The Pleistocene fauna of the Cape south coast revealed through ichnology at two localities

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East of Still Bay on the Cape south coast of South Africa lies a rugged, remote stretch of sea cliffs that expose Late Pleistocene aeolianites. A zone of dense concentration of fossil tracks occurs within this area. Two large rocks, which we call Roberts Rock and Megafauna Rock, were identified ~400 metres apart. These rocks contained a variety of trackways, individual tracks, burrow traces and invertebrate trace fossils on multiple bedding planes. Both rocks were found ex situ, but their context could be determined. Roberts Rock has subsequently slid into the ocean, and Megafauna Rock lies at the base of a coastal cliff. Probable trackmakers include elephant, long-horned buffalo, giant Cape horse, rhinoceros, medium and small artiodactyls, golden mole, birds and invertebrates. Dating studies at an adjacent site, which is comparable to the stratigraphy described here, indicate that both rocks were most likely deposited in Marine Isotope Stage 5e (~128–116 ka). Analysis and description of these tracksites confirms the potential of ichnology to complement the skeletal fossil record and to enhance the understanding of Pleistocene life in southern Africa. The ephemeral nature of such tracksites makes repeated visits to this coastline desirable, both to monitor the fate of known sites and to search for newly exposed trace fossil surfaces.

Significance:

- Roberts Rock and Megafauna Rock are two remarkable fossil tracksites on the Cape south coast, which contain tracks of four members of the Late Pleistocene megafauna. They provide a glimpse of Pleistocene dune life and suggest an area teeming with large mammals.
- These tracks were made on dune surfaces near an interface between the grassland of the Palaeo-Agulhas Plain and the inland Fynbos–Strandveld–Renosterveld. Faunal assemblages from both vegetation zones might therefore be recorded.
- The trace fossil record and body fossil record both have inherent biases, but have the potential to independently provide complementary information on palaeofaunal composition.
- The two rocks have provided the first South African records of fossil elephant tracks (as first described by Dave Roberts and colleagues in 2008), the first rhinoceros track and the first extinct giant Cape horse track, and track evidence of the extinct long-horned buffalo.
- Roberts Rock has slumped into the ocean, and it provides an example of the fate of many exposed tracksites. Conversely, new sites frequently become exposed. This scenario stresses the need for regular ichnological surveys along this track-rich coastline to monitor existing sites and to search for new sites.

Introduction

Late Pleistocene aeolianites, or cemented palaeodunes, are well preserved along the Cape south coast of South Africa. These deposits contain fossil trackways[1-5] preserved fortuitously[6]. An ongoing multidisciplinary project looking at Pleistocene ichnofossils in aeolianites of the Waenhuiskrans Formation, between Witsand in the west and Robberg in the east, a distance of 275 km (Figure 1), was initiated in 2007. To date, more than 100 tracksites have been identified through this project.

Four dominant zones of concentration of tracksites are apparent. One of these zones lies east of Still Bay along a remote, rugged coastline. Here Middle to Late Pleistocene dune cordons of the Waenhuiskrans Formation form coastal cliffs up to 70 m in height, and are overlain by active Holocene dunefields of the Strandveld Formation (Figure 1). These deposits extend for approximately 12 km. This composite dune cordon is separated from older inland lithologies by Rietvlei, an interdune lake.[1,7] Fallen aeolianite blocks lie at the base of the sea cliffs, where they are subjected to gravitational forces and wave and wind erosion. Roberts et al.[1] drew attention to this area, by describing fossil elephant trackways and tracks, and dating them through the early use of optically stimulated luminescence (OSL) in southern Africa. A result of 140±8.3 ka was obtained for the oldest dated layer (below the main elephant track horizon), and 91±4.6 ka for the youngest dated Pleistocene unit. Helm et al. reported on further tracks from this area, including avian tracks[2] and giraffe tracks[3].

One of Roberts' main study sites was a large aeolianite block that had slid down a steep sandy slope from its origin in the cliffs above.[1] It contained a well-preserved, rippled palaeo-surface, 5 m x 3.5 m in size, containing three juvenile elephant trackways and two medium-sized artiodactyl trackways (which Roberts et al.[1] termed 'antelope tracks'). We name this rock 'Roberts Rock'. The instability of the slope and proximity to the ocean made it vulnerable to slumping and to wave action. Multiple visits to the site demonstrated bedding-plane splitting of the block into two halves, with the appearance of further tracks on the newly exposed surfaces. By 2016, Roberts Rock was no longer present, but unexpectedly a large recently fallen aeolianite block lay immediately adjacent to the site, and also contained multiple track-bearing surfaces.

About 420 m to the west of the Roberts Rock site lies another fallen aeolianite block, which was identified in 2016. Multiple large natural mould tracks of variable morphology are evident on its upper surface, which consists of three layers. Large tracks are visible on its sides in cross section and on its underside as natural casts. We name this block 'Megafauna Rock'.

Much of the southern African Late Pleistocene fauna has extant analogues. However, an analysis of Pleistocene tracks requires knowledge of extinct species or subspecies that have been identified through the skeletal fossil record, and openness to interpretation of new track types and the need to analyse tracks systematically, while avoiding assumptions on trackmaker identity based merely on resemblances to the tracks of extant species.

