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Biofilm assists recognition of avian trackways in Late Pleistocene coastal aeolianites, South Africa

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Fourteen fossil avian tracksites have been identified in Late Pleistocene aeolianite deposits on the Cape south coast of South Africa. One of these sites is unusual because of the preferential adherence of organic material (biofilm) to the natural cast tracks. This has enabled the recognition and identification of two ~6 m long, approximately parallel trackways that would otherwise not have been noticed. The trackways are visible from a distance of over 100 metres and contain 20 and 14 individual tracks, respectively. Up to 50 avian tracks are evident at this site. As the biofilm layer continues to thicken, the trackways become increasingly visible. Avian trackways of this length are globally rare. We propose that the biofilm adheres to sections with higher relief on a sedimentary surface, and that an understanding of this mode of preservation can be useful to more easily identify trackways in areas of comparable geological setting.

Keywords: Biofilm, avian trackways, aeolianites, Pleistocene.

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INTRODUCTION

Late Pleistocene aeolianite deposits extend intermittently along much of the South African coastline, where they are exposed in embayments on the coastal plain (Roberts *et al.* 2008; Roberts *et al.* 2013). Coastal aeolian deposits along the Cape south coast are sensitive indicators of palaeoenvironmental fluctuations over time, evidenced in their palaeontological and archaeological content, their orientation and their geometry (Roberts *et al.* 2013). Fossil tracksites on aeolianite surfaces can independently contribute to an understanding of regional palaeoecology and can complement the body fossil record, although there may be a bias to larger, heavier trackmakers that utilized dune surfaces and interdune areas.

Over 100 fossil trackways preserved in Pleistocene aeolianites have been identified by C.W.H. over a stretch of 275 km of the Cape south coast between Witsand and Robberg (Fig. 1). Fourteen of these localities contain avian tracks, representing at least six different footprint morphologies. Eight of the avian tracksites were found within a remote six-kilometre stretch of coastline east of Still Bay. Prior to this study there was only one known avian fossil tracksite in South Africa (Roberts 2008). Nonetheless, the history of avian life in the littoral zone has been studied extensively (Avery 1990).

A single avian trackway (Trackway 1) containing 20 tracks was first noted in 2009 on the underside of an overhanging bedding plane exposure east of Still Bay (Fig. 2). This surface represents the infill layer on a dune surface, and preserves the avian tracks as natural casts, as well as numerous invertebrate traces as natural casts. It lies at an angle of 32°, consistent with the typical angle of repose of a dune surface. It is approximately 20 metres above sea level, is south-facing, and is never exposed to direct sunlight. Tectonic activity through the Pleistocene is considered minimal on the Southern Coastal Plain (Fleming *et al.* 1998), and *in situ* bedding planes therefore lie close to their original angle of deposition. The trackway is inaccessible, as it is much as 6 metres above the unstable rocky slope below.

The trackway is clearly visible from a distance of more than 100 metres in either direction along the coast, due to an obvious effect from a colour contrast. The tracks appear dark brown on a lighter, mostly yellowish rock surface. As this is a natural cast surface (convex hyporeliefs), the footprints form raised protuberances, and it appears that a darker-coloured organic layer is attached to these tracks rather than to the flatter surrounding rock. The brown organic layer is evident on many old exposed surfaces along the coast, and preferentially appears to attach to convex surfaces (Fig. 3).

The area was revisited in 2016 and 2017. The organic material appeared darker than before, and Trackway 1 had become even more obvious. A second, fainter trackway (Trackway 2) with less relief, containing fourteen tracks, had become evident below and approximately parallel to the initially identified trackway (Fig. 4). Trackway 2 had not been noted during initial observa-

