

428 **References**

- 429
- 430 1. AUTHOR
 - 431
 - 432 2. Gaudin T. Pholidota. In: Werdelin L, Sanders WJ, editors. Cenozoic Mammals of Africa.
433 Berkeley: University of California Press; 2010. p. 599–602.

434

- 435 3. Gu T-T, Wu H, Yang F, Gaubert P, Heighton SP, Fu Y, et al. Genomic analysis reveals a
436 cryptic pangolin species. *Proc Natl Acad Sci USA*. 2023;120(40):e2304096120.
437 <https://doi.org/10.1073/pnas.2304096120>
438
- 439 4. Möller LA. *Of the Same Breath: Indigenous Animal and Place Names*. Sun Media
440 Bloemfontein (Pty) Ltd.: Bloemfontein; 2017. <https://doi.org/10.18820/9781928424031>
441
- 442 5. IUCN Red List of Threatened Species. 2023.
443 <https://www.iucnredlist.org/search?query=Pangolins&searchType=species>
444
- 445 6. D'Cruze N, Assou D, Coulthard E, Norrey J, Megson D, Macdonald DW, et al. Snake oil
446 and pangolin scales: insights into wild animal use at "Marché des Fétiches" traditional
447 medicine market, Togo. *Nat Conserv*. 2020;39:45–71.
448 <https://doi.org/10.3897/natureconservation.39.47879>
449
- 450 7. Ingram DJ. 400,000 African pangolins are hunted for meat every year – why it's time to
451 act. *The Conversation Africa* 2019. [https://theconversation.com/400-000-african-](https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540)
452 [pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540](https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540)
453
- 454 8. Malan JA. *Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group) –*
455 *South African Committee for Stratigraphy Lithostratigraphic Series 8*. Pretoria:
456 Department of Mineral and Energy Affairs;1989.
457
- 458 9. Malan JA. 1990. *The stratigraphy and sedimentology of the Bredasdorp Group,*
459 *Southern Cape Province, South Africa*. MSc thesis. Cape Town: University of Cape
460 Town; 1990.
461
- 462 10. Roberts DL, Cawthra HC, Musekiwa C. Dynamics of late Cenozoic aeolian deposition
463 along the South African coast: a record of evolving climate and ecosystems. In: Martini
464 IP, Wanless HR, editors. *Sedimentary Coastal Zones from High to Low Latitudes:*
465 *Similarities and Differences*. Special Publication of the Geological Society of London
466 2013:388. p. 353–387 <http://dx.doi.org/10.1144/SP388.11>
467
- 468 11. Brooke B. The distribution of carbonate eolianite. *Earth-Sci Rev*. 2001;55:135–164.
469 [https://doi.org/10.1016/S0012-8252\(01\)00054-X](https://doi.org/10.1016/S0012-8252(01)00054-X)

- 470
471 12. Marean CW, Cowling RC, Franklin J. The Palaeo-Agulhas Plain: temporal and spatial
472 variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic
473 Region. In: Cleghorn N, Potts AJ, Cawthra HC, editors. The Palaeo-Agulhas Plain: A
474 Lost World and Extinct Ecosystem. *Quat Sci Rev.* 2020;235:106161.
475 <https://doi.org/10.1016/j.quascirev.2019.106161>
476
477 13. Carr AS, Bateman MD, Roberts DL, Murray-Wallace CV, Jacobs Z, Holmes PJ. The last
478 interglacial sea-level high stand on the southern Cape coastline of South Africa. *Quat*
479 *Res.* 2010;73:351–363. <https://doi.org/10.1016/j.yqres.2009.08.006>
480
481 14. Roberts DL, Bateman MD, Murray-Wallace CV, Carr AS, Holmes PJ. Last Interglacial
482 fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South
483 Africa. *Palaeogeogr Palaeoclimatol Palaeoecol.* 2008;257(3):261–279.
484 <https://doi.org/10.1016/j.palaeo.2007.08.005>
485
486 15. Bateman MD, Carr AS, Dunajko AC, Holmes PJ, Roberts DL, McLaren SJ, et al. The
487 evolution of coastal barrier systems: a case study of the Middle-Late Pleistocene
488 Wilderness barriers, South Africa. *Quat Sci Rev.* 2011;30:63–81.
489 <https://doi.org/10.1016/j.quascirev.2010.10.003>
490
491 16. Cawthra HC, Jacobs Z, Compton JS, Fisher EC, Karkanis P, Marean CW. Depositional
492 and sea-level history from MIS 6 (Termination II) to MIS 3 on the southern continental
493 shelf of South Africa. *Quat Sci Rev.* 2018;181:156–172.
494 <https://doi.org/10.1016/j.quascirev.2017.12.002>
495
496 17. Roberts DL, Karkanis P, Jacobs Z, Marean CW, Roberts RG. Melting ice sheets
497 400,000 yr ago raised sea level by 13 m: past analogue for future trends. *Earth Planet*
498 *Sci Lett.* 2012;357–358:226–237. <https://doi.org/10.1016/j.epsl.2012.09.006>
499
500 18. Carr AS, Bateman MD, Cawthra HC, Sealy J. First evidence for onshore marine isotope
501 stage 3 aeolianite formation on the southern Cape coastline of South Africa. *Mar Geol.*
502 2019;407:1–15. <https://doi.org/10.1016/j.margeo.2018.10.003>
503

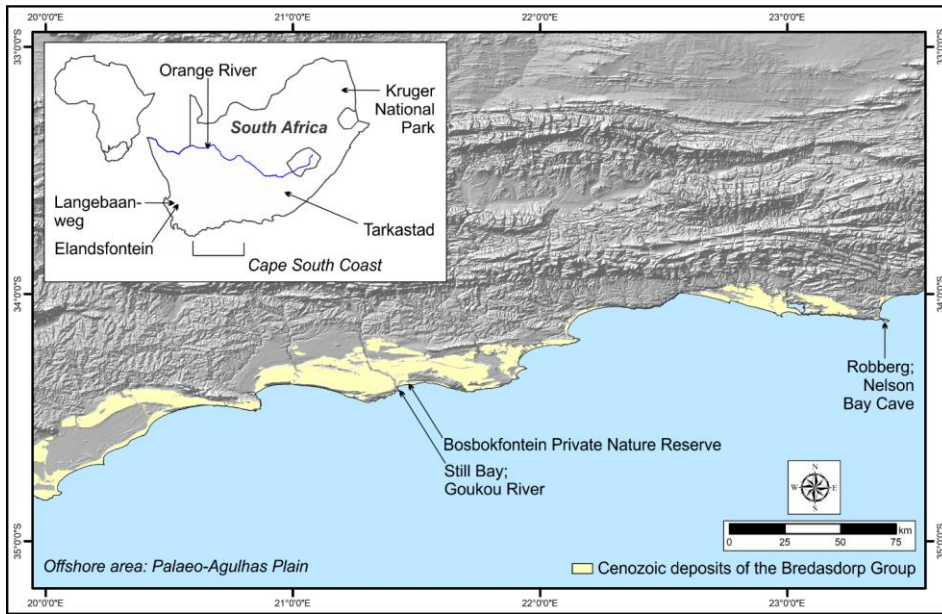
- 504 19. Roberts D, Cole K. Vertebrate trackways in Late Cenozoic coastal eolianites, South
505 Africa. Geological Society of America Abstracts with Programs, XVI INQUA Congress.
506 2003:70(3);196.
507
- 508 20. Belvedere M, Farlow JO. A numerical scale for quantifying the quality of preservation of
509 vertebrate tracks. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur tracks: the
510 next steps. Bloomington and Indianapolis: Indiana University Press; 2016. p. 92–99.
511
- 512 21. Falkingham PL, Gatesy SM. Discussion: defining the morphological quality of fossil
513 footprints. Problems and principles of preservation in tetrapod ichnology with examples
514 from the Palaeozoic to the present by Lorenzo Marchetti et al. Earth-Sci Rev.
515 2020;208:103320. <https://doi.org/10.1016/j.earscirev.2020.103320>
516
- 517 22. Gatesy SM, Falkingham PL. Neither bones nor feet: track morphological variation and
518 'preservation quality'. J. Vertebr. Paleontol. 2017;37:e1314298.
519 <https://doi.org/10.1080/02724634.2017.1314298>
520
- 521 23. AUTHOR ET AL.
522
- 523 24. AUTHOR ET AL.
524
- 525 25. AUTHOR ET AL.
526
- 527 26. Van den Heever A, Mhlongo R, Benadie K. Tracker Manual – a Practical Guide to Animal
528 Tracking in Southern Africa. Struik Nature: Cape Town; 2017.
529
- 530 27. Matthews NA, Noble TA, Breithaupt BH. Close-range photogrammetry for 3-D ichnology:
531 the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors.
532 Dinosaur Tracks: The Next Steps. Bloomington: Indiana University Press; 2016. p. 28–
533 55.
534
- 535 28. Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, et al. 2018.
536 A standard protocol for documenting modern and fossil ichnological data. Palaeontology,
537 2018;61(4):469-480. <https://doi.org/10.1111/pala.12373>
538

- 539 29. Botha J, Gaudin T. An Early Pliocene pangolin (Mammalia; Pholidota) from
540 Langebaanweg, South Africa. *J Vertebr Paleontol.* 2007;27:484–491.
- 541 30. Gaudin TJ, Emry RJ, Wible JR. The phylogeny of living and extinct pangolins
542 (Mammalia, Pholidota) and associated taxa: a morphology based analysis. *J Mammal.*
543 2009;16:235–305.
- 544 31. Avery DM. *A Fossil History of Southern African Land Mammals.* Cambridge University
545 Press: Cambridge; 2019. <https://doi.org/10.1017/9781108647243>
- 546 32. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry,
547 Langebaanweg, South Africa, and a reinterpretation of their geological context. *Ann S Afr*
548 *Mus.* 1981;84(1):1–104.
- 549 33. Klein RG, Avery G, Cruz-Uribe K, Steele TE. The mammalian fauna associated with an
550 archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape
551 Province, South Africa. *J Hum Evol.* 2007;52:164–186.
552 <https://doi.org/10.1016/j.jhevol.2006.08.006>
- 553 34. Klein RG. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province,
554 South Africa): its implications for megafaunal extinctions and environmental and cultural
555 change. *Quat Res.* 1972;2:135–142.
- 556 35. Skead CJ. *Historical Mammal incidence in the Cape Province Vol. I. Western Cape and*
557 *Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei.* Chief Directorate, Nature and
558 Environmental Conservation of the Provincial Administration of the Cape of Good Hope:
559 Cape Town; 1987.
- 560 36. Layard EL. *Catalogue of the specimens in the collection of the South African Museum.*
561 *Part 1. The Mammalia.* Saul Solomon and Co.: Cape Town; 1861.
- 562 37. Shortridge GC. Field notes on the first and second expeditions of the Cape Museum's
563 mammal survey of the Cape Province; and descriptions of some new subgenera and
564 subspecies. *Ann S Afr Mus.* 1942;36:27–99.
- 565 38. Lichtenstein WHC. *Travels in Southern Africa, in the years 1803, 1804, 1805 and 1806.*
566 *Vol. 2 (Translation by Anne Plumtre).* Van Riebeeck Society No. 11: Cape Town; 1815.

- 576
577 39. Burchell WJ. Travels in the Interior of Southern Africa. Vol. 2. Longman, Hurst, Rees,
578 Orme, Brown, and Green: London; 1824.
- 579
580 40. Stuart C, Stuart T. 2019. A Field Guide to the Tracks and Signs of Southern and East
581 African Wildlife. Struik Nature: Cape Town; 2019.
- 582
583 41. AUTHOR ET AL.
- 584
585 42. Liebenberg L. 2000. A Photographic Guide to Tracks and Tracking in Southern Africa.
586 Struik Publishers: Cape Town; 2000.
- 587
588 43. Walker C. Signs of the Wild – A Field Guide to the Spoor & Signs of the Mammals of
589 Southern Africa. Struik Nature: Cape Town; 2018.
- 590
591 44. Gutteridge L, Liebenberg L. Mammals of Southern Africa and their Tracks and Signs.
592 Jacana Media (Pty) Limited: Auckland Park; 2021.
- 593
594 45. Klein RG. Carnivore size and Quaternary climatic change in Southern Africa. Quat Res.
595 1986;26:153–170.
- 596
597 46. Cowling RM, Potts AJ, Franklin J, Midgley GF, Engelbrecht F, Marean CW. Describing a
598 drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the
599 Palaeo-Agulhas Plain. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-
600 Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235:105866.
601 <https://doi.org/10.1016/j.quascirev.2019.105866>
- 602
603 47. AUTHOR ET AL.
- 604
605 48. Liebenberg L. The Art of Tracking – the Origin of Science. David Phillip: Claremont,
606 South Africa; 1990.

