

## Research Article

# An update on Pleistocene tortoise tracks on South Africa's Cape south coast

Charles W. Helm<sup>a</sup> , Andrew S. Carr<sup>b</sup> , Hayley C. Cawthra<sup>a,c</sup> , #oma Daqm<sup>d</sup>, Jan C. De Vynck<sup>a,e</sup> , Mark G. Dixon<sup>a</sup> , Steve Kunta<sup>d,†</sup>, /uce N#amce<sup>d</sup>, Willo M. Stear<sup>a</sup> , Clive R. Thompson<sup>a</sup>  and Jan A. Venter<sup>a,f</sup> 

<sup>a</sup>African Centre for Coastal Palaeoscience, George Campus, Nelson Mandela University, George, South Africa; <sup>b</sup>Institute for Environmental Futures, School of Geography, Geology and the Environment, University of Leicester, Leicester, UK; <sup>c</sup>Geophysics and Remote Sensing Unit, Council for Geoscience, Bellville, South Africa; <sup>d</sup>Nyae Nyae Conservancy, Tsumkwe, Namibia; <sup>e</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa and <sup>f</sup>Department of Conservation Management, George Campus, Nelson Mandela University, George, South Africa

## Abstract

Four new Pleistocene track-bearing aeolianite surfaces have been identified on South Africa's Cape south coast, each portraying evidence of tortoise tracks. Together, they add to and buttress previous reports of tortoise tracks and trackways from the region. Globally, this remains the only area from which fossilized tortoise tracks have been recorded, and for the first time we illustrate the preservation of typical tortoise trackway morphology (involving a 'tramline' pattern with a wide straddle and closely spaced tracks), as observed in the trackways of extant tortoises. One site provides further evidence for the inferred presence of a very large tortoise trackmaker from the region during the Pleistocene. This tortoise was substantially larger than the largest extant tortoises in southern Africa, which bolsters the inference of either an extinct very large tortoise or a large chrono-subspecies of the extant leopard tortoise (*Stigmochelys pardalis*). The mismatch between the body fossil record and trace fossil record with respect to the presence of large tortoises in the southern Cape persists. One trackway was probably registered by a smaller leopard tortoise, and the other trackways may have been registered by an angulate tortoise (*Chersina angulata*).

**Keywords:** Large tortoises; Leopard tortoise; Angulate tortoise; Aeolianites; Trackways

## Introduction

The general absence of reports of tortoise tracks in the global paleoichnological literature is surprising, given that tortoises are a familiar reptile clade with a body fossil record that extends to the Eocene (Vlachos and Rabi, 2018). In fact, the first reported occurrences of fossilized tortoise (family Testudinidae) trackways were identified in Pleistocene aeolianites (cemented dunes) on South Africa's Cape south coast (Helm et al., 2023a). The described ichnosites included particularly interesting evidence of a large trackmaker (>1 m long), which is larger than any extant tortoise in southern Africa. This led to the inference either of an extinct species or a large chrono-subspecies, phenomena which are not evident from the body fossil record (Helm et al., 2023a).

Neoichnologists in southern Africa are fortunate in being able to refer to three comprehensive tracking manuals (Liebenberg, 2000; Stuart and Stuart, 2019; van den Heever et al., 2024). Additionally, the temporal proximity of the Pleistocene implies that Pleistocene tortoise tracks might be similar in morphology to those of extant tortoises. While a variety of track and trackway morphologies were described by Helm et al. (2023a), the classic

pattern of closely spaced tracks in a wide-straddle 'tramline' trackway, noted in the aforementioned manuals, proved elusive. Helm et al. (2023a, p. 108) therefore concluded: "A diligent search for further chelonian tracks and traces on the Cape south coast and elsewhere is indicated."

This search has now yielded three new track-bearing surfaces that exhibit the classical 'tramline' pattern of tortoise trackways. In addition, another tracksite has been identified that contains large tracks, supporting the conclusion of Helm et al. (2023a) of the presence of very large tortoises in the region during the Pleistocene. The purpose of this paper is to summarize the new discoveries and consider their implications.

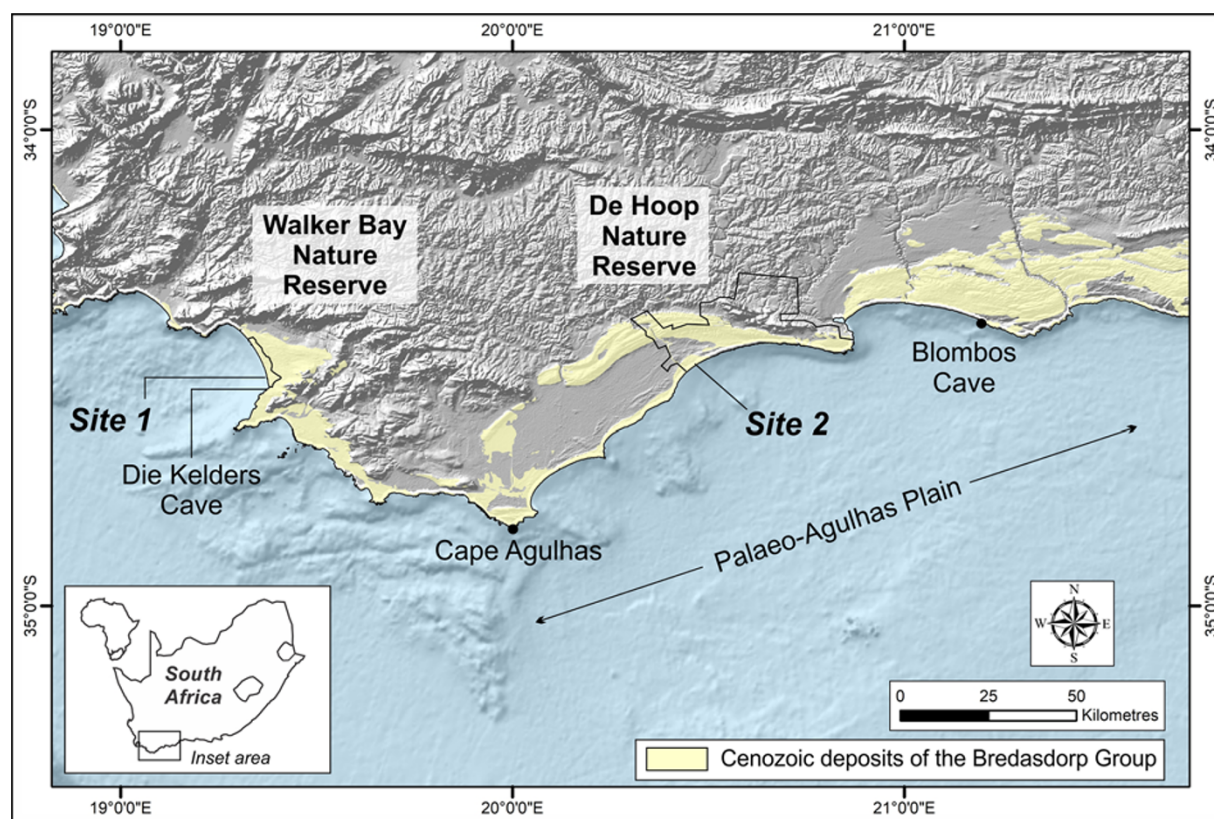
## Geological context

The newly identified ichnosites occur in Middle to Late Pleistocene coastal aeolianites (cemented dunes) of the Waenhuiskrans Formation (Bredasdorp Group; Malan, 1989, 1990; Figs. 1 and 2). Such aeolianites occur predominantly in the coastline's embayments and provide evidence for Pleistocene paleocoastal dune activity, paleoenvironments and paleo-sea-level changes (Roberts et al., 2013). Together with broadly coeval Pleistocene cemented foreshore deposits and lagoonal deposits of the Klein Brak Formation (Malan, 1991), the Waenhuiskrans and Klein Brak formations constitute the majority of coastal Cenozoic outcrops along the Cape south coast of South Africa. They consist mostly of

**Corresponding author:** Charles W. Helm; Email: [helm.c.w@gmail.com](mailto:helm.c.w@gmail.com)

**Cite this article:** Helm C.W. et al., 2026. An update on Pleistocene tortoise tracks on South Africa's Cape south coast. *Quaternary Research*, 1–11. <https://doi.org/10.1017/qua.2026.10078>





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

quartz-dominated clastic sandstones with a significant calcium carbonate component derived largely from marine shells, which facilitates their post-depositional cementation (Malan, 1990). When the tracks were registered in unconsolidated dune sand, the tracksites would have been located near the margin of the Palaeo-Agulhas Plain, the extensive landscape created by exposure of the continental shelf during Pleistocene glacial phases (Cawthra et al., 2020; Marean et al., 2020). Almost all of this plain is currently submerged.