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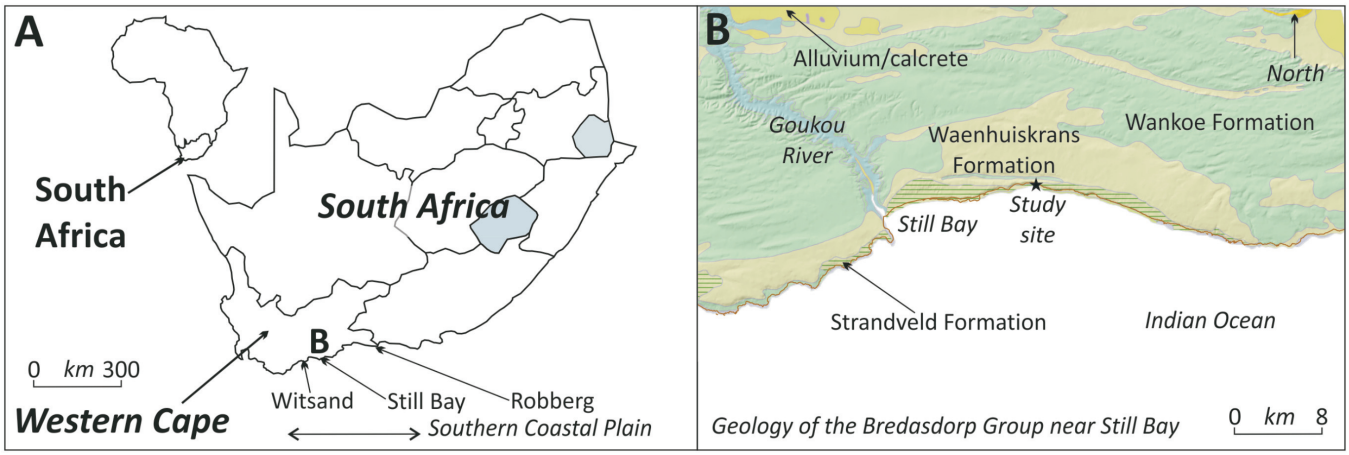


Figure 1. **A**, Location of the study area (east of Still Bay) in relation to the Southern Coastal Plain and within the Western Cape of South Africa. **B**, The geological deposits in this region are dominated by strata of the Cenozoic Bredasdorp Group; the coastal deposits generally constitute outcrops of the Late Pleistocene Waenhuiskrans Formation, draped by a veneer of predominantly Holocene Strandveld Group unconsolidated sediments.

tions, but in retrospect parts of it are barely discernible on the initial photographs. The adherence of the brown organic material onto these convex track casts had undoubtedly assisted with their recognition. Other than the increase in the amount of organic material, the surface had not obviously changed since 2009. As many as 12 indistinct avian tracks of similar size as those in Trackway 1 and Trackway 2 were noted northeast of these trackways on the same palaeosurface during the 2017 visit, and could be measured. In addition, four further probable avian tracks with similar morphology as those of Trackway 1 and Trackway 2, and also appearing darker than the surrounding surface, were identified on a darker older layer ~60 cm to the north of Trackway 1 and ~40 cm to the north of Trackway 2.

GEOLOGICAL CONTEXT

The Cape south coast trackways of the Late Pleistocene, including the avian tracksite, occur in the aeolian Waenhuiskrans Formation which belongs to the Bredasdorp Group. Description and delineation of the Waenhuiskrans Formation was conducted by the South African Committee for Stratigraphy (Malan 1989, 1990) and subsequent work has unravelled the complexity of the stratigraphy and provided chronological control (Roberts *et al.* 2008). The Waenhuiskrans Formation in the area of the avian track site comprises planar-bedded aeolianites of predominantly medium-grained sand, which form cliffs of up to 50 m in height along a 6 km stretch of coastline, much of which is inaccessible during high tides. Storm surges and spring tides impact the coast