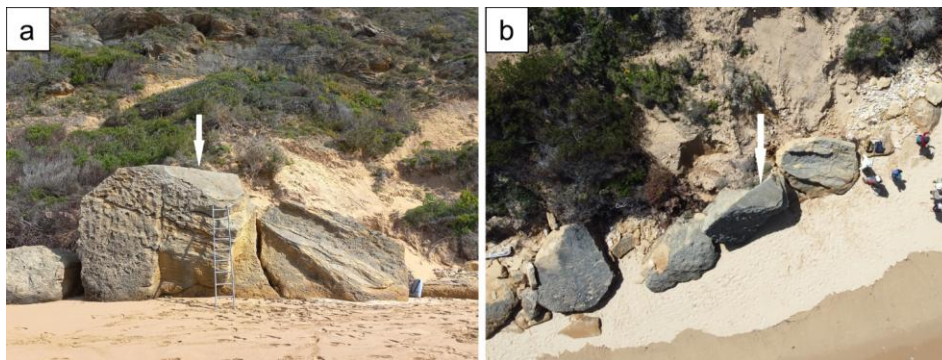
607
608

Figures captions



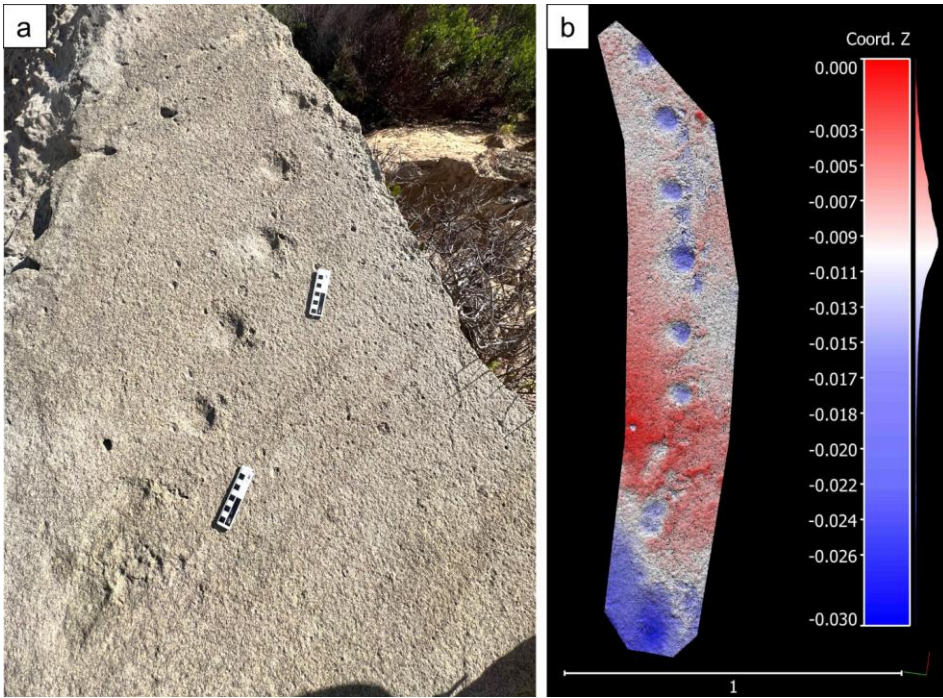
609
610 **Figure 1:** Map of South Africa's coast, indicating the Bosbokfontein site, the extent of Pleistocene
611 deposits, and sites mentioned in the text.

612

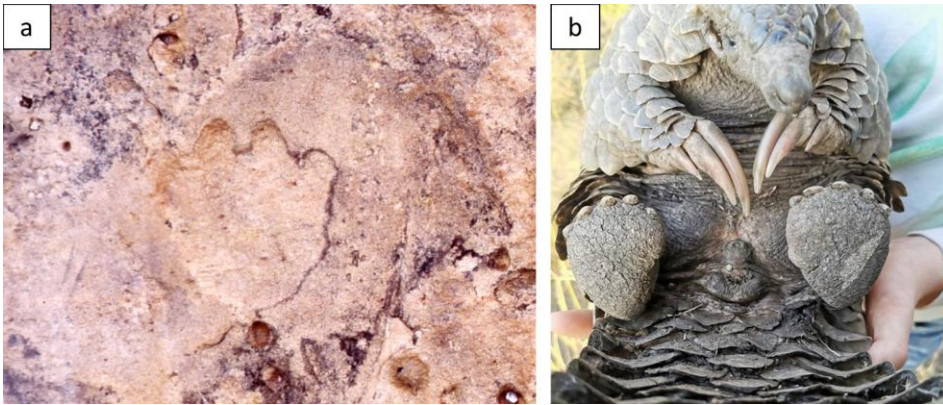


613
614 **Figure 2:** (a) The large loose block containing the purported pangolin trackway on its upper surface; the
615 ladder length is 410 cm. (b) The track-bearing block, viewed from above using a drone; adult human
616 figures for scale. Arrows point to the track-bearing surface.

617

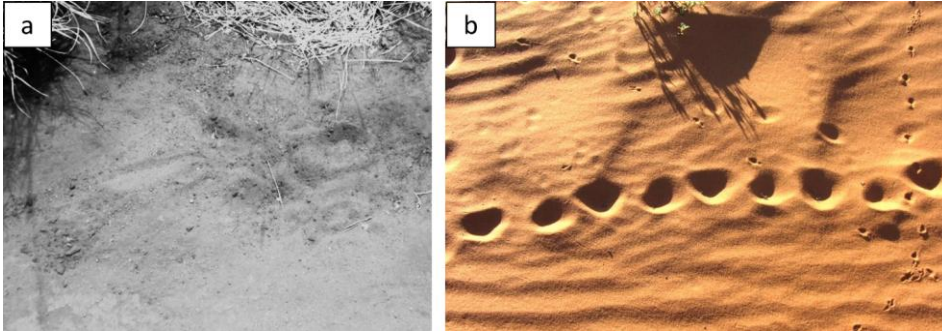


618
 619 **Figure 3:** (a) The purported pangolin trackway; scale bars = 10 cm. (b) Photogrammetry colour mesh of
 620 the trackway; vertical and horizontal scales are in [metres](#).
 621



622

623 **Figure 4:** (a) [A+R](#)ock engraving of a probable pangolin track in Limpopo [P](#)rovince, [S](#)outh Africa;
624 reproduced with permission from Chris and Mathilde Stuart. (b) The forefeet and hindfeet of a [ground](#)
625 [Temminck's](#) pangolin, viewed from below; reproduced with permission from [anonymised].
626



627
628 **Figure 5:** (a) Scuff marks registered by the tail of a [ground-Temminck's](#) pangolin; reproduced with
629 permission from Bruno Nebe. (b) [A+T](#)rackway of a [Temminck'sground](#) pangolin, showing (in this case) a
630 short pace length; reproduced with permission from [anonymised].
631



632
633 **Figure 6:** A [Temminck'sground](#) pangolin walking with a longer pace length; reproduced with permission
634 from [anonymised].

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

1 **A PROBABLE PLEISTOCENE PANGOLIN TRACKWAY FROM SOUTH** 2 **AFRICA'S CAPE SOUTH COAST**

Commented [A1]: Authors?

3 4 **Abstract**

5
6 A fossil trackway, attributed to a probable pangolin trackmaker, has been identified on a
7 Pleistocene aeolianite surface of the Waenhuiskrans Formation in the Bosbokfontein Private
8 Nature Reserve on South Africa's Cape south coast. The trackway comprises eight tracks and
9 two probable tail traces. This appears to be the first description of a pangolin trackway in the
10 global fossil record. The trackway was probably registered during Marine Isotope Stage 6 or 5.
11 Trackway assessment and interpretation involved the integration of indigenous African and
12 western-based ichnological approaches, leading to a reasonably confident conclusion on
13 probable trackmaker identity. Alternative trackmakers (felids, viverrids and canids) were
14 considered, but excluded or regarded as less likely candidates. There are three Cenozoic body
15 fossil records of pangolins from the southwestern Cape. Only the ground pangolin currently
16 occurs in southern Africa. All pangolin species are threatened or endangered.

17 18 **Significance of the main findings**

- 19
20 - A Pleistocene probable pangolin trackway has been identified east of Still Bay.
21 - The identification involved integrating indigenous African and western-based ichnological
22 approaches.
23 - This appears to be the first known fossilised pangolin trackway.
24 - The trackway comprises eight tracks and two probable tail traces.
25 - This discovery could draw attention to the plight of pangolins.

26
27 **KEYWORDS:** pangolin, fossil tracks, aeolianites, Cape south coast, Pleistocene

28 *Figures inserted at the bottom of document.*
29

Introduction

30
31
32 Through the Cape south coast ichnology project over 350 Pleistocene vertebrate ichnosites
33 have been documented along a 350 km stretch of South African coastline. The majority (80%)
34 represent mammal tracks and traces.¹ Until now, no pangolin ichnofossils have been identified,
35 either on the Cape south coast or, to the best of our knowledge, anywhere in the world. Here we
36 describe a trackway on an aeolianite (cemented dune) palaeosurface in the Bosbokfontein
37 Nature Reserve, east of Still Bay on the Cape south coast. The lines of evidence converge on a
38 pangolin as the probable trackmaker.

39
40 The order Pholidota contains a single family, Manidae, with eight established, extant pangolin
41 species from sub-Saharan Africa, India, southern China and southeast Asia to the Philippines.²
42 A cryptic ninth Asian species was added in 2023.³ Four of these species occur in Africa - two
43 are arboreal, and two (the ground pangolin and the giant pangolin) are ground-dwelling. The
44 ground pangolin (*Manis temminckii* or *Smutsia temminckii*) is also known as Temminck's
45 pangolin, the Cape pangolin, or the scaly anteater, and is the only pangolin species to currently
46 occur in southern Africa.² In the Ju/'hoan language the ground pangolin is known as 'n#hòqò',
47 and in Afrikaans as the 'ietermagog'. The latter is probably of Bantu or Tswana derivation.⁴

48
49 All species of extant pangolin are threatened by poaching and habitat loss, and all are classified
50 as vulnerable, endangered, or critically endangered.⁵ Pangolin meat is regarded as a delicacy,
51 and pangolin scales are used in traditional medicines.⁶ There is evidence that pangolins are
52 among the most trafficked wild animals on Earth, and 400,000 African pangolins are estimated
53 to be hunted for their meat annually.⁷

54
55 The tracks described here were initially identified in 2018 by Renée Rust and family. The tracks
56 are evident on the surface of a large fallen aeolianite block. The putative trackmaker remained
57 enigmatic until our joint analysis in 2023. Two of us (anonymised) are indigenous Ju/'hoansi
58 San Master Trackers, and had an immediate, strong sense of what was being examined. This
59 presented the opportunity for indigenous and modern scientific tracking exponents to engage in
60 a productive exchange of ideas, combining culturally honed and experientially grounded
61 intuitions with modern assessment techniques. This collaborative, inter-disciplinary approach
62 has allowed us to arrive at a shared conclusion on probable trackmaker identity.