The two rock sites are situated on the edge of the Palaeo-Agulhas Plain[8], towards the centre of the Greater Cape Floristic Region (GCFR). Most of the Palaeo-Agulhas Plain is currently submerged, but was exposed until as recently as the early Holocene.[9] The plain was characterised by fertile soils, extensive C_4 grasslands, rivers, floodplains and wetlands.[8,10] Extant taxa that are not currently present in the GCFR often dominated assemblages on this plain, including large-bodied grazers such as black wildebeest (*Connochaetes gnou*), while extinct grazers included long-horned buffalo (*Syncerus antiquus*), giant Cape horse (*Equus capensis*) and giant hartebeest (*Megalotragus priscus*).[11-14]

Blue antelope (*Hippotragus leucophaeus*) and quagga (the southern race of *Equus quagga*) survived until the 19th century.[8,15] Typical wetland species were present, including southern reedbuck (*Redunca arundinum*) and hippopotamus (*Hippopotamus amphibius*), indicating the presence of floodplains with perennial wetlands.[8] Immediately inland, in stark contrast with the fertile Palaeo-Agulhas Plain, were Fynbos–Strandveld–Renosterveld vegetation types, which were mostly nutrient poor and high in secondary compounds.[8] Herbivores associated with these vegetation types are specialist browsers such as grysbok (*Raphicerus melanotis)* and grey duiker (*Sylvicapra grimmia*).[8] The tracksites we describe were thus adjacent to a diversity of habitats that contained distinct animal assemblages.

The Cape south coast track record may be preservationally biased in that it tends to record the tracks of larger, heavier trackmakers that walked on sand and created larger, deeper tracks that are more readily evident upon re-exposure. However, the skeletal record may also be biased, as it relies mostly on specimens from caves and rock shelters, representing the remains of hunted prey or animals that lived in such features.[3] As with other fossil-bearing regions, the Cape south coast body fossil record and track record have the potential to complement each other, and to independently provide evidence of the Pleistocene fauna. Tracks, furthermore, have the potential to suggest animal behaviour and relative abundance. The relationship between the track record and extant animals and resulting palaeobiological implications has been addressed by Cohen et al.[16]

Methods

A total of 11 survey visits were made to the coastline east of Still Bay between 2007 and 2017. Global Positioning System (GPS) readings were obtained for Roberts Rock and Megafauna Rock using a handheld device. Locality information was reposited with the African Centre for Coastal Palaeoscience. Measurements and photographs were taken of the track-bearing surfaces and the better-preserved tracks. Photogrammetry was performed on tracks at Megafauna Rock using a Canon PowerShot ELFPH 340 HS camera. Point clouds and digital terrain models were compiled using Agisoft Photoscan Professional (v.1.0.4) and colour topographic profiles were created with CloudCompare (v.2.6.3.beta).

Geological outcrops were investigated in the field through comparison and correlation to known documented and dated deposits in the region. Standard field techniques were applied in understanding the context of the ichnofossils to determine the strata from which they were derived. These methods included measurement of the thickness of aeolian foresets, observation of colour, texture and degree of carbonate cementation, and sedimentary characteristics of the clasts.

Results

Roberts Rock

In 2007 Roberts Rock appeared similar to the description published by Roberts et al.[1] It was tilted at an angle of just over 90°, with the track-bearing surface facing the ocean (Figure 2). By 2009 this large rock had split into two approximately equal halves along a bedding plane. The base of the seaward portion had slumped away from its previous location, and its upper edge rested against the base of the landward portion; the track-bearing surface thus was tilted at ~45°. The position of the landward portion had remained relatively unchanged (Figure 3). This created a shaded recess between these two portions (Figure 4). The newly exposed surfaces exhibited numerous small and medium-sized artiodactyl tracks, similar to those described by Roberts et al.[1] as 'antelope tracks'; these tracks are readily identifiable through the presence of two digit impressions separated by an interdigital sulcus which is open anteriorly and posteriorly. Further large tracks similar to those noted as elephant tracks by Roberts et al.[1] on Roberts Rock were evident; these are also morphologically distinctive, with slightly oval pes tracks and relatively circular manus tracks, both of which are often associated with displacement rims.

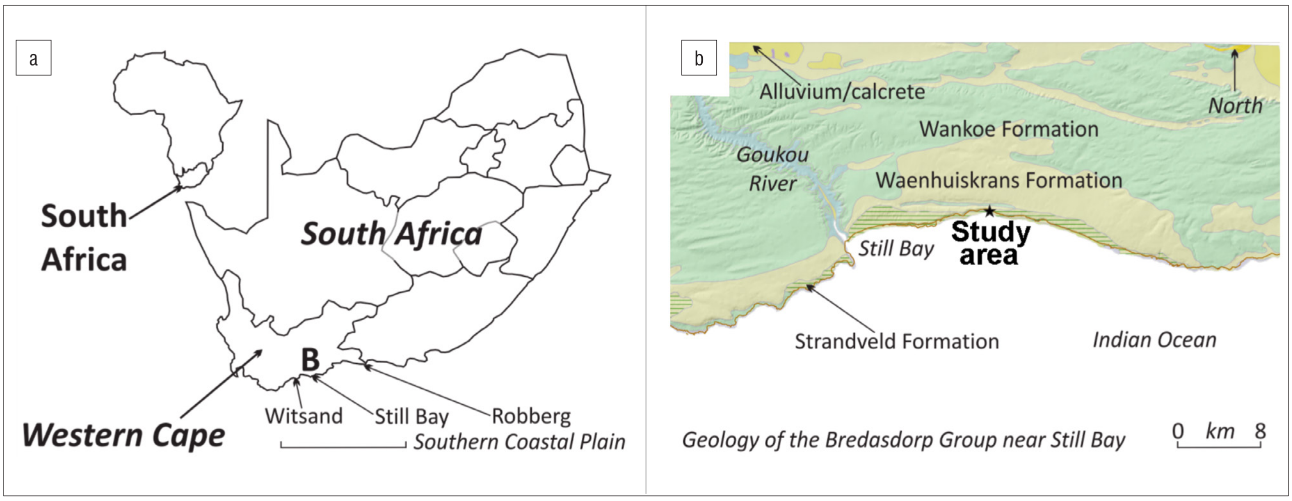


Figure 1: (a) Location of the study area within the Western Cape Province of South Africa. (b) Geological deposits in this region are dominated by strata of the Bredasdorp Group; the coastal deposits constitute outcrops of the Waenhuiskrans Formation, draped by Strandveld Formation unconsolidated sediments.