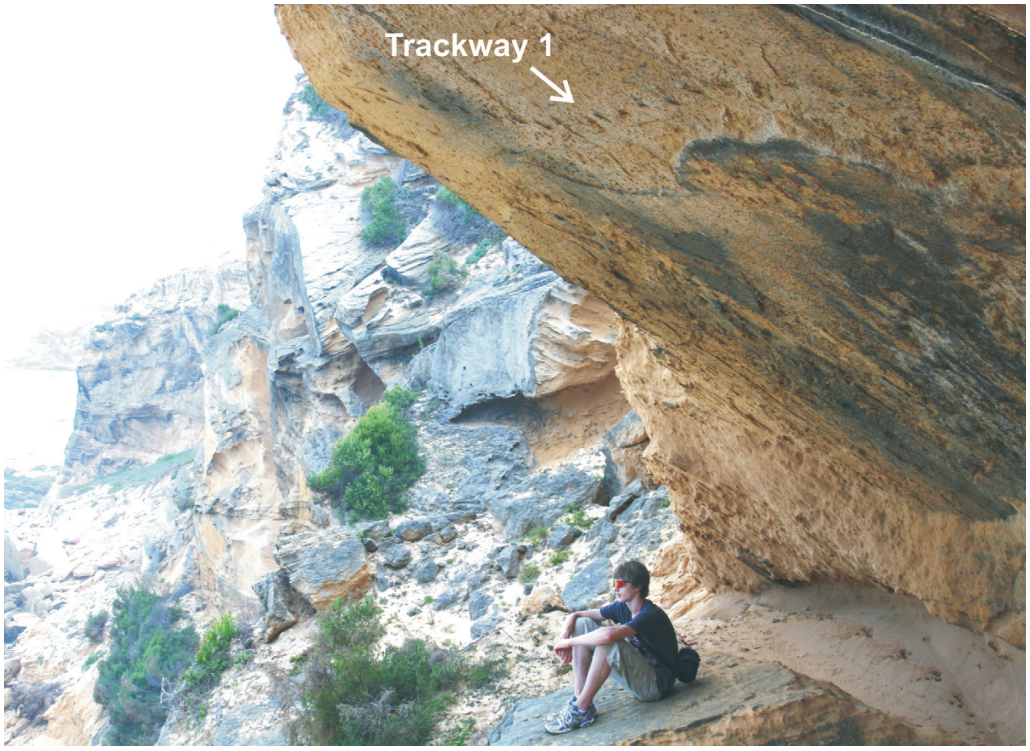


Figure 2. A single avian trackway (Trackway 1), containing 20 tracks running from east (right) to west (left), was first noted in 2009 on the underside of an overhanging exposed bedding plane that represents the infill layer on a dune surface. The trackway is situated approximately 5 metres above the photographer.



Figure 3. Biofilm (dark area) appears to attach preferentially to convex surfaces. Scale bar = 10 cm. The area covered by biofilm extends in a southerly direction from the south-facing cliff surface.

and its deposits, and as portions of the cliffs collapse new tracks are exposed, which are then subjected to erosion and may slump into the ocean.

East of Still Bay, Roberts *et al.* (2008) conducted a detailed sedimentological and ichnological study of a Pleistocene dune cordon, which is stratigraphically correlated to our study site. Roberts *et al.* showed that planar cross-bedded units ranging in thickness from 0.4 to 1.8 m are the dominant primary sedimentary structure in the succession, with foreset dips of up to 37°. The large-scale, steeply dipping planar cross-bedded facies display three aeolian sedimentation processes (grainfall, ripple migration and grainflow) proposed by Hunter (1977). Sedimentary facies are dominated by large-scale planar cross-stratification formed by foreset progradation of large-scale dunes (Roberts *et al.* 2008).

Sets of low-angle-to-horizontal lamination reaching several metres in thickness in the Still Bay outcrops reflect deposition on broad, stable, generally subdued topographies and represent interdune areas (Hunter 1977, 1981;