63

Commented [A2]: I would omit this here

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

67
68

69 Geological context

70

71 Pleistocene carbonate aeolianites (~~cemented dunes~~) of the Waenhuiskrans Formation⁸, part of
72 the Neogene Bredasdorp Group⁹, are exposed along portions of the Cape south coast of South
73 Africa, and have provided evidence for palaeo-shorelines and palaeo-coastal dune activity.¹⁰

74 Carbonate aeolianites are consolidated coastal rock formation consisting of at least partially
75 lithified calcareous wind-blown sand. Globally, aeolianites are fairly common in mid-latitude
76 coastal regions between 20° and 40°.¹¹ Aeolianite surfaces preserve a record of the passage of
77 trackmakers when they comprised unconsolidated sand. Throughout the Pleistocene, global
78 sea-level change meant that the Cape south coast landscape was dynamic. Vertebrate
79 ichnosites encountered on these palaeosurfaces would have been situated at the margin of the
80 Paleo-Agulhas Plain, most of which is presently submerged, but at times sea-level oscillations
81 would have exposed the entire Plain.¹² In contrast, sea level was 6–8 metres higher than at
82 present at the height of the Marine Isotope Stage (MIS) 5e marine transgression at ~126 ka.¹³

83

84 Optically Stimulated Luminescence (OSL) dating of onshore aeolianites has shown that most
85 date to MIS 5 and late MIS 6.¹³⁻¹⁶ MIS 11 deposits¹⁷ and MIS 3 deposits¹⁸ have also been
86 identified, with a resulting age range of dated deposits presently spanning ~400–35 ka. Roberts
87 and Cole provided an explanation for the profusion of ichnosites, postulating a combination of a
88 cohesive moulding agent (moist sand), rapid track burial (facilitated by high sedimentation
89 rates), rapid lithification (via partial solution and re-precipitation of bioclasts), and finally re-
90 exposure of track-bearing surfaces through shoreline erosion.¹⁹

91

92 In general, the grain size of the substrate inversely influences the preservation quality of fossil
93 tracks. In Cape south coast Pleistocene deposits, tracks made on moderately coarse-grained
94 dune surfaces tend to show poor to intermediate preservation quality, certainly inferior to that
95 seen elsewhere in the world, particularly clay or mud substrates on cave floors. Belvedere and
96 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 aerielly 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

97 and 3 represents a track of exceptional quality.²⁰ It is unusual for tracks within the Cape south
98 coast deposits to rise above 2 on this scale.

99
100 Active shoreline erosion causes coastal cliffs to fragment or collapse, sometimes exposing new
101 ichnosites, while known sites deteriorate in quality or loose blocks slump into the ocean.
102 Ichnosites are thus ephemeral. The taphonomic erosive effects of wind and water, either pre-
103 burial or post re-exposure, can result in loss of track preservation quality. In the latter case, even
104 if the tracks displayed anatomical fidelity at the time of re-exposure, over time their quality can
105 deteriorate.¹ The causes of relatively poor preservation (moderately large grain size, pre-burial
106 erosion and post-exposure erosion) may be difficult to distinguish, especially if it is not known
107 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?

108
109 The Bosbokfontein tracksite is located in a remote section of coastline (Figure 1), characterised
110 by aeolianite cliffs as high as 30 m. High tides and storm surges cause cliff sections to collapse,
111 whereupon loose blocks come to rest on unstable slopes or near the high-tide mark at the cliff
112 base.

113
114 One section in this region, situated ~8 km east of the Bosbokfontein site, had been dated prior
115 to our studies.¹³ Ages obtained through OSL dating produced a range of 140 ± 8 ka to 91 ± 5
116 ka. Our subsequent work has yielded several results of relevance here (in each case a five-digit
117 number is preceded by "Leic"). The closest of these lies 4.5 km east of the Bosbokfontein site,
118 where an age of 126 ± 9 ka was obtained (Leic21005).²³ Other results from sites located slightly
119 further east include 161 ± 12 ka (Leic20033), 139 ± 10 ka (Leic20031), 134 ± 9 ka (Leic21008),
120 and 109 ± 9 ka (Leic20024).²³⁻²⁵ It therefore seems likely that the Bosbokfontein track-bearing
121 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?

124 Methods

125
126 Track measurements (in cm) included length, width, depth, pace length, and stride length.
127 External trackway width was measured in cm, representing "the distance between the footfall of
128 left and right feet, measured between the outside extremities of the tracks".²⁶ Global Positioning
129 System locality readings were taken using a hand-held Garmin 60 device. Locality data were

Commented [A9]: repeated

130 stored with the African Centre for Coastal Palaeoscience at Nelson Mandela University, to be
131 made available to researchers upon request.

132
133 The tracksite was photographed, and photogrammetric analysis performed.^{27,28} 3D models were
134 generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal
135 length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 µm). The final images were
136 rendered using CloudCompare (v.2.10-beta). The tracks could be assessed by climbing to the
137 top of the block and examining the surface, but for optimal recording, including photogrammetry
138 studies, access via a portable ladder proved useful. A DJI Mini 2 drone with an inbuilt DJI
139 camera/video was used to obtain further photographs.

140
141 Having viewed the tracksite in detail together, and examined photographs and photogrammetry
142 models, we reviewed our findings and opinions. This permitted further integration of the
143 perspectives and interpretations of Master Trackers and western-trained ichnologists.
144 Furthermore, we engaged with some of southern Africa's tracking (neoichnology) experts,
145 asking for their opinions on trackmaker identity based on photographic and photogrammetric
146 images.

147
148

149 Results

150
151 The tracksite is located within the Bosbokfontein Private Nature Reserve, approximately 6.5 km
152 east of the mouth of the Goukou River and the community of Still Bay. It occurs on the upper
153 surface of a large *ex situ* block, which has tumbled down the vegetated slopes from cliffs above
154 and come to rest above the high-tide mark (Figure 2). The maximum length of the block is ~7 m,
155 with a maximum thickness of 4.5 m. However, the approximately triangular-shaped track-
156 bearing surface is smaller, with maximum dimensions of ~200 x 180 cm. Slight deterioration in
157 the preservation quality of the tracks and trackway occurred since identification in 2018, but
158 assessment and interpretation of tracks and trackway morphology remained feasible.

159
160 The block has come to rest at an angle, and the track-bearing surface faces seaward and
161 skywards, in a southeasterly direction. The trackway, which is ~160 cm in length, is thus aligned
162 in a southeast-northeast direction as the loose block is currently orientated, but this may be
163 subject to change following storm surges. Viewed in cross section, the block exhibits laminar

164 bedding, mostly parallel but with slight distortion in places and faint cross-bedding. Trackmaker
165 direction is inferred to be upslope with respect to the current orientation, and the trackway is
166 interpreted here with the viewer facing landwards and northwest, i.e., as if the trackmaker was
167 progressing upslope. The tracks are preserved in convex epirelief.

168
169 Eight tracks are evident (Figure 3), but the distal track occurs at the edge of the surface and is
170 partial, and the two proximal tracks are partially obscured by two longitudinal 'smudges', aligned
171 in approximately the same direction as the trackway. These are approximately 10.0–12.5 cm
172 long and 4.5–6.0 cm wide. Tracks 3 through 7 therefore offer the best potential for analysis. The
173 trackway curves gently to the left, such that its distal end is orientated ~30° leftward of that of its
174 proximal end. Faint displacement rims partially encircle some of the tracks, suggesting that the
175 tracks were registered on a slightly sloping surface.

176
177 Track lengths (5.5–6.0 cm) and track widths (5.0–5.5 cm) are relatively constant. Tracks 6 and 7
178 appear slightly wider in their distal portions. Pace length in tracks 3 through 7 is relatively
179 constant (18–20 cm). Track depth varies from 1.0 to 1.5 cm, with the distal portions of the tracks
180 slightly deeper than the proximal portions. The external trackway width appears narrow,
181 approximately 7.5 cm.

182
183

184 Discussion

185

186 The prehistoric and historic distribution of southern African 187 pangolins

188

189 The global record of pangolins extends back to the Oligocene Epoch²⁹, as reviewed by Gaudin
190 et al.³⁰ The prehistoric distribution of pangolins in southern Africa in the palaeontological record
191 is meagre for the southern Cape and western Cape: there are only three reported Cenozoic
192 fossils of pangolins from these regions.³¹ These all represent skeletal evidence, and we are not
193 aware of trace fossil records of pangolins in the global ichnology record. The three reported
194 southwestern Cape fossil records are now summarised.

195

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?

196 Hendey reported an unstudied early Pliocene pangolin from the 'E' Quarry at Langebaanweg in
197 the Western Cape Province near the South African west coast.³² Botha and Gaudin²⁹ formally
198 described this specimen as probably ground dwelling, and possibly having engaged in a
199 quadrupedal gait similar to that of the extant giant pangolin (*Manis gigantea*). It was suggested
200 that it may have used its forelimbs more than *M. temminckii*. The specimen was assigned to *M.*
201 *gigantea*, making it the oldest known representative of that species.²⁹

202
203 Klein et al. described a pangolin assigned to the genus *Phataginus* from the Elandsfontein Main
204 site in the Western Cape Province on South Africa's west coast, ~350 km WNW of the tracksite
205 reported on here.³³ It was described as an "extralimital species" that contributed to the
206 exceptional faunal diversity of the site. The age of the faunal assemblage was estimated to be in
207 the range of 1.0–0.6 Ma.³³

208
209 The closest pangolin body fossil site to the Bosbokfontein site, temporally and spatially, was
210 reported by Klein from Nelson Bay Cave near Robberg, 180 km east of Bosbokfontein.³⁴ It was
211 located in Late Pleistocene deposits dating to 18–16 ka. It was described as the "Cape
212 pangolin, *Manis* cf. *temminckii*".³⁴

213
214 The southern African Holocene and historic record is more extensive for the ground pangolin.
215 Possible sources include historical accounts, ethnographic records, rock art and place names.
216 Möller noted that the ground pangolin had a wide distribution and occurred all over southern
217 Africa, and that the lack of early reports might be attributable to its nocturnal habits.⁴ Skead³⁵
218 reported that a probable pangolin had been recorded in 1825 from the Tarkastad or
219 Queenstown area (in the current Eastern Cape Province), and that this probably constituted the
220 southernmost record for the species (~32° S). Skead³⁵ quoted Layard³⁶ that the pangolin was
221 "not now" found in the Cape Colony (i.e., south of the Orange River), perhaps implying that it
222 had occurred previously within it. Shortridge³⁷ reported that it was absent from "Little
223 Namaqualand" but noted a pangolin skin from the Upington area and records south of the
224 Orange River from Prieska and Colesberg. The 1865 type specimen is from Litakun (Latakou),
225 ~250 km north of the Orange River, and north of present-day Kuruman.³⁰ Lichtenstein³⁸ and
226 Burchell³⁹ also reported the occurrence of the pangolin in the Litakun area.

227
228 Möller provided two place names, Ietermagô and Khwaru, that refer to pangolins.⁴ Both are in
229 the Kruger National Park in South Africa's Limpopo Province, ~1,500 km northeast of the

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

230 Bosbokfontein site. They are therefore unhelpful regarding a potential southern Cape
231 distribution range.

232
233 Rock art can provide information on prehistoric pangolin distribution, although it only implies the
234 artist's awareness that the species existed, not its occurrence in that precise locality. Despite
235 consultation with rock art experts, we are not aware of rock art depicting pangolins in southern
236 Africa other than a site in Limpopo Province (Figure 4a), where a frieze of engraved animal
237 tracks of eight species contains an engraving of a possible pangolin hindfoot track.⁴⁰ 'Fragile
238 Images', a YouTube video, includes footage of the engraving at 12 minutes and 10 seconds:
239 <https://www.youtube.com/watch?v=Ra12BKeH7Js> .

240
241 In summary, the body fossil record demonstrates the presence of pangolins in the southwestern
242 Cape region of South Africa during the Pliocene and Pleistocene. The situation is perhaps
243 analogous to that of the giraffe (*Giraffa camelopardalis*), for which there is no body-fossil
244 evidence from the Pleistocene in the southwestern Cape, but a trace fossil record confirms its
245 presence.⁴¹ The giraffe tracksite lies under eight km east of the Bosbokfontein tracksite. The
246 presence of giraffe tracks implies the presence of trees and a probable savanna
247 palaeoenvironment.⁴¹ This may have been suitable for the ground pangolin, with a preferred
248 habitat of savanna woodland. The record from Nelson Bay Cave³⁴ lies just within the last glacial
249 period, when aspects of this habitat might still have been present. Historical records, place
250 names and rock art do not contribute to an understanding of pangolin distribution in the
251 southwestern Cape.

252

253 **Pangolin track morphology**

254

255 Southern African neoichnologists are fortunate in having five tracking manuals to refer to.^{26,39,42-}

256 ⁴⁴ Each describes ground pangolin tracks, reviewed here in order of publication date. Figure 4b
257 depicts the forefeet and hindfeet of a ground pangolin.