Figure 2: Roberts Rock in 2007.

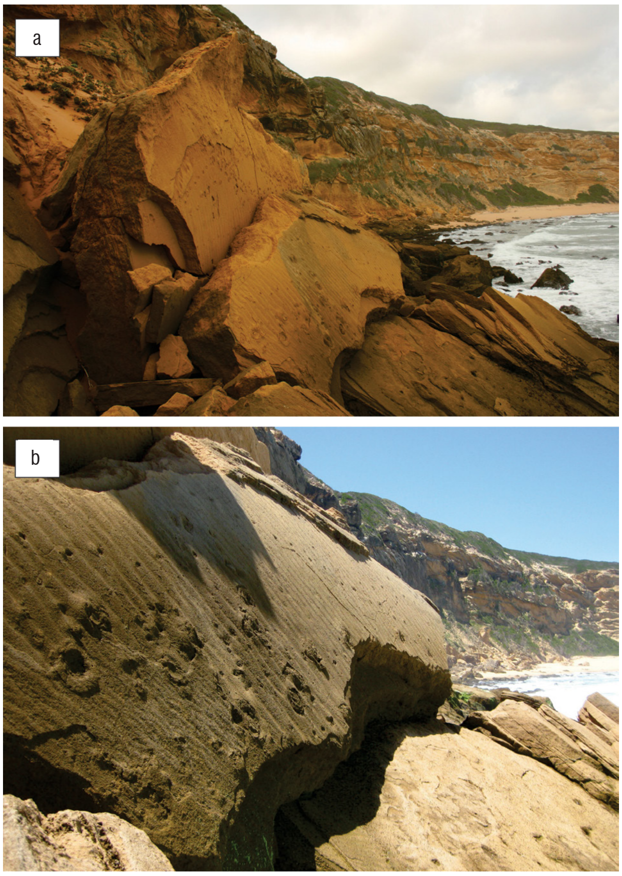


Figure 3: (a) Roberts Rock in 2009, after its separation. (b) The seaward portion of Roberts Rock in 2009 in good light conditions showing elephant and artiodactyl trackways.

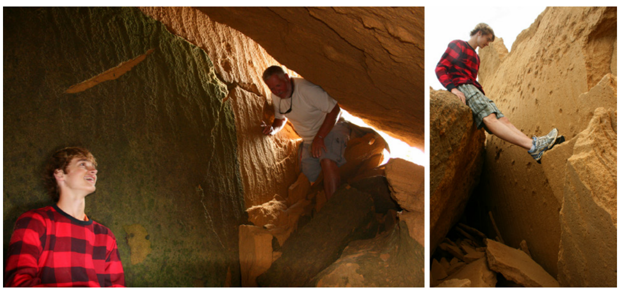


Figure 4: Exploring the gap between the seaward and landward portions of Roberts Rock in 2009. Numerous tracks are evident.

By 2016 Roberts Rock had disappeared into the ocean, and an even larger 12-m long block had slid down the sandy slope, and lay adjacent to the site that Roberts Rock had occupied. The seaward portion of the newly exposed block contained eight exposed surfaces, six of which exhbited tracks or undertracks (Figure 5). Ripple marks were evident on some surfaces.

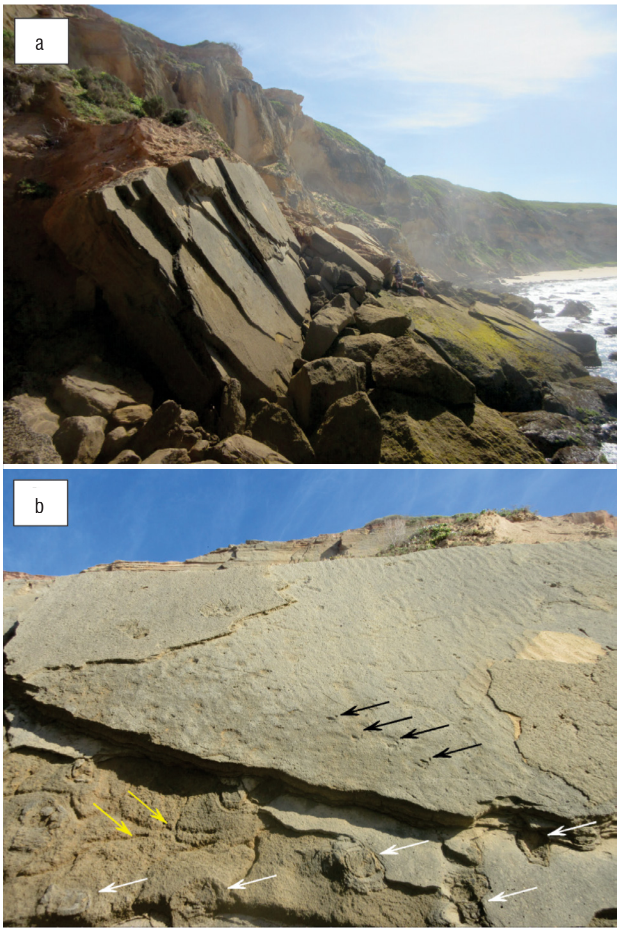


Figure 5: The newly exposed large rock that is situated adjacent to the Roberts Rock site. (a) Eight bedding planes are exposed. (b) Yellow arrows indicate probable golden mole burrow traces; black arrows indicate avian tracks; white arrows indicate elephant tracks.

