Late Pleistocene vertebrate trace fossils of the Walker Bay Nature Reserve

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In the Walker Bay Nature Reserve, on South Africa's Cape southwest coast, a suite of 25 Pleistocene ichnosites has been identified in aeolianite deposits. Dating from one site using optically stimulated luminescence indicates an age of 76 ± 5 ka. Highlights, indicating the global importance of the reserve, include a possible hominin tracksite and the first reported occurrence of fossil snake traces and tortoise tracks. The ichnological findings can be correlated with the substantial archaeological record from the nearby Die Kelders Cave. Elephant tracks are reported from several sites, but are not present in the archaeological record, whereas the plentiful occurrence of burrow traces of appropriate size corroborates the body fossil record from archaeological deposits, in which the Cape dune molerat predominates. The protected nature of the region allows for opportunities for conservation and education. Photogrammetry represents a non-invasive means of preserving and replicating the ichnological findings.

Keywords: Late Pleistocene, aeolianites, hominin tracks, snake traces, burrow traces, OSL dating.

INTRODUCTION

Among the almost 40 published works on Pleistocene trace fossils along South Africa's Cape south coast, two describe the vertebrate ichnological findings in CapeNature reserves. These respectively report on the Goukamma Nature Reserve (Helm *et al*. 2018a) and the Robberg Nature Reserve (Helm *et al*. 2019a). Such articles, representing the understanding of an area at a point in time, may form a benchmark, or at least a point of departure, for further studies.

Pleistocene vertebrate ichnosites have also been found in the Geelkrans Nature Reserve and De Hoop Nature Reserve and are due to be described. The findings and publications form part of the Cape south coast ichnology project, conducted under the auspices of the African Centre for Coastal Palaeoscience at Nelson Mandela University. Since 2008, this project has identified more than 350 vertebrate tracksites within Pleistocene coastal deposits, spanning 350 km of coastline between Arniston in the west and the Robberg Peninsula in the east.

In 2022 a vertebrate tracksite was fortuitously identified by one of us (H.C.C.) in the Walker Bay Nature Reserve, 80 km to the west of Arniston and hence on what can be termed the Cape southwest coast. Findings from the site were reported by Helm *et al*. (2023a). The 4300 hectare Walker Bay Nature Reserve, administered by CapeNature, and contiguous with the Grootbos Private Nature Reserve, comprises six coastal parcels and in total ~17 km of coastline. The largest parcel extends from the Klein River estuary in the northwest to just north of the village of Die Kelders in the southeast (Fig. 1).

At the invitation of the management of the Grootbos Private Nature Reserve, a vertebrate ichnosite survey of the coastal deposits within the Walker Bay Nature Reserve was performed, with the support of CapeNature. In the course of this survey, 25 vertebrate ichnosites were identified. The purpose of this article is to describe these sites and discuss the Pleistocene fauna that most probably registered them.

The area is of interest in a palaeoscience context because of the archaeological findings at Die Kelders Cave (also known as De Kelders Cave or Klipgat Cave), which lies within the reserve. The cave was occupied during the Middle Stone Age (MSA) and Later Stone Age (LSA), and notably preserves early skeletal material of *Homo sapiens*. This material comprises teeth, phalanges and a mandible fragment, from a minimum of 10 individuals, mostly subadults (Grine *et al*. 1991; Grine 2000). Additionally, the site preserves a range of mammalian faunal remains (Klein & Cruz-Uribe 2000; Marean *et al*. 2000; Armstrong 2016).

The sedimentology of the cave and nearby dunes was first described by Tankard & Schweitzer (1976), and in broad terms the cave sediments comprise a basal layer of quartzite boulders ('beach'), an inter-bedded sequence of MSA sandy occupational and non-occupational layers, further layers of variously shelly quartzose sands and a capping LSA shell midden (dating to ~2 ka). In the MSA layers the occupational layers are darker, with a more

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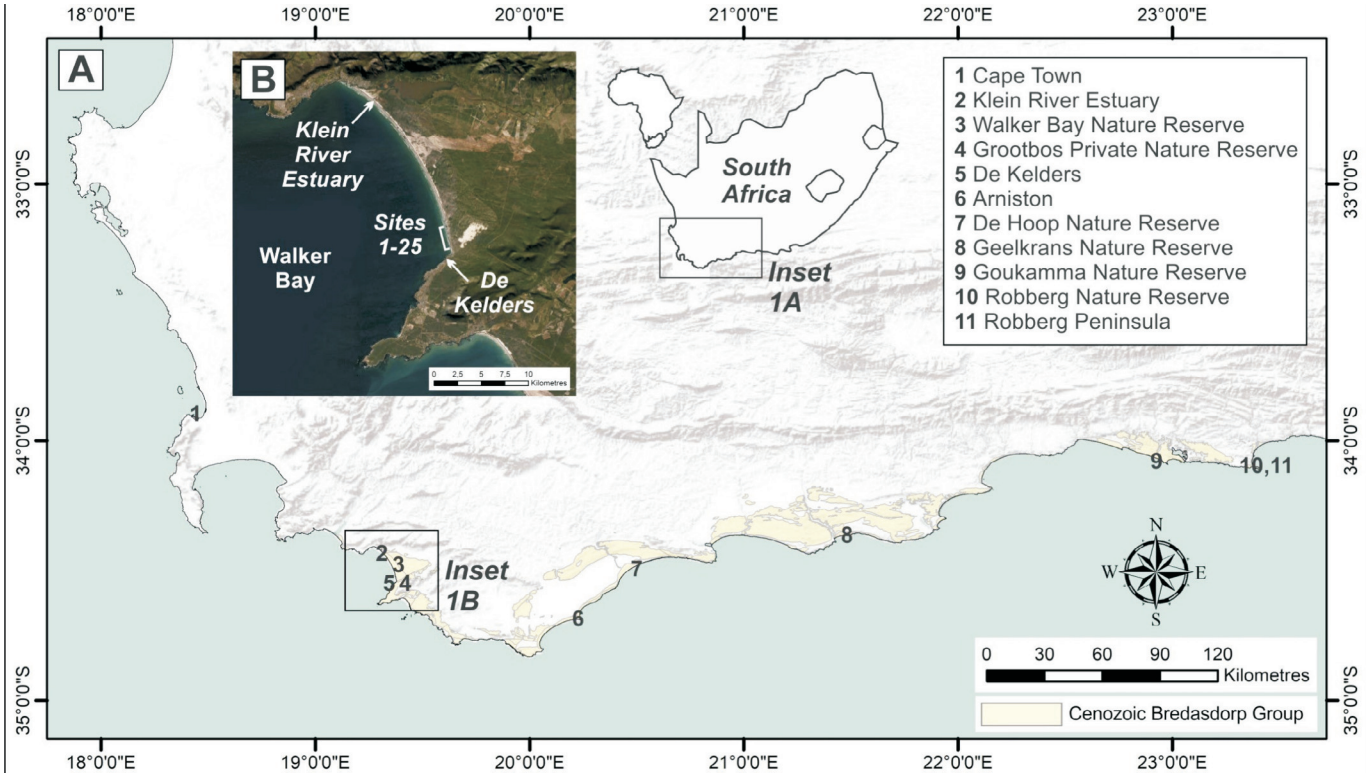

Figure 1. The Cape coast of South Africa, showing Walker Bay, sites mentioned in the text, and Cenozoic deposits of the Bredasdorp Group.

significant fine-grained sediment component. The sands are quartz-rich, sub-rounded and medium- to fine-grained. Tankard & Schweitzer (1976) interpreted the sand fraction to be largely aeolian in origin, and proposed the complete burial of the cave by dune sands for the period ~40 ka to 5 ka. The significant contribution of aeolian sands to the Die Kelders Cave sediments was subsequently corroborated by sedimentological and micromorphological analyses (Goldberg 2000). This work also demonstrated varying degrees of diagenetic alteration throughout the cave, microstratification within the 'occupational layers' and evidence for occupation within layers previously demarked as 'non-occupational'. However, both studies demonstrate the importance of the local aeolian geomorphology for the site's history.

GEOLOGICAL CONTEXT

The coastal portion of the largest sediment package in the Walker Bay Nature Reserve is composed almost exclusively of Holocene beach and dunes in the northwest, but with an increasing number of Pleistocene aeolianite outcrops and cliffs towards the southeast. The identified ichnosites occur in aeolianites of the Waenhuiskrans Formation (Malan 1989a). Pleistocene cemented foreshore deposits and/or lagoonal deposits of the Klein Brak Formation (Malan 1991) may also occur along the coastline. The two formations form part of the Cenozoic Bredasdorp Group (Malan 1990). The aeolianites and cemented beach deposits mostly comprise fine- to medium-grained, quartz-dominated clastic sandstones containing calcium carbonate derived mainly from marine shells.

Inland from the coast lie older, Plio-Pleistocene or Pliocene aeolianite deposits of the Wankoe Formation (Malan 1989b), which also forms part of the Bredasdorp Group. South of the reserve boundary Palaeozoic rocks of the Cape Supergroup are encountered.

Globally, aeolianites (cemented palaeodunes) typically occur between latitudes 20° and 40° in both hemispheres (Brooke 2001). Pleistocene aeolianites on the Cape coast form largely from stacked (often parabolic) dunes, and often include palaeosols of varying degrees of development (e.g. Roberts *et al*. 2008). These deposits have been extensively reported on (e.g. Bateman *et al*. 2004, 2011; Carr *et al*. 2007, 2010; Roberts *et al*. 2008, 2009; Cawthra *et al*. 2018) and have been shown to provide useful palaeoenvironmental and palaeoclimatic information (Roberts *et al*. 2013). Their formation seems to have been largely governed by long-term (glacial-interglacial) sea level changes, which at times moved the required sand source (sandy beaches) out onto the now submerged continental shelf.