258

259 Liebenberg described five toes on the forefeet (the first with a small nail and the central three
260 with long, strongly curved claws), and five toes on the hindfeet, each with a short nail-like claw
261 that is evident in the tracks.⁴² The body was noted to be balanced on the hindfeet when walking,
262 with the forefeet and tail held off the ground. Tracks were noted to show the rounded pads of
263 the hindfeet with four nails usually touching the ground. The occasional tail scrape and traces

264 made by the front edges of the front claws were also noted. Hindfoot tracks were reported as 6
265 cm in length.⁴²

266
267 Van den Heever et al.²⁶ also noted that both forefeet and hindfeet have five toes, and that the
268 first and fifth toes of the front feet are reduced, leaving three middle toes with long curved claws,
269 well adapted for digging. The forefoot track (when present) was noted to record the upper
270 surfaces of the three middle claws, which curl under the foot. The hindfoot was described as
271 padded and triangular, with five toes, and ~5 cm in length. Movement was described as bipedal,
272 with the forefeet seldom touching the ground. Scuff marks made by dragging the tail were
273 reportedly occasionally present.²⁶

274
275 Walker⁴³ described the pangolin as moving along on its hind legs, occasionally dropping onto all
276 fours or using the tail and forelegs for balance. Claws were noted to be prominent, and claws 2,
277 3 and 4 (presumably on the forefeet) were well-developed and recurved. Pangolins were noted
278 to walk mainly on their hind legs in an upright position. Hindfoot tracks were reportedly ~4.5 cm
279 long and wide.⁴³

280
281 Stuart and Stuart described (questionably in our opinion) a “typical tramline-like trail”, resulting
282 from the fairly wide spacing of the hindfeet, on which the ground pangolin normally walks, with
283 the short, heavily clawed forefeet held clear off the ground.⁴⁰ The forefeet were noted to be used
284 mostly for digging. Hindfoot track length of 6 cm was reported, with slight intoeing. An image of
285 a pangolin trackway was not provided.⁴⁰

286
287 Gutteridge and Liebenberg described the “interesting spoor” of the pangolin, which usually
288 moves bipedally on the rounded hindfeet.⁴⁴ These were noted to drag, as the pangolin walks in
289 a kind of shuffle. The unique marking made by the tail was also noted. Hindfoot track length was
290 reported as be 6.5 cm.⁴⁴

291
292 While there are slight differences in the focus of these descriptions, there is substantial
293 agreement, involving a predominantly bipedal gait, with hindfoot tracks 4.5–6.5 cm in size,
294 occasional forefoot traces, and occasional tail drag marks.

295

296 **Interpretation and trackmaker identity**

297

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

307
308 Other plausible trackmaker candidates included felids such as serval (*Leptailurus serval*),
309 caracal (*Caracal caracal*) and African wild cat (*Felis lybica*), the viverrids African civet
310 (*Civettictis civetta*), rusty genet (*Genetta maculata*) and large-spotted genet (*Genetta genetta*),
311 and canids such as jackals and foxes (in a soft, sandy substrate the claw impressions of canids
312 might not be preserved). There is no evidence in the Pleistocene fossil record or among extant
313 southern African species of other animals that could have made these tracks. One caveat is that
314 carnivoran size (hence track size) varied during the Pleistocene, being reportedly larger during
315 glacial phases.⁴⁵

316
317 The tracks, 5-6 cm in size, are consistent with those of both extant pangolin and serval,
318 although a pangolin’s hindfoot track length is marginally greater than those of a serval’s forefoot
319 and hindfoot. *Contra* Stuart and Stuart⁴⁰, the narrow external trackway width is consistent with
320 the trackways of both pangolin and, on occasion, serval. However, the trackway widths of
321 caracal⁴⁴ and especially civet (our own observations) are distinctly broader. While the African
322 wild cat can also produce a round track, the smaller size of its track and pace length exclude it.
323 Similar considerations exclude both species of genet. Jackal tracks, in the 5 cm range, are
324 relatively slender and more elongated (especially in the case of the smaller hind foot), definitely
325 not “soos ‘n ronde stok wat in die grond ingedruk is”. The same is true of fox tracks (Cape and
326 Bat-eared), with the front foot of the Bat-eared fox (*Octocyon megalotis*) measuring but 4.5
327 cm⁴⁴, and the hind foot even smaller,

328
329 Whereas ground pangolin hindfoot tracks are triangular (with the apex pointing backwards,
330 away from the direction of travel) and well-preserved serval tracks exhibit pad and digit
331 impressions, none of these features might be present in Cape south coast aeolianites. This may

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.

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

338
339 The inference of trackmaker direction is based on some tracks appearing slightly wider in their
340 distal portions, the overall indentation pattern, and the orientation of the 'smudges'. These
341 impressions at the proximal end of the trackway and in line with it are consistent with the scuff-
342 marks made by the pangolin tail (Figure 5a), and less consistent with tail traces made by servals
343 or other potential trackmakers.

344
345 Pace length is consistently 18-20 cm, and therefore the distance between tracks is about three
346 times the size of each track. While a pangolin sometimes walks with a shuffle and a relatively
347 short pace length (Figure 5b) it can also walk with a longer pace length, as in the Bosbokfontein
348 trackway and in Figure 6a.

349
350 Another potential distinguishing factor involves the relative lightness of the gait. A serval, like all
351 cats, walks or runs lightly. A ground pangolin, bulky, slower and bipedal, has a more ponderous
352 gait. Therefore pangolin tracks tend to be deeper than serval tracks. While this is not an
353 absolute criterion, the depth of the tracks in question (1.0 – 1.5 cm), bolstered by the notion of
354 the round end of a stick poked into the ground, suggests a pangolin trackmaker.

355
356 Opinions from expert southern African trackers were most helpful. We approached Opinions
357 from expert southern African trackers were most helpful. We approached [anonymised],
358 [anonymised], [anonymised], [anonymised], and [anonymised].

359 Their feedback was measuredly supportive. None thought the tracks were inconsistent with
360 those of a pangolin. [anonymised] provided a confident assessment:

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

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

Commented [A21]: The figure have only one image

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

Commented [A24]: lc

Commented [A25]: what is this?

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

367 [anonymised] provided a detailed comment:

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

375
376 In the less likely scenario that the tracks were registered by a serval, a 'direct register' would be
377 inferred whereby the hindfoot was placed precisely on top of the forefoot track. (Stealth hunters
378 often employ this economical, sound-minimising foot-placement pattern.) From a prehistoric
379 distribution perspective, a serval trackmaker is plausible. Avery reported Pliocene serval records
380 from Gauteng Province, and Pleistocene and Holocene records from, *inter alia*, the
381 southwestern Cape.³¹

382
383 Our overall conclusion is that the trackway cannot be attributed with absolute certainty to any
384 trackmaker. However, it is most consistent with a ground pangolin trackmaker, distinctly more
385 than a serval or any other candidate species. The Pleistocene distribution range of the ground
386 pangolin included the southwestern Cape, in a situation that is analogous to that of the giraffe,
387 the preferred habitat of both species being savanna woodland. Such habitat might have been
388 present on the now-submerged Palaeo-Agulhas Plain.⁴⁶

389

390

391

391 **Conclusions**

392

393 A ground pangolin probably walked across a soft, sandy dune surface near the margin of the
394 Palaeo-Agulhas Plain, most likely during MIS6 or MIS 5, leaving a trackway. Eight tracks and,
395 suggestively, two tail traces are preserved and amenable to interpretation. For many, fossil
396 trackways are to body fossils what movies are to photographs, and evocative trackways tell a
397 story of something that might have walked by yesterday, or over 100,000 years ago.

398
399 While the loose block containing the track-bearing surface is too large to physically recover, the
400 photogrammetry data can be used to make a replica of the trackway, which could be exhibited
401 in the Blombos Museum of Archaeology in Still Bay. What to date is probably the first reported
402 pangolin trackway in the world could thus serve to draw attention to the plight of pangolins
403 worldwide.

404
405 In a recent publication we described the advantages of collaboration between indigenous
406 Master Trackers and western-trained ichnologists in interpreting Pleistocene trackways.⁴⁷ The
407 title of a book by Liebenberg specified that the art of tracking was “the origin of science”.⁴⁸ In our
408 experience, the outcomes and conclusions that result are richer for integrating ancient and
409 modern science.

410

411

412 Acknowledgements

413

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

417

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

420

421

422 References

423

424 1. AUTHOR

425

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

428

Commented [A26]: There are many missing references

- 429 3. Gu T-T, Wu H, Yang F, Gaubert P, Heighton SP, Fu Y, et al. Genomic analysis reveals a
430 cryptic pangolin species. *Proc Natl Acad Sci USA*. 2023;120(40):e2304096120.
431 <https://doi.org/10.1073/pnas.2304096120>
432
- 433 4. Möller LA. *Of the Same Breath: Indigenous Animal and Place Names*. Sun Media
434 Bloemfontein (Pty) Ltd.: Bloemfontein; 2017. <https://doi.org/10.18820/9781928424031>
435
- 436 5. IUCN Red List of Threatened Species. 2023.
437 <https://www.iucnredlist.org/search?query=Pangolins&searchType=species>
438
- 439 6. D'Cruze N, Assou D, Coulthard E, Norrey J, Megson D, Macdonald DW, et al. Snake oil
440 and pangolin scales: insights into wild animal use at "Marché des Fétiches" traditional
441 medicine market, Togo. *Nat Conserv*. 2020;39:45–71.
442 <https://doi.org/10.3897/natureconservation.39.47879>
443
- 444 7. Ingram DJ. 400,000 African pangolins are hunted for meat every year – why it's time to
445 act. *The Conversation Africa* 2019. [https://theconversation.com/400-000-african-](https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540)
446 [pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540](https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540)
447
- 448 8. Malan JA. *Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group) –*
449 *South African Committee for Stratigraphy Lithostratigraphic Series 8*. Pretoria:
450 Department of Mineral and Energy Affairs;1989.
451
- 452 9. Malan JA. 1990. *The stratigraphy and sedimentology of the Bredasdorp Group,*
453 *Southern Cape Province, South Africa*. MSc thesis. Cape Town: University of Cape
454 Town; 1990.
455
- 456 10. Roberts DL, Cawthra HC, Musekiwa C. Dynamics of late Cenozoic aeolian deposition
457 along the South African coast: a record of evolving climate and ecosystems. In: Martini
458 IP, Wanless HR, editors. *Sedimentary Coastal Zones from High to Low Latitudes:*
459 *Similarities and Differences*. Special Publication of the Geological Society of London
460 2013:388. p. 353–387 <http://dx.doi.org/10.1144/SP388.11>
461
- 462 11. Brooke B. The distribution of carbonate eolianite. *Earth-Sci Rev*. 2001;55:135–164.
463 [https://doi.org/10.1016/S0012-8252\(01\)00054-X](https://doi.org/10.1016/S0012-8252(01)00054-X)

- 464
465
466
467
468
469
470
471
472
473
474
475
476
477
478
479
480
481
482
483
484
485
486
487
488
489
490
491
492
493
494
495
496
497
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, Karkanis 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, Karkanis 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>

- 498 19. Roberts D, Cole K. Vertebrate trackways in Late Cenozoic coastal eolianites, South
499 Africa. Geological Society of America Abstracts with Programs, XVI INQUA Congress.
500 2003:70(3);196.
501
- 502 20. Belvedere M, Farlow JO. A numerical scale for quantifying the quality of preservation of
503 vertebrate tracks. In: Falkingham PL, Marty D, Richter A, editors. Dinosaur tracks: the
504 next steps. Bloomington and Indianapolis: Indiana University Press; 2016. p. 92–99.
505
- 506 21. Falkingham PL, Gatesy SM. Discussion: defining the morphological quality of fossil
507 footprints. Problems and principles of preservation in tetrapod ichnology with examples
508 from the Palaeozoic to the present by Lorenzo Marchetti et al. Earth-Sci Rev.
509 2020;208:103320. <https://doi.org/10.1016/j.earscirev.2020.103320>
510
- 511 22. Gatesy SM, Falkingham PL. Neither bones nor feet: track morphological variation and
512 'preservation quality'. J. Vertebr. Paleontol. 2017;37:e1314298.
513 <https://doi.org/10.1080/02724634.2017.1314298>
514
- 515 23. AUTHOR ET AL.
516
- 517 24. AUTHOR ET AL.
518
- 519 25. AUTHOR ET AL.
520
- 521 26. Van den Heever A, Mhlongo R, Benadie K. Tracker Manual – a Practical Guide to Animal
522 Tracking in Southern Africa. Struik Nature: Cape Town; 2017.
523
- 524 27. Matthews NA, Noble TA, Breithaupt BH. Close-range photogrammetry for 3-D ichnology:
525 the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors.
526 Dinosaur Tracks: The Next Steps. Bloomington: Indiana University Press; 2016. p. 28–
527 55.
528
- 529 28. Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, et al. 2018.
530 A standard protocol for documenting modern and fossil ichnological data. Palaeontology,
531 2018;61(4):469-480. <https://doi.org/10.1111/pala.12373>
532

