Research Article

Pleistocene small-mammal and arthropod trackways from the Cape south coast of South Africa

Martin G. Lockley[a,b], Charles W. Helm[a]* , Hayley C. Cawthra[a,c], Jan C. De Vynck[a], Mark G. Dixon[a] and Jan A. Venter[a,d]

[a]African Centre for Coastal Palaeoscience, PO Box 77000, Nelson Mandela University, Gqeberha, 6031, South Africa; [b]Dinosaur Trackers Research Group, Campus Box 172, University of Colorado Denver, PO Box 173364, Denver, 80217-3364, USA; [c]Geophysics and Remote Sensing Unit, Council for Geoscience, Western Cape regional office, PO Box 572, Bellville, 7535, South Africa and [d]Department of Conservation Management, George Campus, Nelson Mandela University, Madiba Drive, George, 6530, South Africa

Abstract

A trackway and burrows of a small rodent-sized bounding mammal (attributed to the Cape gerbil, *Gerbilliscus afra*) and a traceway of a large arachnid (spider) from the Pleistocene Waenhuiskrans Formation represent two biological groups not previously reported from this track-rich dune facies, which is widely distributed along the Cape south coast of South Africa. This may be due to biases against the preservation of small tracks. Trackways of hopping or bounding rodent-sized mammals are rare in the fossil record, occurring at only two known Mesozoic sites and three Cenozoic sites. Where these occur in dune facies, they are commonly associated with arachnid and other arthropod surface trails. The arachnid trace fossils commonly include the spider traceway *Octopodichnus*, known from the Permian to Recent, which is also the temporal range of the eponymous *Octopodichnus* ichnofacies. The abundance of small-mammal tracks associated with dune ichnofaunas led to the naming of the late Palaeozoic and Mesozoic *Chelichnus* ichnofacies, which is largely co-extensive with the *Octopodichnus* ichnofacies at this time. However, the recognition of similar mammal–arthropod dune facies assemblages in the Cenozoic requires adjusting our understanding of their distribution in space and time, and extends the known distribution of dune ichnofacies.

Keywords: Late Pleistocene, Cape south coast, Trackways, Aeolianites, Burrows, Ichnofacies

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INTRODUCTION

In recent years the Cape south coast ichnology project has focused on the description of tracks and traces on paleosurfaces in Late Pleistocene aeolianite and cemented foreshore deposits, representing the remains of dune, beach, and lagoon environments. The majority of tracks represent large mammals, birds, and reptiles, although the two former groups also include traces of smaller animals, inferred to represent mongoose and small avians (Helm et al., 2018, 2020a, b). Golden mole burrows were recently reported (Lockley et al., 2021), and coprolites (including those of a small carnivore) offer further avenues of study to be reported elsewhere. Invertebrate traces are commonplace, but have not been formally described, and no inventory of invertebrate sites has yet been compiled.

While this trace fossil record does not suffer from the biases inherent in the regional body fossil record (which represents mostly hunted and scavenged prey in caves and rock shelters, by agents such as hominins, hyenas, porcupines, and owls), it has its own set of biases. Larger, heavier animals create larger, deeper tracks, which are easier to identify on Pleistocene paleosurfaces upon re-exposure, even when these surfaces exhibit substantial erosion (e.g., Helm et al., 2021a). In addition, dune and beach sands do not provide ideal substrates for track registration and preservation, compared with finer-grained and more cohesive sediments.

Haubold (1996, p. 23) introduced the term 'phantom taxa' to refer to ichnotaxa based on "fragmentary tracks, incomplete trackways and other preservational variations of optimal track morphology and trackway pattern." Lucas (2001) also reminded us that "the concept of extramorphological variation [was] introduced by Peabody (1948) who noted that extramorphologic characters include characters arising from the type of recording material." Thus, Lucas coined the term "taphotaxon" to encompass what Peabody termed extramorphological characters. This allows us to distinguish suboptimal preservation of footprint ichnotaxa under the concept of taphotaxa (see Haubold, 1997, and Lockley, 2000, for review of relevant concepts).