Elephant and artiodactyl tracks, similar to those described above, were present. Linear traces resembling burrows, up to 10 cm in diameter, were evident. Two small tridactyl trackways were evident, with relatively narrow digit impressions. Because of the instability of the vertically orientated bedding planes and associated access challenges, measurements were not obtained for these two trackways. Numerous smaller trace fossil features were noted. Vestiges of the track surfaces of Roberts Rock were evident among rocks of the intertidal area.

The aeolianites which make up Roberts Rock and the rock which lay adjacent to the site it had occupied are derived from the same geological unit in the sequence. The aeolianite is of calcarenite composition and is medium-grained, moderately sorted sand, interspersed with shell fragments and sparse heavy mineral grains. These stratified deposits comprise low angle planar cross bed foresets which dip up to 20°.

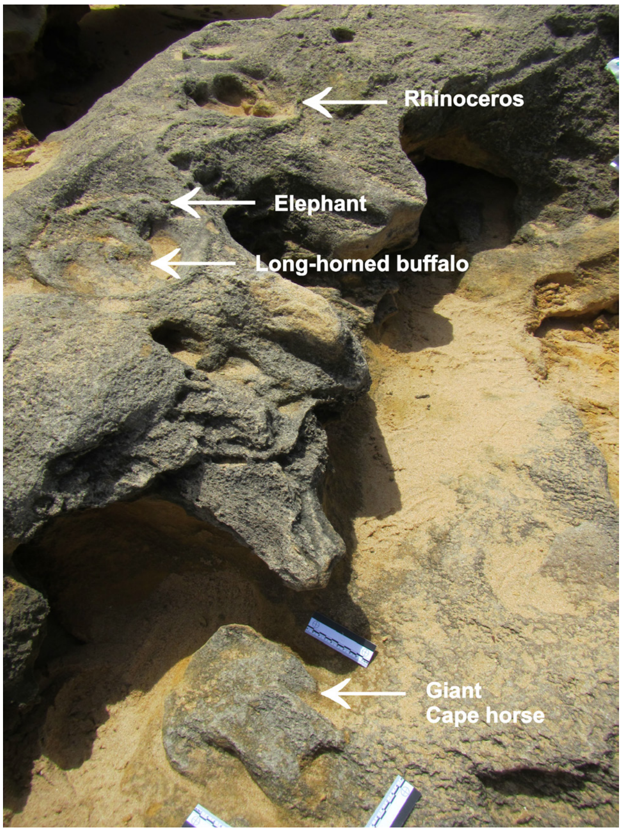
Megafauna Rock

Megafauna Rock was not identified during visits to the area before 2016. The most likely explanation is that it was present but not noticed, as from a distance it does not exhibit features to suggest that it displays fossil tracks. It lies at the upper end of a small beach. The bedding plane from which it has originated can be identified less than 10 m above its present position. Although derived from the same geological unit as Roberts Rock, Megafauna Rock is from a massive, well-cemented part of the succession. The beds range in thickness from 10 cm to 40 cm and dip shallowly.

Megafauna Rock measures 5 m x 5 m and is over 2.5 m high (Figure 6). On its upper natural-mould surface, which contains three levels, four large track morphologies are evident (Figure 7). Most common are the round or oval depressions. Length and width dimensions of two such tracks are respectively 34 cm x 31 cm and 31 cm x 29.5 cm.

Some of these tracks contain a layer of infill, and impressed into one such infill layer is a large artiodactyl track (Figure 8), with two characteristic digit impressions separated by an interdigital sulcus that is open anteriorly and posteriorly. Track length (13.5 cm) is less than track width (16 cm).

Figure 6: Megafauna Rock.



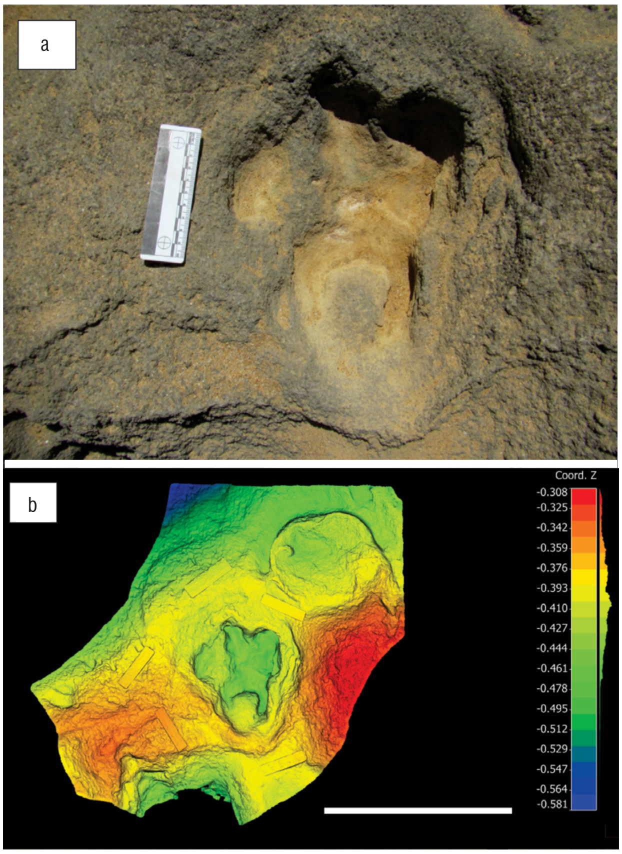
Scale bar = 10 cm

Figure 7: Upper surface of Megafauna Rock; arrows indicate tracks.