- 533 29. Botha J, Gaudin T. An Early Pliocene pangolin (Mammalia; Pholidota) from
534 Langebaanweg, South Africa. *J Vertebr Paleontol.* 2007;27:484–491.
- 535 30. Gaudin TJ, Emry RJ, Wible JR. The phylogeny of living and extinct pangolins
536 (Mammalia, Pholidota) and associated taxa: a morphology based analysis. *J.Mammal.*
537 2009;16:235–305.
- 539 31. Avery DM. *A Fossil History of Southern African Land Mammals.* Cambridge University
540 Press: Cambridge; 2019. <https://doi.org/10.1017/9781108647243>
- 542 32. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry,
543 Langebaanweg, South Africa, and a reinterpretation of their geological context. *Ann S Afr*
544 *Mus.* 1981;84(1):1–104.
- 546 33. Klein RG, Avery G, Cruz-Uribe K, Steele TE. The mammalian fauna associated with an
547 archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape
548 Province, South Africa. *J Hum Evol.* 2007;52:164–186.
549 <https://doi.org/10.1016/j.jhevol.2006.08.006>
- 551 34. Klein RG. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province,
552 South Africa): its implications for megafaunal extinctions and environmental and cultural
553 change. *Quat Res.* 1972;2:135–142.
- 555 35. Skead CJ. *Historical Mammal incidence in the Cape Province Vol. I. Western Cape and*
556 *Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei.* Chief Directorate, Nature and
557 Environmental Conservation of the Provincial Administration of the Cape of Good Hope:
558 Cape Town; 1987.
- 560 36. Layard EL. *Catalogue of the specimens in the collection of the South African Museum.*
561 *Part 1. The Mammalia.* Saul Solomon and Co.: Cape Town; 1861.
- 563 37. Shortridge GC. Field notes on the first and second expeditions of the Cape Museum's
564 mammal survey of the Cape Province; and descriptions of some new subgenera and
565 subspecies. *Ann S Afr Mus.* 1942;36:27–99.
- 567 38. Lichtenstein WHC. *Travels in Southern Africa, in the years 1803, 1804, 1805 and 1806.*
568 *Vol. 2 (Translation by Anne Plumtre).* Van Riebeeck Society No. 11: Cape Town; 1815.

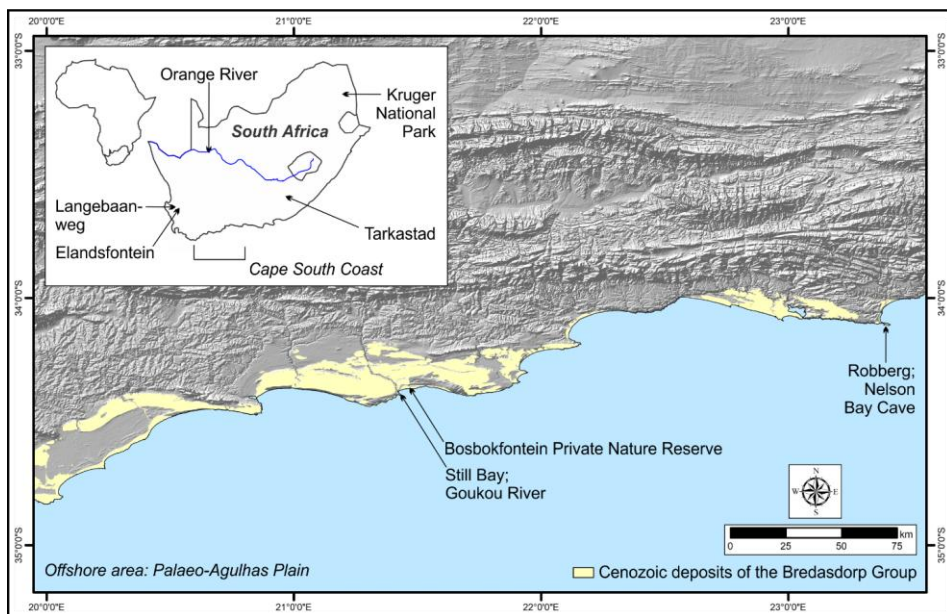
- 570
571 39. Burchell WJ. Travels in the Interior of Southern Africa. Vol. 2. Longman, Hurst, Rees,
572 Orme, Brown, and Green: London; 1824.
- 573
574 40. Stuart C, Stuart T. 2019. A Field Guide to the Tracks and Signs of Southern and East
575 African Wildlife. Struik Nature: Cape Town; 2019.
- 576
577 41. AUTHOR ET AL.
- 578
579 42. Liebenberg L. 2000. A Photographic Guide to Tracks and Tracking in Southern Africa.
580 Struik Publishers: Cape Town; 2000.
- 581
582 43. Walker C. Signs of the Wild – A Field Guide to the Spoor & Signs of the Mammals of
583 Southern Africa. Struik Nature: Cape Town; 2018.
- 584
585 44. Gutteridge L, Liebenberg L. Mammals of Southern Africa and their Tracks and Signs.
586 Jacana Media (Pty) Limited: Auckland Park; 2021.
- 587
588 45. Klein RG. Carnivore size and Quaternary climatic change in Southern Africa. Quat Res.
589 1986;26:153–170.
- 590
591 46. Cowling RM, Potts AJ, Franklin J, Midgley GF, Engelbrecht F, Marean CW. Describing a
592 drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the
593 Palaeo-Agulhas Plain. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-
594 Agulhas Plain: A Lost World and Extinct Ecosystem. Quat Sci Rev. 2020;235:105866.
595 <https://doi.org/10.1016/j.quascirev.2019.105866>
- 596
597 47. AUTHOR ET AL.
- 598
599 48. Liebenberg L. The Art of Tracking – the Origin of Science. David Phillip: Claremont,
600 South Africa; 1990.

Commented [A27]: please complete

Commented [A28]: Please complete

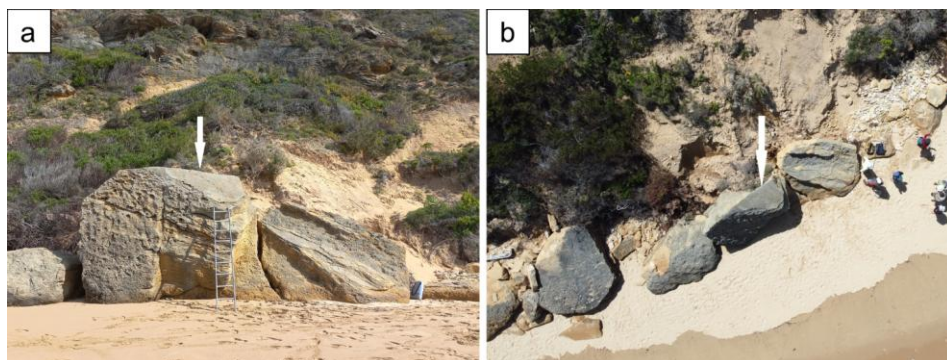
601 **Figures captions**

602



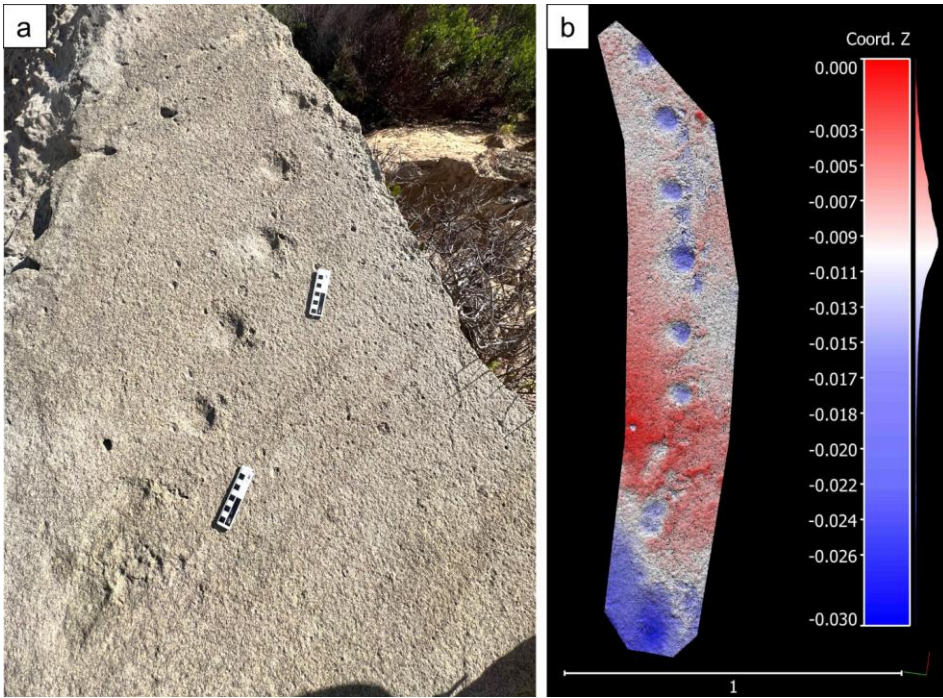
603
604
605
606

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

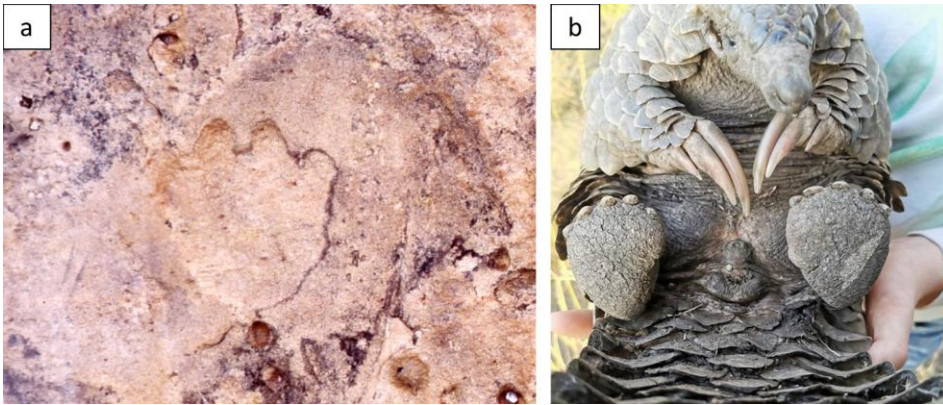


607
608
609
610
611

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.

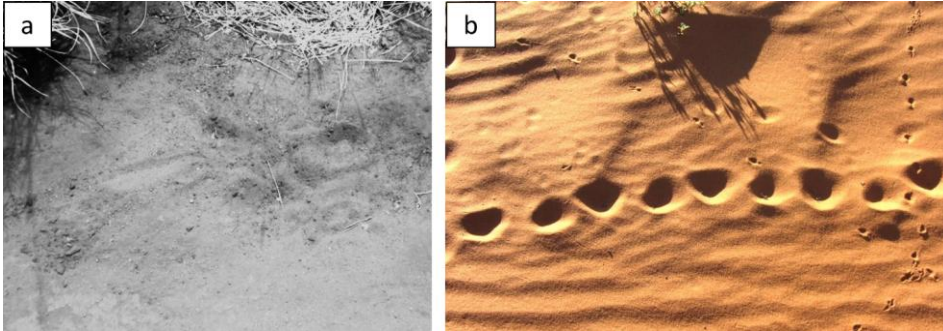


612
 613 **Figure 3:** (a) The purported pangolin trackway; scale bars = 10 cm. (b) Photogrammetry colour mesh of
 614 the trackway; vertical and horizontal scales are in metres.
 615



616

617 **Figure 4:** (a) A rock engraving of a probable pangolin track in Limpopo Province; reproduced with
 618 permission from Chris and Mathilde Stuart. (b) The forefeet and hindfeet of a ground pangolin, viewed
 619 from below; reproduced with permission from [anonymised].
 620



621
 622 **Figure 5:** (a) Scuff marks registered by the tail of a ground pangolin; reproduced with permission from
 623 Bruno Nebel. (b) A trackway of a ground pangolin, showing (in this case) a short pace length; reproduced
 624 with permission from [anonymised].
 625



626
 627 **Figure 6:** A ground pangolin walking with a longer pace length; reproduced with permission from
 628 [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.