Roberts & Cole (2003) provided a plausible explanation for the notable abundance of trace fossils in Cape coastal aeolianites. Specifically, cohesive moist sand provides an effective moulding agent, while high sedimentation rates promote swift burial of tracks. Deposits are then rapidly lithified through partial solution and re-precipitation of bioclasts, following which shoreline erosion re-exposes the track-bearing surfaces. As Quaternary tectonic activity was minimal along what is now the Cape coast (Fleming *et al*. 1998), *in situ* bedding planes can be assumed to lie close to their original angles of deposition.

A moist substrate is considered paramount to the preservation of tracks with high anatomical fidelity. Belvedere & Farlow (2016) proposed a four-point scale (0-1-2-3) in which level 3 indicates a perfectly registered and preserved track. In general, tracks made in sandy sub-

strates such as the Pleistocene Cape coastal dunes and beaches do not rise above level 2 on this scale, and many of the sites described here fall between 1 and 2 on the scale. This is related to grain size, as the finest-grained sediments have the highest potential to yield tracks of optimal quality (Helm 2023). Some palaeosurfaces on the Cape coast display a thin crust or 'veneer' of fine-grained material soon after exposure (Helm 2023). Moist sand grains may have been bound by microbial activity similar to that described by Seilacher (2008). Such veneers may have sealed surfaces of sand soon after track formation and preserved detail before burial, facilitating the subsequent separation of layers to reveal the palaeosurfaces. However, challenges in identifying the types of footprints associated with microbial mats have also been reported (Marty *et al*. 2009), leading to difficulties in distinguishing poorly defined true tracks from modified true tracks, overtracks and transmitted tracks.

Poor preservation quality of tracks and hence a lack of anatomical fidelity, in addition to resulting from the effect of substrate grain size, can also result from the erosive effects of wind, water, trampling by humans, or the passage of vehicles over track-bearing surfaces. Distinguishing the causes of relatively poor preservation (Gatesy & Falkingham 2017) is thus not always straightforward, although prolonged sub-aerial exposure of track-bearing surfaces allows more time for erosive forces to operate. In the Walker Bay Nature Reserve, we attribute poor preservation quality to both causes, although the details may vary from site to site.

At the time of registration, the ichnosites would have been situated near the margin of the Palaeo-Agulhas Plain (the landscape created by exposure of the continental shelf during periods of lower sea-level), most of which is currently submerged. Pleistocene sea-level oscillations led to substantial variability in the exposure of the Palaeo-Agulhas Plain and the location of the palaeoshoreline (Cawthra *et al*. 2020, Marean *et al*. 2020). For example, at ~91 ka the coastline at Walker Bay was 8–10 km seaward of today's coast, when sea levels were 45 m lower than at present. At ~79 ka the coastline was ~2 km from today's coast, when sea levels were ~25 m lower than at present and at the time of the Last Glacial Maximum (~20 ka), the coastline was ~40 km seaward of the modern coast (Waelbrock *et al*. 2002). At ~126 ka (the last interglacial, or Marine Isotope Stage (MIS) 5e) the coastline would have been situated inland from the present-day coast, as the sea level was 6–8 metres higher than at present (Carr *et al*. 2010). At ~400 ka during MIS 11 sea level was as much as 13 metres higher than the present (Roberts *et al*. 2013).

METHODS

Four visits were conducted to the areas of aeolianite exposures in the Walker Bay Nature Reserve between 2022 and 2024. Global Positioning System readings were obtained for tracksites using a handheld device. Measurements of track length, track width and, where appropriate, pace length and stride length were recorded (*sensu* Van den Heever *et al*. 2017; *sensu* Stuart & Stuart 2019). Burrow diameters and lengths were measured. All results were recorded in centimetres. Standard field techniques were applied in understanding the context of the ichnofossils, and strike and dip measurements of *in situ* surfaces were obtained. A sample was obtained for optically stimulated luminescence (OSL) dating. Details of the associated methodology are presented in the supplementary materials and follow those reported in Helm *et al*. (2023a,b).

Photographs were taken of tracks, and photogrammetric analysis (Matthews *et al*. 2016; Falkingham *et al*. 2018) was performed where appropriate. 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).

Locality data were reposited with the African Centre for Coastal Palaeoscience at Nelson Mandela University, and with CapeNature. Discussions were held with CapeNature and staff of the Grootbos Private Nature Reserve regarding potential preservation and education initiatives, and data were shared with Heritage Western Cape.

RESULTS

The survey focused on the 3 km stretch of coastal aeolianite cliffs at the southern end of Walker Bay. Twenty-five vertebrate ichnosites were identified. The majority of these sites were clustered in the 1.5-km-long middle portion of the surveyed coastline: the southern portion (north of Die Kelders Cave) and northern portion were largely devoid of ichnosites. Tracks were preserved as natural impressions (epirelief) or natural casts (hyporelief) and in profile, and burrows were preserved as endichnia, *sensu* Martinsson (1970). In some cases features such as displacement rims suggested that 'true tracks' were being examined, but in other cases the lack of good track preservation quality made it impossible to exclude the presence of transmitted tracks (Marty *et al*. 2016).

The sites are presented below from south to north, accompanied by brief interpretive comments, followed by a discussion of selected highlights. The level of track preservation was moderate, which is probably related to the majority of tracks having been registered in soft, relatively coarse-grained sand. Consequently, in many cases the trackmaker could not be identified to family level. In contrast, fossil burrow traces were commonly encountered and some were well preserved.

Site 1

A very rough four-wheel-drive road leads from the main parking area at the south end of the reserve to the edge of the aeolianite cliffs. *En route* the mostly sandy road crosses aeolianite surfaces. One of these contains at least five round or oval tracks in concave epirelief, without other distinguishing features, in a linear pattern (Fig. 2a). Track diameter is >30 cm. The linear pattern suggests a trackway, and the lack of distinctive morphology other than size and shape is characteristic of elephant tracks.

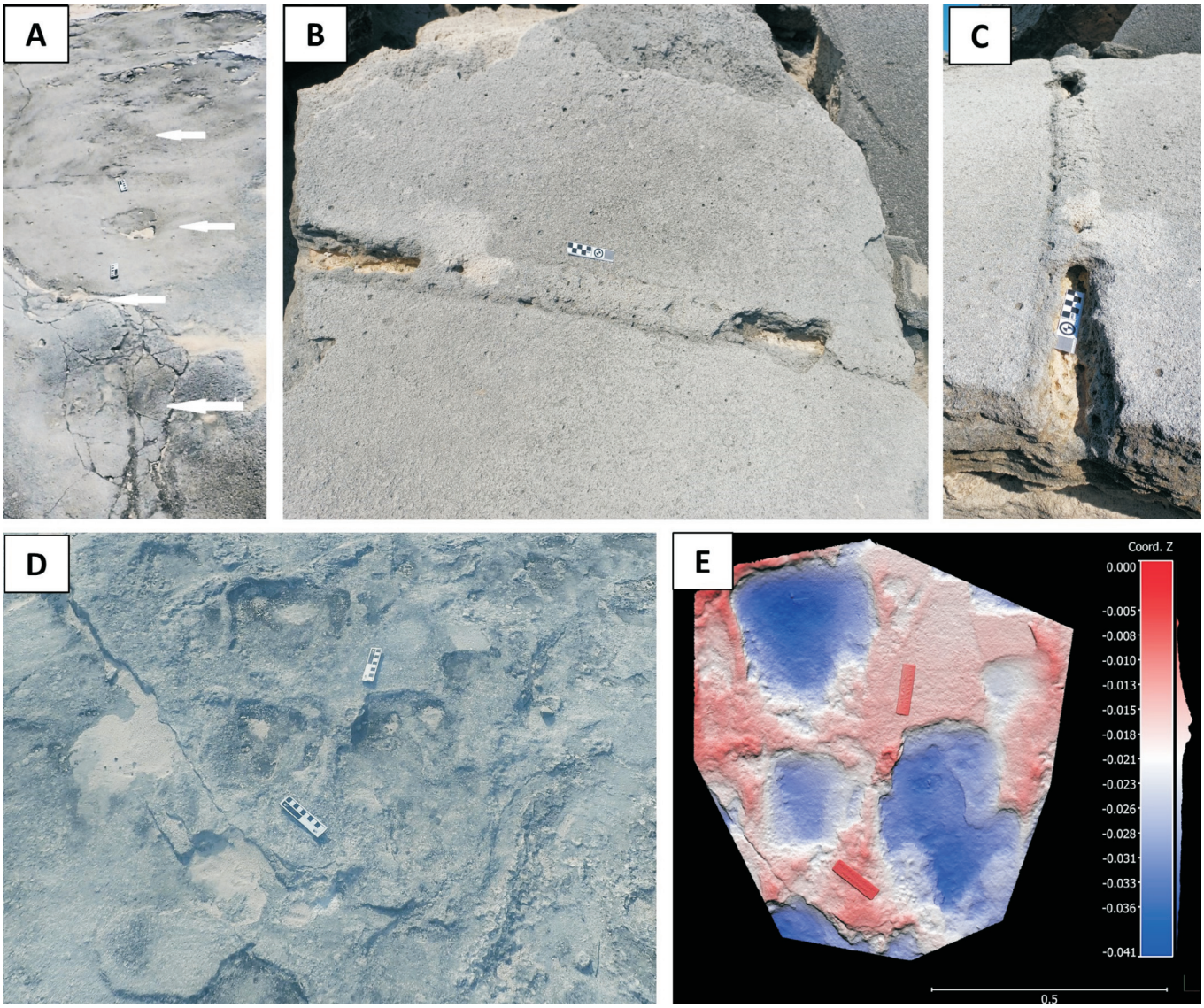

Figure 2. **A**, Arrows indicate tracks at Site 1; scale bars = 10 cm. **B** and **C**, Hollow linear feature at Site 2; scale bars = 10 cm. **D**, The site 3 possible rhinoceros tracksite; scale bars = 10 cm. **E**, 3D colour photogrammetry model of possible rhinoceros tracks at Site 3; vertical and horizontal scales are in metres.