More than 350 Pleistocene vertebrate ichnosites have been identified in these Cape south coast deposits (Helm, 2023). Roberts and Cole (2003) argued that the abundance of trace fossils in Cape south coast aeolianites reflected a combination of cohesive moist sand (an effective molding agent) and high sedimentation rates (swift track burial), with rapid lithification ensured through the partial solution of bioclasts and re-precipitation of matrix cement. Thereafter, shoreline erosion has re-exposed the track-bearing surfaces. Quaternary tectonic activity is thought not to be of major relevance on this coastline (Fleming et al., 1998), consequently in-situ bedding planes lie relatively close to their original angles of deposition.

The relatively coarse grain size of unconsolidated dune sand leads to imperfect track quality and anatomical fidelity, although finer-grained substrates and moist, cohesive sand may preserve tracks of higher quality (Helm, 2023). Poor preservation can also result from prolonged exposure to erosive forces following sub-aerial re-exposure. Once exposed, tracksites are ephemeral, and many track-bearing surfaces become eroded or fragmented, or slump into the sea.

Dating results are available for the aeolianite deposits in the Walker Bay Nature Reserve. Although the in-situ tracksite

described below (Site 1b) was not directly dated in this study, it lies just 20 meters from a site that has been sampled and dated using optically stimulated luminescence (OSL). This method provides an estimate of the burial duration (depositional age) of the sands upon which the trackways form (although given the uncertainties in the ages, these are considered essentially simultaneous events). This site was shown to date to  $76 \pm 5$  ka (Helm et al., 2024a). Further OSL ages have been reported for Walker Bay aeolianites at the southern end of the embayment near Die Kelders Cave 1. Here a sequence of four samples spanning the exposed thickness of aeolianite at the coast ranged between  $93 \pm 6$  ka and  $83 \pm 6$  ka (Helm et al., 2023b, and references therein). The Walker Bay tracks are therefore likely associated with Marine Isotope Stages (MIS) 5c to 5a.

Site 2 has not been dated, and no ages have yet been reported for the aeolianites or cemented foreshore deposits on the coast of the De Hoop Nature Reserve. We aim to address this in future studies.

### Extant tortoise track morphology

Tortoise track morphology was reviewed in detail by Helm et al. (2023a; Fig. 3), with size being the major distinguishing factor between the traces of extant southern African species, from the tiny speckled padloper (*Chersobius signatus*) to the large leopard tortoise (*Stigmochelys pardalis*) (Liebenberg, 2000; Stuart and Stuart, 2019; van den Heever et al., 2024). In summary, most species have five claws on the front feet and four claws on the hind feet, although the impressions of all the claws are not necessarily apparent in the tracks. Typically, the track of the manus faces inwards and the track of the pes faces outwards (van den Heever et al., 2024). Claw

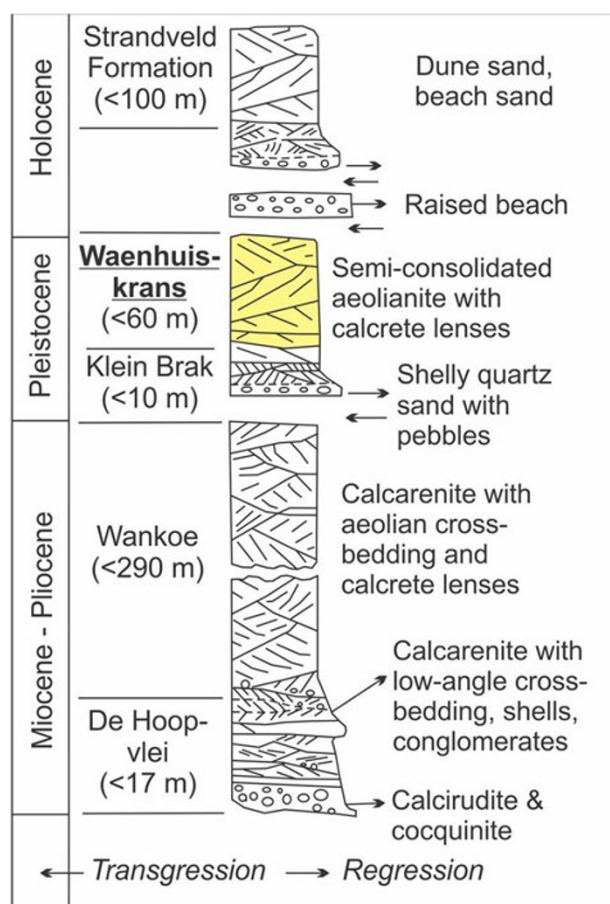


Figure 2. Stratigraphy of the Bredasdorp Group.

impressions are often deeply registered, in particular those of digits I, II, and III; the digit IV claw impression is typically fainter and the digit V claw impression of the manus may be absent. When only claw impressions are apparent, the term 'toe-tip traces' can be used, and these often occur in triplets. Depending on speed of travel, the pes track may be registered on, partially on, or behind the manus track. In soft substrates, such as unconsolidated sandy dune surfaces, pes and manus tracks may coalesce into amorphous rounded depressions.

Of relevance here are characteristic 'tramline trackways', with a wide straddle and relatively closely spaced tracks (Stuart and Stuart, 2019). Such tramlines contain clear, widely separated left and right lines of tracks (a wide straddle) that form part of a double-line unit (Stuart and Stuart, 2019). This can be considered the prototypical tortoise trackway. Other origins of tramline trackways were discussed in Helm et al. (2023a), the majority of which (e.g., crocodiles, lizards, terrapins, sea-turtles, frogs, and invertebrates) can be excluded in this study on grounds of size or environment.

## Methods

In light of the findings in Helm et al. (2023a), including the absence of prototypical tortoise trackways as described above, a search was initiated with the goal of identifying further tortoise tracksites. Global Positioning System readings were taken at the identified tracksites, using a hand-held device. Locality data were

reposited at the African Centre for Coastal Palaeoscience at Nelson Mandela University, George, to be made available to researchers upon request.

Photographs were taken at all sites. Track length, track width, pace length, and interdigital distance were measured. External straddle was recorded as the distance between the outer borders of the two lines of the 'tramline', measured perpendicular to the direction of travel (sensu van den Heever et al., 2024). Displacement rims were noted when present. In order to estimate the length of the trackmakers, we used two ratios described in Helm et al. (2023a): (1) the ratio of total trackmaker length to external straddle, and (2) the ratio of total trackmaker length to inter-claw distance.

Photographs were taken for photogrammetric analysis (Matthews et al., 2016). 3D models were generated with Agisoft Metashape Professional (v. 1.0.4) using an Olympus Tough model TG-6 camera (focal length 4.5 mm; resolution 4000 × 3000; pixel size 1.56 × 1.56 µm). The final images were rendered using CloudCompare (v.2.10-beta).

In addition, and in contrast to our previous study, our research team now includes San Indigenous Master Trackers #D, SK, and /N (Helm et al., 2025a), who in this instance reviewed tracksites both in the field and through photogrammetry images. Our different perspectives and training allowed for the fusion of different approaches and insights, leading to consensus.