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

1 A PROBABLE PLEISTOCENE PANGOLIN (ORDER PHOLIDOTA) 2 TRACKWAY FROM SOUTH AFRICA'S CAPE SOUTH COAST

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

3 4 Abstract

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

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

19 20 21 22 Significance of the main findings

- 23
24 - A Pleistocene probable pangolin trackway has been identified east of Still Bay, Western Cape
25 province, South Africa.
26 - The identification involved integrating indigenous African and western-based ichnological
27 approaches.
28 - This appears to be the first known fossilised pangolin trackway.
29 - The trackway comprises eight tracks and two probable tail traces.
30 - This discovery could draw attention to the plight of pangolins.

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

31 32 33 Introduction

34
35 Through the Cape south coast ichnology project over 350 Pleistocene vertebrate ichnosites
36 have been documented along a 350 km stretch of South African coastline. The majority (80%)
37 represent mammal tracks and traces.¹ Until now, no pangolin ichnofossils have been identified,
38 either on the Cape south coast or, to the best of our knowledge, anywhere in the world. Here we
39 describe a trackway on an aeolianite (cemented dune) palaeosurface in the Bosbokfontein
40 Nature Reserve, east of Still Bay on the Cape south coast. The lines of evidence converge on a
41 pangolin as the probable trackmaker.

42
43 The order Pholidota contains a single family, Manidae, with eight recognized, extant pangolin
44 species from sub-Saharan Africa, India, southern China and southeast Asia to the Philippines.²
45 A cryptic ninth Asian species was detected in 2023³, and awaits formal description. Four of
46 these species occur in Africa - two are arboreal, and two (Temminck's pangolin and the giant
47 pangolin) are ground-dwelling. Temminck's pangolin (*Smutsia temminckii*, previously *Manis*
48 *temminckii*) is also known as the ground pangolin, the Cape pangolin, or the scaly anteater, and
49 is the only pangolin species to currently occur in southern Africa.² In the Ju/'hoan language
50 Temminck's pangolin is known as 'n#hòqò', and in Afrikaans as the 'ietermagog'. The latter is
51 probably of Bantu or Tswana derivation.⁴

52
53 All species of extant pangolin are threatened by poaching and habitat loss, and all are classified
54 as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List of Threatened
55 Species.⁵ Pangolin meat is regarded as a delicacy, and pangolin scales are used in traditional
56 medicines.⁶ There is evidence that pangolins are among the most trafficked wild animals on
57 Earth, and 400,000 African pangolins are estimated to be hunted for their meat annually.⁷

58
59 The tracks described here were initially identified in 2018 by Renée Rust and family. The tracks
60 are evident on the surface of a large fallen aeolianite block. The putative trackmaker remained
61 enigmatic until our joint analysis in 2023. Two of us (#D, /N) are indigenous Ju/'hoansi San
62 Master Trackers, and had an immediate, strong sense of what was being examined. This
63 presented the opportunity for indigenous and modern scientific tracking exponents to engage in
64 a productive exchange of ideas, combining culturally honed and experientially grounded
65 intuitions with modern assessment techniques. This collaborative, inter-disciplinary approach
66 has allowed us to arrive at a shared conclusion on probable trackmaker identity.

67

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.

Commented [A8]: As per Reviewer 1 suggestion.

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

71
72

73 Geological context

74

75 Pleistocene carbonate aeolianites of the Waenhuiskrans Formation⁸, part of the Neogene
76 Bredasdorp Group⁹, are exposed along portions of the Cape south coast of South Africa, and
77 have provided evidence for palaeo-shorelines and palaeo-coastal dune activity.¹⁰ Carbonate
78 aeolianites are consolidated coastal rock formations consisting of at-least-partially lithified
79 calcareous wind-blown sand. The trackway described here would have been registered on an
80 unconsolidated dune surface, which is now consolidated and cemented into aeolianite. Globally,
81 aeolianites are fairly common in mid-latitude coastal regions between 20° and 40°. ¹¹ Throughout
82 the Pleistocene, global sea-level change meant that the Cape south coast landscape was
83 dynamic. Vertebrate ichnosites encountered on these palaeosurfaces would have been situated
84 at the margin of the Paleo-Agulhas Plain, most of which is presently submerged, but at times
85 sea-level oscillations would have exposed the entire plain.¹² In contrast, sea level was 6–8
86 metres higher than at present at the height of the Marine Isotope Stage (MIS) 5e marine
87 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.

88

89 Optically Stimulated Luminescence (OSL) dating of onshore aeolianites has shown that most
90 date to MIS 5 and late MIS 6.¹³⁻¹⁶ MIS 11 deposits¹⁷ and MIS 3 deposits¹⁸ have also been
91 identified, with a resulting age range of dated deposits presently spanning ~400–35 ka. Roberts
92 and Cole provided an explanation for the profusion of ichnosites, postulating a combination of a
93 cohesive moulding agent (moist sand), rapid track burial (facilitated by high sedimentation
94 rates), rapid lithification (via partial solution and re-precipitation of bioclasts), and finally re-
95 exposure of track-bearing surfaces through shoreline erosion.¹⁹

96

97 In general, the grain size of the substrate inversely influences the preservation quality of fossil
98 tracks. In Cape south coast Pleistocene deposits, tracks made on moderately coarse-grained
99 dune surfaces tend to show poor to intermediate preservation quality, certainly inferior to that
100 seen elsewhere in the world, for example in clay or mud substrates on cave floors. Belvedere
101 and Farlow introduced a four-point preservation scale, in which 0 represents an unidentifiable

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

102 track, and 3 represents a track of exceptional quality.²⁰ It is unusual for tracks within the Cape
103 south coast deposits to rise above 2 on this scale.

104
105 Active shoreline erosion causes coastal cliffs to fragment or collapse, sometimes exposing new
106 ichnosites, while known sites deteriorate in quality or loose blocks slump into the ocean.
107 Ichnosites are thus ephemeral. The taphonomic erosive effects of wind and water, either pre-
108 burial or post re-exposure, can result in loss of track preservation quality. In the latter case, even
109 if the tracks displayed anatomical fidelity at the time of re-exposure, over time their quality can
110 deteriorate.¹ The causes of relatively poor preservation, such as moderately large grain size (in
111 this case medium-grained sand), pre-burial erosion and post-exposure erosion, may be difficult
112 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.

113
114 The Bosbokfontein tracksite is located in a remote section of coastline (Figure 1), characterised
115 by aeolianite cliffs as high as 30 m. High tides and storm surges cause cliff sections to collapse,
116 whereupon loose blocks come to rest on unstable slopes or near the high-tide mark at the cliff
117 base.

118
119 One section in this region, situated ~8 km east of the Bosbokfontein site, had been dated prior
120 to our studies.¹³ Ages obtained through OSL dating produced a range of 140 ± 8 ka to 91 ± 5
121 ka. Our subsequent work has yielded several results of relevance here (in each case a five-digit
122 number is preceded by "Leic"). The closest of these lies 4.5 km east of the Bosbokfontein site,
123 where an age of 126 ± 9 ka was obtained (Leic21005).²³ Other results from sites located slightly
124 further east include 161 ± 12 ka (Leic20033), 139 ± 10 ka (Leic20031), 134 ± 9 ka (Leic21008),
125 and 109 ± 9 ka (Leic20024).²³⁻²⁵ Although direct stratigraphic correlation between these sites is
126 not feasible, due to an absence of laterally persistent layers or marker beds, it nonetheless
127 seems likely that the Bosbokfontein track-bearing surface occurs in deposits within the age
128 range of ~161–91 ka, from MIS 6 or MIS 5.

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

130 131 Methods

132
133 Track measurements (in cm) included length, width, depth, pace length, and stride length.
134 External trackway width was measured in cm, representing "the distance between the footfall of
135 left and right feet, measured between the outside extremities of the tracks".²⁶ Global Positioning

136 System locality readings were taken using a hand-held Garmin 60 device. Locality data were
137 stored with the African Centre for Coastal Palaeoscience at Nelson Mandela University, to be
138 made available to researchers upon request.

139

140 The tracksite was photographed, and photogrammetric analysis performed.^{27,28} 3D models were
141 generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal
142 length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 μm). The final images were
143 rendered using CloudCompare (v.2.10-beta). The tracks could be assessed by climbing to the
144 top of the block and examining the surface, but for optimal recording, including photogrammetry
145 studies, access via a portable ladder proved useful. A DJI Mini 2 drone with an inbuilt DJI
146 camera/video was used to obtain further photographs.

147

148 Having viewed the tracksite in detail together, and examined photographs and photogrammetry
149 models, we reviewed our findings and opinions. This permitted further integration of the
150 perspectives and interpretations of Master Trackers and western-trained ichnologists.

151 Furthermore, we engaged with some of southern Africa's tracking (neoichnology) experts,
152 asking for their opinions on trackmaker identity based on photographic and photogrammetric
153 images.

154

155

156 Results

157

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

166

167 The block has come to rest at an angle, and the track-bearing surface faces seaward and
168 skywards, in a southeasterly direction. The trackway, which is ~160 cm in length, is thus aligned
169 in a southeast-northeast direction as the loose block is currently orientated, but this may be

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

170 subject to change following storm surges. Viewed in cross section, the block exhibits laminar
171 bedding, mostly parallel but with slight distortion in places and faint cross-bedding. The relative
172 absence of cross-bedding suggests that the tracks might have been registered on a more level
173 interdune area. The trackway is interpreted here with the viewer facing landwards and
174 northwest, as if the trackmaker was progressing up the current slope of the loose block. The
175 tracks are preserved in concave epirelief.

176
177 Eight tracks are evident (Figure 3), but the distal track occurs at the edge of the surface and is
178 partial, and the two proximal tracks are partially obscured by two elongated depressions,
179 aligned in approximately the same direction as the trackway. These are approximately 10.0–
180 12.5 cm long and 4.5–6.0 cm wide. Tracks 3 through 7 therefore offer the best potential for
181 analysis. The trackway curves gently to the left, such that its distal end is orientated ~30°
182 leftward of that of its proximal end. Faint displacement rims partially encircle some of the tracks,
183 suggesting that the tracks were registered on a slightly sloping surface.

184
185 Track lengths (5.5–6.0 cm) and track widths (5.0–5.5 cm) are relatively constant. Tracks 6 and 7
186 appear slightly wider in their anterior portions. Pace length in tracks 3 through 7 is relatively
187 constant (18–20 cm). Track depth varies from 1.0 to 1.5 cm, with the anterior portions of the
188 tracks slightly deeper than the posterior portions. The external trackway width appears narrow,
189 approximately 7.5 cm.

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.

191 Discussion

194 The prehistoric and historic distribution of southern African pangolins

195
196
197 The global record of pangolins extends back to the Oligocene Epoch²⁹, as reviewed by Gaudin
198 et al.³⁰ The prehistoric distribution of pangolins in southern Africa in the palaeontological record
199 is meagre for the southern Cape and western Cape: there are only three reported Cenozoic
200 fossils of pangolins from these regions.³¹ These all represent skeletal evidence, and we are not
201 aware of trace fossil records of pangolins in the global ichnology record. The three reported
202 southwestern Cape fossil records are now summarised.

203
204 Hendey reported an unstudied early Pliocene pangolin from the 'E' Quarry at Langebaanweg in
205 the Western Cape province near the South African west coast.³² Botha and Gaudin²⁹ formally
206 described this specimen as probably ground dwelling, and possibly having engaged in a
207 quadrupedal gait similar to that of the extant giant pangolin (*Smutsia gigantea*). It was
208 suggested that it may have used its forelimbs more than *S. temminckii*. The specimen was
209 assigned to *S. gigantea*, making it the oldest known representative of that species.²⁹

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

210
211 Klein et al. described a pangolin assigned to the genus *Phataginus* from the Elandsfontein Main
212 site in the Western Cape province on South Africa's west coast, ~350 km WNW of the tracksite
213 reported on here.³³ It was described as an "extralimital species" that contributed to the
214 exceptional faunal diversity of the site. The age of the faunal assemblage was estimated to be in
215 the range of 1.0–0.6 Ma.³³

216
217 The closest pangolin body fossil site to the Bosbokfontein site, temporally and spatially, was
218 reported by Klein from Nelson Bay Cave near Robberg, 180 km east of Bosbokfontein.³⁴ It was
219 located in Late Pleistocene deposits dating to 18–16 ka. It was described as the "Cape
220 pangolin, *Manis* cf. *temminckii*".³⁴

221
222 The southern African Holocene and historic record is more extensive for *Temminck's pangolin*.
223 Possible sources include historical accounts, ethnographic records, rock art and place names.
224 Möller noted that *Temminck's pangolin* had a wide distribution and occurred all over southern
225 Africa, and that the lack of early reports might be attributable to its nocturnal habits.⁴ Skead³⁵
226 reported that a probable pangolin had been recorded in 1825 from the Tarkastad or
227 Queenstown area (in the current Eastern Cape province), and that this probably constituted the
228 southernmost record for the species (~32°S). Skead³⁵ quoted Layard³⁶ that the pangolin was
229 "not now" found in the Cape Colony (i.e., south of the Orange River), perhaps implying that it
230 had occurred previously within it. Shortridge³⁷ reported that it was absent from "Little
231 Namaqualand" but noted a pangolin skin from the Upington area and records south of the
232 Orange River from Prieska and Colesberg. The 1865 holotype is from Litakun (Latakou), ~250
233 km north of the Orange River, and north of present-day Kuruman.³⁰ Lichtenstein³⁸ and Burchell³⁹
234 also reported the occurrence of the pangolin in the Litakun area.