Site 2

A loose slab contains a linear tubular structure, 140 cm in length and ~10 cm in external diameter (Fig. 2b, c). The internal diameter of ~7 cm could be measured in two areas where the wall of the structure had been eroded away. Although no tapering was noted over the length of the feature, a rhizolith could not be excluded, as there was possible evidence of an alteration in the appearance of the surrounding rock due to chemical interaction with organic plant matter (Durand *et al*. 2018; Helm 2023). Alternatively, this may represent compaction of the surrounding sediment through the passage of a fossorial species, suggesting a burrow trace. The absence of obvious claw scratch marks in the portion of the internal wall that could be visualized contributes to the equivocal nature of the structure. If it is indeed a burrow trace, the diameter suggests a golden mole origin.

Site 3

The above-mentioned road crosses another *in situ* surface, on which several large depressions occur in a linear pattern (Fig. 2d, e). The passage of many 4WD vehicles over this surface has probably contributed to erosion of these features, which are 30–40 cm in length. Due to the irregularities in their outlines, in combination with their dimensions, they resemble poorly preserved rhinoceros tracks, although a hippopotamus origin is also plausible.

Site 4

An *in situ* vertical aeolianite cliff exposure contains a near-vertical structure, 200 cm in height and 10 cm in diameter, although the lower 33 cm of the structure is wider, measuring a maximum of 25 cm in diameter (Fig. 3a). It has a mostly linear form, save for a single direction change of 45°. A loose slab at the foot of the cliff exhibits the 'counterpart' to the cliff, showing 140 cm of the structure and the above-mentioned widened portion more clearly (Fig. 3b). No tapering of the structure over its length was present, and there was no evidence of an altered appearance of the surrounding rock, i.e. there were no features to suggest a rhizolith (Durand *et al*. 2018; Helm 2020). A burrow trace, with the widened area suggesting a chamber, appears likely. If this interpretation

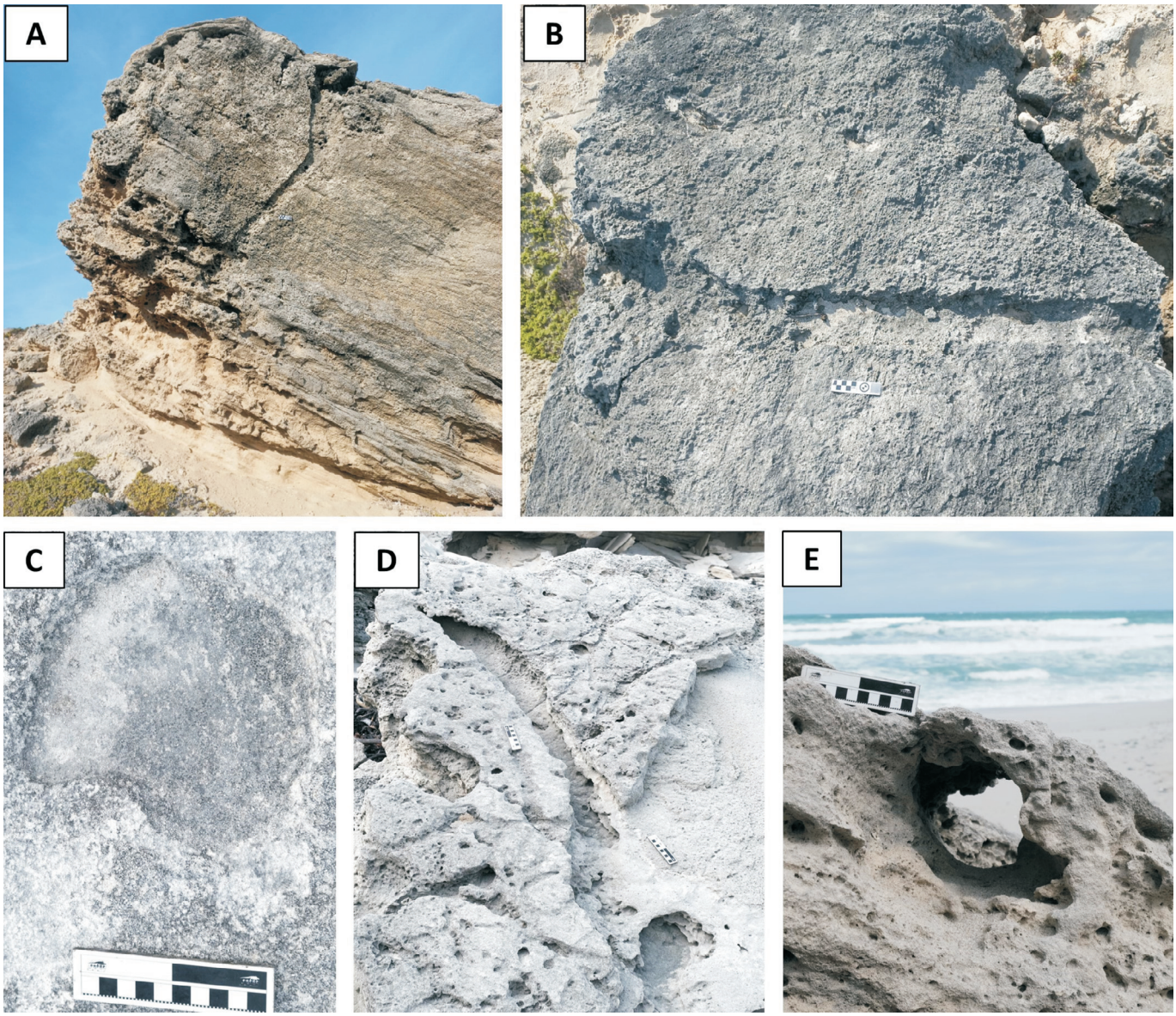

Figure 3. **A**, *In situ*, near-vertical burrow trace at Site 4. **B**, Loose slab showing the 'counterpart' and the probable chamber at the left end of the trace. **C**, A single, large, probable bovid track at Site 5. **D**, A well-preserved burrow trace at Site 6. **E**, The view from the one end of the burrow trace reveals its hollow nature. All scale bars = 10 cm.

is correct, then the burrow diameter of 10 cm suggests a molerat origin. The site will be described in more detail elsewhere.

Site 5

A single track was noted in epirelief, 14 cm long and 14 cm wide, with an outline suggestive of a large bovid track (Fig. 3c).

Site 6

A well-preserved tubular structure, 100 cm long, 10 cm in diameter, and open at both ends, was identified on the surface of a loose slab (Fig. 3d, e). As with Site 4, in the absence of any features that suggest a rhizolith, the structure is interpreted as a burrow trace, and the diameter suggests a molerat origin.

Site 7

An *in situ*, fairly level surface was crossed by three essentially parallel rows of closely spaced, round tracks ~5 cm in diameter (Fig. 4a). These are interpreted as tortoise trackways, and will be described in detail elsewhere.

Site 8

Three cavities, their centres separated by 220 cm and 135 cm, were noted in the same horizon in *in situ* deposits (Fig 4b). Cavity width and height range from 30 to 43 cm, and the greatest depth is 230 cm. They may represent large burrow traces, such as those made by an aardvark (*Orycteropus afer*). They will be described in detail elsewhere.

Site 9

A composite track (not consistent with a single impression, and hence probably representing the registration of more than one track), 13 cm long and 12 cm wide, with a prominent displacement rim, is not identifiable conclusively to family level, but a bovid origin appears likely (Fig. 4c). Other larger, unidentifiable tracks were noted on the same rock, as well as sinuous invertebrate traces.