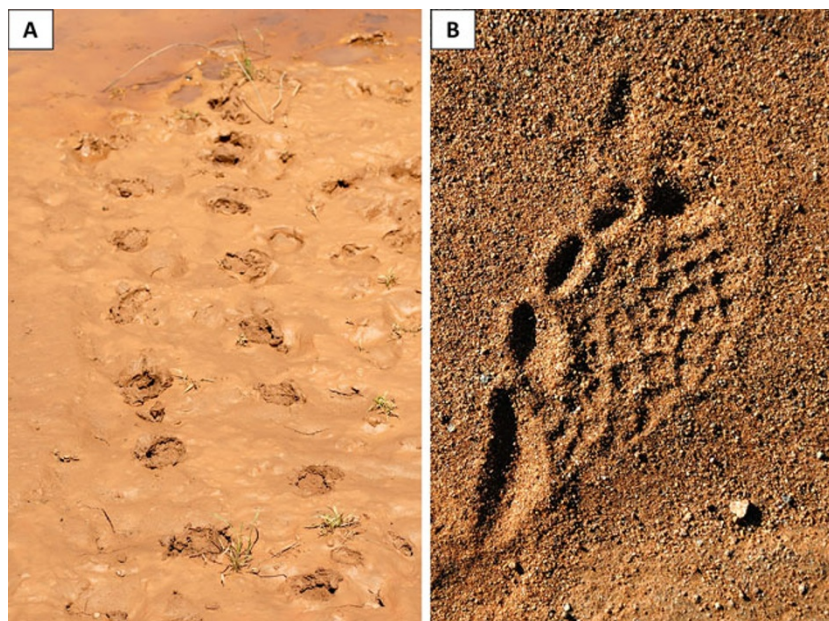
## Results and interpretation

Four Pleistocene Cape south coast ichnosites are described here. All are located within protected areas managed by CapeNature (Fig. 1). Sites 1a, 1b, and 1c, collectively referred to as Site 1, are located approximately five meters apart on the coastline of the Walker Bay Nature Reserve. This wide, west-facing embayment is characterized by extensive and thick (> 6 m) Holocene (uncemented) dunes that cover sporadically exposed Pleistocene aeolianites, which presumably are the paleo-analogue of the modern embayment–dune system. This is a remarkably rich area for ichnofossils: within 50 meters of Site 1 are the traces or tracks of armadillo (*Oryzomys azer*), the extinct long-horned buffalo (*Syncerus antiquus*), a puff-adder (*Bitis arietans*), a probable hominin, the African elephant (*Loxodonta africana*), other large trackmakers, vertebrate burrows, and invertebrate traces (Helm et al., 2023b, 2024a, 2025b). The three track-bearing surfaces are described below from west to east. Site 2 lies approximately 105 km to the east, on the coast within the De Hoop Nature Reserve, within meters of the tracks of lion (*Panthera leo*) and eland (*Taurotragus oryx*). The stratigraphic context of Site 1 and Site 2 is provided in Figures 4 and 5.

### Site 1a

The Site 1a trackway (Fig. 6) occurs on the surface of a thin, fragile, roughly triangular set of two loose slabs that readily can be joined together along the line along which the slab has fractured. The dimensions of the slabs, once fitted together, are ~35 cm in maximum length and width. The site, which lies ~2 meters to the west (seaward) of Site 1b, was identified by turning over and examining all loose slabs in the vicinity of Site 1b and Site 1c.

The trackway has a 'tramline' morphology, with an external straddle of 11 cm. The parallel 'lines' of the tramline contain 9 or 10 closely spaced, round or oval tracks, each ~1.5–2.5 cm in size,



**Figure 3.** (A) A leopard tortoise trackway registered in wet mud, showing the wide external straddle. (B) A particularly well-preserved leopard tortoise left hindfoot track, showing scale impressions; note that the claw impressions are registered deeper than the foot pad impression. The depression ahead of the second claw impression probably represents a scuff mark created by the claw during protraction. Photographs reproduced with kind permission of Chris and Mathilde Stuart.

preserved in concave epirelief. When the tracks are oval, then the major axis lies in the direction of travel. The level of preservation is not sufficient to allow digit impressions to be identified. The dimensions of the external straddle and of the individual tracks suggest a medium-sized tortoise trackmaker, such as the angulate tortoise (*Chersinia angulata*). The similarity of the recorded dimensions to those at Site 1c (described below) imply a trackmaker of similar size. The proximity of the sites, just meters apart, raises the possibility of a single trackmaker, and that the Site 1a loose slab represents a broken-off portion of the in-situ surface that contains the Site 1c tracks.

#### Site 1b

Figure 7 illustrates the spatial relationship between Site 1b, which is situated on a loose slab, and Site 1c, which is situated on a relatively level in-situ surface. The photographs were taken facing west, and proximity to the ocean is portrayed.

Site 1b comprises an aeolianite surface measuring 70 cm in maximum length and 40 cm in maximum width (Fig. 8). A repeating pattern of traces is evident, in a consistent arrangement of sets of two, three, or four depressions, with the sets orientated sub-parallel to each other and exhibiting curvilinear morphology. The distance between the sets varies from 4–9 cm. The traces are preserved in concave epirelief and are typically surrounded by shallow displacement rims. Each depression is typically round, with a diameter of ~2 cm. Invertebrate traces are evident on the same surface.

The sets are interpreted as right-sided ‘toe-tip traces’ from the right tramline of a large tortoise, inferred to be travelling from bottom to top in Figure 8. In this interpretation the left side of the tramline is not evident because it would be located off to the left of the surface. Examination of surrounding surfaces did not reveal any other evidence of the passage of a large tortoise trackmaker. The ‘interclaw distance’ was most easily calculated in the sets of three or four depressions, measuring the distance between the impressions of digits 1–3 or digits 1–4, and dividing by two or

three, respectively. The mean distance between claw impressions was thus measured to be 3.3 cm.