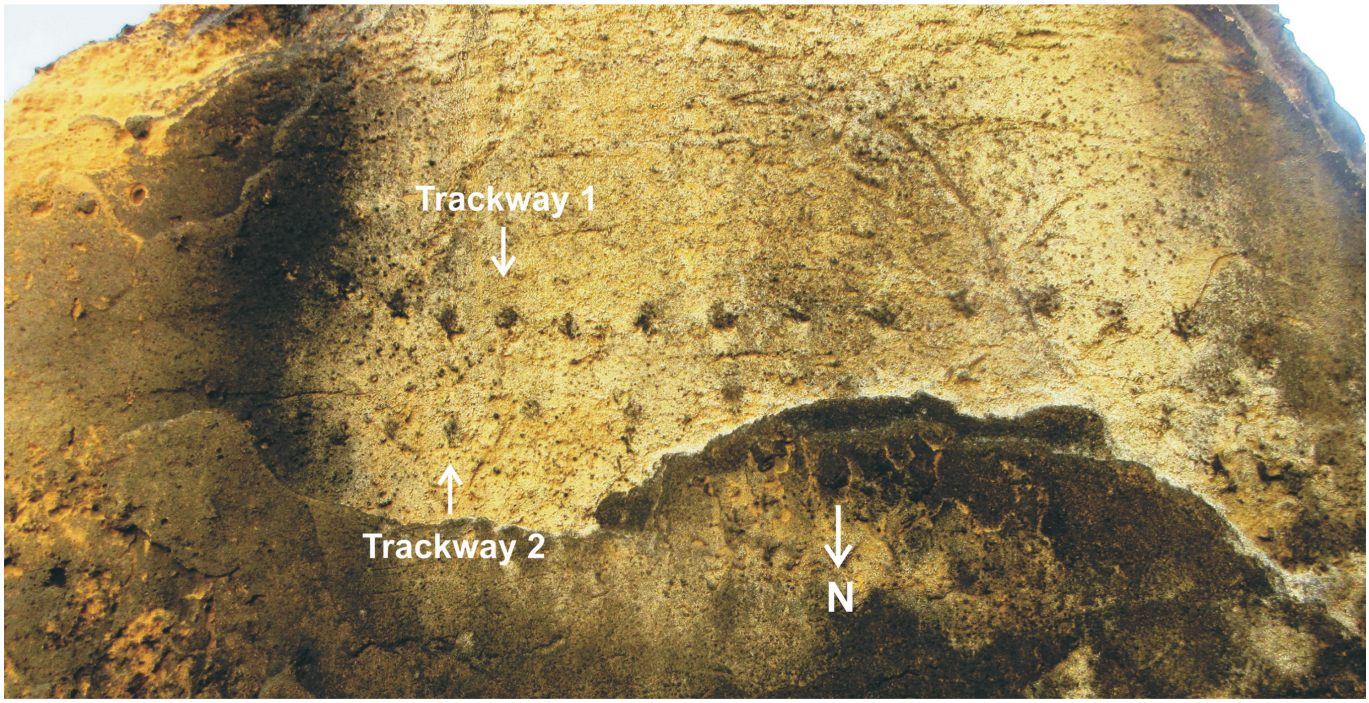


Figure 4. By 2016 a second trackway (Trackway 2) had become visible, approximately parallel to Trackway 1.

Fryberger *et al.* 1979). Such low relief areas are extensively developed in modern south coast dunefields (Roberts *et al.* 2008) and vertebrate trace fossils are relatively abundant in this facies.

Optically stimulated luminescence (OSL) and amino acid racemization (AAR) dating east of Still Bay (Roberts *et al.* 2008) provides ages ranging from Marine Isotope Stage (MIS) 5e to 5b and termination of Late Pleistocene aeolian sedimentation at ~90 ka. The Waenhuiskrans Formation Pleistocene aeolianite is separated from the overlying unconsolidated 8 ka Holocene dunes by a major hiatus. Because of the present interglacial MIS 1 highstand, MIS 5 aeolianites are being actively and rapidly eroded by storm wave activity. Fresh blocks of material are frequently dislodged. MIS 5 aeolianites relate to sea levels below the MIS 5e maximum highstand of about 6.2 m above Mean Sea Level and consequently would be vulnerable to erosion during the MIS 1 highstand (Roberts *et al.* 2008, 2012). These dating studies of the Waenhuiskrans Formation by Roberts *et al.* (2008) were performed at an elephant trackway site 400 metres to the east of the avian track site. Stratigraphic correlation of the elephant site with the avian track site showed that the avian tracks are stratigraphically higher than the elephant site and were laid down after the MIS 5e highstand. The closest stratigraphically correlatable date generated from the adjacent elephant trackway site (Roberts *et al.* 2008) provides a minimum age of the unit of 91 ± 4.6 ka.