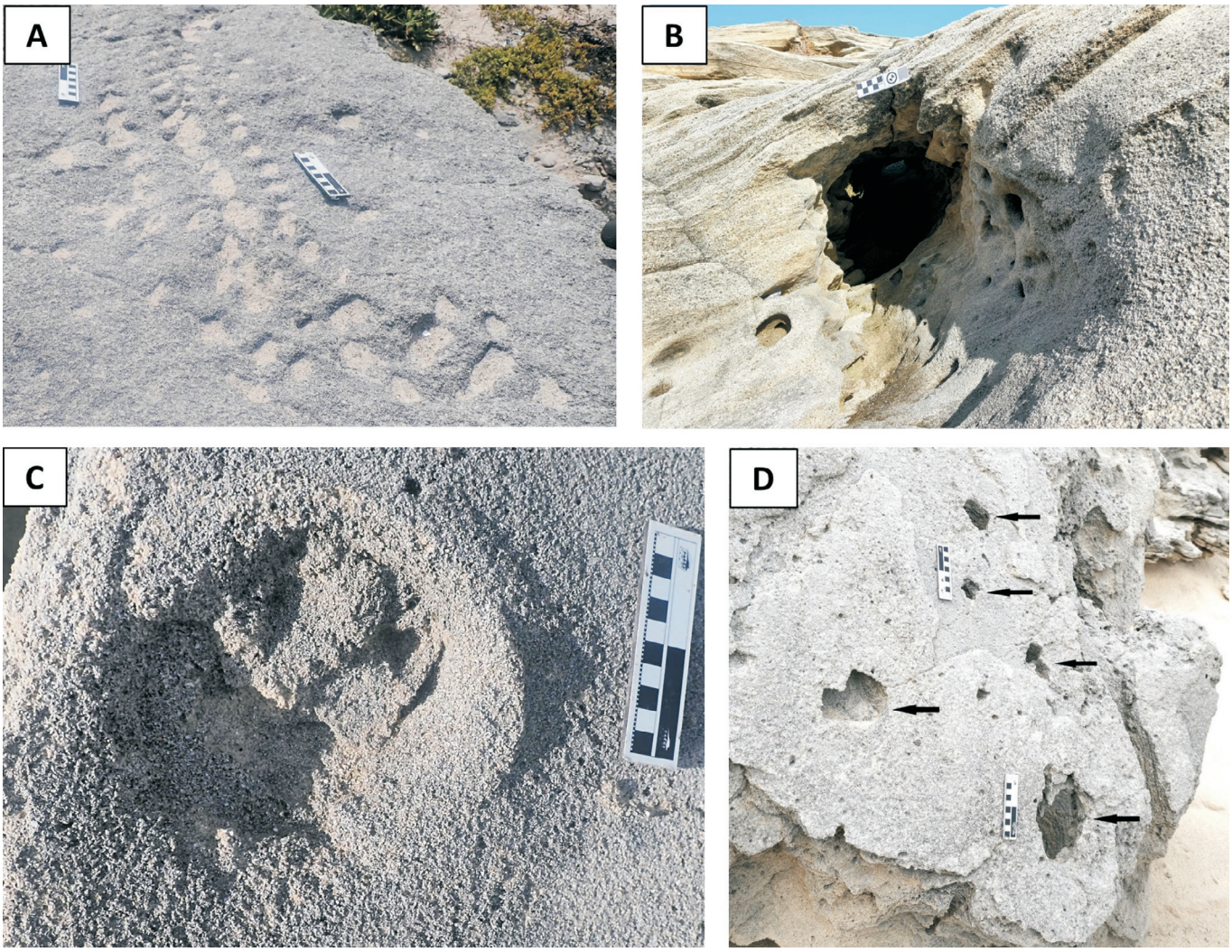

Figure 4. **A**, Angled view of tortoise tracks at Site 7. **B**, Large cavity at Site 8, interpreted as a probable aardvark borrow trace. **C**, A composite track, probably of bovid origin, at Site 9. **D**, Arrows indicate possible burrow traces of various sizes at Site 10. All scale bars = 10 cm.

Site 10

Cavities and tubular structures occur commonly in bioturbated aeolianites exposed beside a pathway down through the cliffs to the beach. Three diameters were noted: ~10–14 cm, ~6–7 cm, and ~4 cm (Fig. 4d). The discrete pattern of these diameters suggests that these are possible unfilled burrow traces, although a non-biogenic origin cannot be excluded.

Site 11

A track-bearing layer was noted in profile in an aeolianite cliff exposure (Fig. 5a). On closer inspection, some of the tracks could be viewed in convex hyporelief on the ceiling of a small overhang. The surface is fairly level, sloping slightly up to the south, with a maximum length of 118 cm (from north to south), and maximum width of 25 cm (from west to east). It is a complex site as tracks are evident in two layers.

The long axis of each of the five tracks is orientated from north to south. Two of the tracks have measurable dimensions, respectively ~20 cm long, 10 cm wide, and 6 cm deep (middle), and 21 cm long, 10 cm wide, and 8 cm deep (Fig. 5b). A pace length of 45 cm and a stride length of 88 cm could be measured. In profile, the northern ends of the tracks were slightly steeper than the southern ends, suggesting trackmaker direction from north to south. The track depth suggests that the tracks were made in soft sand, hence digit impressions would be unlikely to be preserved. Although the surface is too small to permit detailed assessment, the suggestion is of bipedal trackways with a narrow external width, and possibly consistent with hominin trackways. If this interpretation is correct, then the pace length suggests a possible walking gait. However, other origins of tracks with these dimensions cannot be excluded, such as overstepping equids (Helm *et al*. 2019b), and the limited size of the exposure implies that a quadrupedal origin cannot be excluded. A sample for OSL dating was obtained six metres south of the tracksite, 10 cm lower in stratigraphic section, as discussed below.

Site 12

A loose slab at the foot of the aeolianite cliffs contains a trackway comprising four tracks, ~5 cm in length and ~4 cm in width. Pace length varied from 28–32 cm, and stride length was 55 cm. Although some morphological detail is evident in the second and third tracks, this was insufficient to allow attribution to any family. The right track as viewed in Fig. 6a is interpreted as a transmitted track. The differential diagnosis includes small bovid and small carnivoran trackmakers.

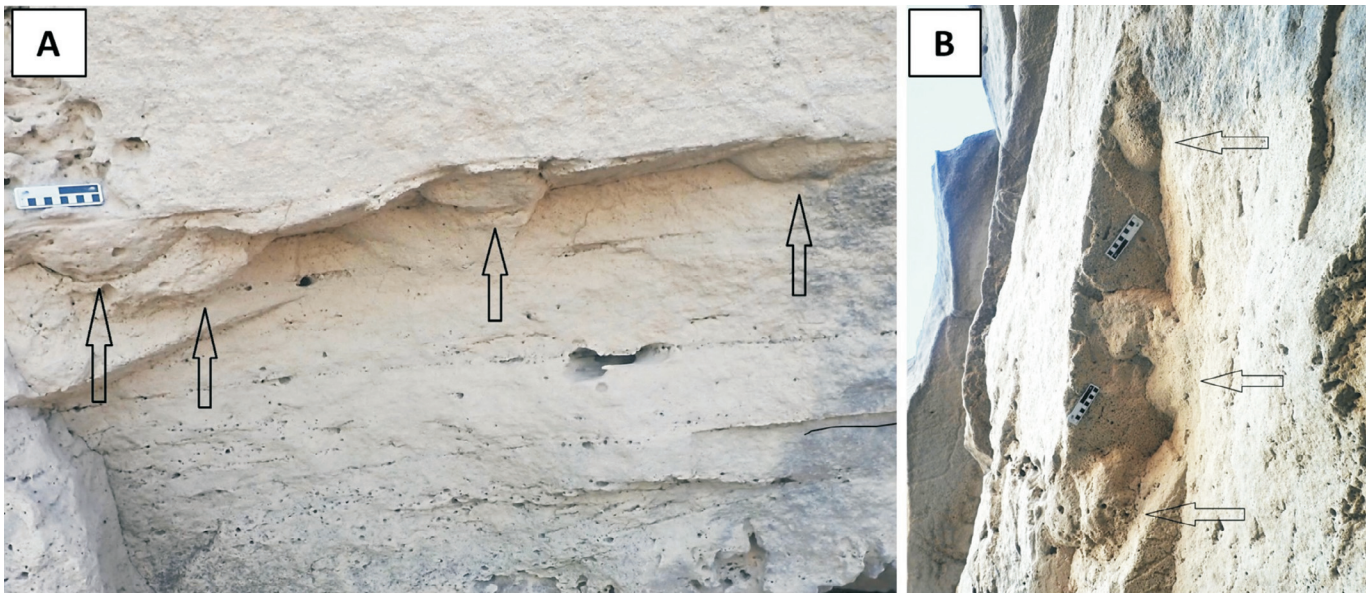

Figure 5. **A** and **B**, Arrows indicate possible hominin tracks in profile and in hyporelief at Site 11. All scale bars = 10 cm.

Site 13

Tracks are evident in profile in several horizons in the cliffs (Fig. 6b); the lower tracks just above the beach level are round and large, measuring >30 cm in diameter (Fig. 6c). They probably represent elephant tracks in profile and hyporelief.

Site 14

This site provided the first identification in the world of a fossilized surface trail of a snake, and has been described in detail (Helm *et al*. 2023a). Here a large, fallen loose slab (close to three metres in maximum width and length, and at least 40 cm thick) contains a large bovid trackway in