A single large tridactyl track with rounded digit impressions (Figure 9) occurs on the same level (length = 24 cm, width = 20 cm, depth = 5.5 cm).

Scale bar = 10 cm

Figure 8: Large artiodactyl track, probably made by long-horned buffalo, impressed upon infill layer of large elephant track on Megafauna Rock.

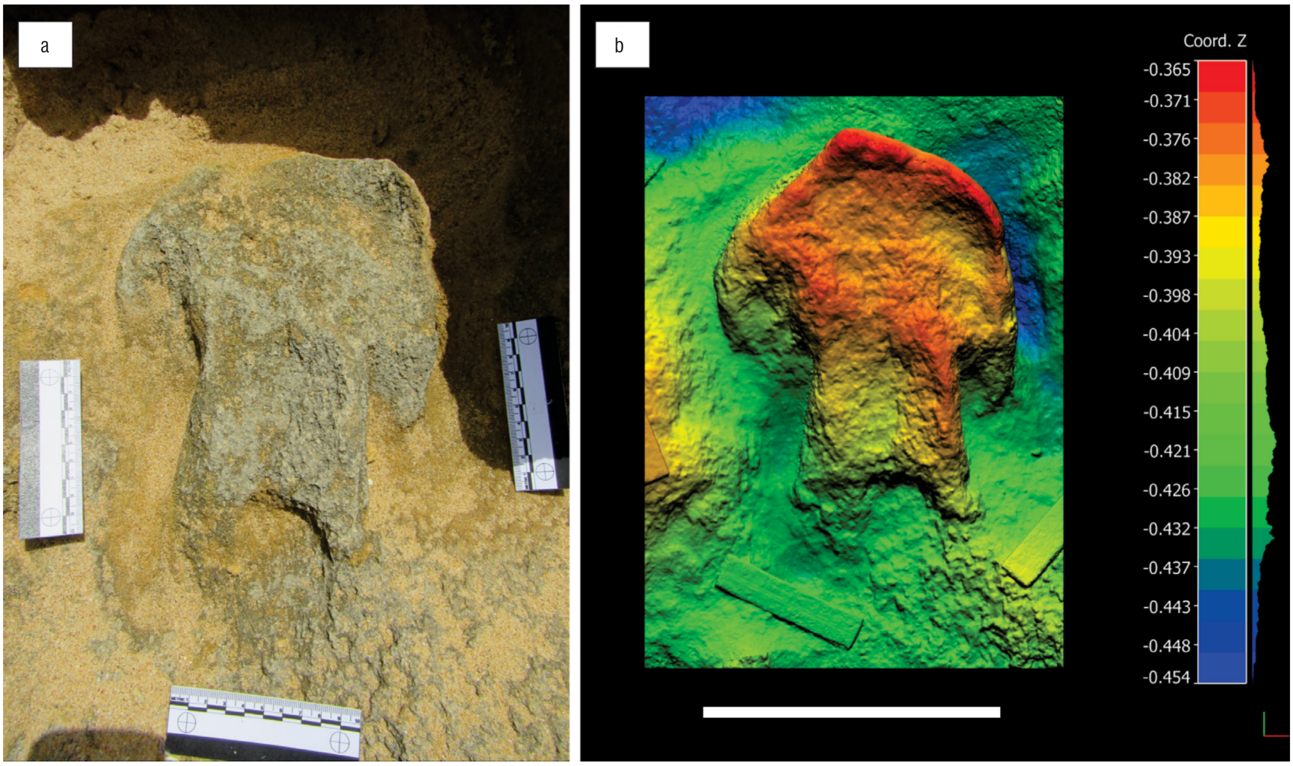


(a) Scale bar = 10 cm; (b) length of white horizontal scale bar = 0.4 m

Figure 9: (a) Large, three-toed, probable rhinoceros track on Megafauna Rock. (b) Photogrammetry colour mesh: probable rhinoceros track (centre) and at least one elephant track (upper right). 3D model was generated with Agisoft Photoscan Professional (v. 1.0.4) using 33 images from a Canon PowerShot ELFPH 340 HS (focal length 4.5 mm; resolution 4608 x 3456; pixel size of 1.33853 x 1.33853 um). Photos were taken an average of 0.42 m from the surface. The surface model error is 0.144403 pix. The final images presented here were rendered using CloudCompare (v.2.6.3.beta). Vertical scale bar is in metres.

One level below these tracks is a raised, symmetrical feature (Figure 10). Maximum length = 27 cm, and maximum width = 20 cm. There is no evidence of a cloven hoof anteriorly, and a 'frog' is probably evident posteriorly.

The sides of Megafauna Rock display large tracks in cross section. What is visible of its underside contains numerous large natural casts.



(a) Scale bar = 10 cm; (b) length of white horizontal scale bar = 0.2 m

Figure 10: (a) Probable *Equus capensis* track on Megafauna Rock. (b) Photogrammetry colour mesh: probable *Equus capensis* track on Megafauna Rock. 3D model was generated with Agisoft Photoscan Professional (v. 1.0.4) using 32 images from a Canon PowerShot ELFPH 340 HS (focal length 4.5 mm; resolution 4608 x 3456; pixel size of 1.33853 x 1.33853 μm). Photos were taken an average of 0.4 m from the surface. The surface model error is 0.138061 pix. The final images presented here were rendered using CloudCompare (v.2.6.3.beta). Vertical scale bar is in metres.