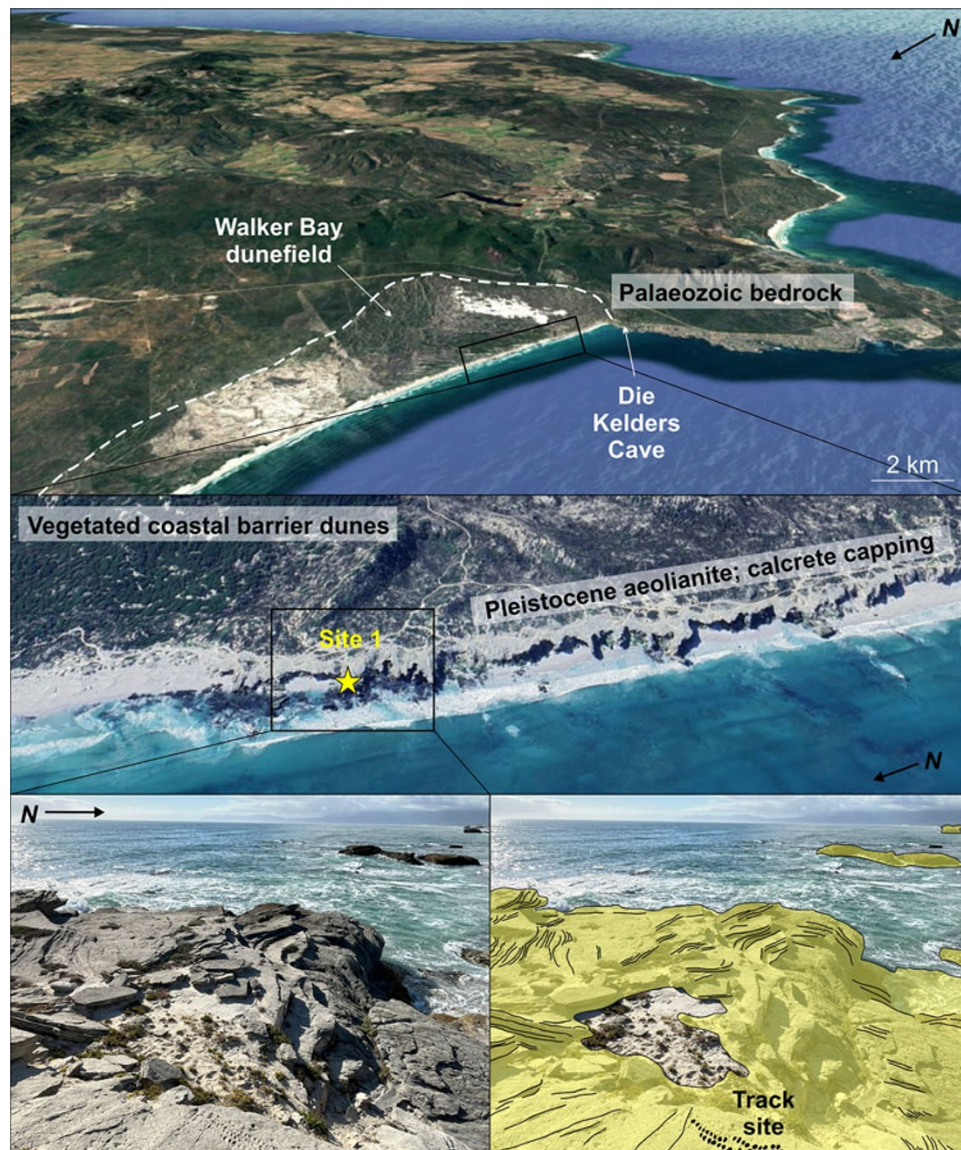
#### Site 1c

Site 1c is more complex: three parallel, curvilinear rows of closely spaced, round or slightly oval depressions extend for ~30 cm across an in-situ, relatively level aeolianite surface (Fig. 9). Each depression measures 2–3 cm in diameter. The traces are preserved in concave epirelief. The external straddle between the left and middle rows, and between the middle and right rows, is constant at ~11.4 cm. A direction change is evident at either end of these rows (at the top and bottom of the photogrammetry image in Fig. 9d) and larger, composite tracks are present. The most plausible interpretation is that a medium-sized tortoise turned around and doubled back on its tracks; however, in returning, one set of tracks followed the route taken by the ipsilateral set of tracks on the outward journey. In this scenario the middle row of tracks was thus registered twice, once on the outward journey and again on the return journey. This pattern has been encountered in our examination of the trackways of extant tortoises, although more commonly the tortoise follows precisely the same path on the return journey (i.e., both lines of the tramline are registered twice). On soft, sandy substrates, mammals will also preferentially tread in existing tracks rather than register fresh tracks (e.g., Helm et al., 2024a, fig. 8c and d).

Tracks of a medium-sized tortoise were noted in unconsolidated dune sand nearby (Fig. 10). These were probably registered by the angulate tortoise (*Chersinia angulata*) given that it remains the commonest tortoise in the region.

#### Site 2

Site 2 is situated in the De Hoop Nature Reserve on the coast east of Koppie Alleen, in a track-rich area. The loose track-bearing aeolianite slab measures ~2 meters in maximum length and ~1 meter in maximum width. It is episodically covered by a deep layer of beach sand, but at times is exposed, revealing the tracks.



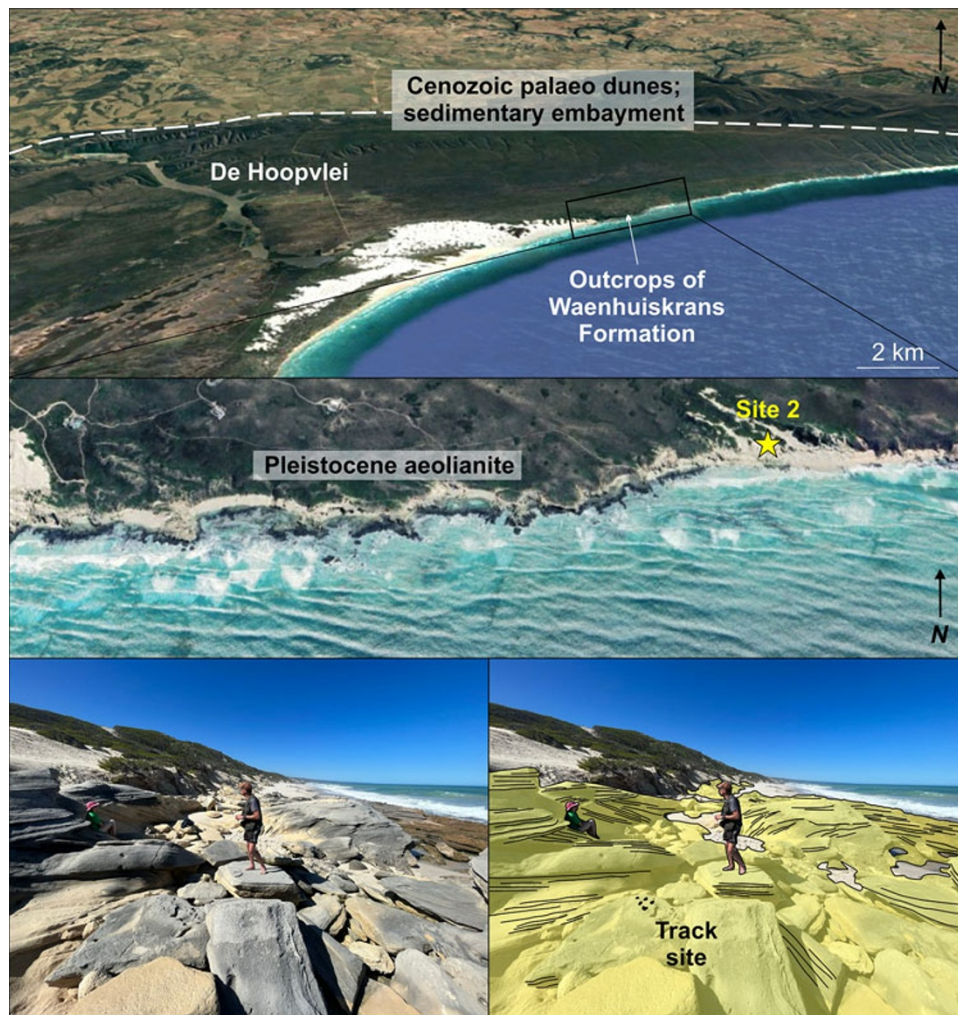
**Figure 4.** The stratigraphic context of Site 1.

The tracks are preserved in concave epirelief. A tramline trackway is distinctly present, with the left line of the tramline (as viewed in Fig. 11) displaying 34 tracks and the right line displaying 20 tracks. The right line is shorter because it is truncated by the edge of the rock surface. The lines of the tramway are parallel to one another, with a constant external straddle of  $\sim 30$  cm. Subtle matching movements to right or left are detectable in the left and right lines of the tramline. There is no evidence of digit morphology in the traces, and the tracks appear round and amorphous. Curvilinear invertebrate traces cross the surface, along with more recent slightly curved but parallel, sharply demarcated incisions, which are probably due to the grinding action of another rock on the surface at some point following re-exposure. Where these marks cross the left line of the tramline trackway they do not extend into the tracks. A large tortoise trackway is inferred, registered by a larger trackmaker than at Site 1a or Site 1c but smaller than at Site 1b.

#### Estimation of trackmaker length

Following Helm et al. (2023a), two ratios were determined from the findings described above: (1) total body length to external straddle = 1.53; and (2) total body length to distance between claw impressions = 29.8. The assumption is made here that the ratio of total body length to external straddle is isometric, but it is acknowledged that this is not known with certainty.