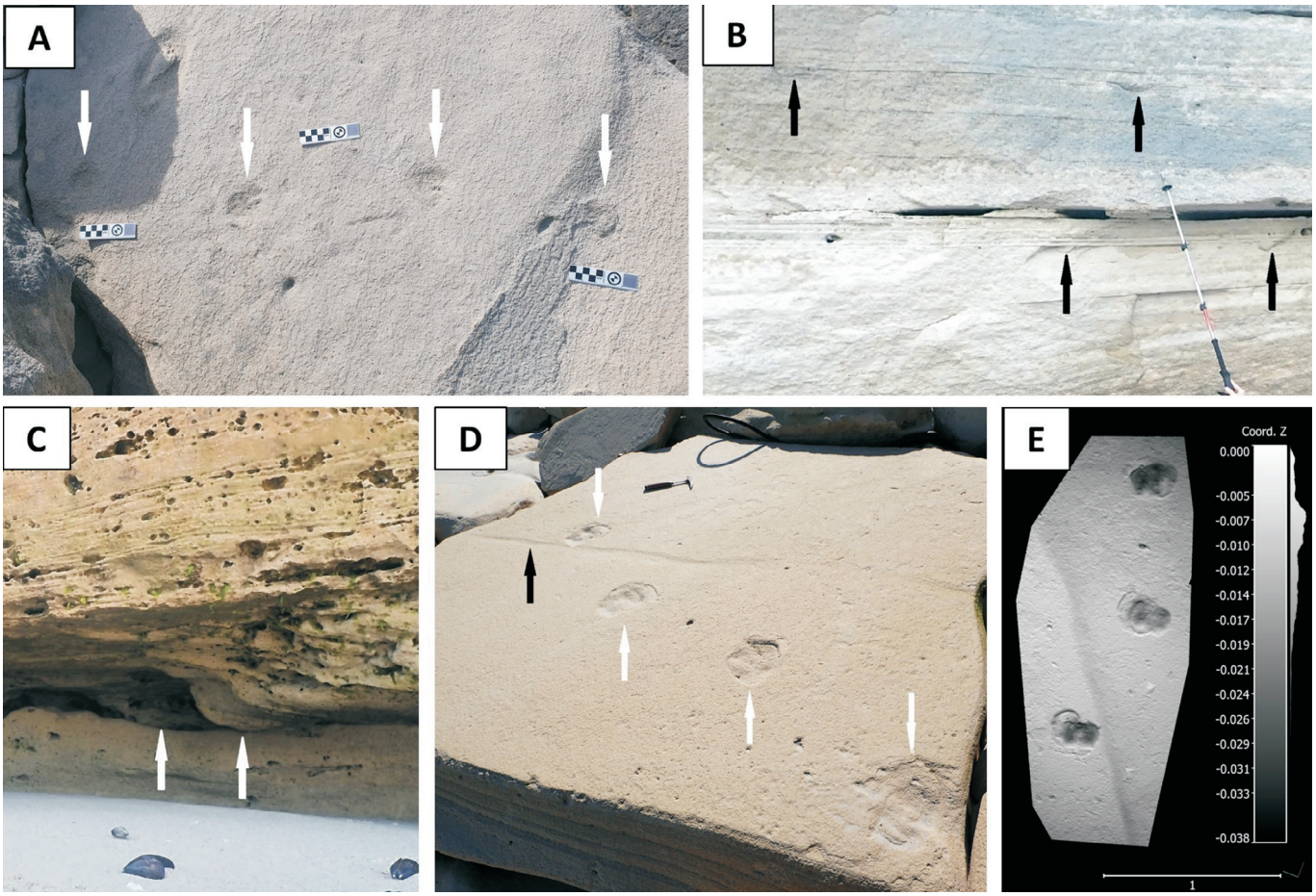

Figure 6. **A**, Arrows indicate a short trackway at Site 12; scale bars = 10 cm. **B**, Arrows indicate small tracks evident in profile in the cliff at Site 13; the length of the hiking pole = 93 cm. **C**, Arrows indicate large tracks in hyporelief under an overhang just above beach level at Site 13. **D**, White arrows indicate the large bovid trackway at Site 14, and the black arrow indicates the snake trace; the length of the geological hammer = 33 cm. **E**, 3D greyscale photogrammetry greyscale model of the Site 14 tracks and trace; vertical and horizontal scales are in metres.

epirelief, showing evidence of an interdigital sulcus (Fig. 6d, e). Five tracks are present in concave epirelief, mostly with a direct register, but showing subtle evidence in some cases of an imperfect direct register (with the hindfoot impression having been imprinted imperfectly over the forefoot impression). Track width (mean 17 cm) consistently exceeds track length (mean 13 cm); pace length was measured at ~75 cm. One of the tracks slightly distorts a long, shallower, slightly sinuous furrow feature (280 cm in length and varying from 6–9 cm in width), containing in places a narrow central groove (Fig. 6d, e). At a subsequent visit the surface was covered with a layer of algae, and at further visits the slab was algae-free but was covered by sand. The interpretation was of a long-horned buffalo (*Syncerus antiquus*) which had crossed a puff adder trail.

Site 15

A trackway of five large, unidentifiable tracks (20 cm × 20 cm) was noted to cross the upper part of a loose slab. The size and dimensions are potentially consistent with a juvenile elephant, rhinoceros or hippopotamus trackmaker. One of these exhibits downslope displacement rims (Fig. 7a).

Site 16

Three fallen slabs were noted on the beach near the high-tide mark at the base of low cliffs. The upper slab contained several oval tracks, as much as 30 cm in length, without obvious digit impressions (Fig. 7b). Possible elephant tracks are inferred. The two lower slabs were once joined. They contain oval tracks, as much as 30 cm long and 25 cm wide (Fig. 7c). Again, elephant tracks are inferred. Surrounding loose slabs contain fainter large tracks, which may have been registered by elephant, rhinoceros or hippopotamus.

Site 17

Tracks ~30 cm long and ~20 cm wide are evident on a surface above the cliff-top, where vehicles park (Fig. 7d). They suggest a tetradactyl trackmaker, possibly a hippopotamus.

Site 18

Five sets of round tracks were identified on the ceiling of an *in situ* overhang (Fig. 7e, f). Many of these appear to be 'double tracks', suggesting overprinting. While tracks preserved in convex hyporelief might be anticipated, the

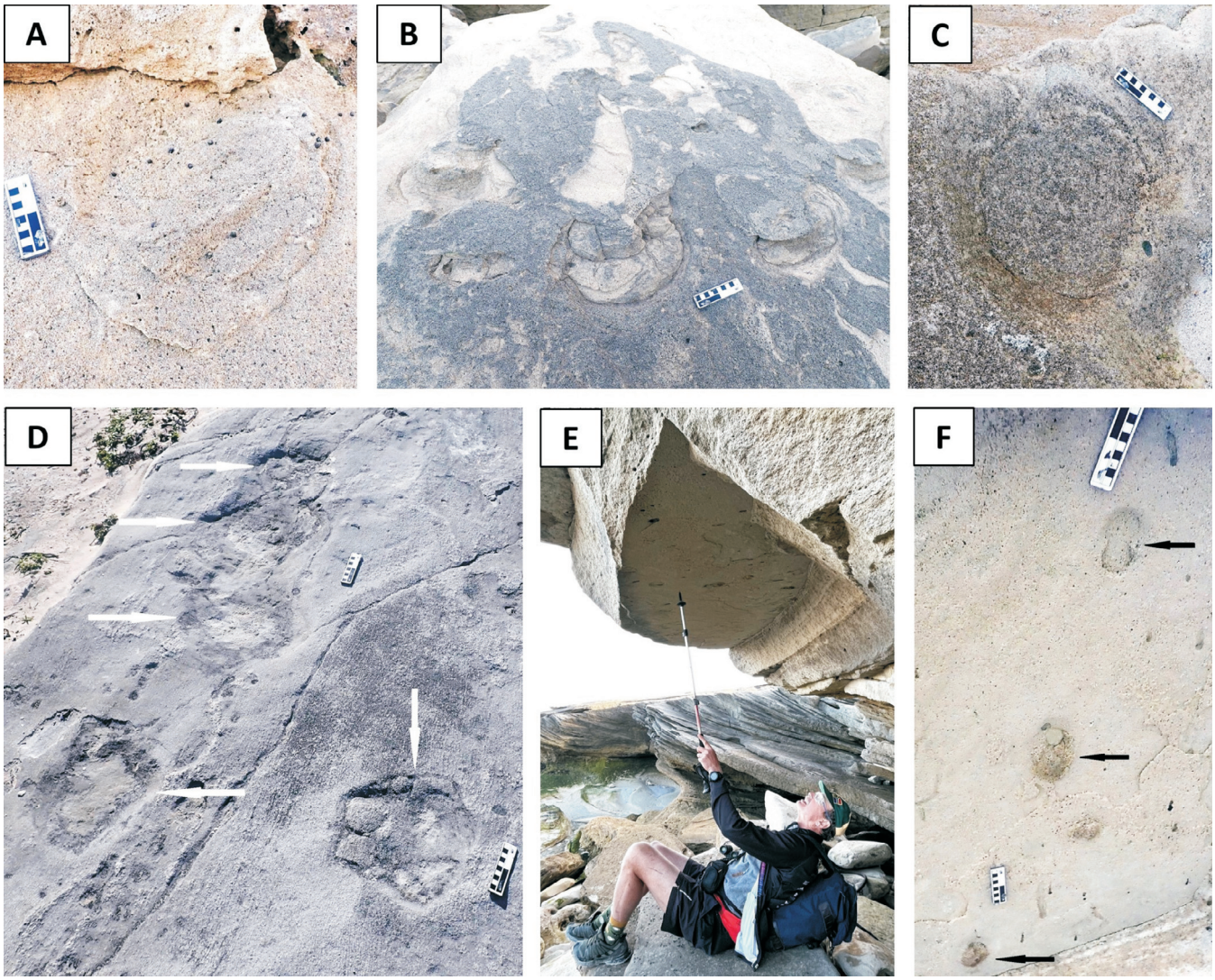

Figure 7. **A**, Large track with a substantial displacement rim at Site 15. **B** and **C**, Large tracks at Site 16, possibly attributable to elephant trackmakers. **D**, Large, probable tetradactyl track at Site 17, possibly registered by a hippopotamus. **E** and **F**, Sets of tracks, possibly registered by a carnivoran, are evident on the ceiling of an overhang at Site 18. All scale bars = 10 cm.

tracks appear as shallow indented areas on the ceiling. The most parsimonious interpretation is that the areas of track infill, initially preserved in convex hyporelief as natural casts, have broken off from the surface. A similar phenomenon has been encountered at other Cape coastal sites. Typical track length is 6 cm. The tracks may have been registered by a carnivoran, although this is not certain. Overprinting is commonly encountered in equid trackways, but the tracks are too small to have been registered by any known extant or extinct adult southern African equid.

Site 19

A single track is evident in profile and in hyporelief (Fig. 8a). It is 19 cm in length and 5 cm deep, but cannot be identified to family level.

Site 20

Three sets of paired tracks are evident on the surface of a large fallen block, measuring ~12 cm × 9–10 cm (Fig. 8b). Although poor morphological detail means that the trackmakers cannot be identified with confidence, the size and shape suggest possible large bovid tracks. The tracks are slightly raised on an epirelief surface, and hence probably represent pedestalled tracks, due to differential compaction of trampled sediments and subsequent differential erosion of non-trampled, less compacted sediment.

Site 21

This complex site contains tracks in profile and in epirelief. In one case, when viewed in profile, four layers of tracks occur close to (but not always directly above) each other over a height of 27 cm (Fig. 8c, d). The lack of direct superimposition, coupled with variation in track morphology as viewed in profile, and compared with the evidence of deformation in underlying layers evident in two cases, make the possibility of these features being transmitted tracks or overtracks most unlikely. Some of the other tracks at the site, registered in concave epirelief, contain downslope displacement rims but exhibited poor preservation detail (Fig. 8e).

Site 22

A possible trackway comprising eight tracks was noted on an epirelief *in situ* surface (Fig. 9a). While most of these are very poorly preserved, the best preserved track exhibits morphology and size consistent with tracks of the extinct giant Cape zebra, *Equus capensis*, in that it exhibits an unbroken hoof wall, and measures 13 cm in length and 12 cm in width (Fig. 9b). It can be compared with the tracks in a trackway attributed to *E. capensis* (Helm *et al*. 2023d, fig. 5).