Recently, ichnologists have expressed concerns about the "morphological quality of preservation" of tracks and how it may affect ichnotaxonomy and ichnological interpretation more generally (Belvedere and Farlow, 2016; Gatesy and Falkingham, 2017; Marchetti et al., 2019a). In this regard, tracks on Pleistocene paleosurfaces on the Cape south coast seldom rise above level 2 on the four-point (0-1-2-3) quality-of-preservation

*Corresponding author email address: helm.c.w@gmail.com

scale developed by Belvedere and Farlow (2016). Factors that lead to sub-optimal track preservation include sediment consolidation, moisture and microbe content, substrate grain size, and the effects of erosion and weathering in a coastal setting, which inevitably lead to biases against the identification of smaller, lighter trackmakers.

Nonetheless, under favorable circumstances, Pleistocene paleosurfaces on the Cape south coast have the capacity to preserve relatively fine detail, and thorough examination under optimal lighting conditions allows the identification of tracks and traces of smaller creatures. Two such examples are described here—one, a small-mammal trackway (with associated burrows), and the other, an invertebrate traceway. The tracksites were identified in 2019, and were situated ∼140 m apart on loose aeolianite slabs on a remote stretch of coastline east of Still Bay.

GEOLOGICAL CONTEXT

Aeolianites, or cemented paleodune deposits, are distributed globally, generally in mid-latitude regions between 20° and 40° (Fairbridge and Johnson, 1978; Brooke, 2001). Late Pleistocene examples of this rock form are well preserved along the Cape south coast of South Africa, and form the Waenhuiskrans Formation (Malan, 1989). Late Pleistocene shoreface, foreshore, and lagoonal deposits of the Klein Brak Formation (Malan, 1991) are also preserved along this coastline, but have not been encountered in the immediate area described herein. These two formations form part of the Bredasdorp Group.

Through the ongoing, multidisciplinary Cape south coast ichnology project (initiated in 2007), >300 tracksites have been identified in the study area between the town of Arniston in the west and the Robberg peninsula in the east, a distance of 350 km (Fig. 1). Numerous sites within this area have been dated through Optically Stimulated Luminescence, with the majority being from Marine Isotope Stage (MIS) 5 and MIS 6 (Roberts et al., 2008; Carr et al., 2010; Bateman et al., 2011; Cawthra et al., 2018). MIS 11 deposits (Roberts et al., 2012) and MIS 3 deposits (Carr et al., 2019) are less common. The tracksite frequency has been explained by Roberts and Cole (2003) as a result of four processes: (1) moist sand provided a cohesive molding agent; (2) high sedimentation rates enabled rapid track burial; (3) rapid lithification followed via partial solution and re-precipitation of bioclasts; and (4) shoreline erosion has re-exposed the track-bearing surfaces. In addition, we infer some binding of sand by microbial activity.

East of Still Bay, a remote, rugged section of coastline, 6 km in length, comprises continuous cliffs as much as 70 m in height. Here, Pleistocene dune cordons are overlain by active Holocene dunefields of the Strandveld Formation. Planar cross-bedded units ranging in thickness from 0.4–18 m form the dominant primary sedimentary structure (Roberts et al., 2008). The large-scale units are laterally persistent for tens of meters. Foreset dips of up to 37°, the angle of repose of wind-blown sand, are present. Foreset progradation of large-scale dunes has led to sedimentary facies that are dominated by large-scale planar cross-stratification. The foreset orientation indicates a dominance of westerly winds, broadly similar to present-day wind conditions (Roberts et al., 2008).

Storm surges and high spring tides contribute to cliff collapse. Loose slabs and blocks are dislodged, and tumble down to lie at the base of the cliffs, at or below the high tide mark, where they are subjected to further wave and wind erosion. Over time, many of these loose blocks slump into the sea.

Roberts et al. (2008) first drew attention to this area, describing fossil elephant trackways and tracks in the Waenhuiskrans Formation. Roberts et al. (2008) presented OSL dates for the main elephant tracksite, which is situated ∼750 m east of the two sites described here: a result of 140 ± 8.3 ka was obtained for the oldest dated unit, and a result of 91 ± 4.6 ka was obtained for the youngest dated unit. This currently remains the only reliably dated sequence on this stretch of coast. Although paleosols at the dated sequence are laterally persistent, permitting stratigraphic correlation to one nearby tracksite (Helm et al., 2018), they do not extend west as far as the sites described here. Nonetheless, the expectation is that these cliffs represent an age range of deposits from MIS 6 to MIS 5b.

