Research Article

Morphology of Pleistocene elephant tracks on South Africa's Cape south coast and probable elephant trunk-drag impressions

Charles W. Helm[a]* 🔟, Martin G. Lockley[a,b], Lizette Moolman[c], Hayley C. Cawthra[a,d], Jan C. De Vynck[a], Mark G. Dixon[a], Willo Stear[a] and Guy H.H. Thesen[a]

[a]African Centre for Coastal Palaeoscience, P.O. Box 77000, Nelson Mandela University, Port Elizabeth 6031, South Africa; [b]Dinosaur Trackers Research Group, Campus Box 172, University of Colorado at Denver, P.O. Box 173364, Denver 80217-3364, USA; [c]Scientific Services, South African National Parks, P.O. Box 3542, Knysna 6570, South Africa and [d]Geophysics and Remote Sensing Unit, Council for Geoscience, Western Cape Regional Office, P.O. Box 572, Bellville 7535, South Africa

Abstract

Aeolianites and cemented foreshore deposits on South Africa's Cape south coast have the capacity to record and preserve events that transpired on them when they were composed of unconsolidated sand. Thirty-five Pleistocene elephant tracksites have been identified along this coastline. This abundance of sites along what was the margin of the vast Palaeo-Agulhas Plain allows for an appreciation of the forms that elephant tracks and traces can take in the context of the global proboscidean track record. They point to a significant regional elephant presence from Marine Isotope Stage (MIS) 11 (∼400 ka) through MIS 5 (∼130–80 ka) to MIS 3 (∼35 ka) and also indicate repeated use of certain dune areas. They buttress Holocene and historical evidence that elephants made use of open areas in the region, and that the remaining "Knysna elephants" retreated into dense afrotemperate forest for protection in recent centuries. Analogies can be drawn between Pleistocene elephant tracks and Mesozoic dinosaur tracks, and some of the Cape south coast elephant tracks are among the largest Cenozoic (and hence, Quaternary) tracks ever to be described. A newly identified tracksite in this area may provide the first reported evidence of elephant trunk-drag impressions.

Keywords: Pleistocene, Cape south coast, African elephant, Palaeo-Agulhas Plain, Knysna elephants, Ichnology, Tracksites, Trunk-drag impressions

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INTRODUCTION

The Cape south coast of South Africa contains an array of Pleistocene tracks and trace fossils in aeolianites (cemented dunes) and cemented foreshore deposits (e.g., Helm et al., 2020a). The capacity of these dune and beach surfaces to record events that transpired on them has been demonstrated, including the passage of humans (Helm et al., 2018a), other mammals (Helm et al., 2018b; Lockley et al., 2021), birds (Helm et al., 2017, 2020b), reptiles (Lockley et al., 2019; Helm et al., 2020c), and invertebrates (Helm et al., 2020a). Since 2007, more than 300 such coastal tracksites have been identified within a 350-km stretch of coastline that extends from the town of Arniston in the west to the Robberg Peninsula in the east (Helm et al., 2020a) (Fig. 1). Recent exploration of the coastline farther east has led to the identification of additional sites at Woody Cape in Algoa Bay (Lockley et al., 2021).

The profusion of elephant tracksites in these deposits stands in contrast to a paucity of skeletal material. To date, no Pleistocene elephant bones have been detected in these aeolianites and cemented foreshore deposits. However, an elephant tusk dated to 130 ka was found in a coastal aeolianite at Durban, ∼1000 km northeast of our study area. We are also aware of at least five occurrences of elephant skeletal material occurring in Holocene dunes in our study area (De Mond, Still Bay, Cape Vacca, Nautilus Bay, Robberg Beach).

The African bush elephant (*Loxodonta africana*) is the largest extant land mammal in the world, and adults are more than twice as heavy as any other land mammal (Prothero, 1995). Adult bulls weigh up to 6000 kg (Langman et al., 1995), and track lengths of as much as 58 cm (Liebenberg, 2000) and 57 cm (Van den Heever et al., 2017) have been reported. Roberts et al. (2008) provide the first description of fossil elephant tracks in southern Africa, from a Pleistocene site on the Cape south coast. Thirty-five Pleistocene elephant tracksites have subsequently been identified along this coastline (e.g., Helm et al., 2018c, 2019a, 2019b, 2020a). These sites would have been situated at the margin of the vast Palaeo-Agulhas Plain, which was alternately exposed and inundated during Pleistocene sea-level oscillations (Cawthra et al., 2018, 2020). The southernmost documented fossil elephant
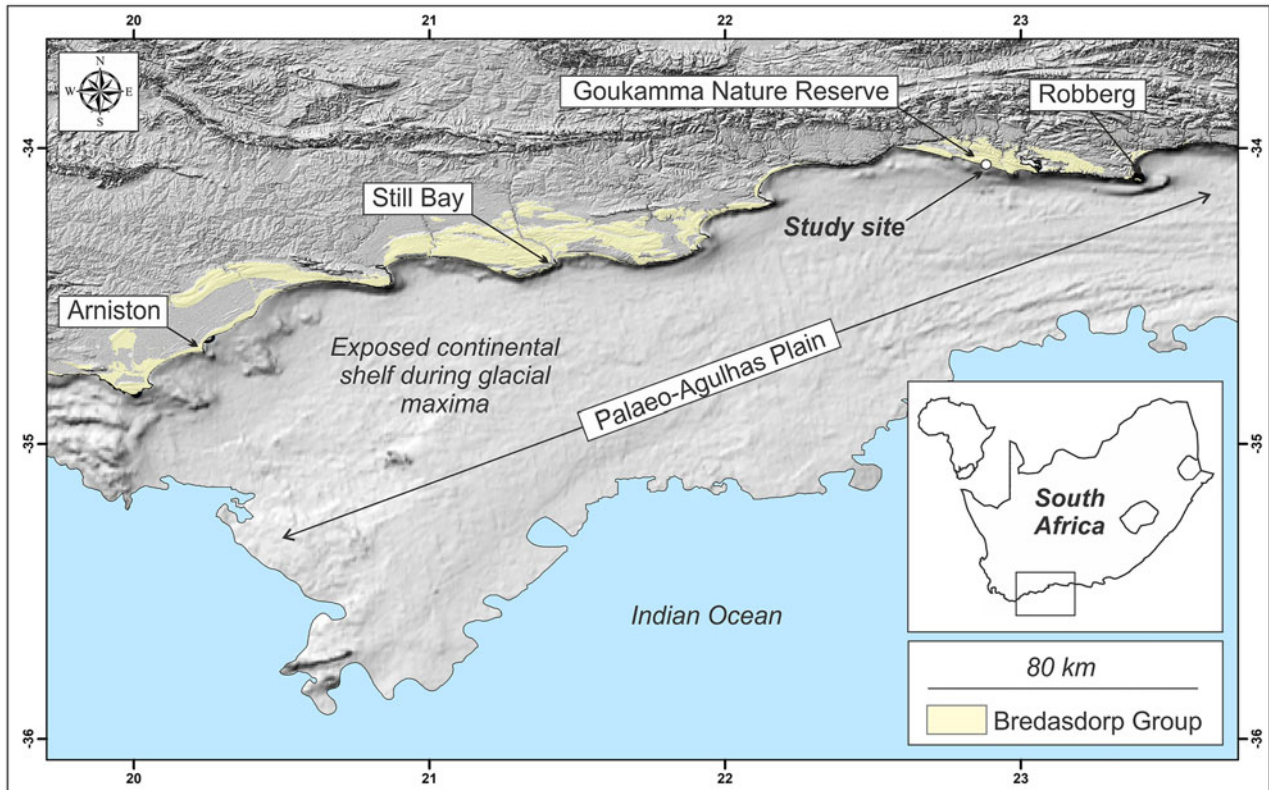
Figure 1. Map of the Cape south coast of South Africa, indicating the main study area and the study site.

track is from Arniston, which lies close to the latitude of Cape Agulhas, the southernmost point of mainland Africa. Additional elephant tracks could be identified offshore through sub-marine studies of submerged aeolianite and cemented foreshore deposits (Cawthra et al., 2015), but bio-armouring on reefs is expected to render this a challenge.