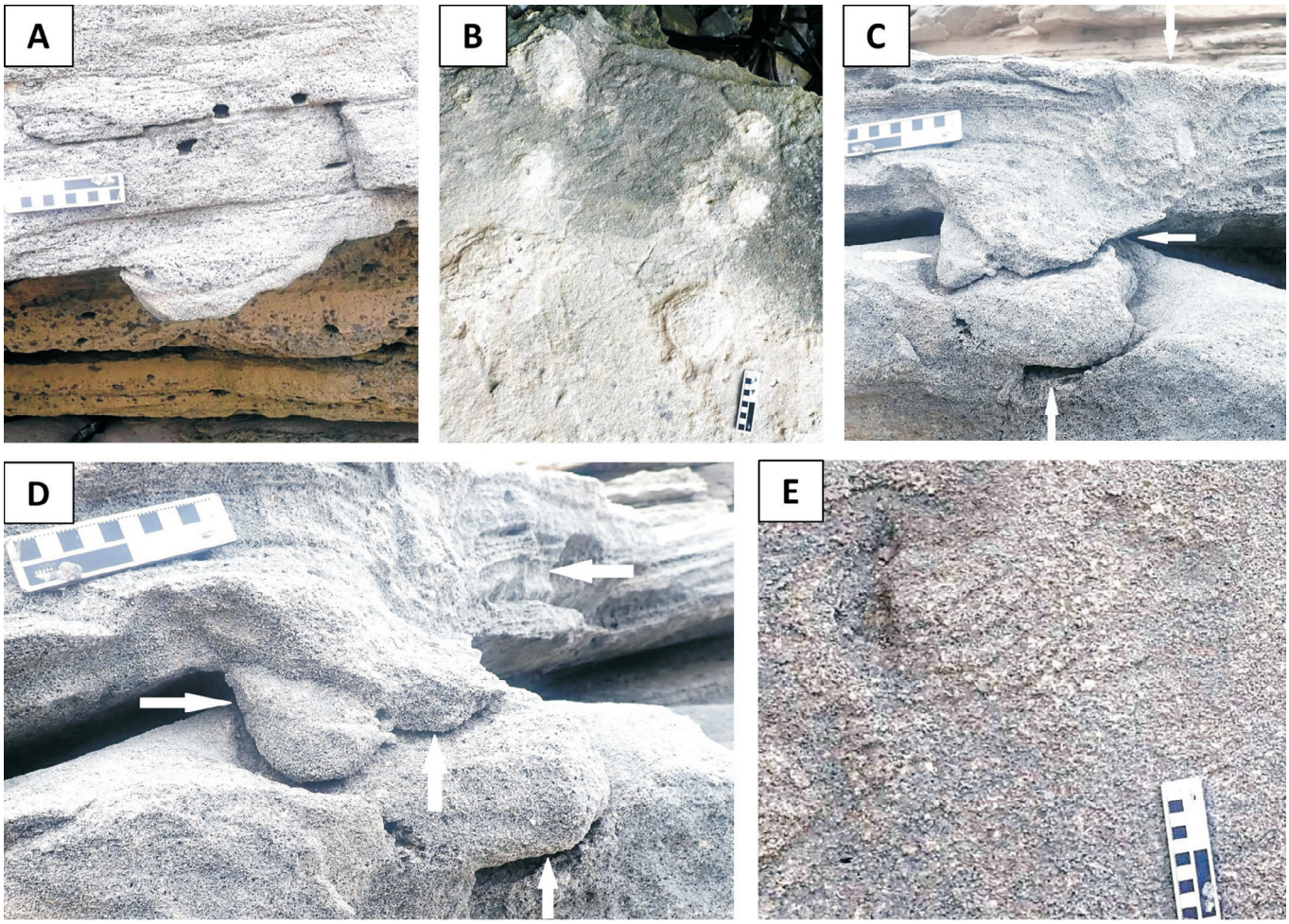

Figure 8. **A**, An unidentifiable large track at Site 19, evident in profile and in hyporelief. **B**, Paired pedestalled tracks at Site 20. **C** and **D**, Two views of superimposed tracks at Site 21, indicated by arrows; deformation of underlying layers is evident below the top right track. **E**, Poorly preserved track registered in epirelief at Site 21, with a displacement rim showing concentric arcs. All scale bars = 10 cm.

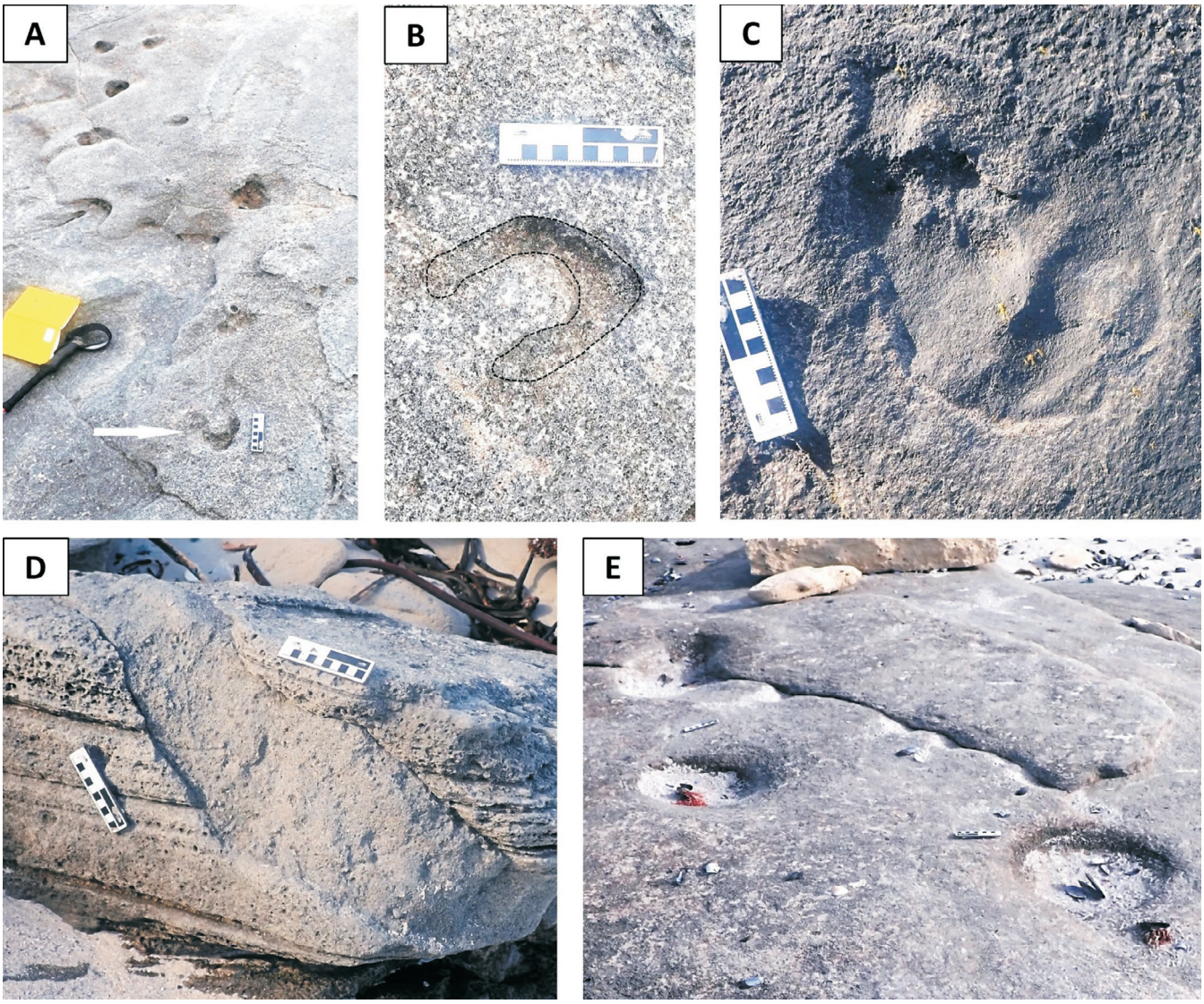

Figure 9. **A**, Arrow indicates the only well-preserved track in a possible giant Cape zebra trackway at Site 22. **B**, Line drawing of the track indicated by the arrow in A. **C**, A tridactyl, possible rhinoceros track at Site 23. **D**, A substantial, infilled burrow trace at Site 24. **E**, Round depressions in a linear pattern at Site 25, consistent with elephant tracks. All scale bars = 10 cm.

Site 23

A single track with apparent tridactyl morphology, 23 cm long and 19 cm wide, was noted on a loose slab (Fig. 9c). The apparent bifid heel impression and the impressions of the medial and lateral outer digits suggest a rhinoceros track, although the middle digit impression appears atypically 'off-centre' and not as rounded as usual for this family.

Site 24

A substantial feature, 60 cm long and 18 cm wide, was noted in profile in a loose slab in the intertidal area, causing a break in the architecture of the surrounding bedding planes (Fig. 9d). It is interpreted as a completely infilled burrow trace. The infilled sediments may represent burrow back-filling by a fossorial species, or subsequent filling of a hollow burrow through wave action. In the latter case the surrounding deposits would need to have already undergone substantial cementation.

Site 25

Eight rounded depressions, ~30 cm in diameter, without digit depressions, were noted in linear patterns (Fig. 9e). While the lack of morphological detail may be related to poor preservation quality, the linear patterns suggest trackways, and the amorphous nature of the features is consistent with elephant tracks, which only exhibit digit impressions in very well-preserved cases.

Although not the focus of the survey, note is made here of well-preserved invertebrate traces three metres to the south of Site 11 and on the same horizon (Fig. 10a). Fossilized remnants of trees and roots were noted in several places. Furthermore, the capacity of Waenhuiskrans Formation aeolianites in the Walker Bay to preserve not just fossil tracks, but also fossil bone, has recently been confirmed. Mike Fabricius, a guide at the Grootbos Private Nature Reserve, identified a vertebra (Fig. 10b) and a probable humerus (Fig. 10c) embedded in a fallen aeolianite block north of Die Kelders Cave in 2023. An intensive search could yield further skeletal material.