At Site 1b the mean distance between claw impressions = 3.3 cm. This yields an estimated trackmaker length of 98.3 cm. At Site 1a and Site 1c the external straddle = 11.4 cm, yielding an estimated trackmaker length of 17.4 cm. At Site 2 the external straddle =  $\sim 30$  cm, yielding an estimated trackmaker length of 45.9 cm. By comparison, the external straddles of the tortoise trackways in unconsolidated sand that we measured in the Walker Bay Nature Reserve were 9.3 cm and 11.5 cm, yielding estimated trackmaker lengths of 14.2 cm and 17.6 cm, respectively.



**Figure 5.** The stratigraphic context of Site 2.

## Discussion

### Trackmaker species and ‘tramline’ trackways

At present, the largest tortoise that occurs in southern Africa is the leopard tortoise (*Stigmochelys pardalis*), and the maximum length of extant specimens is ~70 cm (Branch, 1994). There is a geographic size difference, as the largest specimens are encountered at the northern end of its distribution range in Sudan, and at the southern end in South Africa (Branch, 2016). The length estimate from Site 1b of 98.3 cm is clearly substantially greater than the largest reported extant leopard tortoises, although less than the result of 106 cm (using the same total-body-length to external-straddle ratio) reported by Helm et al. (2023a). The fact that two sites of very large tortoise trackmakers have now been identified bolsters the previous conclusion that either an extinct tortoise species or a large leopard tortoise chrono-subspecies occurred in the region during the Pleistocene. While a very large terrapin trackmaker cannot be fully excluded at Site 1b, ‘toe-tip tracks’ on a dune surface are much more likely to have been registered by a tortoise (Branch, 2016). The notion of a large chrono-subspecies is arguably supported by evidence that some vertebrates were larger during the Pleistocene than their extant counterparts, which has

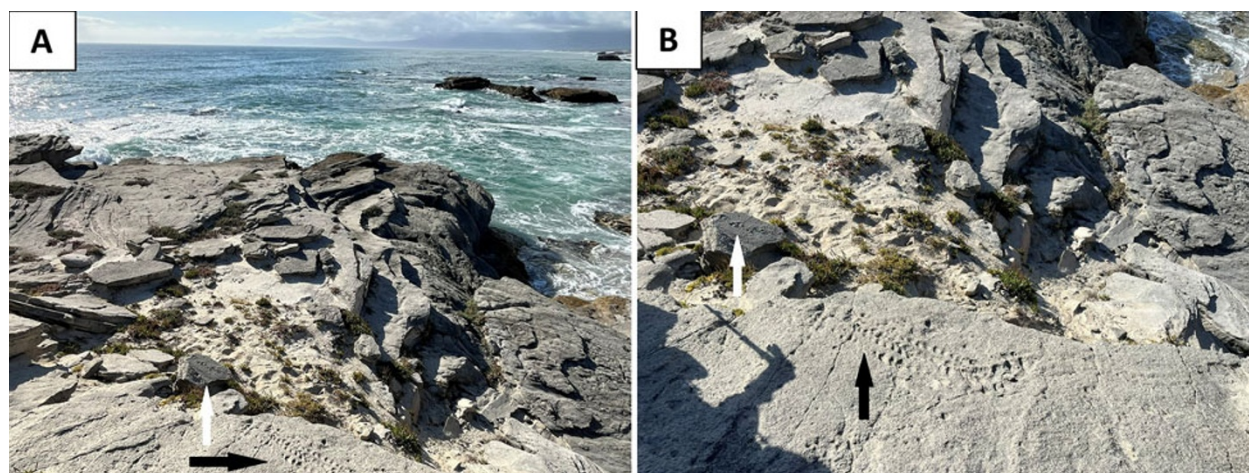
been reported in carnivorans (Klein, 1986), birds (Tyrberg, 2007; Helm et al., 2020), and some reptiles (Slavenko et al., 2016).

There is only one leopard tortoise body fossil site in the southern Cape, at Blombos Cave, which lies 65 km east of Site 2 (Fig. 1), where a single specimen was recorded (Thompson and Henshilwood, 2014). The mismatch noted by Helm et al. (2023a) between the body fossil record and the trace fossil record thus persists, bolstered by the findings at Site 1b and Site 2: the single body fossil specimen stands in contrast to the increasing number of ichnosites, indicating the presence of large and very large tortoises during the Pleistocene. A possible explanation was provided by Helm et al. (2023a), namely that the considerable mass of large tortoises rendered them difficult to transport, and that they were more probably butchered and eaten where they were encountered. The findings at Site 2 of a total length estimate of 45.9 cm suggest the presence of a smaller leopard tortoise, although a very large chrono-subspecies of a smaller tortoise such as the angulate tortoise (*Chersina angulata*) cannot be excluded.

The angulate tortoise is the most abundant regional tortoise in archaeological excavations from the Middle Stone Age (MSA) and Later Stone Age (LSA) (Klein et al., 2004). It is medium-sized, with a maximum total body length of 35 cm (Hofmeyr, 2009).



**Figure 6.** (A) The tramline trackway at Site 1a; scale bar = 10 cm.



**Figure 7.** (A and B) White arrows indicate Site 1b; black arrows indicate Site 1c.

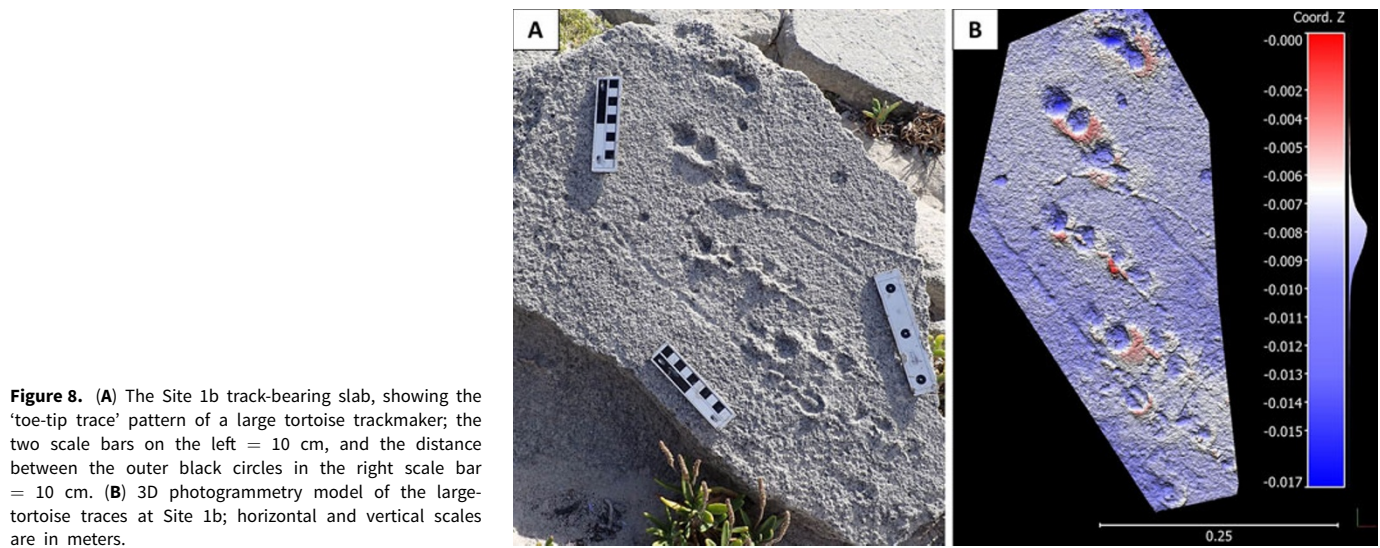
Excavations at Blombos Cave yielded a near-exclusive occurrence (3190 specimens) of this tortoise species (Thompson and Henshilwood, 2014). Klein and Cruz-Uribe (2000) described this tortoise and the Cape dune molerat as by far the commonest species identified in MSA and LSA archaeological deposits at Die Kelders Cave 1, from a large sample size of 174,816 bones that could be attributed to body part or taxon. This cave, also known as Klipgat Cave, is located just 1.4 km south of Site 1 (Fig. 1). Klein et al. (2004) also noted that *Chersina angulata* has been the dominant species in the region in historic times. The angulate tortoise appears to be a good match for the trackmaker at Site 1a and Site 1c, where the two sites might represent portions of a single trackway.