Whereas southern African tracking guidebooks (Liebenberg, 2000; Van den Heever et al., 2017; Walker, 2018; Stuart and Stuart, 2019) depict elephant tracks and trackways as a series of depressions in the substrate, the fossil track record is more complex and includes tracks preserved as natural casts in hyporelief and tracks preserved in cross section. Analogies can be drawn between Pleistocene elephant tracks and Mesozoic dinosaur tracks in terms of, for example, their ability to deform underlying sediment layers. Furthermore, elephant tracks may be eroded into recognisable forms and shapes.

The abundance of Pleistocene elephant tracksites on the Cape south coast allows for an appreciation of the forms such tracks can take and the unusual associated features that might not have been previously documented. Therefore, the purpose of this article is to (1) consider the range of elephant track morphologies recorded thus far on the Cape south coast in the context of the global proboscidean track record; (2) consider a newly identified site in the area that may provide the first palaeoichnological evidence of elephant trunk-drag impressions; and (3) provide an interpretation of this evidence against known behaviour of the extant African elephant.

ELEPHANTS AND THEIR TRACKWAYS

The proboscidean lineage can be traced to the Paleocene (Shoshani, 1998), and proboscidean tracks have a wide geographical distribution. McDonald et al. (2007) provide 52 references for Proboscidea traces in a bibliography of Cenozoic vertebrate track-sites. The Cape coastal sites of South Africa add new site reports and provide the only Pleistocene records in southern Africa other than a single occurrence near Durban, more than 800 km to the northeast (Cawthra, 2012). The only other southern African record that we are aware of is from Namibia, where Bennett et al. (2010) describe Holocene elephant tracks in the Kuiseb Delta. Elsewhere in Africa, Pliocene elephant tracks have been noted in Laetoli, Tanzania (Musiba et al., 2008), and Pleistocene elephant tracks were found in Ileret, Kenya (Roach et al., 2016).

In North America, Lea (1996) documents proboscidean tracks in Pleistocene aeolianites in Alaska. Mammoth tracks in New Mexico (Lucas et al., 2007) and late Pleistocene mammoth tracks and trample grounds in Alberta, Canada (McNeil et al., 2007), have also been recorded. In Asia, Matsukawa and Shibata (2015) describe a variety of Plio-Pleistocene proboscidean tracks and trackways in fluvio-lacustrine environments in Japan. In Europe, Milàn et al. (2007) describe upper Pleistocene/lower Holocene dwarf proboscidean tracks in aeolianites on the island of Rhodes, Greece; Neto De Carvalho (2009) describes mid-Pleistocene elephant tracks in aeolianites in Portugal; Milàn et al. (2015) describe upper Pleistocene/lower Holocene dwarf elephant tracks in aeolianites on Cyprus; Pillola and Zoboli (2017) report on Pleistocene dwarf mammoth tracks in aeolianites on the island of Sardinia; and Muñiz et al. (2019) describe late Pleistocene proboscidean tracks in weakly cemented coastal dune sediments in Gibraltar. Most of these tracks are preserved in aeolianites, and together with other examples from the global ichnology record, they provide evidence of widespread proboscidean travel over dune and interdune surfaces.

Figure 2. The main palaeosurface described by Roberts et al. (2008), containing elephant and other tracks.

Three representatives of the Proboscidea order and the Elephantidae family are extant: the African bush elephant (*L. africana*), the smaller African forest elephant (*L. cyclotis*), and the Asian elephant (*Elephas maximus*). There is no body fossil evidence to suggest that earlier elephant species, such as *L. atlantica*, survived later than 400 ka in southern Africa (Klein et al., 2007; Carruthers et al., 2008).The elephant tracks described herein occur in deposits ranging in age from Marine Isotope Stage (MIS) 11 (∼400 ka) through MIS 5 (∼130–80 ka) to MIS 3 (∼35 ka). For the MIS 5 and MIS 3 tracksites, *L. africana* is the most plausible source. However, it is not impossible that the MIS 11 tracksites were made by *L. atlantica*; it was reputedly larger than *L. africana*, so its tracks could be inferred to be somewhat larger (Klein et al., 2007; Carruthers et al., 2008).

ELEPHANT TRACK MORPHOLOGY

L. africana tracks exhibit large, round forefoot (manus) impressions and narrower, oval hindfoot (pes) impressions, usually without evidence of digit impressions (Liebenberg, 2000; Van den Heever et al., 2017; Stuart and Stuart, 2019). Adult tracks cannot be confused with those of any other Pleistocene trackmaker in southern Africa. However, juvenile tracks could be confused with poorly preserved tracks of other large members of the southern African Pleistocene megafauna, such as the hippopotamus (*Hippopotamus amphibius*) and the rhinoceros (*Diceros bicornis* or *Ceratotherium simum*). Hippopotamus tracks can be as much as 28 cm in length and typically show four digit impressions (Van den Heever et al., 2017; Stuart and Stuart, 2019). Rhinoceros tracks can be as much as 30 cm in length and typically show three digit impressions (Van den Heever et al., 2017; Stuart and Stuart, 2019). However, when made in noncohesive substrates, or when the quality of preservation is poor, digit impressions may not be reliably registered or preserved. In such cases, juvenile elephant tracks could be confused with those of these species.

Extinct members of the southern African Pleistocene megafauna, such as the long-horned (or giant) buffalo (*Syncerus antiquus*) or the giant Cape horse (*Equus capensis*), made tracks that were significantly smaller than elephant tracks and should not be confused with them, except perhaps in the case of poorly preserved juvenile elephant tracks. Abiotic causes of soft sediment deformation structures (Molina et al., 2002) may cause features with similar appearances in cross section, but we have not yet encountered such features in Pleistocene deposits on the Cape south coast. In summary, identification of fossil elephant tracks is usually relatively straightforward. In all the above citations, we have not found reference to putative trunk-drag impressions of the kind suggested below.

Belvedere and Farlow (2016) propose a four-point scale (0-1-2-3) for quantifying the preservation quality of vertebrate tracks. In general, tracks in aeolianites do not exhibit outstanding preservation (Haubold et al., 1995; Lucas and Heckert, 1995). Tracks in dune facies (and coarse beach sand) usually do not rise above level 2 on this scale. In the case of elephant tracks, this means that subtle features like digit impressions are not apparent. However, track size and shape can usually still be determined.

As noted above, Roberts et al. (2008) describe the first fossil elephant trackways and tracks from southern Africa from a site on the Cape south coast. Optically stimulated luminescence (OSL) dating yielded a result of 140 ± 8.3 ka for the oldest dated layer (below the main elephant track horizon) and 91 ± 4.6 ka for the youngest dated layer. The main surface had dimensions of 5 × 3.5 m, with three purported juvenile elephant trackways on a well-preserved, ripple-marked palaeosurface (Fig. 2). Over time, the block split in two, exposing numerous artiodactyl tracks, before slumping into the sea by 2016 (Helm et al., 2019b).

The morphologies of elephant tracks and trackways in epirelief as impressions (natural moulds) on palaeosurfaces are of the kind

Figure 3. (A) Manus and pes pairs of fossil elephant tracks, Garden Route National Park; scale bar = 30 cm between outer black circles. (B) An elephant trackway east of Still Bay, exhibiting displacement rims and infill. (C) One of the authors measuring an underwater elephant track on the Robberg Peninsula. (D) Convolution of the bedding plane layers due to elephant tracks, seen in cross section in the Goukamma Nature Reserve; scale bar = 15 cm.

described in southern African tracking books (Liebenberg, 2000; Van den Heever et al., 2017; Walker, 2018; Stuart and Stuart, 2019). They often take the form of manus and pes pairs (Fig. 3A) and display considerable displacement rims and sometimes contain an infill layer (Fig. 3B). The displacement rims are usually more prominent on the downslope sides of the impression and thus aid in track interpretation. Some of these natural mould tracks have even been documented underwater (Fig. 3C). Natural cast tracks, evident in hyporelief on the ceilings of caves and overhangs, exhibit similar morphological features, which is not unexpected.