DISCUSSION

The cluster of 25 confirmed and potential vertebrate ichnosites along less than 2 km of coastline represents a

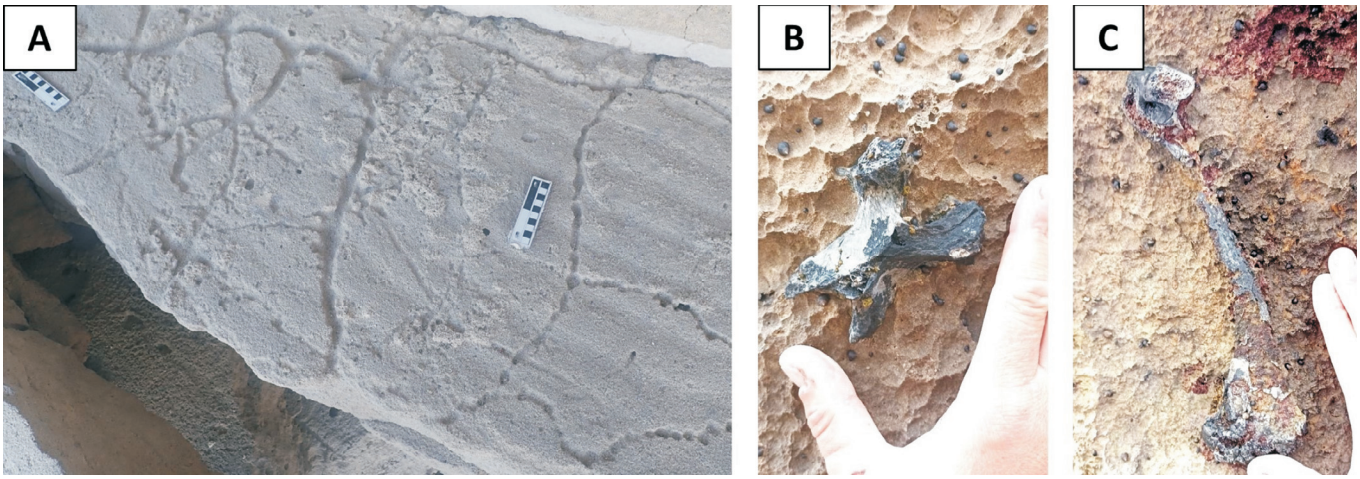

Figure 10. **A**, Invertebrate traces adjacent to Site 11; scale bars = 10 cm. **B** and **C**, Vertebrate fossils embedded in an aeolianite block near Die Kelders Cave: **B** shows a vertebra, and **C** a probable humerus; adult human hand for scale – the distance from the tip of the index finger to the web between thumb and index finger = 14 cm. Photographs courtesy of Mike Fabricius.

high density. Along with other stretches of Cape aeolianite coastline, it suggests an area teeming with Pleistocene life. The most noteworthy findings include a possible hominin tracksite, the first record in the global ichnological record of a snake trace (Helm *et al*. 2023a), large bovid tracks, probable large equid tracks, megafauna tracks (of elephant, possible rhinoceros, and hippopotamus), tortoise tracks, and burrow traces of various sizes. Although the quality of preservation is poor compared with tracks registered in finer-grained substrates, many tracks are nonetheless interpretable.

A temporal approach rather than a phenetic or phylogenetic approach was followed, using southern African tracking manuals (Liebenberg 2000; Van den Heever *et al*. 2017; Stuart & Stuart 2019; Gutteridge & Liebenberg 2021) as guides to the morphologies of Late Pleistocene tracks, while recognizing that through the body fossil record certain species are known to have become extinct in the interim. Furthermore, the existence of hitherto undescribed extinct Late Pleistocene species in the region, that might be apparent only in the ichnological record, needs to be considered. A cautious approach was therefore followed, whereby tracks were analysed first on their merits, followed by attempts to assign them to a trackmaker if feasible. This approach was necessarily constrained by the often-poor level of track preservation.

Possible hominin tracks

The morphology of hominin tracks in profile was addressed by Helm *et al*. (2019b). While the tracks at Site 11 may meet these criteria, the small size of the surface exposure unfortunately limits detailed interpretation and the confidence with which any conclusions can be reached. Interpretation was further facilitated by the tracks being visible in convex hyporelief, exhibiting dimensions consistent with hominin tracks and allowing for the measurement of pace length and stride length. Together these imply a possible hominin origin and a possible walking gait. The absence of digit impressions can be explained by the apparent soft, non-cohesive nature of the substrate. Tracks registered on more than one layer imply repeated use of an area over time. That the trackmaker was moving from north to south in the direction of the known archaeological site of Die Kelders Cave, 1.4 km away, may be coincidental or may indicate a preferred bearing.

This possible hominin tracksite can be added to the list of other possible, probable or unequivocal hominin tracksites on the Cape coast, currently comprising 12 sites on the east coast (Mountain 1966), south coast (Helm *et al*. 2018b, 2020, 2023c) and west coast (Roberts 2008; Helm *et al*. 2022). Situated on the Cape southwest coast, it is the first possible example to be identified between Langebaan on the west coast and Still Bay on the south coast, a direct distance of 350 km or 600 km along the coast. As discussed below, the OSL age of 76 ± 5 ka is consistent with other reported results from the region (Helm *et al*. 2023a), and establishes a benchmark for the Walker Bay coastal tracksites.

A snake trail

The first report of a fossilized snake trail was described by Helm *et al*. (2023a) from what is referred to herein as Site 14. It is therefore only briefly summarized here. As one of the bovid tracks is superimposed on the furrow, slightly deforming it, it can be concluded that the furrow feature probably predated the registration of the trackway, and that diagenetic or more recent erosional causes of the furrow feature can be excluded. The furrow dimensions and morphology suggest the passage of a large snake employing predominantly rectilinear motion. This conclusion is further confirmed by the intermittent presence of a central groove, consistent with a tail-tip impression (Van den Heever *et al*. 2017). A puff-adder (*Bitis arietans*) origin is likely. *Anguichnus linearis* gives a formal ichnotaxonomic label to this trace, representing rectilinear motion (Helm *et al*. 2023a). It currently remains the only known example of its kind.

Large bovid tracks

The tracks that form the Site 14 trackway are substantially wider than they are long, and exhibit morphology and size consistent with an extinct long-horned buffalo (*Syncerus antiquus*) trackmaker; no extant bovids in south-

ern Africa routinely register tracks that are significantly wider than they are long (Helm *et al*. 2018a). Tracks of similar size but exhibiting approximately similar length and width, as at Site 5 and Site 9, fall into an intermediate category, and could have been made either by *S. antiquus* or by the Cape buffalo (*S. caffer*).

The Site 20 tracks, if indeed they are of bovid origin, offer an intriguing list of possible trackmaker candidates. These include two extinct species, the blue antelope (*Hippotragus leucophaeus*) and giant hartebeest (*Megalotragus priscus*) and one extirpated species, the roan antelope (*Hippotragus equinus*). The mode of preservation, of pedestalling in convex epirelief, is highly unusual. The likely explanation is that the sandy sediment was compressed beneath the tracks, and that subsequent wind caused the surrounding areas to be preferentially deflated, leaving raised tracks (Lockley 1991).

Equid tracks

The only well-preserved track at Site 22 is 13 cm in length and 12 cm in width, with evidence of an unbroken hoof wall. It appears consistent with tracks of the extinct giant Cape zebra, *Equus capensis* (Helm *et al*. 2023d).

Megafauna tracks

Tracks are attributed to elephants at several sites. These identifications are made on the basis of size and shape and the absence of other defining characteristics (Helm *et al*. 2021). *Loxodonta africana* is the only candidate proboscidean trackmaker species. The tracks are of interest because elephant bones have not been detected in the skeletal record from Die Kelders Cave, as discussed below.

The possible hippopotamus tracks at Site 17 are inferred on the basis of size and possible tetradactyl morphology, although this is not certain. Probable hippopotamus (*Hippopotamus amphibius*) tracks have been identified elsewhere on the Cape coast, but perfectly preserved tracks of high anatomical fidelity are yet to be identified (Helm 2023).

If the attribution for the Site 17 tracks is correct, proximity to a water source can be inferred. Hippopotami may travel large distances by night, but return to wetland areas by day. The Klein River estuary, 11 km to the north, may have formed a suitable environment. Lenhoff (1995) showed a 3 km wide valley-like depression in the bedrock offshore of the present-day Klein River mouth, orientated in a NE–SW direction, and interpreted this feature as a submarine extension of the Klein River valley, cut into bedrock at times of lower sea levels. This depression was followed onto the shelf 8 km seaward, before being buried with sediment. Although this is smaller than the adjacent Bot River palaeochannel (Rogers 1985), an ancestral Klein River seemingly existed in this area in a similar position to today.

The partial tracks at Site 3 resemble those of a rhinoceros, but although digit impressions are plausibly identified the partial and eroded nature of these tracks precludes a confident identification. Similar considerations apply to the tracks at Site 16. The single large track at Site 23 appears to exhibit tridactyl morphology, but the middle digit impression is atypical. While these tracks are tentatively assigned to rhinoceros trackmakers, identification of further tracks would assist in confidently asserting this. Of the two southern African rhinoceros species, the black rhinoceros (*Diceros bicornis*) was historically more common than the white rhinoceros (*Ceratotherium simum*) in the southwestern Cape, and has been recorded more often in the body fossil record (Klein *et al*. 2007). The only Cape coastal fossil rhinoceros track that thus far can be identified to species level was from the Robberg Nature Reserve, and was attributed to *D. bicornis* (Helm *et al*. 2019a).