This stretch of coastal cliffs forms a zone of concentration of tracksites and, to date, 80 vertebrate tracksites have been identified here. Some of these have led to important paleoenvironmental inferences (Helm et al., 2018, 2019a; Lockley et al., 2019, 2021) and paleoanthropological implications (Helm et al., 2019b, 2021b). The two sites described here would have been situated at the edge of the Palaeo-Agulhas Plain, most of which is currently submerged. Substantial changes in Pleistocene climates led to glacio-eustatic sea-level oscillations, with maximum regressions exposing the entire Plain (Marean et al., 2020).

METHODS

Global Positioning System readings were taken, using a hand-held device. Locality data was reposited with the African Centre for Coastal Palaeoscience at Nelson Mandela University, South Africa, to be made available to bona fide researchers upon request. Tracksites were interpreted in the field through correlation to dated deposits and examination of cliff sections above the sites. Access to the tracksites was only possible during spring low tides.

Measurements of the trackways and burrows included length, width, and depth, and, where plausible, pace length. Thicknesses of foresets were measured. Results were recorded in centimeters. Tracings were made on clear acetate film. In addition to photographs that were taken of the tracks, traces, and and burrows described here, photographs were also taken of a Cape gerbil (*Gerbilliscus afra*) making tracks after release from a Sherman trap, and of bounding gait patterns in snow in British Columbia, Canada.

RESULTS

Small-mammal trackway and burrows

The small-mammal trackway is preserved in epirelief on a loose, north-facing aeolianite slab at the high tide mark. The precise origin in the cliffs above cannot be reliably determined. The mid-portion of the trackway contains the best-preserved track impressions, whereas the surface appears more eroded, with loss of track detail at either end. The trackway is interpreted as comprising 12 sets of relatively evenly spaced tracks, most of them in pairs (Fig. 2).