In contrast, elephant tracks in cross section display some surprising features that invite comparisons with dinosaur tracks. In both cases, the tracks were the largest of their time made by the heaviest creatures and therefore had the greatest impact on underlying layers of sediment, possibly resulting in turbation of trampled areas. One example, in the Goukamma Nature Reserve, exhibits substantial convolution of the bedding plane layers in cross section (Helm et al., 2018c, Fig. 3D). The origin of these features is readily determined by following the layers to where the bedding plane surfaces are exposed, where they exhibit typical elephant tracks. Laury (1980) describes trampling, referred to as "megabioturbation," by Pleistocene mammoths. Laporte and Behrensmeyer

(1980) describe various Quaternary examples of substrate reworking, or trampling, in East Africa. Examples of dinosaur tracks deforming underlying sediments, known as "dinoturbation," are presented in Figure 4.

As is the case with dinosaur tracks, elephant tracks deform these underlying layers in a predictable pattern, creating undertracks or "transmitted tracks." In cross section, each successive lower layer is deformed to a slightly lesser degree, but the horizontal dimensions of each layer are slightly greater than those in the layer immediately above (Fig. 5A). In this respect, Figure 5A can be compared with Figure 4A, which shows similar features in a dinosaur track. As a result, a bedding plane surface representing one of these underlying surfaces may exhibit enormous depressions, which in fact are transmitted tracks. Such was the case on the Robberg Peninsula, where Helm et al. (2019a) recorded track lengths of 70 cm, 65 cm, and 62 cm (Fig. 5B). Even with the understanding that these were transmitted tracks, and therefore probably somewhat larger than the original tracks, it can be claimed that they are among the largest Cenozoic tracks ever to be described and hence among the largest Quaternary tracks recorded. Confirmation that these were elephant transmitted tracks was obtained through crawling into a tight recess and finding further tracks on this surface that contained infill layers
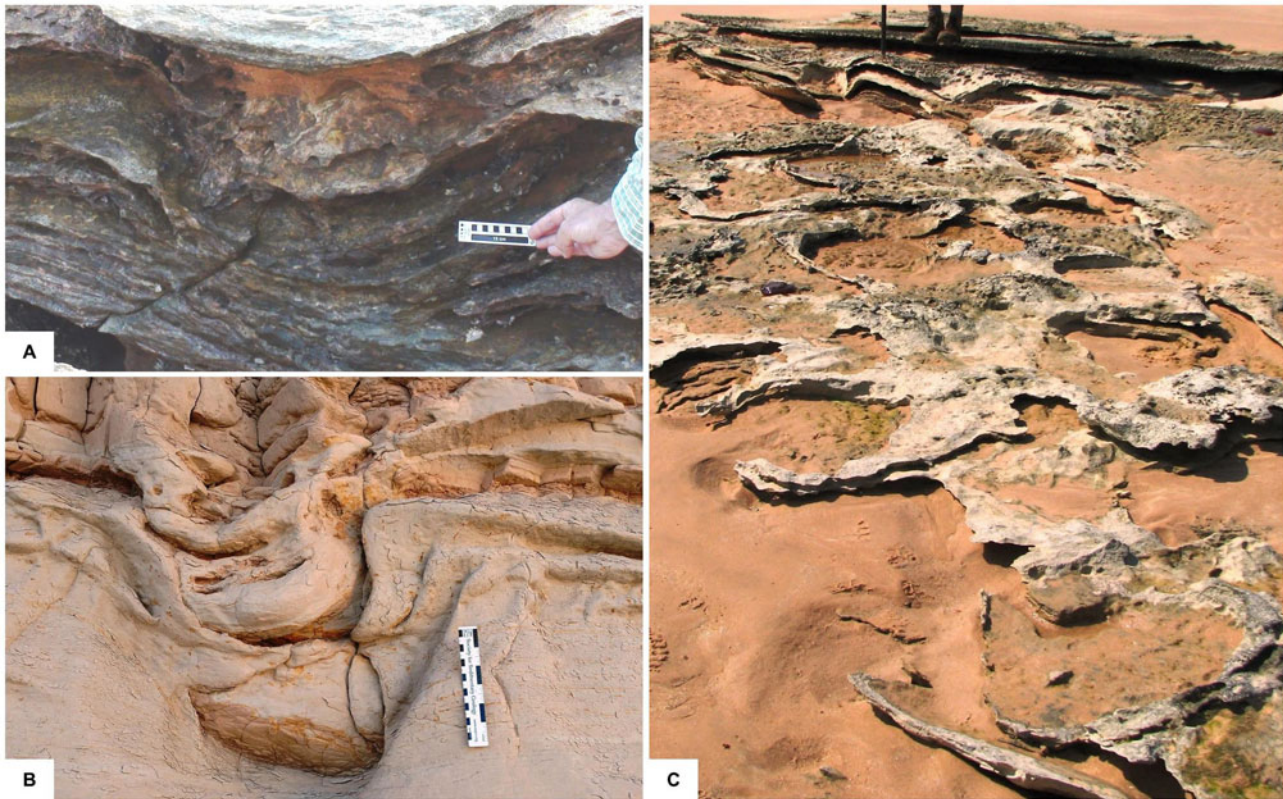
Figure 4. (A) Deformation of underlying layers beneath a Cretaceous dinosaur track in Western Australia; scale bar = 10 cm. (B) Substantial deformation of underlying layers beneath a Cretaceous dinosaur track in China; scale bar = 15 cm. (C) Dinoturbation in Cretaceous sediments near Broome, Western Australia.

in the form of typical elephant tracks. Stewart et al. (2020) describe large Pleistocene proboscidean tracks (diameters of as much as 63 cm) in the Arabian Peninsula. Elephant tracks in cross section can also assist in determining the "way-up" of loose, ex situ blocks and slabs. At the Robberg Peninsula site, the orientation of a gigantic block that had tumbled down from overlying cliffs could be determined at a distance by noting the direction in which elephant tracks had been registered (Fig. 5C).

Tracks registered by smaller, lighter trackmakers may not be discernible on poorly preserved surfaces. However, because of their size and depth, elephant tracks may be identifiable on such surfaces (Fig. 5D) and may therefore be recorded with disproportionate frequency.

Depending on the nature of the substrate, elephant tracks may be extraordinarily deep. As with dinosaur tracks, if tracks were registered in moist muddy substrates, leading to deep depressions, and a layer of sand provided the infill layer, the latter is often preserved while the muddy layer is often eroded. This leads to the phenomenon where the layer of infill is obvious in cross section and may reach depths of 30 cm (Fig. 6A and B). Again, comparison with the dinosaur tracks shown in Figure 4 is of value. Where such infill layers in tracks are resistant to erosion, remarkable forms may result (Fig. 7A–C).

Deformations on the Cape south coast consistent with elephant tracks in cross section have been noted in seven discrete layers over a stratigraphic sectional height of 10 m of aeolianites at one site (Helm et al., 2018c). At another site, a section measuring 26 m displayed multiple discrete layers containing such

structures in aeolianites. Where bedding plane surfaces are exposed in epirelief at these sites, elephant tracks are evident. From such observations, inferences on repeated use over time of an area of dune surfaces have been made, although the time interval that such sections represent cannot accurately be determined (Helm et al., 2018c). Palaeosurfaces containing elephant tracks do not necessarily slump into the sea or erode away. It has been demonstrated that elephant tracks on Cape south coast palaeobeaches can serve as precursors to pothole formation (Helm et al., 2021) (Fig. 7D).