METHODS

Global Positioning System (GPS) readings were obtained for the tracksite using a handheld device. Accurate measurement of the trackways was impossible due to challenging access to the overhanging palaeosurface. Measurements were taken of the dimensions of the track-bearing surface, and basic measurements (track length, pace length) were taken of Trackway 1 using a scale bar mounted on a long pole (Fig. 5), as well as of the tracks further northeast. In 2017 the brown material that was noted to be coating the tracks was sampled from an area a short distance from the trackways for microscopic analysis. Pieces of substratum were chipped off the rock face and frozen for transport to the laboratory. Samples were thawed and surface material was scraped off with a scalpel, placed on microscope slides in fresh water and viewed under a Leitz Diaplan compound microscope (Wetzlar, Germany) equipped with an Olympus D50 digital camera. An ethnobotanical survey included the questioning of local residents on their understanding and traditional uses of the brown material found on rock surfaces in the region (De Vynck *et al.* 2016). Locality information for this site is reposited at the African Centre for Coastal Palaeoscience, Nelson Mandela University, and at the Peace Region Palaeontology Research Centre.

RESULTS

The track-bearing overhang surface measures 7 m from east to west, and up to 6 m from north to south at a 32° angle. The tracks appear as natural casts. The slightly sinuous trackways run from east to west across the dune palaeosurface (perpendicular to the slope), with a probable sharp turn at their proximal ends, and are approximately parallel to one another. Trackway 1 comprises 20 tracks and is under 4 m in total exposed length; Trackway