Discussion

Inferred chronology and significance of the Last Interglacial

Based on stratigraphic correlation to the dated layers of Roberts et al.[1], we suggest that Megafauna Rock most likely dates to Marine Isotope Stage (MIS) 5e. The geological stratum in which it occurs is the same unit described by Helm et al.[3] in which giraffe tracks were described. MIS 5e extended from ~128 ka to 116 ka[17] with a peak sea-level highstand at 126±7.1 ka[18], and was associated with a relative sea-level range of 6.6–8 m higher than present on the Cape south coast[19]. This was a time associated with polar temperatures ~3–5 °C warmer than at present[20] and a global mean temperature 1.5 °C higher than at present[21,22]. With the effects of the present interglacial, the study of sea-level indicators from MIS 5e is fundamental to achieving a sense of palaeoclimatic and palaeoenvironmental regimes as suitable analogues. Accurate dating of Megafauna Rock through OSL, and resulting estimates of the extent of the exposed Palaeo-Agulhas Plain and the distance to the coastline at the time the tracks were registered, may enable more robust palaeoenvironmental conclusions to be drawn.

Avian tracks

We ascribe an avian origin to the two short tridactyl trackways with relatively narrow digit morphology on the rock that lies adjacent to the Roberts Rock site. We do not consider these to be distinctive enough to allow for further speculation on trackmaker identity. However, they add to the archive of fossil avian tracks in southern Africa. We have identified 14 such tracksites, representing at least six morphologies, in Pleistocene aeolianites on the Cape south coast, of which 8 are in the area east of Still Bay.[2,4] One of these sites is close to Megafauna Rock, and contains two of the longest known fossil avian trackways in the world.[2] Prior to our studies there was only one published reference to an avian fossil trackway in South Africa.[23]

Elephant tracks

The occurrence of elephant tracks at both Roberts Rock and Megafauna Rock is not surprising. Roberts' initial description[1] of Roberts Rock placed it at the western edge of a 300 m, laterally persistent, low-angled, laminated facies containing numerous elephant tracks; bioturbation was noted, with tracks evident in successive bedding planes over a vertical extent of 4 m.

The slightly oval pes and more rounded manus tracks are distinctive, and there is no plausible trackmaker other than the African elephant (*Loxodonta africana*).[24-27] There is no fossil evidence to suggest that earlier elephant species such as *Loxodonta atlantica* survived later than 400 ka.[14] We have now identified fossil elephant tracks at many sites along the Cape south coast, including Dana Bay, Goukamma (six sites)[4] and Brenton-on-Sea[5]. One cross-sectional Goukamma site exhibits tracks in a section up to 26 m in thickness.[4] While the elephant tracks at Roberts Rock and Megafauna Rock represent some of the southernmost evidence of elephants in the world[1], submarine studies may expand the range further south onto the Palaeo-Agulhas Plain.[28]

The Cape south coast sites are collectively the only known Pleistocene elephant tracksites in southern Africa, and there is a single documented occurrence of a Pleistocene elephant tusk in an intertidal platform in aeolianite near Durban.[29] Pliocene elephant tracks have been reported from Laetoli in Tanzania.[30] Pleistocene elephant tracks were reported from near Ileret in Kenya[31], and Holocene elephant tracks have been reported from Namibia[32,33].

The African elephant is highly adaptable, and ranged across Africa in numbers of more than 20 million before European colonisation, after which their numbers decreased to an estimated 400 000 today.[34,35] A remnant population survives near the Cape south coast in the Southern Afrotemperate Forest around Knysna, which was once connected with the rest of the southern African population.[36] Evidence suggests that elephants used a variety of habitats and migrated extensively in the GCFR, even crossing mountain passes into the Karoo, eastern Cape thicket and beyond.[37,38] Based on dentition and modern diets, African elephants are considered mixed feeders, favouring woody browse during the dry season and C_4 grasses during the wet season.[39,40] Evidence suggests that their diets contained a higher degree of C_4 grasses in the Pleistocene.[40] The grassy plains, meandering rivers and seasonally waterlogged floodplains of the Palaeo-Agulhas Plain[10] would potentially have been an important seasonal resource for elephants, driving a seasonal migration[15,29] between the grazing resources in the wet season and the forests in the southern Cape, river drainage thickets of the Karoo hinterland, or thicket areas of the eastern Cape in the dry season.

Artiodactyl tracks

Artiodactyl tracks are the most common ichnofossils noted in Late Pleistocene aeolianites on the Cape south coast through the course of our project. Often such tracks cannot be identified to genus level, and can simply be described as 'large artiodactyl', 'medium artiodactyl' or 'small artiodactyl', as on Roberts Rock where small and medium artiodactyl tracks predominated. However, tracks of buffalo species are an exception, being distinctive in size (slightly larger than eland or kudu, smaller than giraffe). Two buffalo species are known from the GCFR: the extant Cape buffalo (*Syncerus caffer*) and the extinct long-horned buffalo (*Syncerus antiquus*). In analysing fossil artiodactyl tracks of this size, we note two morphologies: tracks that are longer than they are wide, consistent with tracks of the extant *Syncerus caffer*, and tracks that are wider than they are long, as noted first in a long trackway at Goukamma[4]; there are no extant artiodactyl tracks in southern Africa that exhibit such dimensions.[24-27] The artiodactyl track on Megafauna Rock is much wider than it is long (Figure 8).

In contending that *Syncerus antiquus* is the most plausible trackmaker, we note the observations of Lockley[41] that wider, longer and often more curved horns are associated with wider, more curved tracks, and that *Syncerus antiquus* had extremely long, laterally extending horns. Cattle farmers in southern Africa indicate that they can distinguish tracks of short-horned cattle from those of Nguni cattle which have horns of medium length, the latter being proportionately wider (Smit N 2016, oral communication, October 16). The track on Megafauna Rock, although single, corroborates the trackway evidence from the Goukamma site regarding track dimensions of this extinct buffalo species.[4] Its occurrence within the infill layer of an elephant track is unusual.