As noted above, the only previously published report of fossilized tortoise tracks did not provide evidence of the prototypical ‘tramline trackway’. In contrast, the current study presents evidence

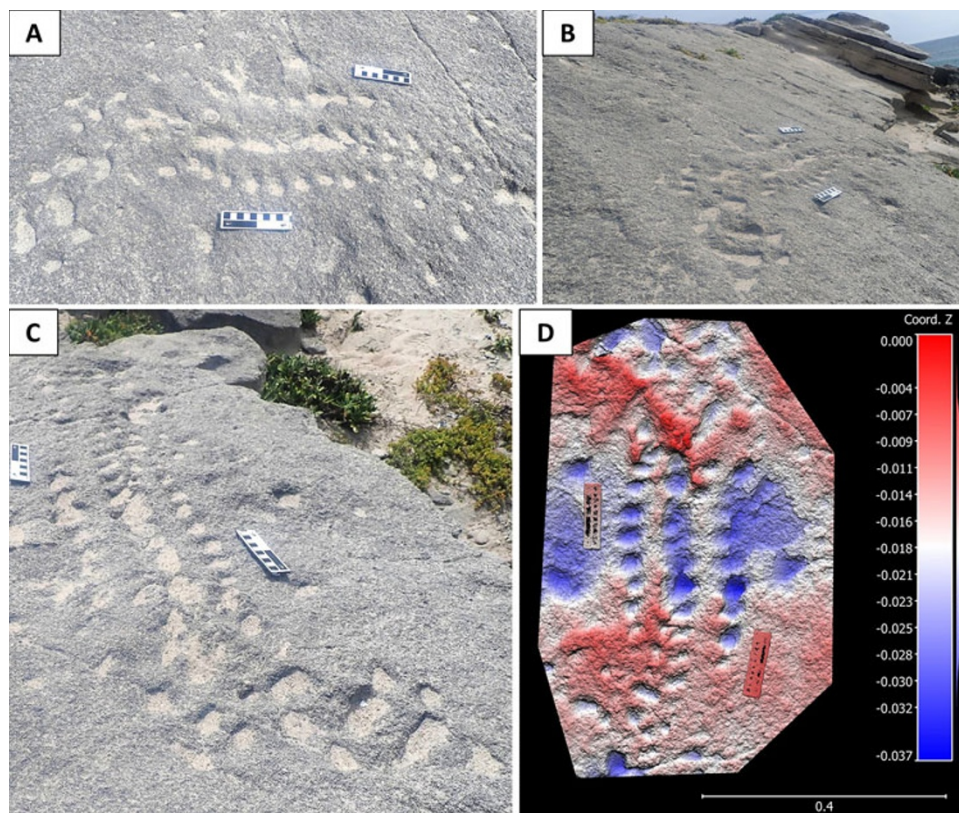
of tramline trackways from sites 1a, 1c, and 2. Furthermore, Site 1b would possibly have shown similar evidence had the track-bearing surface been of sufficient size. Line drawings of the features at Site 1a, 1b, 1c, and Site 2 are presented in Figure 12.

### Geoheritage value

The importance of the Cape south coast ichnosites in the preservation of regional and global geoheritage has been addressed (Helm et al., 2024b). The loose block containing the previously reported main large-tortoise trackway has slumped inexorably into the sea (Helm et al., 2023a). This focuses attention on the three track-bearing surfaces described here. Photogrammetry, which provides a non-invasive means of data recording, has been performed on all three surfaces. Therefore, data from all three ichnosites are replicable and are potentially available for exhibition. Nonetheless, the



**Figure 8.** (A) The Site 1b track-bearing slab, showing the 'toe-tip trace' pattern of a large tortoise trackmaker; the two scale bars on the left = 10 cm, and the distance between the outer black circles in the right scale bar = 10 cm. (B) 3D photogrammetry model of the large-tortoise traces at Site 1b; horizontal and vertical scales are in meters.

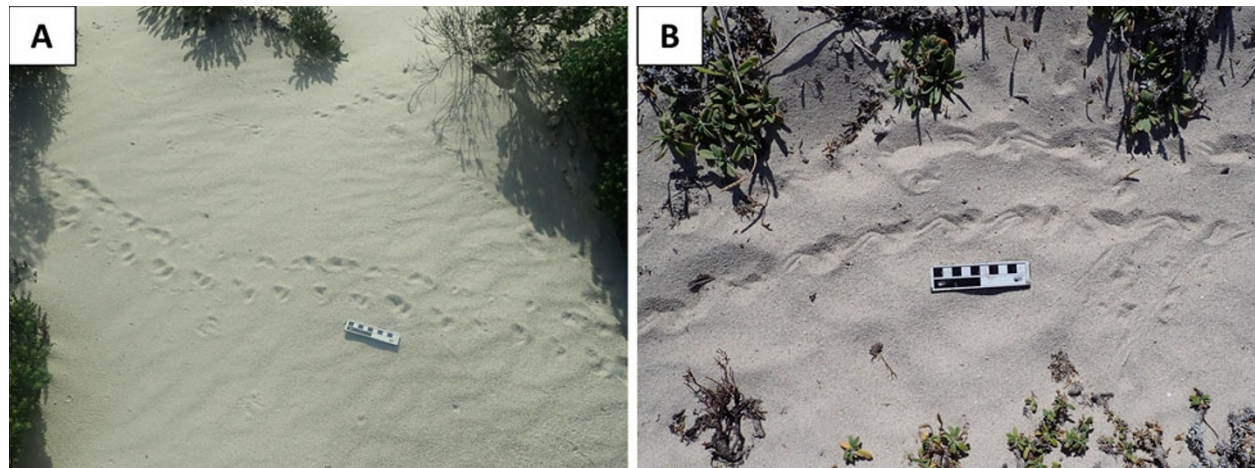


**Figure 9.** (A–C) Views from different angles of the Site 1c tracks, scale bars = 10 cm. (D) 3D photogrammetry model of the Site 1c tracks; horizontal and vertical scales are in meters.

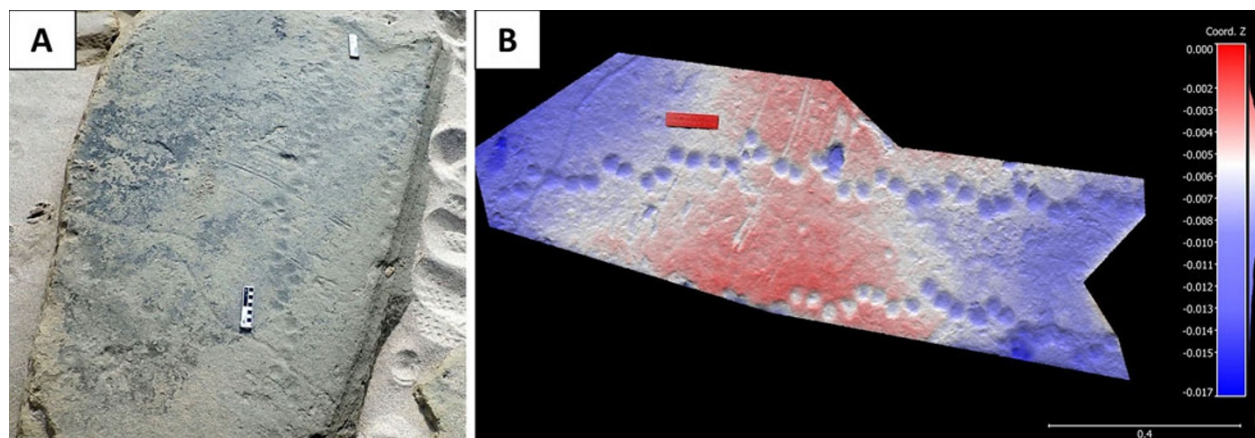
merits of physical recovery and curation in a suitable repository need to be considered and weighed against the risk of damage during recovery.