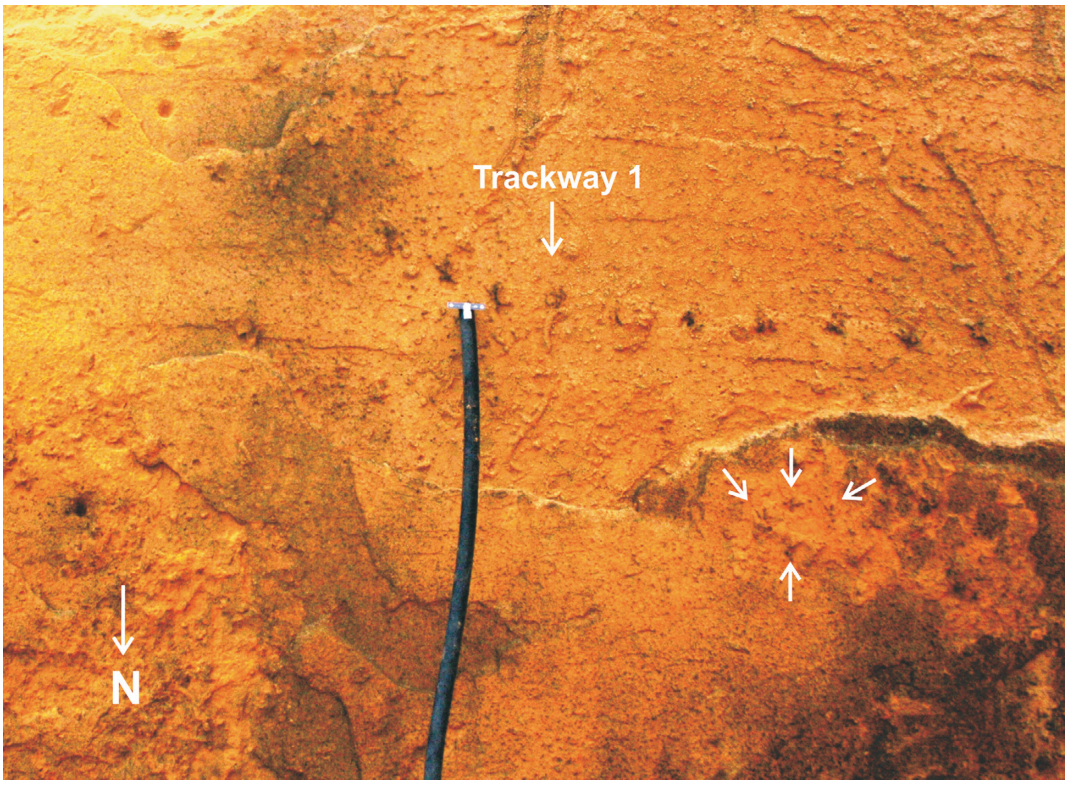


Figure 5. A scale bar (distance between the white circles = 10 cm) on a pole was used to take basic measurements of Trackway 1 in 2009. Although Trackway 2 was not identified at this stage, in retrospect parts of it can be noted. Four further probable avian tracks on the darker older layer north of Trackway 1 are indicated with arrows.

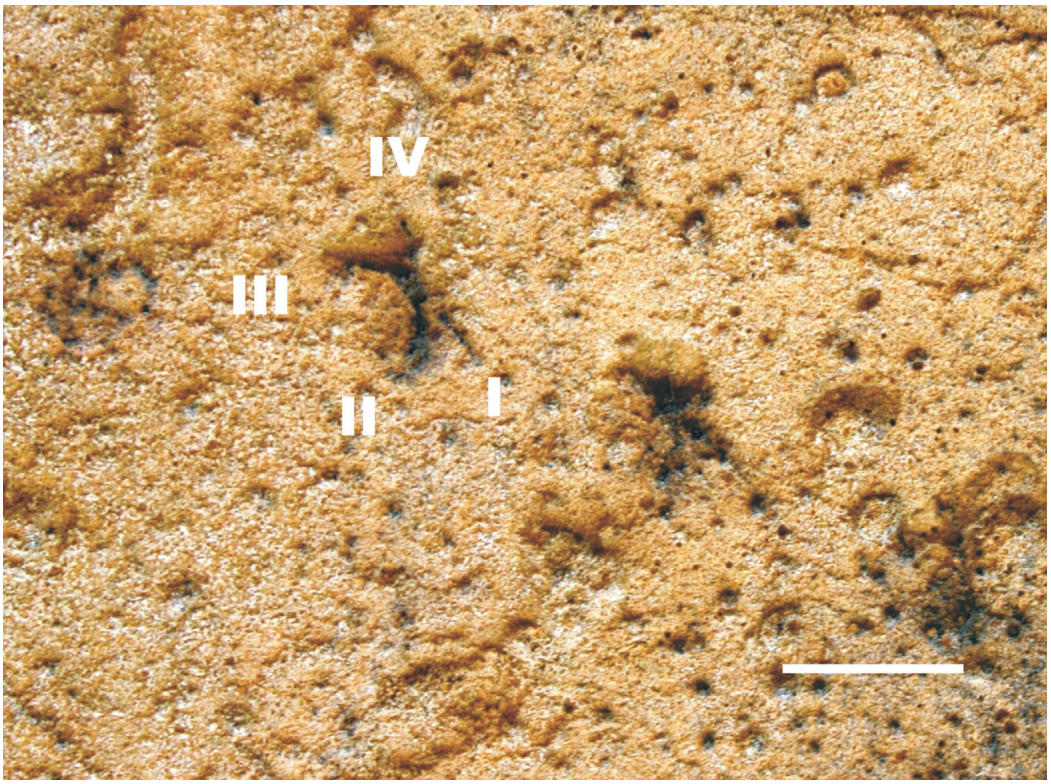


Figure 6. Close-up of four tracks from Trackway 1. Digit numbers I–IV are indicated. White horizontal scale bar = 10 cm.

2 comprises at least 14 tracks and is ~2.5 m in total exposed length. Mean track length is ~10 cm. Pace length is slightly variable, ~16–20 cm in the better preserved portions of Trackway 1. Although morphology is not well preserved (it is not possible to discern whether or not webbing is present) the better-preserved tracks are anisodactyl with a posteromedially directed hallux (digit I) (Fig. 6). The two trackways exhibit similar morphology.