The long-horned buffalo, *S. antiquus,* was common in the GCFR up to the beginning of the present interglacial, becoming locally extinct at ~10–12 ka.[42] Its decline is thought to be related to changing climate and the associated sea-level rise that inundated a large proportion of the Palaeo-Agulhas Plain, resulting in loss of suitable habitat in the early Holocene.[42-44] The smaller Cape buffalo, *S. caffer,* remained fairly common in the southern Cape up to the 18th century, especially from Mossel Bay eastwards.[37,38]

Both *S. antiquus* (~800 kg) and *S. caffer* (~650 kg) are very large ruminants, with the latter already at the extreme of ruminant body size limits.[45] Both species would have required bulk grazing resources in the GCFR which would have provided sufficient energy to sustain them during times of lower availability. Regional migration on the Palaeo-Agulhas Plain between C_4 and C_3 grasslands (e.g. between bimodal and winter rainfall areas) is possible. The C_4 grasslands with wetter habitats on the Palaeo-Agulhas Plain would have played a prominent role in the survival of both species, arguably more so in the case of *S. antiquus*. Klein[43] noted that the hypsodont teeth and long horns of *S. antiquus* indicated a preference for open grasslands. Sinclair[46] noted a preference for riverine grasslands and riverine forest for *S. caffer*. In comparing the habitat requirements of *S. antiquus* and *S. caffer*, Vrba[47] considered *S. caffer* to be less tolerant of very open environments. Peters[48] considered such arguments in analysing the faunal succession at the Ishango site in eastern central Africa, which may have relevance to similar successions on the Cape south coast. Once accurate dating has been performed at Megafauna Rock, and the extent of exposure of the Palaeo-Agulhas Plain at the time the tracks were made can be determined, such considerations may be helpful in palaeoenvironmental interpretation.

Rhinoceros track

The dimensions and morphology of the deep tridactyl impression with rounded digit impressions on Megafauna Rock is suggestive of a rhinoceros trackmaker (Figure 9). This inference is tempered with caution because only one track is evident. However, the presence of other large, well-preserved vertebrate tracks on this surface supports the likelihood this impression is a track rather than a non-biogenic feature. No extant member of the southern African fauna produces three-toed tracks of this size other than rhinoceros, although we acknowledge that in sandy substrates impressions made by the two middle toes of hippopotamus (*Hippopotamus amphibius*) can sometimes appear to fuse, potentially creating a resemblance to a rhinoceros track.[27] We are not able to distinguish whether this track was made by black rhinoceros or white rhinoceros, but the dimensions of this track are smaller than that made by an adult white rhinoceros.[24-27] This is the first documentation of a probable fossil rhinoceros track in southern Africa. Pliocene rhinoceros tracks have been reported at Laetoli in Tanzania.[27]

Black rhinoceros (*Diceros bicornis*) was recorded throughout the GCFR until as recently as the 18th century.[38] White rhinoceros (*Ceratotherium simum*) disappeared from the fossil record in the southwestern Cape ~17 000 years ago.[42] While both species are present in the body fossil record of the GCFR during the Pleistocene[42], *D. bicornis* is encountered more frequently[14]. *D. bicornis* is a browser preferring low-growing woody shrubs, and *C. simum* is a grazer preferring short grass species in the wet season and taller grass species in the dry season.[49] Both species are water dependent.[50] *C. simum* would have tended to inhabit the Palaeo-Agulhas Plain with its C4 dry and short grasslands, and *D. bicornis* would have tended to inhabit Fynbos–Strandveld–Renosterveld areas inland with suitable browse vegetation.

Equid track

The large, symmetrical raised feature on Megafauna Rock (Figure 10) has equid features, and its dimensions are more than double the length and width of tracks of extant zebra species, which are typically ~10 cm in length.[24-27] The morphological features and size suggest a large horse species such as the giant Cape horse (*Equus capensis*) as the trackmaker. While some of the attributes of this track can be attributed to overprinting, the dimensions noted remain substantially larger than those of any extant equid species, and there is no candidate for equid tracks of this size from the body fossil record other than *E. capensis*. We acknowledge that Pleistocene body size may correlate with climate regimes, with carnivore size noted as being larger during glacial phases.[51] However, there is no indication that extant zebra species were similarly affected.

While Roberts et al.[1] noted the presence of equid tracks in aeolianites along the Cape south coast, the track on Megafauna Rock was the first identification of an equid track of this size in southern Africa. Whereas the other tracks on the upper surface of Megafauna Rock are natural mould impressions, this feature is raised. The preservation mechanism can be attributed to compaction of sediment below the track, making it more resistant to erosion than the surrounding matrix.[52] Such a preservation mechanism can be replicated on Cape south coast beaches under suitable conditions: initial compression of surface layers of sand by the trackmaker, followed by wind of sufficient strength removing the softer sand around the track, leaving an elevated 'pedestal track'. Subsequently, fossil equid tracks have been noted at Goukamma[4], Brenton-on-Sea and Robberg. As with the inferred long-horned buffalo and rhinoceros tracks on Megafauna Rock, the presence of only a single track provides a limited database.

Equus capensis occurrence in the GCFR can be traced to the early Pleistocene[53], but like *S. antiquus* it went locally extinct at ~10–12 ka[42]. The giant Cape horse[54], at ~450 kg, was larger than its close relatives, the Cape mountain zebra (*Equus zebra*, ~234 kg)[50] and the quagga or plains zebra (*Equus quagga,* ~235 kg)[55].