Associations of trackmakers are of potential importance. Along the Goukamma Nature Reserve coastline, elephant tracks were found close to a long trackway interpreted as having been made by a long-horned (giant) buffalo. Trackways interpreted as having been made by the extinct Cape subspecies of the African lion (*Panthera leo melanochaitus*) also occur close by (Helm et al., 2018c). East of Still Bay, a probable long-horned buffalo track was centrally registered within a large elephant track on a surface containing multiple elephant tracks (Helm et al., 2019b) (Fig. 8). At Brenton-on-Sea, elephant tracks were found on layers adjacent to those containing hominin tracks (Helm et al., 2018a).

GEOLOGICAL CONTEXT

The origin and age of Cape south coast sediment accumulations, episodes of dune building, and the accumulation of coastal sand deposits and their association with Pleistocene sea-level fluctuations have been investigated geologically in some detail during
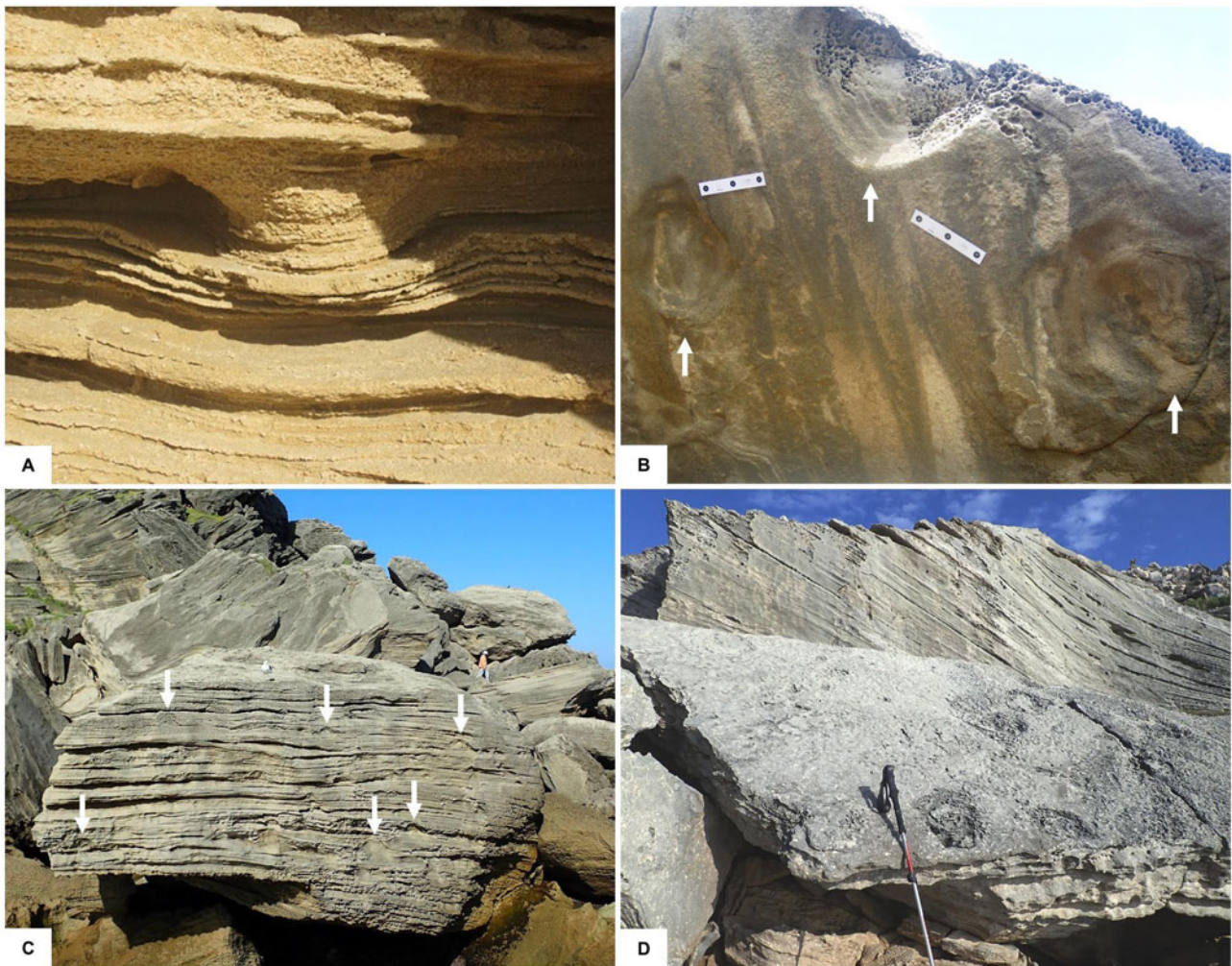
Figure 5. (A) An elephant track seen in section, illustrating deformation of underlying layers. (B) Elephant transmitted tracks (indicated by white arrows) recorded on the Robberg Peninsula; scale bars = 30 cm between outer black circles. (C) The orientation of this large block (adult human figure provides scale) can be determined at a distance by noting the orientation in cross section of elephant tracks (indicated by white arrows). (D) Elephant tracks can be identified on this surface in De Hoop Nature Reserve despite erosion and poor preservation.
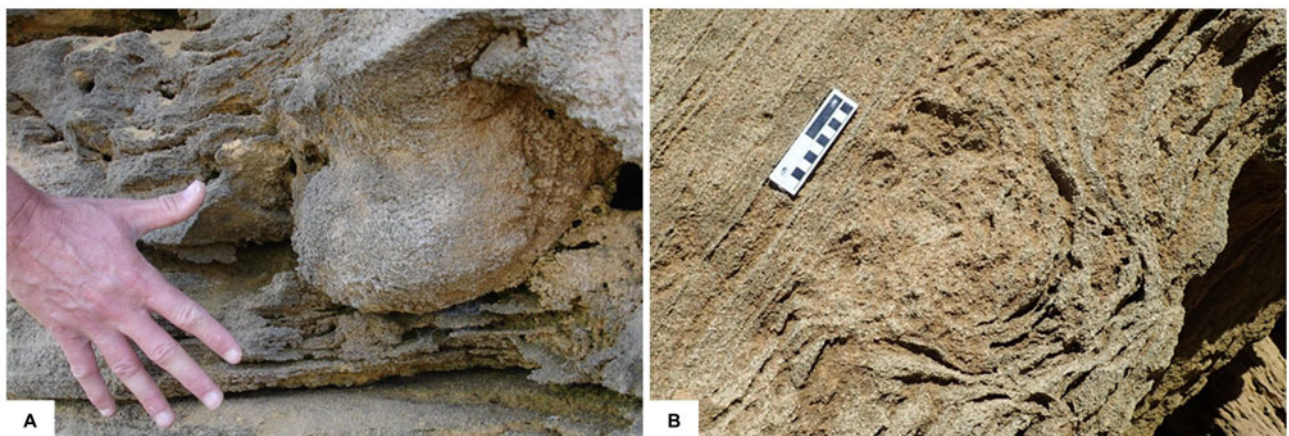

Figure 6. (A) and (B) Deep infill layers seen in cross section at sites east of Still Bay. In both cases, the track dimensions are not large enough to exclude rhinoceros or hippopotamus as trackmakers, but numerous elephant tracks are evident where these surfaces are exposed, increasing the probability that the trackmaker was a juvenile elephant. Scale bar in (B) = 10 cm.

Figure 7. (A), (B), (C) Eroded elephant tracks and infill layers may take on remarkable forms (indicated by white arrows); scale bars in (A) and (C) = 10 cm. (A) and (C) are in the Goukamma Nature Reserve, and (B) is east of Still Bay. (D) Potholes in linear patterns on the Cape south coast, for which elephant tracks were likely precursors.

the last decade (e.g., Carr et al., 2010; Fisher at al., 2010; Jacobs, 2010; Bateman et al., 2011; Roberts et al., 2013; Carr et al., 2019). OSL studies from numerous sites along the Cape south coast have demonstrated that two significant sea-level high stands preserved deposits from the interglacial periods MIS 11 (~400 ka) (Jacobs et al., 2011; Roberts et al., 2012) and MIS 5e (~125 ka) (Carr et al., 2010; Cawthra et al., 2018); evidence for deposits laid down during MIS 4 and MIS 3 have recently been reported from the continental shelf (Cawthra et al., 2018) and the Robberg Peninsula (Carr et al., 2019). Roberts et al. (2013) note that these types of deposits can be sensitive palaeoenvironmental indicators, as recorded in their orientation, geometry, and palaeontological and archaeological content.