The twelve tracks evident to the northeast of the main trackway area are indistinct, and are only minimally darker than the surrounding surface. They run initially from north to south (upslope), curving to southwest distally. Two trackways are possibly evident, curving distally towards the area of the proximal tracks of Trackway 1 and Trackway 2. One short four-track segment could be measured, exhibiting a pace length of 9–11 cm. The hallux is only evident in one of these tracks, for which the track length is 7 cm. This track has similar morphology to those in Trackway 1 and Trackway 2.

The four probable avian tracks on the older, darker surface south of the main trackways are clearly darker than the surrounding surface. They are orientated northwards. Two of these tracks may form a short trackway. The palaeosurface also exhibits numerous invertebrate traces.

Microscopy revealed adherent colonies of a unicellular (?chroococcoid) cyanobacterium about 5 μm in diameter, yellowish-brown in colour, often subdivided into subcells (diads, triads, or tetrads) (Fig. 7). A fragment of a filamentous cyanobacterium was also present. A frustule of a very small diatom was present, along with small amounts of probably inorganic matter, coated with bacteria. These characteristics are consistent with a biofilm as described

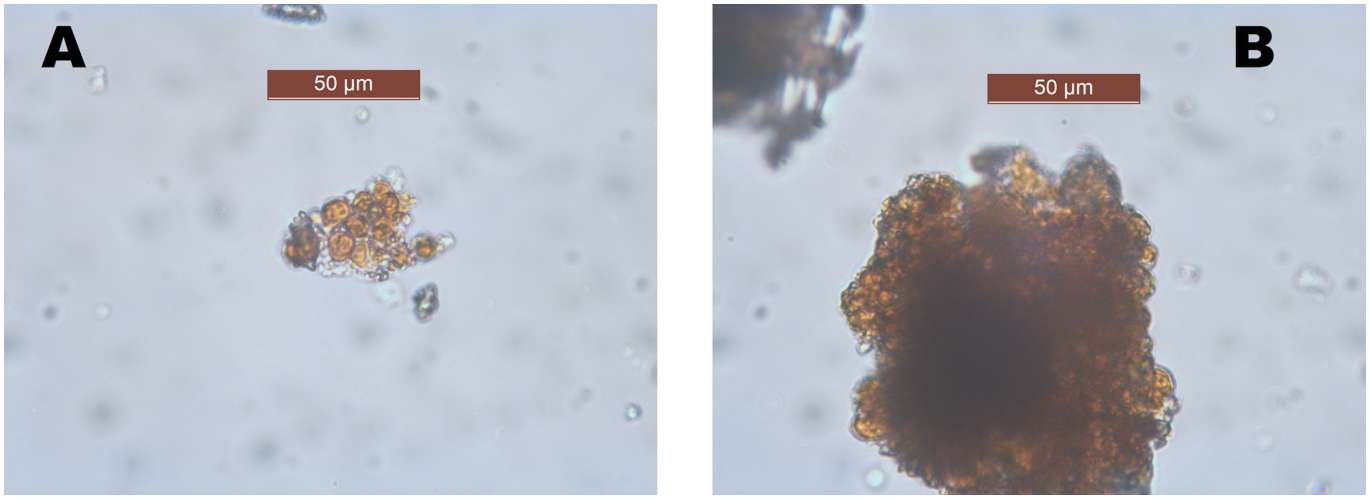


Figure 7. **A** & **B**, Agglomerations of cyanobacterial cells that comprise most of the biofilm material; the transparent particles appear to be mainly fine sand, and cell walls of dead cells.

by Gorbushina (2007): a miniature, self-sufficient microbial ecosystem on a solid mineral surface that is exposed to the atmosphere.

Ethnobotanical questioning of local residents about such discolourations on rock surfaces in the region yielded the term 'klipsweet' (De Vynck *et al.* 2016).

DISCUSSION AND CONCLUSIONS

To date, the only previously reported South African fossil avian tracksite was from an aeolianite surface at Nahoon, 650 km to the east of the site described here (Mountain 1966; Roberts 2008). It contained a short avian trackway of three tracks, and possibly a second indistinct avian trackway, as well as three hominin tracks (the first found in southern Africa), a deep tetrapod trackway, and two shallow felid tracks (Roberts 2008).