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

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

235

236 Möller provided two place names, Ietermagô and Khwaru, that refer to pangolins.⁴ Both are in
237 the Kruger National Park in South Africa's Limpopo Province, ~1,500 km northeast of the
238 Bosbokfontein site. They are therefore unhelpful regarding a potential southern Cape
239 distribution range.

240
241 Rock art can provide information on prehistoric pangolin distribution, although it only implies the
242 artist's awareness that the species existed, not its occurrence in that precise locality. Despite
243 consultation with rock art experts, we are not aware of rock art depicting pangolins in southern
244 Africa other than a site in Limpopo province (Figure 4a), where a frieze of engraved animal
245 tracks of eight species contains an engraving of a possible pangolin hindfoot track.⁴⁰ 'Fragile
246 Images', a YouTube video, includes footage of the engraving at 12 minutes and 10 seconds:
247 <https://www.youtube.com/watch?v=Ra12BKeH7Js>.

248
249 In summary, the body fossil record demonstrates the presence of pangolins in the southwestern
250 Cape region of South Africa during the Pliocene and Pleistocene. The situation is perhaps
251 analogous to that of the giraffe (*Giraffa camelopardalis*), for which there is no body-fossil
252 evidence from the Pleistocene in the southwestern Cape, but a trace fossil record confirms its
253 presence.⁴¹ The giraffe tracksite lies less than eight km east of the Bosbokfontein tracksite. The
254 presence of giraffe tracks implies the presence of trees and a probable savanna
255 palaeoenvironment.⁴¹ This may have been suitable for Temminck's pangolin, with a preferred
256 habitat of savanna woodland. The record from Nelson Bay Cave³⁴ lies just within the last glacial
257 period, when aspects of this habitat might still have been present. Historical records, place
258 names and rock art do not contribute to an understanding of pangolin distribution in the
259 southwestern Cape.

260

261 Pangolin track morphology

262

263 Southern African neoichnologists are fortunate in having five tracking manuals to refer to.^{26,39,42-}

264 ⁴⁴ Each describes Temminck's pangolin tracks, reviewed here in order of publication date.

265 Figure 4b depicts the forefeet and hindfeet of a Temminck's pangolin.

266

267 Liebenberg described five toes on the forefeet (the first with a small nail and the central three
268 with long, strongly curved claws), and five toes on the hindfeet, each with a short nail-like claw
269 that sometimes registers an impression in the tracks.⁴² The body was noted to be balanced on

270 the hindfeet when walking, with the forefeet and tail held off the ground. Tracks were noted to
271 show the rounded pads of the hindfeet with four nails usually touching the ground. The
272 occasional tail scrape and traces made by the front edges of the front claws were also noted.
273 Hindfoot tracks were reported as 6 cm in length.⁴²

274
275 Van den Heever et al.²⁶ also noted that both forefeet and hindfeet have five toes, and that the
276 first and fifth toes of the front feet are reduced, leaving three middle toes with long curved claws,
277 well adapted for digging. The forefoot track (when present) was noted to record the upper
278 surfaces of the three middle claws, which curl under the foot. The hindfoot was described as
279 padded and triangular, with five toes, and ~5 cm in length. Movement was described as bipedal,
280 with the forefeet seldom touching the ground. Scuff marks made by dragging the tail were
281 reportedly occasionally present.²⁶

282
283 Walker⁴³ described the pangolin as moving along on its hind legs, occasionally dropping onto all
284 fours or using the tail and forelegs for balance. Claws were noted to be prominent, and claws 2,
285 3 and 4 (presumably on the forefeet) were well-developed and recurved. Pangolins were noted
286 to walk mainly on their hind legs in an upright position. Hindfoot tracks were reportedly ~4.5 cm
287 long and wide.⁴³

288
289 Stuart and Stuart described (questionably in our opinion) a “typical tramline-like trail”, resulting
290 from the fairly wide spacing of the hindfeet, on which **Temminck’s** pangolin normally walks, with
291 the short, heavily clawed forefeet held clear off the ground.⁴⁰ The forefeet were noted to be used
292 mostly for digging. Hindfoot track length of 6 cm was reported, with slight intoeing. An image of
293 a pangolin trackway was not provided.⁴⁰

294
295 Gutteridge and Liebenberg described the “interesting spoor” of the pangolin, which usually
296 moves bipedally on the rounded hindfeet.⁴⁴ These were noted to drag, as the pangolin walks in
297 a kind of shuffle. The unique marking made by the tail was also noted. Hindfoot track length was
298 reported as being 6.5 cm.⁴⁴

299
300 While there are slight differences in the focus of these descriptions, there is substantial
301 agreement, involving a predominantly bipedal gait, with hindfoot tracks 4.5–6.5 cm in size,
302 occasional forefoot traces, and occasional tail drag marks.

303

Commented [A23]: Reviewer 1 typo correction.

304 Interpretation and trackmaker identity

305

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

315

316 Other plausible trackmaker candidates include felids such as serval (*Leptailurus serval*), caracal
317 (*Caracal caracal*) and African wild cat (*Felis lybica*), the viverrids African civet (*Civettictis*
318 *civetta*), rusty genet (*Genetta maculata*) and large-spotted genet (*Genetta genetta*), and canids
319 such as jackals and foxes (in a soft, sandy substrate the claw impressions of canids might not
320 be preserved). Bipedal avian trackmakers would be expected to leave at least some evidence of
321 didactyl, tridactyl or tetradactyl morphology⁴⁵, and the two elongated depressions are
322 inconsistent with an avian origin. There is no evidence in the Pleistocene fossil record or among
323 extant southern African species of other animals that could have made these tracks. One caveat
324 is that carnivoran size (hence track size) varied during the Pleistocene, being reportedly larger
325 during glacial phases.⁴⁶

326

327 The tracks, 5–6 cm in size, are consistent with those of both extant Temminck's pangolin and
328 serval, although a pangolin's hindfoot track length is marginally greater than those of a serval's
329 forefoot and hindfoot. *Contra* Stuart and Stuart⁴⁰, the narrow external trackway width is
330 consistent with the trackways of both Temminck's pangolin and, on occasion, serval. However,
331 the trackway widths of caracal⁴⁴ and especially civet (our own observations) are distinctly
332 broader. While the African wild cat can also produce a round track, the smaller size of its track
333 and pace length exclude it. Similar considerations exclude both species of genet. Jackal tracks,
334 in the 5 cm range, are relatively slender and more elongated (especially in the case of the
335 smaller hind foot), definitely not “soos ‘n ronde stok wat in die grond ingedruk is”. The same is
336 true of fox tracks (Cape and Bat-eared), with the front foot of the Bat-eared fox (*Octocyon*
337 *megalotis*) measuring but 4.5 cm⁴⁴, and the hind foot even smaller,

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

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

338
339 Whereas **Temminck's** pangolin hindfoot tracks are triangular (with the apex pointing backwards,
340 away from the direction of travel) and well-preserved serval tracks exhibit pad and digit
341 impressions, none of these features might be present in Cape south coast aeolianites. This may
342 either be due to a soft, non-cohesive substrate at the time the tracks were registered, the effects
343 of grain size, or pre-burial or post-re-exposure erosion.¹ Consequently, the tracks of both
344 **Temminck's** pangolin and serval might appear round, without further morphological details. In
345 such a situation, trackmaker identity would depend more on trackway morphology than of
346 individual tracks. In the Bosbokfontein trackway, however, there is a hint of a triangular track
347 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.

348
349 The inference of trackmaker direction is based on some tracks appearing slightly wider in their
350 **anterior** portions, the overall indentation pattern, and the orientation of the **two elongated**
351 **depressions**. These impressions at the proximal end of the trackway and in line with it are
352 consistent with the scuff-marks made by the pangolin tail (Figure 5a), and less consistent with
353 tail traces made by servals or other potential trackmakers.

354
355 Pace length is consistently **18–20** cm, and therefore the distance between tracks is about three
356 times the size of each track. While a pangolin sometimes walks with a shuffle and a relatively
357 short pace length (Figure 5b) it can also walk with a longer pace length **when not foraging**, as in
358 the Bosbokfontein trackway and in **Figure 6**.

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

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

359
360 Another potential distinguishing factor involves the relative lightness of the gait. A serval, like all
361 cats, walks or runs lightly. A **Temminck's** pangolin, bulky, slower and bipedal, has a more
362 ponderous gait. Therefore, pangolin tracks tend to be deeper than serval tracks. While this is
363 not an absolute criterion, the depth of the tracks in question (**1.0–1.5** cm), bolstered by the
364 notion of the round end of a stick poked into the ground, **is more consistent** with a pangolin
365 trackmaker.

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

366
367 Opinions from expert southern African trackers were most helpful. We approached
368 [anonymised], [anonymised], [anonymised], [anonymised], [anonymised], and [anonymised].

369 Their feedback was measuredly supportive. None thought the tracks were inconsistent with
370 those of a pangolin. [anonymised] provided a confident assessment:

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

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

377 [anonymised] provided a detailed comment:

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

385
386 Furthermore, one of the three very knowledgeable anonymous reviewers of this manuscript
387 (under strict confidentiality of the peer review process) sent the image of the fossilised trackway to
388 two colleagues who have worked with Temminck's pangolin for many years on a day-to-day basis.
389 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.

390
391 In the less likely scenario that the tracks were registered by a serval, a 'direct register' would be
392 inferred whereby the hindfoot was placed precisely on top of the forefoot track. (Stealth hunters
393 often employ this economical, sound-minimising foot-placement pattern.) From a prehistoric
394 distribution perspective, a serval trackmaker is plausible. A very reported Pliocene serval records
395 from Gauteng Province, and Pleistocene and Holocene records from, *inter alia*, the
396 southwestern Cape.³¹

397
398 Our overall conclusion is that the trackway cannot be attributed with absolute certainty to any
399 trackmaker. However, it is most consistent with a Temminck's pangolin trackmaker, distinctly
400 more than a serval or any other candidate species. The Pleistocene distribution range of the
401 Temminck's pangolin included the southwestern Cape, in a situation that is analogous to that of
402 the giraffe, the preferred habitat of both species being savanna woodland. Such habitat might
403 have been present on the now-submerged Palaeo-Agulhas Plain.⁴⁷

404

405

406

Conclusions

407

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

413

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

419

420 In a recent publication we described the advantages of collaboration between indigenous
421 Master Trackers and western-trained ichnologists in interpreting Pleistocene trackways.⁴⁸ The
422 title of a book by Liebenberg specified that the art of tracking was “the origin of science”.⁴⁹ In our
423 experience, the outcomes and conclusions that result are richer for integrating ancient and
424 modern science.