Burrow traces

Distinguishing between burrow traces and rhizoliths in Cape coastal aeolianites can be challenging, as alluded to above. Whereas clear evidence of claw scratch marks in the walls render a burrow identification essentially unequivocal (Cardonatto & Melchor 2021), these were not noted at any of the purported burrow sites described here. The absence of distinctive rhizolith attributes was therefore used to help distinguish between these phenomena.

Stuart & Stuart (2019) provide descriptions of the various extant fossorial species that inhabit southern Africa, of varying size and thus varying burrow dimensions. The available evidence on the Cape coast suggests four main groups, assigned according to burrow size (Helm 2023). The smallest burrows include those of the Cape gerbil (*Gerbilliscus afra*), as described by Lockley *et al*. (2022). Intermediate-size burrows are typically created by golden moles (Helm *et al*. 2019a), and larger burrows by the Cape dune molerat (*Bathyergus suillus*). Helm (2023) described a burrow attributed to the latter species that included probable claw scratch marks on the surface of a burrow cast. Klein & Cruz-Uribe (2000) reported that MSA molerats were larger than today's molerats, so slightly larger MSA burrow diameters can be anticipated. Cavities greater than 30 cm in diameter may represent burrows created by the aardvark (*Orycteropus afer*) and will be described in detail elsewhere.

The Walker Bay Nature Reserve aeolianites contain abundant evidence of burrow traces; only the most impressive and obvious sites have been described here. They include all four of the above-mentioned size ranges.

Tortoise tracks

The only tortoise tracks and trackways to have been reported thus far in the global ichnology record are by Helm *et al*. (2023e), who described primarily the tracks of a very large tortoise from the Cape south coast. The tracks of smaller tortoises were also described, but the typical features of a tortoise trackway (a 'tramline' trackway with two parallel lines of closely spaced tracks and a wide external width) were not recorded. Site 7 provides such evidence. Findings from the site will therefore be described in detail elsewhere.

The angulate tortoise (*Chersina angulata*), was the commonest tortoise in the region during the MSA. Its abundance in the Die Kelders Cave deposits matches that of the Cape dune molerat and led to an inference of warm, dry days, at least seasonally (Klein & Cruz-Uribe 2000). The

angulate tortoise is by far the commonest species to be reported from MSA samples in the Western Cape (Klein *et al*. (2004). For example, Thompson & Henshilwood (2014), noted an almost exclusive occurrence of this species in excavations at Blombos Cave on the coast west of Still Bay. It remains a common tortoise in the region.

Superimposition of tracks

The observation at Site 21 of four layers of tracks, appearing approximately above one another, merits further discussion. While this might be a coincidental finding, it may represent a genuine phenomenon, whereby trackmakers may preferentially walk in previously registered tracks. A possible reason might be the enhanced compression in an existing track compared to the surrounding substrate, which then provides for more efficient motion and less energy expenditure. The notion of these being transmitted tracks is not supported by the evidence at the site.

Comparing the ichnological record and the body fossil record

Klein & Cruz-Uribe (2000) provided a comprehensive list of the large mammalian and tortoise fauna from MSA deposits in Die Kelders Cave, based on a large sample-size of 174 816 bones that could be attributed to body part or taxon. This allows comparisons to be drawn between the body fossil record and the ichnological record, although the latter record remains sparse by comparison. The body fossil record from the MSA is dominated by the Cape dune molerat (*Bathyergus suillus*) and the angulate tortoise (*Chersina angulata*). Hippopotamus (*Hippopotamus amphibius*), the extinct long-horned buffalo (*Syncerus antiquus*), and extinct giant Cape zebra (*Equus capensis*) are present in both records. Ancestral MSA humans (*Homo sapiens*) can possibly be added to this list.

The possible rhinoceros tracks cannot be identified to species level. Klein & Cruz-Uribe (2000) recorded the remains of both black rhinoceros (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*) in Die Kelders Cave.

Species that are suggested in the trace fossil record that were not recorded by Klein & Cruz-Uribe (2000) include the African elephant (*Loxodonta africana*) and the aardvark (*Orycteropus afer*). Skeletal material of snakes formed a minority of the MSA fauna described by Klein & Cruz-Uribe and was not further analysed.

The absence of elephant bones in the body fossil record might represent the 'schlepp effect,' in which larger size and distance from camp are related to the probability of a carcass not being transported by humans, leading to the relative under-representation of larger animals (Perkins & Daly 1968; Parkington & Poggenpoel 1971; Thackeray (1979). Thirty-five Pleistocene elephant tracksites have previously been recorded on the Cape south coast (Helm *et al*. 2021).

OSL dating and the palaeo-coastline

Initial dating studies of the Die Kelders Cave area were performed by Feathers & Bush (2000) and Schwarcz & Rink (2000), and later re-analysed by Millard (2008). Helm *et al*. (2023a) reported five new OSL ages from aeolianites immediately above (Shfd05025) Die Kelders Cave and from a small embayment 150 m to the east (Leic13025-Leic13028). The latter group spanned a total exposed aeolianite thickness of 10 m and produced an age range spanning 93 ± 6 to 83 ± 6 ka (Helm *et al*. 2023a). All of these ages are significantly older than Tankard & Schweitzer's (1976) proposed phase of cave burial, but overlap with the upper proposed age range for the MSA occupation of the site of ~50–85 ka; Millard, 2008). These were overlain by a palaeosol, above which (cemented) Holocene dune sediments are preserved (6.1 ± 0.4 ka; Leic13027). The aeolianite ages imply a MIS 5c/5b age range, followed by a hiatus in dune accumulation during MIS 4-2, broadly consistent with reported aeolianite ages from near Cape Agulhas (Carr *et al*. 2010) and elsewhere along the Cape south coast (e.g. Bateman *et al*. 2011).

The OSL age (Leic23004) obtained in the present study was sampled six metres south of Site 9 and 1.4 km north of Die Kelders Cave, producing an age of 76 ± 5 ka (see supplementary material for details), which is within measurement uncertainties of the two younger aeolianite ages reported for the Die Kelders environs (Helm *et al*. 2023a). The two sets of results therefore buttress one another and provide a benchmark from which other sites in the reserve can be evaluated. Ideally, new samples and more extensive OSL dating will more accurately determine the ages of ichnosites.

The above ages enable an estimation of the location of the coastline at the time the tracks were registered. Using the ages of 93 ± 6 ka – 83 ± 6 ka and 76 ± 5 ka, and correlating them with the plotted coastline localities, it is likely that the coastline lay 8–10 km (~91 ka) or 2 km (~79 ka) seaward of today's coast when the tracks and traces were registered.

Can the sites described here be considered to form not just a zone of concentration of tracks, but a megatracksite (Lockley & Meyer 2022)? And is the Cape coastal palaeoenvironment sufficiently distinct to justify the proposal of a 'coastal dune and beach' ichnofacies or ichnocoenosis? For the latter, a more detailed understanding of the invertebrate ichnofauna would be required (Helm 2023) and for the former, more OSL ages would be required from Walker Bay to better delineate stratigraphic relationships. A challenge is that laterally persistent track-bearing facies are useful in classifying megatracksites, and this is a rarity in Cape coastal aeolianites unless palaeosols are present, which is not the case for the sites described here. For now, therefore, these intriguing concepts remain speculative.

Conservation and interpretation

The dating studies thus far performed provide information that is germane to the conservation importance of the reserve. The currently available data suggest a likely age range from 75 to 95 ka, a result consistent with expectations from the regional record of late Pleistocene coastal evolution and dune formation (e.g. Bateman *et al*. 2011) and (given the identified possible hominin trackway) the local and regional archaeological record (e.g. Feathers & Bush 2000; Millard 2008; Jacobs *et al*. 2020).

Regarding interpretation and education, the Walker Bay

Nature Reserve is ideally located in many respects. It lies a mere 150 km by road from the metropolis of Cape Town, and forms part of an area frequented by South African and international tourists. Die Kelders Cave, within the reserve, contains impressive interpretive exhibits that focus on Stone Age occupation of the site. Guides from the Grootbos Private Nature Reserve, which is contiguous with the Walker Bay Nature Reserve, already interpret the coastline for their clients. Furthermore, the tracksites are accessible with relative ease. These factors augur well for further education and interpretation initiatives. For example, interpretive panels on Pleistocene vertebrate ichnology could be added to the Die Kelders Cave exhibits, tourist guides could add interpretation of the tracksites to their repertoire, and CapeNature websites could include information on the fossil tracks.

While recovery and curation of selected specimens could be considered, this is often challenging and runs the risk of inadvertent destruction. Manual casting runs similar risks and has essentially become obsolete. In contrast, photogrammetric analysis forms a non-invasive, risk-free form of replication, yielding digital 3D models and the potential for creating exact replicas through 3D printing. Furthermore, obtaining repeated photogrammetric models at intervals over time can provide information on the rate of erosion of sites and the resulting deterioration in track preservation (Díaz Martínez *et al.* 2018). Collaboration with CapeNature and other interested parties provides a ready path forward.

CONCLUSIONS

The suite of 25 vertebrate Pleistocene ichnosites in the Walker Bay Nature Reserve, concentrated within less than 2 km of coastline, form an impressive zone of fossil track density. The presence of the world's currently only confirmed surface fossil snake trace (*Anguichnus linearis*) and possible fossil hominin tracks attest to the reserve's global ichnological importance. The study of the reserve's invertebrate trace fossils and a further search for body fossils offer avenues for further research.

Ichnology helps to complement and independently corroborate the traditional body fossil record from the region, including the record from the Die Kelders Cave MSA deposits, and thus enhances our understanding of both the regional Pleistocene vertebrate fauna and of the hominin presence. The area, already protected as a nature reserve, is well suited to education and interpretation initiatives. Photogrammetry provides a non-invasive means of preserving and replicating the most important sites. The ichnological richness described herein justifies repeated surveys, especially following storm surge events, in the hope of identifying newly exposed sites at an early stage when their state of preservation is optimal. Indeed, it is likely that a more intensive search will yield many more vertebrate ichnosites in the Walker Bay Nature Reserve.

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