Much younger African bird tracks are reported from 0.5–1.7 ka Holocene sediments in Namibia (Bennett *et al.* 2010). Ellenberger (1974) described a late Triassic site at Mokanametsong in the Quthing District of Lesotho with bird-like trackways – this would be by far the oldest evidence of birds in the world, but it is plausible that these tracks may be those of small theropod dinosaurs with bird-like track characteristics. The fourteen Late Pleistocene newly-identified sites on the Cape south coast, including the site described here, substantially enlarge the archive of southern African fossil avian tracks, and will be described elsewhere.

The two parallel trackways rendered visible by the biofilm layer represent the longest identified fossil avian trackways in the region. Fossil avian trackways of this length are rare, and this site adds to a sparse global record. Similar reported tracksites include: (i) a Miocene site in Mexico with a trackway of 15 turkey-like tracks (Lockley & Bishop 2014); (ii) a Pleistocene avian track surface from the Carson City Prison site, Nevada, U.S.A., recorded in a sketch map in 1889 showing 8 heron-like trackways, each with more than 20 tracks (Lockley & Hunt 1995); and (iii) a long tridactyl trackway, probably made by a shorebird, on an Oligocene palaeosurface at the La Playa Fósil site in Spain (Rabal-Garcés 2017).

The limited information that can be gleaned from the track morphology suggests that a member of a family such as the extant Numididae (guineafowl) or Phasianidae (spurfowl) could be considered as a plausible track maker (Stuart & Stuart 2000). The challenges of moving along a dune slope perpendicular to the angle of the slope can also be expected to create asymmetries in morphology between left and right tracks (Razzolini & Klein 2017), and with morphology that is different from the potentially optimal morphologies that might be registered on horizontal surfaces with ideal substrate conditions.

The tracks that have been identified northeast of Trackway 1 and Trackway 2 are slightly smaller, with a shorter pace length, but were made under different conditions, moving north (upslope). It is conceivable that they represent the same trackmakers, and that the differences observed reflect differences in gait associated with travel up a steep dune slope.

The microscopy results indicate characteristics that are consistent with a biofilm as described by Gorbushina (2007). Biofilms often occur on rock surfaces, and are characterized by patchy growth. Biofilms cause chemical and physical changes as they penetrate the rock substrate and eventually contribute to weathering of the surface.

Communities of algae and cyanobacteria are not uncommon on sedimentary surfaces, and can produce microbially-induced sedimentary structures (Stimson *et al.* 2017). As demonstrated at this site, biofilm also attaches selectively to the convex irregularities on a rock surface formed by low relief natural casts. At this site in particular, avian tracks are made visible by biofilms adhering preferentially to natural casts, possibly because these convex irregularities provide a larger and more rugose surface compared with the flat surface of a smooth bedding plane.

Up to fifty avian tacks have been identified at this tracksite, most of which are rendered easily visible due to the presence of a biofilm layer. Further tracks make become evident on this surface through this process in future.

Noting the consistency in time of day of our visits, and the similarity of light conditions, we conclude that the changes we have noted over time are genuine and not influenced by factors such as changes in lighting.

De Vynck *et al.*'s ethnobotanical survey (2016) identified the traditional name of 'klipsweet' (translated as 'rock sweat' or 'stone sweat') for the dark discolouration on rock surfaces in the region. The survey established that this was thought to be excretions of midges, and that at one point this substance was apparently used for medicinal purposes, but that details of this use are no longer known. Further such studies may be useful with a view to establishing such details.

This report represents a novel and potentially useful additional approach to ichnologic field surveys: the use of biofilms in tracksite recognition in addition to standard methods of searching for tracksites. A phase of trackway enhancement can probably be anticipated as the biofilm layer continues to attach to the tracks, followed by a period of slow track disappearance as the lithophagic effect of the biofilm begins to predominate. Awareness of the potential for biofilm layers to enhance or render visible such ichnofossils can inform the search for further trackways in these coastal aeolianites and further afield.

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