The ichnological discoveries above allow for palaeoenvironmental inferences to be drawn; they complement the evidence available through the body fossil record, thus filling unanticipated gaps in this record.

At a global level, aeolianite deposits are mostly found in mid-latitude regions, typically between 20° and 40° (Brooke, 2001); aeolianite outcrops occur intermittently along much of the South African coast. The Pleistocene aeolianites encountered on the Cape south coast form the Waenhuiskrans Formation (Malan, 1989). The Pleistocene cemented foreshore deposits form part of the Klein Brak Formation, along with shoreface

and lagoonal deposits (Malan, 1991). The two formations form part of the Bredasdorp Group. Where they crop out, these deposits alternate with expanses of beach and unconsolidated Holocene dunes, remnant Neogene dune ridges, Palaeozoic quartzite exposures of the Cape Supergroup, granite exposures of the Cape Granite Suite, and Neoproterozoic metasedimentary successions (Newton et al., 2006). Because Quaternary tectonic activity is considered minimal along this coastline (Fleming et al., 1998), bedding planes in the Pleistocene formations lie at, or very close to, their original angles of deposition. In the case of aeolianites, this is often the angle of repose of windblown sands (Roberts et al., 2012); cross bedding may be evident, while interdune areas and cemented foreshore deposits typically exhibit bedding plane layers that lie closer to the horizontal plane. Distinguishing between these types of deposits is not always simple, even with microscopy. Given the frequency of transition zones between beaches and dunes, as well as sea-level fluctuations that prompt calcium carbonate diagenesis at different levels of the stratigraphy, this is not surprising.

OSL studies from numerous sites along the Cape south coast have demonstrated that, while the great majority of Pleistocene deposits are from MIS 5 (~130–80 ka), substantially older and younger deposits also occur. For example, Roberts et al. (2012) demonstrate that both MIS 11 and MIS 5 deposits occur at

Figure 8. East of Still Bay, a probable long-horned buffalo track is centrally registered within a large elephant track. Scale bar = 10 cm.

Dana Bay. The MIS 11 deposits date to ∼400 ka (Roberts et al., 2012), and elephant tracks are apparent in these layers (Helm et al., 2021). In contrast, Carr et al. (2019) demonstrate that some deposits on the Robberg Peninsula are much younger, dating to MIS 3 and as young as 35 ka. Again, elephant tracks are evident in the MIS 3 deposits (Helm et al., 2019a).

METHODS

The site containing possible elephant trunk-drag impressions is located in the Goukamma Nature Reserve and was visited at low tide, during a period in which it was exposed and not covered by sand. Track length, width, and depth were recorded in centimetres, along with measurements of pace length where applicable. Track numbers were assigned from 1 (most landward) through 13 (most seaward). Dimensions were recorded for the groove features described below, along with distances from the median trackway axis. A GPS reading was taken, using the World Geodetic System 84 datum. A sample was obtained for OSL dating from a suitable layer located 1.8 m lower in the stratigraphic section.

We climbed nearby cliffs, which permitted an aerial view of the site. Standard field techniques were applied in understanding tracksite context. Dip and strike measurements were taken on primary bedding planes, bed thicknesses were measured, and textures were described.

Locality data were reposited with the African Centre for Coastal Palaeoscience and Garden Route National Park to be made available to researchers upon request. Photographs were taken, including photogrammetric analysis (Matthews et al., 2016). Three-dimensional models were generated with Agisoft Metashape Professional (version 1.0.4), using an Olympus Tough model TG-6 camera (4.5 mm focal length, 4000 × 3000 resolution, pixel size 1.56 × 1.56 μm). The final images were rendered using CloudCompare (version 2.10-beta).

RESULTS

The Goukamma Nature Reserve tracksite is in an area containing a high concentration of elephant tracks in multiple layers, seen in epirelief and cross section, as well as bovid tracks of various sizes, including well-preserved long-horned buffalo tracks with dewclaw impressions. The area also contains a medium-sized bovid coprolite site and a small carnivore coprolite site, both of which are associated with tracks. The strike of the bedding planes in this area varies from 293° to 330°, and dip measurements vary from 12° to 30°, indicating a succession of dune layers and a predominant wind direction at the time of deposition from the southwest.

A series of at least 13 features, consistent in size and shape with elephant tracks, was noted along the strike (293°) of one of these bedding plane surfaces, hence in a direction that traverses the side of the dune slope (Fig. 9). A dip measurement of less than 30° was recorded. Twelve of these features are depressions; track 8 is an eroded remnant of the infill layer of a track. This natural cast phenomenon provides further confirmation that the depressions apparent on the surface were registered when it was made up of unconsolidated sand.

The trackway extends the full length of the bedding plane surface, which is rough and cracked in places and has suffered the effects of erosion, especially at the seaward end. The quality of track preservation is therefore poor in places, and in some cases, dimensions could not reliably be determined. Digit impressions were not identified. In two cases, tracks are contiguous and were thus not amenable to reliable measurement. Nonetheless, enough detail was evident to permit interpretation. Direction of travel could not unequivocally be determined. We chose to describe the trackway and associated features facing southeast, i.e. in a landward-to-seaward direction.

Two cracks in the surface cross the trackway, the distal crack being wider than the proximal crack (Figs. 9 and 10). The
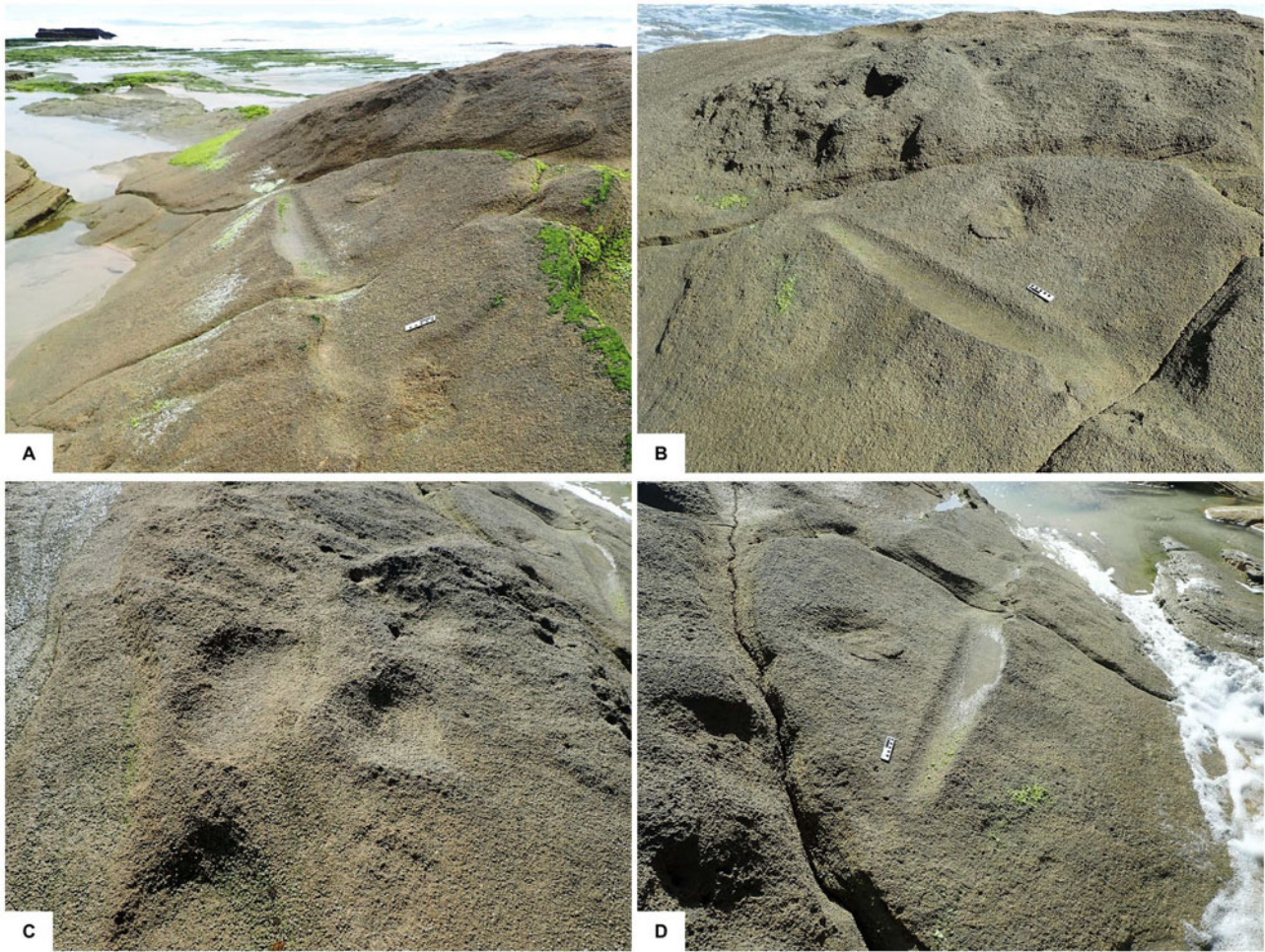
Figure 9. A sloping aeolianite surface in the Goukamma Nature Reserve, showing elephant tracks and two elongated grooves interpreted as possible trunk-drag impressions (indicated by arrows). (A) and (B) are facing southeast, and (C) and (D) are facing northwest; scale bars = 10 cm.