All equids are non-ruminants which are tolerant of poor quality forage, but they require a high rate of intake.[56] *E. quagga* is considered to be a grazer that takes browse occasionally.[57] *E. zebra* is also predominantly a grazer, but takes browse more readily.[58] Extant equids are water dependent and normally stay within 12 km of the nearest water source.[50] *E. quagga* is described as a savanna species which prefers more open areas in woodland habitats.[50] Considering the food and habitat requirements of extant species and the fact that *E. capensis* was a very large animal, the C_4 grasslands of the Palaeo-Agulhas Plain would have been a key resource for this species.

Burrow traces and invertebrate traces

The dimensions of the large burrow traces evident on the large block that lies adjacent to the Roberts Rock site probably make an invertebrate origin unlikely. We considered root casts, as they are found in the region, usually in palaeosols. However, such root casts tend to cross foresets, and tend to taper. While we do not ascribe an origin for these features with certainty, we suggest that they were most likely made by a fossorial species such as a golden mole. Similar, better preserved burrow traces have been found closer to Still Bay, at Goukamma and at Robberg. Early to Middle Tertiary golden mole burrow traces have been described from the Tsondab Sandstone Formation in the Namib Desert.[59] Numerous smaller traces are present consistent with an invertebrate origin. While these burrow traces do not form a current focus of our study, they may form a fruitful subject for future study.

Megafauna Rock – palaeoenvironmental considerations

Megafauna Rock represents an important record from the perspective of understanding faunal distributions in the GCFR. The site location, at what would probably have been a dune setting in an ecotone between the grassland of the Palaeo-Agulhas Plain and the inland Fynbos–Strandveld–Renosterveld, allows for the potential of observing faunal assemblages from both vegetation types. Fossil remains of *S. antiquus* from Late Pleistocene sites are generally associated with bones of typical grazers, including *E. capensis*.[49] The track assemblage on Megafauna Rock thus independently supports the body fossil record. All four species whose tracks are found on Megafauna Rock were water dependent. The concentration of tracks on different bedding planes on one rock (indicating repeated use over time) suggests proximity to a water source. Quick et al.[7] analysed a core sample from Rietvlei, 3 km northwest of Megafauna Rock, with dates extending back to 36 ka. A similar interdune lake could have existed at the time the tracks were registered, as was suggested by Roberts et al.[1]

Areas of concentration

Tracksite zones appear to be concentrated in space and time. An area of concentration east of Still Bay extends laterally parallel to the coast, as well as vertically, implying repeated use of certain areas. Roberts Rock and Megafauna Rock occur within this track-rich zone. In adjacent areas that seem to offer suitable opportunities for track-bearing exposures, none are observed over stretches of more than a kilometre. Proximity to water sources is one possible reason for such zones of concentration. Roberts et al.[1] also suggested the possibility of a seasonal migration trail. Through neoichnological studies, Cohen at al.[12] have suggested how track analysis can be used to estimate population density and recurrent behaviour. The applicability of such suggestions to the tracksites of the Cape south coast, including the sites we describe here, should be considered with caution, as meaningful interpretation would require large sample sizes. Furthermore, the challenges are acknowledged of differentiating between many tracks made by a single individual versus a few tracks made by multiple individuals.

Rate of tracksite exposure and loss

High tides and storm surges impact these coastal cliffs. Cliff collapse and slumping are frequent, as weakly cemented aeolianites readily cleave along bedding planes. Rocks containing track-bearing surfaces may be seen in situ, or ex situ at the base of cliffs, as in the case of Roberts Rock and Megafauna Rock. The rapid changes that occurred in the space of less than a decade at Roberts Rock are testimony to the ephemeral nature and instability of such sites. Repeat visits enabled an observation of the ichnofauna on a succession of surfaces that would not have been apparent from a single visit. It is likely that other sites have been lost to coastal erosion without being recorded. Fortunately, Megafauna Rock appears to be a more stable unit, and it lies above the zone of intertidal erosion. Repeat coastal surveys to document new tracksites and to determine the fate of known sites are desirable.

Conclusions

Roberts Rock and Megafauna Rock form two ichnological highlights of an area rich in trace fossils. Both exhibit impressive track density, and both indicate continued impact on substrates in space and time in definable zones. They provide windows into Late Pleistocene dune life in the southern Cape, and suggest an area teeming with life.

Together they contribute to the understanding of the Late Pleistocene southern Cape megafauna, including the first documentation of elephant tracks, probably the first rhinoceros and giant Cape horse tracks, and ichnological evidence of the long-horned buffalo.

Dating of Megafauna Rock and other tracksites of significance by OSL is anticipated to contribute to further palaeoenvironmental inferences, as the sites would be placed within a temporal framework. The slumping of Roberts Rock into the ocean is a loss to ichnology, mitigated by its replacement by an even larger track-bearing rock. At least it was studied repeatedly during its exposure. As an example of the ephemeral nature of exposed tracksites and the likely exposure of new sites, this case stresses the need for regular ichnological surveys along this track-rich coastline.

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Authors’ contributions

C.W.H.: lead author, corresponding author, conceptualisation, data collection, data analysis, writing, project leadership, track analysis. H.C.C.: sample analysis, data analysis, contribution on geological context, field stratigraphy, review of drafts and revisions. J.C.d.V.: data collection, data analysis, discoverer of Megafauna Rock, review of drafts and revisions. M.G.L.: data collection, data analysis, contribution on ichnological content, review of drafts and revisions. R.T.M.: data analysis, photogrammetry, review of drafts and revisions. J.V.: data analysis, contribution on palaeobiology and palaeoenvironment, review of drafts and revisions.

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