Despite the global importance associated with being the only currently known sites that exhibit the typical tortoise trackway morphology, the Site 1c surface is *in situ* and the Site 2 surface, although on a loose slab, is remote, heavy, and would probably require helicopter retrieval. In contrast, the loose slabs containing

the Site 1a and Site 1b tracks are lighter and more manageable, and vehicle access to within 20 meters of the site could be provided. Given that the Site 1b loose slab provides the only remaining evidence of a very large tortoise trackmaker in southern Africa, and that the Site 1a loose slab contains the only currently known, easily recoverable example in the world of a fossilized tramline trackway registered by a tortoise, their recovery and safe curation should be viewed as a priority.



**Figure 10.** (A and B) Medium-sized tortoise trackways in unconsolidated sand near Site 1; scale bars = 10 cm. Numerous longitudinal claw-drag impressions are evident in (B).



**Figure 11.** (A) The tramline trackway at Site 2 in the De Hoop Nature Reserve; scale bars = 10 cm. (B) 3D photogrammetry model of the Site 2 traces; horizontal and vertical scales are in meters.

### Quaternary megafauna extinctions

Several large vertebrate species are known through the body fossil record to have become extinct in the region during the Quaternary, with accompanying loss of biodiversity (Klein, 1980; Faith, 2014). In some cases, the trace fossil record corroborates the regional body fossil record: identifying the tracks of the giant Cape zebra (*Equus capensis*) or long-horned buffalo (*Syncerus antiquus*) are obvious examples (Helm et al., 2018, 2023b, c). Likewise, tracks consistent with those of a very large suid are probably attributable to *Metridiochoerus*, the extinct giant warthog, and will be reported elsewhere.

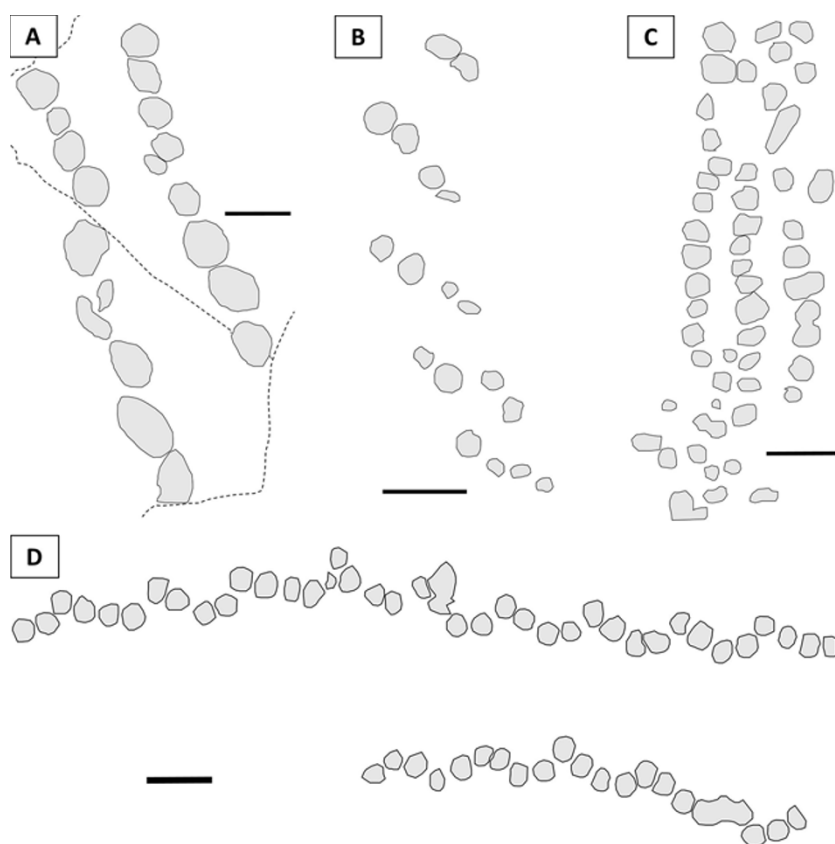
In contrast, thus far there is no evidence in the body fossil record of the existence of larger-than-expected birds or very large tortoises, yet the trace fossil record provides regional evidence of their passage (Helm et al., 2020). In the case of birds, this may be consistent with a global trend (Tyrberg, 2007), and tortoise giantism has been a recurring theme in the fossil record (Itescu et al., 2014; Vlachos and Rabi, 2018). Our ichnological observations also support the presence of larger-than-expected marine invertebrates and terrestrial invertebrates, which will be reported elsewhere.

Whether the large tortoise trackmaker described here is an extinct species or a large variant, it most certainly is no longer

present today, providing an example (unsuspected from the body fossil record) of faunal turnover and possible extinction during the late Quaternary. The most comprehensive summary of African megafaunal extinction (Faith, 2014) predated our discovery of ichnological evidence of very large tortoises on the Cape south coast. Intriguingly, there is evidence in the Australian record of both Quaternary megafauna extinctions and dwarfing of other lineages (Webb, 2008). As the track record of very large tortoises in Cape south coast aeolianites hopefully expands over time, this topic can be productively revisited.

### Conclusions

The ichnosites described here serve three major functions. Firstly, Site 1a, Site 1c, and Site 2 provide the first paleoichnological examples of the prototypical tortoise trackway, which comprises a tramline appearance with a wide straddle and closely spaced tracks. Secondly, Site 1b provides a second example of very large, fossilized tortoise tracks, bolstering the contention that either an extinct species or a large chrono-subspecies of the leopard tortoise inhabited what is now the Cape south coast during the Pleistocene.



**Figure 12.** Line drawings of the features described in the text. (A) Site 1a; scale bar = 5 cm; dashed lines indicate cracks in the surface or the edges of the surface. (B) Site 1b; scale bar = 10 cm. (C) Site 1c; scale bar = 10 cm. (D) Site 2; scale bar = 10 cm.

Thirdly, Site 2 provides another probable example of a leopard tortoise registering tracks in the region during the Pleistocene, adding to the number of such sites and to the mismatch in this respect between the trace fossil record and the body fossil record. The Site 1a and Site 1b track-bearing surfaces are the most amenable to physical recovery and have substantial geoheritage value.

**Acknowledgments.** We thank the CapeNature staff of Walker Bay Nature Reserve and De Hoop Nature Reserve, and Mike Fabricius, Jeanne van Tonder, and the staff of Grootbos Private Nature Reserve, for their assistance and support. We thank Linda Helm and Guy Thesen for their perspicacity, Carina Helm for her assistance, and the Discovery Wilderness Trust for funding the visit of San Indigenous Master Trackers from Namibia to the Cape south coast. We thank Greg Botha, an anonymous Reviewer, and Associate Editor Tyler Faith for their thorough reviews and insightful comments: incorporating their suggestions led to an improved manuscript. We cherish our memories of our co-author Steve Kunta, who passed away in 2025.