proximal crack passes through track 4. Furrows are present on other portions of the surface, probably attributable to postdepositional water erosion resulting from repeated inundation of the surface during tidal action. The concentration of tracks is greater at the seaward end. Elephants often reuse tracks and trails, and the possibility that the tracks in this portion represent more than one trackway cannot be excluded.

A total trackway length of ∼5 m was measured. Data for the measurable tracks, which are consistent in shape and size with an elephant trackmaker, are presented in Table 1. Track 5, situated on a less-eroded section of the surface, is the best preserved and exhibits a substantial downslope displacement feature.

The striking feature of this trackway is a set of two wide grooves, located within it or close beside it (one on either side) and approximately parallel to it. The proximal groove, which is evident downslope (east) of the trackway, exhibits better preservation, as it occurrs in a less-eroded portion of the surface. The length, including the three smaller proximal areas described hereafter, is 270 cm; it measures135 cm without these three features. Maximum width is 20 cm. A slight displacement rim is present at its medial and lateral margins. Its lateral margin (relative to the trackway) displays a slight outward convexity; the proximal end of this lateral margin exhibits three smaller successive areas with outer convexity. These are

closely associated with tracks 2 and 4 and with small displacement rims, which appear to cover these portions of the groove feature (i.e. the tracks appear to slightly distort the groove feature and to have been registered on top of it). Only vestigial track 3 could be detected beside the middle of these three areas of convexity/distortion. At is proximal end, the groove lies within or close to the median axis of the trackway, whereas distance from the groove to this axis reaches a maximum of ∼60 cm at its distal end.

The distal groove feature (seaward and upslope of the trackway) is present in a more eroded portion of the surface; hence, the quality of preservation is not as good as in the case of the proximal groove. However, it could be determined that its proximal end correlates approximately with the distal end of the proximal groove. It is at least 110 cm in length, with a maximum measured width of 15 cm. It displays more of an outward convexity than the proximal groove, evident in both its medial and lateral margins. Its proximal origin appears to be close to track 5, and the maximum distance from the median axis of the trackway is ∼40 cm. If the observed pattern evident in the proximal and distal groove features recurred, the resulting grooves would be positioned beyond the northern and southern limits of the track-bearing surface.

The tracksite is only exposed at low tide and is subject to intense wave action during high tides and storm surges. It is
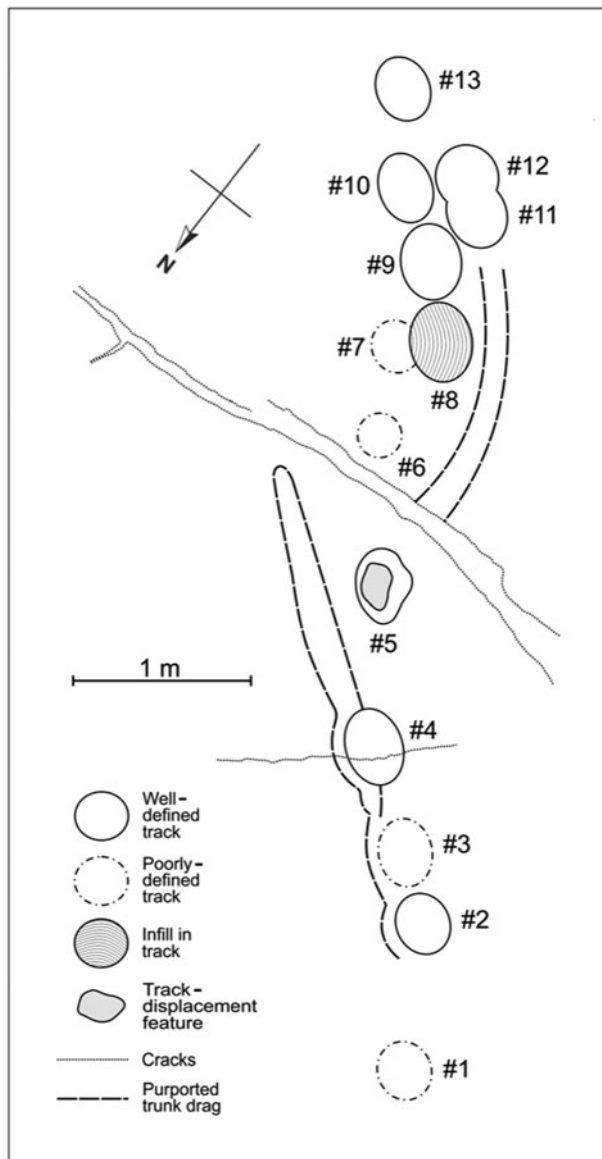
Figure 10. Plan of an elephant trackway and purported trunk-drag impressions in the Goukamma Nature Reserve.

Table 1. Track dimensions of the elephant trackway in the Goukamma Nature Reserve, Cape south coast, South Africa, from north to south.

Track number	Dimensions (cm)
2	35 × 30
4	44 × 32
5	42 × 32
8	45 × 35
9	43 × 34
10	40 × 30
12	42 × 40
13	47 × 40

also frequently covered by sand. Over the past decade, it has only been exposed on two brief occasions, in 2015 and 2019. A plan view of the trackway is presented in Figure 10. Photogrammetry images are presented in Figure 11, showing displacement rims at the margins of the proximal groove feature, with the lateral displacement rim more prominent than the medial displacement rim (consistent with its downslope position).