425

426

Acknowledgements

427

428
429 We thank Linda Helm, Louis Liebenberg, Christina Mars, Richard McKibbin, Andrew Paterson,
430 Wendy Panaino, Renée and Niekie Rust, Chris and Mathilde Stuart, Alex Van den Heever, and
431 Richard Webb for their assistance. **We are grateful to the three anonymous reviewers for their
432 thorough and helpful comments, which led to substantial improvements in the manuscript.**

433

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

436

437

References

- 438
- 439
- 440 1. AUTHOR
- 441
- 442 2. Gaudin T. Pholidota. In: Werdelin L, Sanders WJ, editors. Cenozoic Mammals of Africa.
- 443 Berkeley: University of California Press; 2010. p. 599–602.
- 444
- 445 3. Gu T-T, Wu H, Yang F, Gaubert P, Heighton SP, Fu Y, et al. Genomic analysis reveals a
- 446 cryptic pangolin species. *Proc Natl Acad Sci USA*. 2023;120(40):e2304096120.
- 447 <https://doi.org/10.1073/pnas.2304096120>
- 448
- 449 4. Möller LA. *Of the Same Breath: Indigenous Animal and Place Names*. Sun Media
- 450 Bloemfontein (Pty) Ltd.: Bloemfontein; 2017. <https://doi.org/10.18820/9781928424031>
- 451
- 452 5. IUCN Red List of Threatened Species. 2023.
- 453 <https://www.iucnredlist.org/search?query=Pangolins&searchType=species>
- 454
- 455 6. D'Cruze N, Assou D, Coulthard E, Norrey J, Megson D, Macdonald DW, et al. Snake oil
- 456 and pangolin scales: insights into wild animal use at "Marché des Fétiches" traditional
- 457 medicine market, Togo. *Nat Conserv*. 2020;39:45–71.
- 458 <https://doi.org/10.3897/natureconservation.39.47879>
- 459
- 460 7. Ingram DJ. 400,000 African pangolins are hunted for meat every year – why it's time to
- 461 act. *The Conversation Africa* 2019. [https://theconversation.com/400-000-african-](https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540)
- 462 [pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540](https://theconversation.com/400-000-african-pangolins-are-hunted-for-meat-every-year-why-its-time-to-act-111540)
- 463
- 464 8. Malan JA. *Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group) –*
- 465 *South African Committee for Stratigraphy Lithostratigraphic Series 8*. Pretoria:
- 466 Department of Mineral and Energy Affairs;1989.
- 467
- 468 9. Malan JA. 1990. *The stratigraphy and sedimentology of the Bredasdorp Group,*
- 469 *Southern Cape Province, South Africa*. MSc thesis. Cape Town: University of Cape
- 470 Town; 1990.
- 471

- 472 10. Roberts DL, Cawthra HC, Musekiwa C. Dynamics of late Cenozoic aeolian deposition
473 along the South African coast: a record of evolving climate and ecosystems. In: Martini
474 IP, Wanless HR, editors. Sedimentary Coastal Zones from High to Low Latitudes:
475 Similarities and Differences. Special Publication of the Geological Society of London
476 2013:388. p. 353–387 <http://dx.doi.org/10.1144/SP388.11>
477
478 11. Brooke B. The distribution of carbonate eolianite. *Earth-Sci Rev.* 2001;55:135–164.
479 [https://doi.org/10.1016/S0012-8252\(01\)00054-X](https://doi.org/10.1016/S0012-8252(01)00054-X)
480
481 12. Marean CW, Cowling RC, Franklin J. The Palaeo-Agulhas Plain: temporal and spatial
482 variation in an extraordinary extinct ecosystem of the Pleistocene of the Cape Floristic
483 Region. In: Cleghorn N, Potts AJ, Cawthra HC, editors. The Palaeo-Agulhas Plain: A
484 Lost World and Extinct Ecosystem. *Quat Sci Rev.* 2020;235:106161.
485 <https://doi.org/10.1016/j.quascirev.2019.106161>
486
487 13. Carr AS, Bateman MD, Roberts DL, Murray-Wallace CV, Jacobs Z, Holmes PJ. The last
488 interglacial sea-level high stand on the southern Cape coastline of South Africa. *Quat*
489 *Res.* 2010;73:351–363. <https://doi.org/10.1016/j.yqres.2009.08.006>
490
491 14. Roberts DL, Bateman MD, Murray-Wallace CV, Carr AS, Holmes PJ. Last Interglacial
492 fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South
493 Africa. *Palaeogeogr Palaeoclimatol Palaeoecol.* 2008;257(3):261–279.
494 <https://doi.org/10.1016/j.palaeo.2007.08.005>
495
496 15. Bateman MD, Carr AS, Dunajko AC, Holmes PJ, Roberts DL, McLaren SJ, et al. The
497 evolution of coastal barrier systems: a case study of the Middle-Late Pleistocene
498 Wilderness barriers, South Africa. *Quat Sci Rev.* 2011;30:63–81.
499 <https://doi.org/10.1016/j.quascirev.2010.10.003>
500
501 16. Cawthra HC, Jacobs Z, Compton JS, Fisher EC, Karkanis P, Marean CW. Depositional
502 and sea-level history from MIS 6 (Termination II) to MIS 3 on the southern continental
503 shelf of South Africa. *Quat Sci Rev.* 2018;181:156–172.
504 <https://doi.org/10.1016/j.quascirev.2017.12.002>
505

- 506 17. Roberts DL, Karkanas P, Jacobs Z, Marean CW, Roberts RG. Melting ice sheets
507 400,000 yr ago raised sea level by 13 m: past analogue for future trends. *Earth Planet*
508 *Sci Lett.* 2012;357–358:226–237. <https://doi.org/10.1016/j.epsl.2012.09.006>
- 509
510 18. Carr AS, Bateman MD, Cawthra HC, Sealy J. First evidence for onshore marine isotope
511 stage 3 aeolianite formation on the southern Cape coastline of South Africa. *Mar Geol.*
512 2019;407:1–15. <https://doi.org/10.1016/j.margeo.2018.10.003>
- 513
514 19. Roberts D, Cole K. Vertebrate trackways in Late Cenozoic coastal eolianites, South
515 Africa. *Geological Society of America Abstracts with Programs, XVI INQUA Congress.*
516 2003:70(3);196.
- 517
518 20. Belvedere M, Farlow JO. A numerical scale for quantifying the quality of preservation of
519 vertebrate tracks. In: Falkingham PL, Marty D, Richter A, editors. *Dinosaur tracks: the*
520 *next steps.* Bloomington and Indianapolis: Indiana University Press; 2016. p. 92–99.
- 521
522 21. Falkingham PL, Gatesy SM. Discussion: defining the morphological quality of fossil
523 footprints. *Problems and principles of preservation in tetrapod ichnology with examples*
524 *from the Palaeozoic to the present by Lorenzo Marchetti et al.* *Earth-Sci Rev.*
525 2020;208:103320. <https://doi.org/10.1016/j.earscirev.2020.103320>
- 526
527 22. Gatesy SM, Falkingham PL. Neither bones nor feet: track morphological variation and
528 'preservation quality'. *J. Vertebr. Paleontol.* 2017;37:e1314298.
529 <https://doi.org/10.1080/02724634.2017.1314298>
- 530
531 23. AUTHOR ET AL.
- 532
533 24. AUTHOR ET AL.
- 534
535 25. AUTHOR ET AL.
- 536
537 26. Van den Heever A, Mhlongo R, Benadie K, Thomas I. *Tracker Manual – a Practical*
538 *Guide to Animal Tracking in Southern Africa.* Struik Nature: Cape Town; 2024.
- 539

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

- 540 27. Matthews NA, Noble TA, Breithaupt BH. Close-range photogrammetry for 3-D ichnology:
541 the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors.
542 Dinosaur Tracks: The Next Steps. Bloomington: Indiana University Press; 2016. p. 28–
543 55.
- 544 28. Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, et al. 2018.
545 A standard protocol for documenting modern and fossil ichnological data. *Palaeontology*,
546 2018;61(4):469–480. <https://doi.org/10.1111/pala.12373>
- 547 29. Botha J, Gaudin T. An Early Pliocene pangolin (Mammalia; Pholidota) from
548 Langebaanweg, South Africa. *J Vertebr Paleontol.* 2007;27:484–491.
- 549 30. Gaudin TJ, Emry RJ, Wible JR. The phylogeny of living and extinct pangolins
550 (Mammalia, Pholidota) and associated taxa: a morphology based analysis. *J.Mammal.*
551 2009;16:235–305.
- 552 31. Avery DM. A Fossil History of Southern African Land Mammals. Cambridge University
553 Press: Cambridge; 2019. <https://doi.org/10.1017/9781108647243>
- 554 32. Hendey QB. Palaeoecology of the Late Tertiary fossil occurrences in 'E' Quarry,
555 Langebaanweg, South Africa, and a reinterpretation of their geological context. *Ann S Afr*
556 *Mus.* 1981;84(1):1–104.
- 557 33. Klein RG, Avery G, Cruz-Uribe K, Steele TE. The mammalian fauna associated with an
558 archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape
559 Province, South Africa. *J Hum Evol.* 2007;52:164–186.
560 <https://doi.org/10.1016/j.jhevol.2006.08.006>
- 561 34. Klein RG. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province,
562 South Africa): its implications for megafaunal extinctions and environmental and cultural
563 change. *Quat Res.* 1972;2:135–142.
- 564 35. Skead CJ. Historical Mammal incidence in the Cape Province Vol. I. Western Cape and
565 Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei. Chief Directorate, Nature and
566 Environmental Conservation of the Provincial Administration of the Cape of Good Hope:
567 Cape Town; 1987.

- 576
577 36. Layard EL. Catalogue of the specimens in the collection of the South African Museum.
578 Part 1. The Mammalia. Saul Solomon and Co.: Cape Town; 1861.
- 579
580 37. Shortridge GC. Field notes on the first and second expeditions of the Cape Museum's
581 mammal survey of the Cape Province; and descriptions of some new subgenera and
582 subspecies. *Ann S Afr Mus.* 1942;36:27–99.
- 583
584 38. Lichtenstein WHC. Travels in Southern Africa, in the years 1803, 1804, 1805 and 1806.
585 Vol. 2 (Translation by Anne Plumtre). Van Riebeeck Society No. 11: Cape Town; 1815.
- 586
587 39. Burchell WJ. Travels in the Interior of Southern Africa. Vol. 2. Longman, Hurst, Rees,
588 Orme, Brown, and Green: London; 1824.
- 589
590 40. Stuart C, Stuart T. 2019. A Field Guide to the Tracks and Signs of Southern and East
591 African Wildlife. Struik Nature: Cape Town; 2019.
- 592
593 41. AUTHOR ET AL.
- 594
595 42. Liebenberg L. 2000. A Photographic Guide to Tracks and Tracking in Southern Africa.
596 Struik Publishers: Cape Town; 2000.
- 597
598 43. Walker C. Signs of the Wild – A Field Guide to the Spoor & Signs of the Mammals of
599 Southern Africa. Struik Nature: Cape Town; 2018.
- 600
601 44. Gutteridge L, Liebenberg L. Mammals of Southern Africa and their Tracks and Signs.
602 Jacana Media (Pty) Limited: Auckland Park; 2021.
- 603
604 45. AUTHOR ET AL.
- 605
606 46. Klein RG. Carnivore size and Quaternary climatic change in Southern Africa. *Quat Res.*
607 1986;26:153–170.
- 608
609 47. Cowling RM, Potts AJ, Franklin J, Midgley GF, Engelbrecht F, Marean CW. Describing a
610 drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the
611 Palaeo-Agulhas Plain. In: Clegghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), *The Palaeo-*

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

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

614
615 48. AUTHOR ET AL.

616
617 49. Liebenberg L. The Art of Tracking – the Origin of Science. David Phillip: Claremont,
618 South Africa; 1990.

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

Figure captions

619
620
621
622 **Figure 1:** Map of South Africa's coast, indicating the Bosbokfontein site, the extent of Pleistocene
623 deposits, and sites mentioned in the text.
624
625 **Figure 2:** (a) The large loose block containing the purported pangolin trackway on its upper surface; the
626 ladder length is 410 cm. (b) The track-bearing block, viewed from above using a drone; adult human
627 figures for scale. Arrows point to the track-bearing surface.
628
629 **Figure 3:** (a) The purported pangolin trackway; scale bars = 10 cm. (b) Photogrammetry colour mesh of
630 the trackway; vertical and horizontal scales are in metres.
631
632 **Figure 4:** (a) **Rock** engraving of a probable pangolin track in Limpopo Province; reproduced with
633 permission from [anonymised], (b) The forefeet and hindfeet of a **Temminck's** pangolin, viewed from
634 below; reproduced with permission from [anonymised],
635
636 **Figure 5:** (a) Scuff marks registered by the tail of a **Temminck's** pangolin; reproduced with permission
637 from [anonymised], (b) A trackway of a **Temminck's** pangolin, showing (in this case) a short pace length;
638 reproduced with permission from [anonymised],
639
640 **Figure 6:** A **Temminck's** pangolin walking with a longer pace length; reproduced with permission from
641 [anonymised],