## References

- Branch B., 1994. *Field Guide to the Snakes and Other Reptiles of Southern Africa*. Struik, Cape Town, 326 p.
- Branch, B., 2016. *Tortoises Terrapins and Turtles of Africa*. Struik Publishers, Cape Town, 128 p.
- Cawthra, H.C., Cowling, R.M., Andò, S., Marean, C.W., 2020. Geological and soil maps of the Palaeo-Agulhas Plain for the Last Glacial Maximum. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), *The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem*. *Quaternary Science Reviews* **235**, 105858. <https://doi.org/10.1016/j.quascirev.2019.07.040>
- Faith, J.T., 2014. Late Pleistocene and Holocene mammal extinctions on continental Africa. *Earth-Science Reviews* **128**, 105–121. <https://doi.org/10.1016/j.earscirev.2013.10.009>
- Fleming, K., Johnston, P., Zwart, D., Yokoyama, Y., Lambeck, K., Chappell, J., 1998. Refining the eustatic sea-level curve since the Last Glacial Maximum using far- and intermediate-field sites. *Earth and Planetary Science Letters* **163**, 327–342. [https://doi.org/10.1016/S0012-821X\(98\)00198-8](https://doi.org/10.1016/S0012-821X(98)00198-8)
- Helm, C.W., 2023. Pleistocene vertebrate trace fossils from the Cape south coast of South Africa: inferences and implications. Ph.D. thesis, Nelson Mandela University, George, South Africa, 400 p.
- Helm, C.W., McCrea, R.T., Cawthra, H.C., Thesen, G.H.H., Mwankunda, J.M., 2018. Late Pleistocene trace fossils in the Goukamma Nature Reserve, Cape south coast, South Africa. *Palaeontologia Africana* **52**, 89–101.
- Helm, C.W., Lockley, M.G., Cawthra, H.C., De Vynck, J.C., Helm, C.J.Z., Thesen, G.H.H., 2020. Large Pleistocene avian tracks on the Cape south coast of South Africa. *Ostrich* **91**, 275–291.
- Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Lockley, M.G., Stear, W., Venter, J.A., 2023a. Large Pleistocene tortoise tracks on the Cape south coast of South Africa. *Quaternary Research* **112**, 93–110. <https://www.doi.org/10.1017/qua.2022.50>
- Helm, C.W., Bateman, M.D., Carr, A.S., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Lockley, M.G., Stear, W., Venter, J.A., 2023b. Pleistocene fossil snake traces on South Africa's Cape south coast. *Ichnos* **30**, 98–114. <https://doi.org/10.1080/10420940.2023.2250062>
- Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Gräbe, P.-J., Thesen, G.H.H., Venter, J.A., 2023c. Tracking the extinct giant Cape zebra (*Equus capensis*) on the Cape south coast of South Africa. *Quaternary Research* **114**, 178–190. <https://doi.org/10.1017/qua.2023.1>
- Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., 2024a. Late Pleistocene vertebrate trace fossils of the Walker Bay Nature Reserve. *Palaeontologia Africana* **58**, 37–52. <https://hdl.handle.net/2381/27959250>
- Helm, C.W., Carr, A.C., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Lockley, M.G., Rust, R., Stear, W., Thesen, G.H.H., Van Berkel, F., Venter, J.A., 2024b. Pleistocene ichnological geoheritage in national parks on the Cape coast. *Koedoe* **66**, a1786. <https://doi.org/10.4102/koedoe.v66i2.1786>
- Helm, C., Cawthra, H., Daqm, #., De Vynck, J., NAmce, /., Thompson, C., 2025a. A Pleistocene hyenid trackway from the Cape south coast of

- South Africa. *Quaternary Research* **123**, 59–69. <https://doi.org/10.1017/qua.2024.31>
- Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Gräbe, P.-J., Rust, R., Stear, W., 2025b. Pleistocene aardvark (*Orycteropus afer*) burrow traces on South Africa's Cape coast. *Quaternary Research* **124**, 139–152. <https://doi.org/10.1017/qua.2024.48>
- Hofmeyr, M.D., 2009. *Chersina angulata* (Schweigger 1812)—angulate tortoise, South African bowsprit tortoise. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., Mittermeier, R.A. (Eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs **5**, 030.1–030.6. <http://dx.doi.org/10.3854/crm.5.030.angulata.v1.2009>
- Itescu, Y., Karraker, N.E., Raia, P., Pritchard, P.C., Meiri, S., 2014. Is the island rule general? Turtles disagree. *Global Ecology and Biogeography* **23**, 689–700. <https://doi.org/10.1111/geb.12149>
- Klein, R.G., 1980. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. *Annals of the South African Museum* **81**, 223–83.
- Klein, R.G., 1986. Carnivore size and Quaternary climatic change in southern Africa. *Quaternary Research* **26**, 153–170.
- Klein, R.G., Cruz-Uribe, K., 2000. Middle and Later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* **38**, 169–195. <https://doi.org/10.1006/jhev.1999.0355>
- Klein, R.G., Avery, G., Cruz-Uribe, K., Halkett, D., Parkington, J.E., Steele, T., Volman, T.P., Yates, R., 2004. The Ysterfontein 1 Middle Stone Age site, South Africa, and early human exploitation of coastal resources. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 5708–5715. <https://doi.org/10.1073/pnas.0400528101>
- Liebenberg, L., 2000. *A Photographic Guide to Tracks and Tracking in Southern Africa*. Struik Publishers, Cape Town, 144 p.
- Malan, J.A., 1989. *Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group)*. South African Committee for Stratigraphy (SACS), Lithostratigraphic Series **8**, 1–10. Department of Mineral and Energy Affairs, Geological Survey, Pretoria.
- Malan, J.A., 1990. *The Stratigraphy and Sedimentology of the Bredasdorp Group, Southern Cape Province, South Africa*. M.Sc. thesis, University of Cape Town, 197 p.
- Malan, J.A., 1991. *Lithostratigraphy of the Klein Brak Formation (Bredasdorp Group)*. South African Committee for Stratigraphy (SACS), Lithostratigraphic Series **13**. Department of Mineral and Energy Affairs, Geological Survey, Pretoria.
- Marean, C.W., Cowling, R.C., Franklin, J., 2020. 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, A.J., Cawthra, H.C. (Eds.), *The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem*. *Quaternary Science Reviews* **235**, 106161. <https://doi.org/10.1016/j.quascirev.2019.106161>
- Matthews, N.A., Noble, T.A., Breithaupt, B.H., 2016. Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), *Dinosaur Tracks: The Next Steps*. Indiana University Press, Bloomington, pp. 28–55.
- Roberts, D., Cole, K., 2003. Vertebrate trackways in Late Cenozoic coastal eolianites, South Africa. XVI INQUA Congress, Reno, Nevada. *Geological Society of America Abstracts with Programs*, **70**(3), 196.
- Roberts, D.L., Cawthra, H., Musekiwa, C., 2013. Dynamics of late Cenozoic aeolian deposition along the South African coast: a record of evolving climate and ecosystems. In: Martini, I.P., Wanless, H.R. (Eds.), *Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences*. *Geological Society of London Special Publication* **388**, 353–387.
- Slavenko, A., Tallwin, O.J.S., Itescu, Y., Raia, P., Meiri, S., 2016. Late Quaternary reptile extinctions: size matters, insularity dominates. *Global Ecology and Biogeography* **25**, 1308–1320.
- Stuart, C., Stuart, T., 2019. *A Field Guide to the Tracks and Signs of Southern and East African Wildlife*. Struik Nature, Cape Town, 488 pp.
- Thompson, J.C., Henshilwood, C.S., 2014. Tortoise taphonomy and tortoise butchery patterns at Blombos Cave, South Africa. *Journal of Archaeological Science* **41**, 214–229. <https://doi.org/10.1016/j.jas.2013.08.017>
- Tyrberg, T., 2007. The Late Pleistocene continental avian extinction—an evaluation of the fossil evidence. *Oryctos* **7**, 249–269.
- van den Heever, A., Mhlongo, R., Benadie, K., Thomas, I., 2024. *Tracker Manua—A Practical Guide to Animal Tracking in Southern Africa*. Struik Nature, Cape Town, 376 pp.
- Vlachos, E., Rabi, M., 2018. Total evidence analysis and body size evolution of extant and extinct tortoises (Testudines: Cryptodira: Pan-Testudinidae). *Cladistics* **34**, 652–683.
- Webb, S., 2008. Megafauna demography and late Quaternary climatic change in Australia: A predisposition to extinction. *Boreas* **37**, 329–345. <https://onlinelibrary.wiley.com/doi/epdf/10.1111/j.1502-3885.2008.00026.x>