DISCUSSION

Elephant trunk-drag impressions

The available evidence, as summarized above, indicates an elephant trackway along with two sequential, deep, wide, elongate groove features that are aligned approximately with the longitudinal axis of the trackway. The evidence in the case of the proximal groove suggests that it was registered prior to the tracks being registered: if this impression was made by an elephant trunk, this would be consistent with elephant anatomy in which the trunk is positioned anteriorly to the limbs and registration of the trunk impression precedes the subsequent footfalls of the manus and pes. Furthermore, the presence of slight displacement rims just outside the medial and lateral margins of this groove suggests that it was made through a compressive rather than erosive force. If the sand was unconsolidated, as the evidence suggests, the forward motion of a trunk would produce a "bow wave" effect, which would in turn create the aforementioned displacement rims, resulting less from medially and laterally directed compressive forces and more from the buildup of bow wave sediment. The more prominent lateral displacement rim is consistent with its downslope position. The distal groove does not contain evidence of such rims, and an erosional cause cannot be excluded. Van den Heever et al. (2017, p. 79), referring to trunk-drag impressions associated with trackways made by bull elephants, use the term "serpentine" (Fig. 12) to describe the resulting pattern, and a number of other authors (see below) use terms like "snakelike." Indeed, this seems to be an apt term to describe the pattern made by the groove features, with their varying degrees of outward convexity. Furthermore, in considering potential elephant trunk-drag marks made while traversing a sloping dune surface, a more linear appearance would be expected for the downslope drag mark, and a more curved appearance would be expected for the upslope drag mark; this is consistent with the documented features. Photographs of elephant trunk-drag marks are available on various websites (e.g., Elephant Voices, n.d.).

The trails of extant African bush elephants contain numerous features other than tracks. These include droppings, urine, flattened grass, broken branches and trees, bark stripped from trees, chewed material scuff marks, mud smeared on trees, and trunk-drag marks (Van den Heever et al., 2017). Indeed, at one Pleistocene elephant tracksite, we identified probable elephant coprolites, which are the object of further analysis. Furthermore, polished rock surfaces as much as 3 m above ground level have been attributed to rubbing action by mammoths in California (Haynes, 2006; KQED, 2009).

The trunk of *L. africana*, with more than 150,000 muscle fibres, is a structurally complex and highly flexible organ (Shoshani, 1998) with fine neuromotor control (Onodera and Hicks, 1999). Aside from its mechanical and physiological functions, it is used to socialise (Poole and Granli, 2011) and can
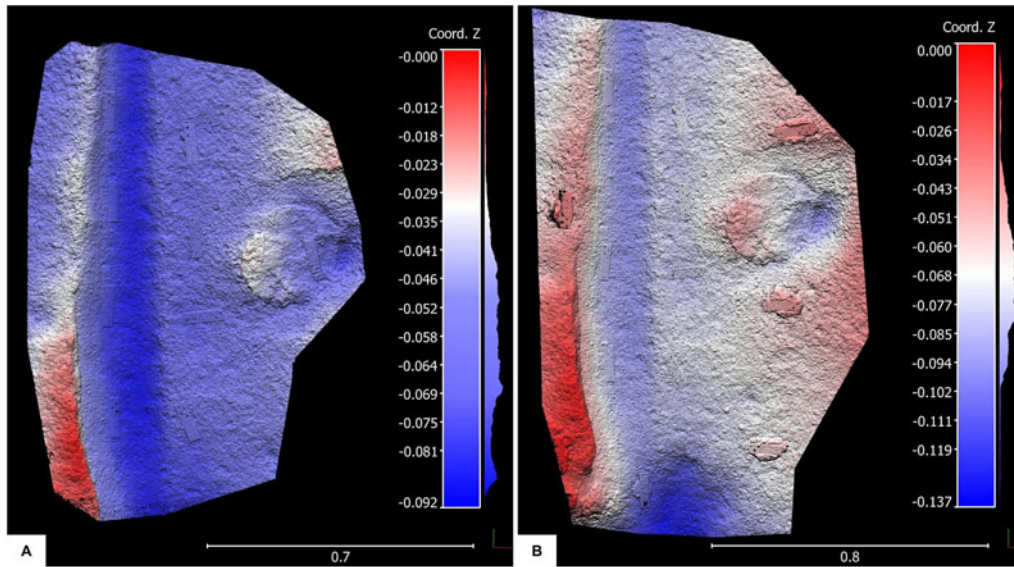
Figure 11. Photogrammetry colour mesh of a purported elephant trunk-drag impression; vertical and horizontal scales are in metres. (A) 18 images were used, and the photographs were taken at an average of 56.7 cm from the surface; the reprojection error is 0.296 pix. (B) 21 images were used, and the photographs were taken at an average of 54.8 cm from the surface; the reprojection error is 0.251 pix; a portion of track 5 is also evident.
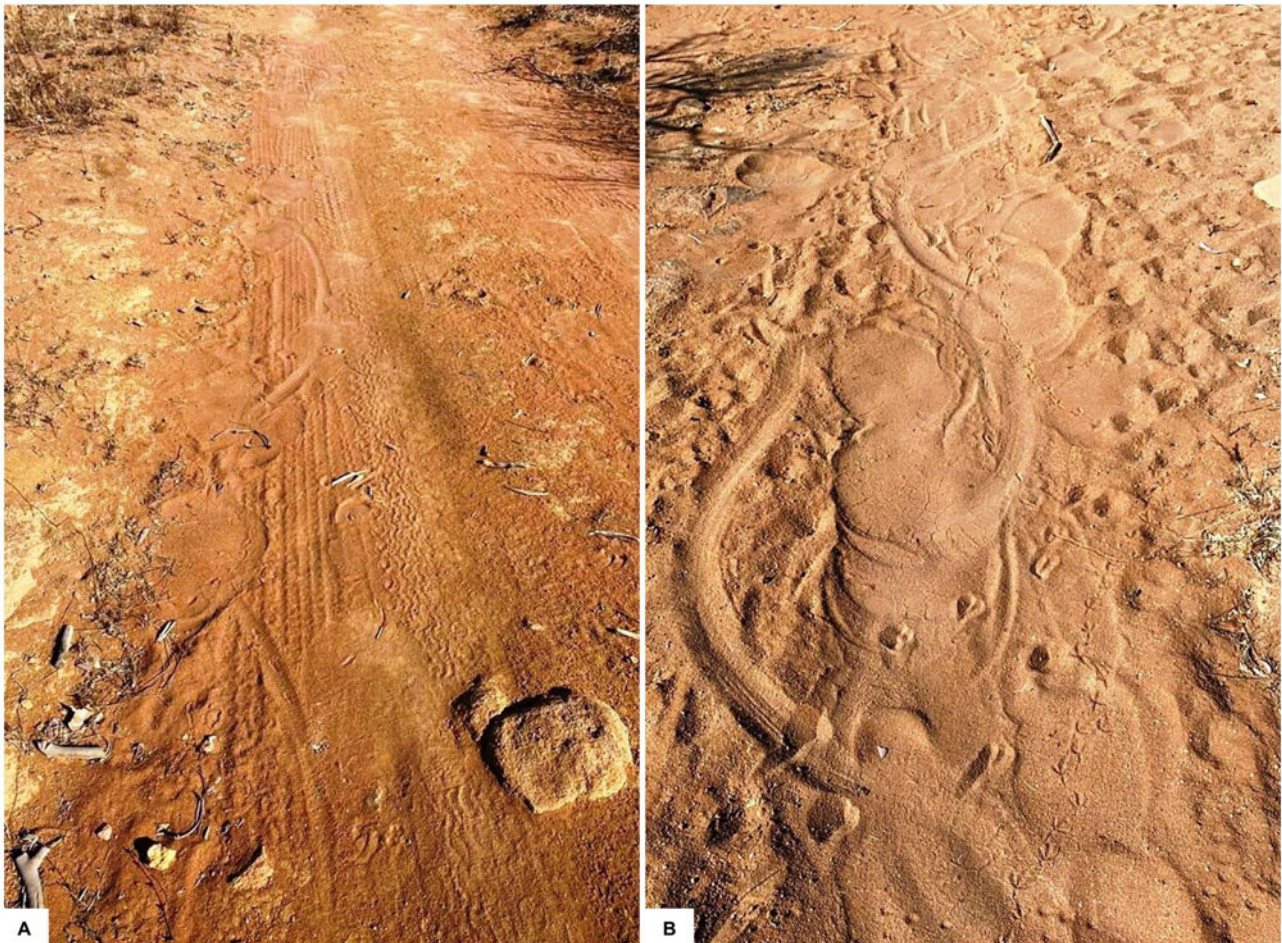

Figure 12. Trunk-drag impressions of *L. africana*, showing their serpentine nature (reproduced with the permission of A. Van den Heever).

indicate various emotions, such as aggression, play, greeting, and affection (Vidya and Sukumar, 2005). Most adult males over the age of 24 years experience musth, a temporary state of heightened testosterone levels in their blood (Hall-Martin and Van der Walt, 1984) and urine (Poole et al., 1984). During musth, elephant males can be particularly aggressive and increase their home ranges through extensive wandering (Poole, 1987; Hall-Martin, 1987). They also often use their trunks for ritualised reproductive displays at this time (Kahl and Armstrong, 2002).

Extant *L. africana* may register trunk-drag impressions under a variety of circumstances. Poole and Granli (2011, p. 118) note that "musth males may drag . . . the distal portion of the trunk on the ground, making a rasping sound. This behaviour leaves a snake-like mark on the ground. . . . Musth males may trunk-drag as a threat at very close range." Likewise, Kahl and Armstrong (2002, p. 167) note that "while standing, or more commonly while walking, a musth male may bounce or drag the distal portion of his trunk on the ground. One sometimes sees a snakelike drag-mark in the sand, where this has been done in the recent past." Douglas-Hamilton et al. (2006) describe a dying matriarch dragging her swollen trunk along the ground, and Van den Heever et al. (2017, p. 79) state that tracks "are often accompanied by drag marks made by the trunk. Bull elephants, in particular, tend to drag their trunk, creating a serpentine trail." Van den Heever (personal communication, 2020) also notes that small trunk impressions (unlike those described here) can be made by (usually) a bull elephant sniffing the ground in pursuit of a female herd or by an elephant collecting dust to throw onto its back; more commonly, tired elephants (usually bulls) drag their trunks on flat terrain, creating intermittent drag marks.

Among the above possibilities, the first two may be the most consistent with the features observed at our study site. It should also be noted that the behaviour of the African and Asian elephant are not identical. Kahl and Armstrong (2002, p. 168) describe the latter's more elaborate "trunk bounce," in which "the trunk is bounced forcefully on the ground and the elephant—not necessarily a musth male in the Asian species—utters a loud, booming vocalization."

Other than trunk drag marks, are there other agents that could have caused the features that have been documented? The first possibility is that the grooves simply represent erosional features that the elephant happened to pass through or that have subsequently been formed. If three or more successive groove features were evident, the case for trunk-drag impressions would be stronger. If only one groove feature was present, the case would be weaker. The presence of two such features, as described, lies between these extremes and suggests such an origin without being conclusive. As noted above, an erosional cause cannot be excluded for the distal groove.

Could the grooves have been created by an elephant using something other than its trunk? Elephants may gouge out grooves with their tusks and may create long scuff marks with their feet, especially when injured (Van den Heever, A., personal communication, 2020). However, on an angled dune surface, such behaviour would likely have caused discernible irregularities in the trackway, and the sequence of two grooves, one on each side of the trackway, makes these possibilities less likely. *L. africana* also may drag sticks, branches, and other objects that they hold in their trunks. It is not implausible that the drag marks described were not made by the trunk but by an object that was held in the trunk.

Palaeoenvironment and the Palaeo-Agulhas Plain

Marean et al. (2020) note that *L. africana* is well represented in Pleistocene trackways but not in body fossil assemblages and so postulate that (1) the regular presence of elephants may have been a factor in maintaining and spreading grasslands on the Palaeo-Agulhas Plain; and (2) there may have been a regular movement of elephants between the Palaeo-Agulhas Plain and the interior. A migration corridor for large animals involving the Palaeo-Agulhas Plain has previously been suggested (Fisher et al., 2010; Marean et al., 2014; Cawthra et al., 2015; Hodgkins et al., 2020). African elephants seasonally shift their ranges between different vegetation types, for example, by selecting open woodlands, shrublands, and grassland in the wet season and woody vegetation in the dry season (Loarie et al., 2009).

Regarding the first postulate, the mosaic of woodland and grassland, meandering rivers, and seasonally waterlogged flood-plains of the Palaeo-Agulhas Plain (Cowling et al., 2020) would have provided extensive potential habitat for elephants. Elephants are ecosystem engineers (Wright and Jones, 2006), and their presence may result in large-scale effects and changes in the landscape (Fritz, 2017). As large-bodied and generalist foragers, elephants at high densities can reduce woody vegetation in dry savannas (Guldemond and Van Aarde, 2008) and can transform woody habitats to open habitats such as mosaics or grasslands (Sinclair, 1973). These newly transformed habitats, in turn, attract mixed feeders and grazers (Haynes, 2012). Specifically, elephants affect ecological processes through feeding, digging, and movement (Kerley et al., 2009).

The number of Pleistocene elephant tracksites on the Cape south coast, from at least three MIS stages and indicating repeated use of certain areas over time, signifies a substantial presence on the landscape. The speculation by Marean et al. (2020) that elephants had a role in maintaining and spreading grasslands on the Palaeo-Agulhas Plain appears to be justified.

Implications for the Knysna elephant population

L. africana is estimated to have ranged across Africa in numbers of more than 20 million prior to European colonisation; this has decreased substantially to recent estimates of less than 400,000 (Douglas-Hamilton and Burrill, 1991; Chase et al., 2016). Based on an estimated 3000 elephants that may have roamed the southern and western Cape in precolonial times (Kerley et al., 2003), ~1000 elephants may have occupied the Outeniqua-Tsitsikamma area just inland from the Cape south coast (Boshoff et al., 2002). These numbers were decimated in the 19th century as a result of the ivory market and habitat transformation (Carruthers et al., 2008), and by 1900, only an estimated 30–50 elephants remained (Hall-Martin, 1992). The survival of this small relict population near Knysna may be attributed to the fact that hunters had difficulty in finding them in the dense forest terrain (Skead, 2011). Whereas in recent times, the Knysna elephants have been confined to the afrotemperate forests, historical records indicate that they occupied areas outside the forest and immediate surrounding fynbos before the 18th century (Boshoff et al., 2016). It has been suggested that the Knysna elephants retreated into the forest and surrounding fynbos for protection and would not have utilised only these two habitats year-round if they had access to others (Moolman et al., 2019a).

Today, only one Knysna elephant remains. She is an adult female in her 40s (Moolman et al., 2019b) and inhabits an area ~18 km from the elephant tracksite containing the purported trunk-drag marks. The Knysna elephants were the most southerly group of elephants in Africa, the only free-ranging elephants in South Africa, and one of only four relict populations in South Africa (Hall-Martin, 1992). Genetic studies (Essop et al., 1996; Eggert et al., 2008) provide evidence that the Knysna elephants formed part of a single South African population. The Pleistocene elephant tracksites described here, from a variety of ages, combined with the evidence from Holocene sites and historical records, indicate a substantial regional elephant presence in open areas dating to MIS 11. They support the contention that elephants retreated into the forest for safety reasons in recent centuries.

CONCLUSIONS

The abundance of Pleistocene elephant tracksites identified along South Africa's Cape south coast allows for an appreciation and review of the varied forms that elephant tracks and traces can take. Features of Pleistocene elephant tracks are in many ways analogous to those of Mesozoic dinosaur tracks. The regional Pleistocene elephant presence evident through a number of MIS stages and at certain locations suggests a role in maintaining and spreading grasslands on the Palaeo-Agulhas Plain. Furthermore, it supports the Holocene and historical evidence that elephants made use of open areas, and that the remaining elephants on the Cape south coast retreated into dense afrotemperate forest in recent centuries.

While the available evidence is not conclusive, we suggest that the elongated groove features noted in the Goukamma Nature Reserve and described here represent the first reported example in the global trace fossil record of elephant trunk-drag marks. A possible behavioural explanation for these features is that they were created by a bull elephant during musth while traversing a dune slope.

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