The total trackway length is 43 cm, and is symmetrical about the mid line (i.e., the tracks occur as pairs indicating registration of a hopping or bounding gait rather than a series of alternating left and right footprints). The maximum straddle (measured from the most lateral margins of the tracks) is ∼4.0 cm, whereas the average straddle is less (∼3.5 cm). Dimensions for the best-preserved tracks that occur in non-overlapping pairs are ∼1.5 cm long, and ∼1.0 cm wide (i.e., the long axis is oriented parallel to the trackway mid-line). The individual tracks exhibit an oval configuration, and bilateral symmetry. Some tracks appear
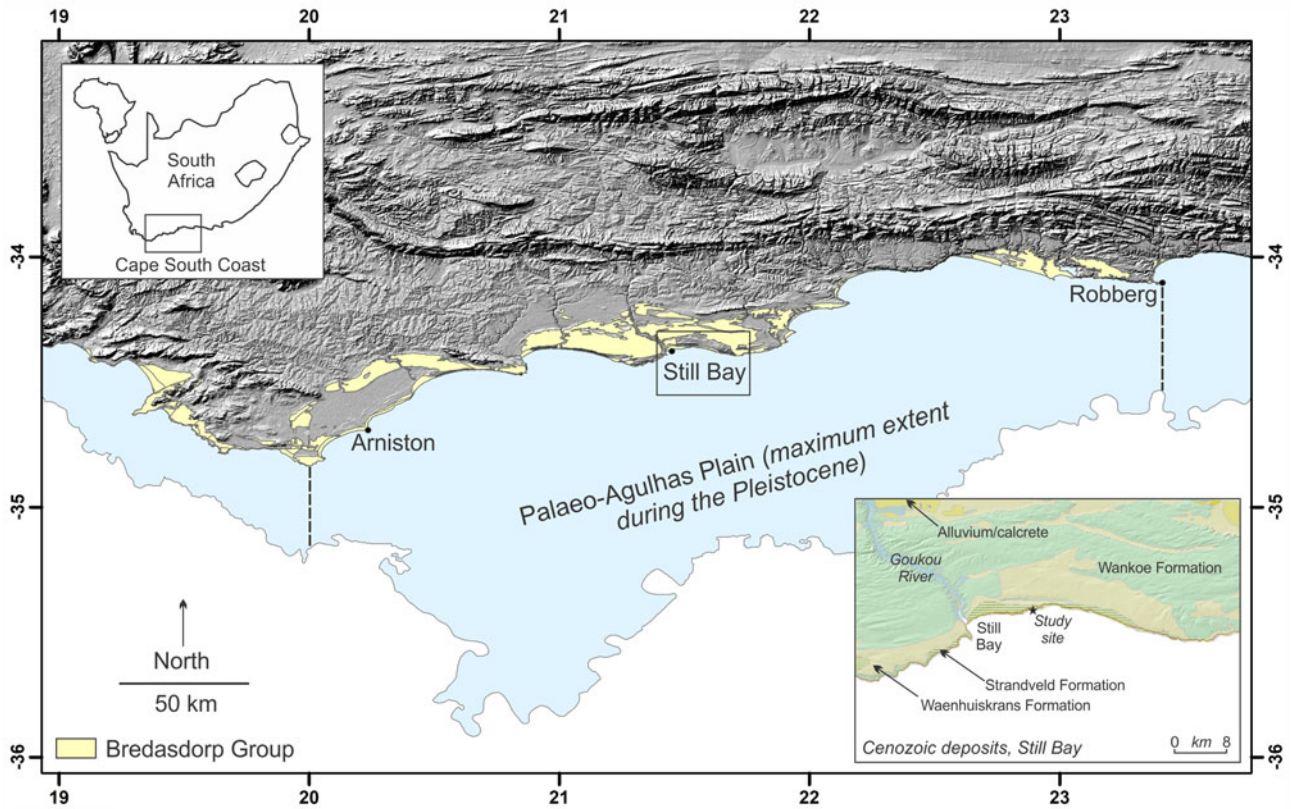
Figure 1. Locality map showing Bredasdorp Group sediments on the Cape south coast, and, in the bottom inset, the study site east of Still Bay.
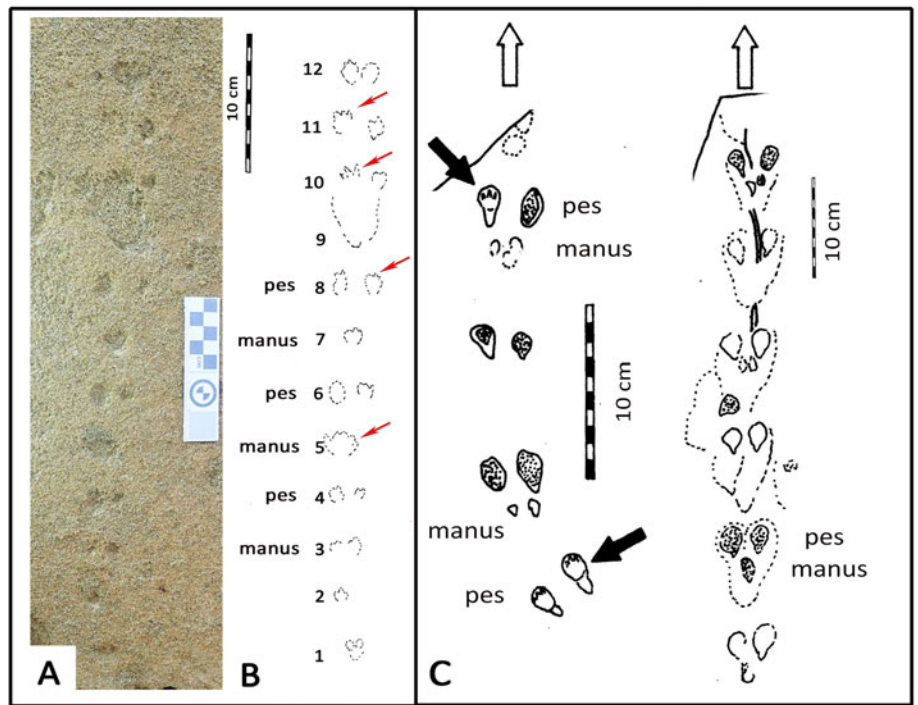

Figure 2. Photograph (**A**) and line drawing (**B**) of small-mammal trackway from the Waenhuiskrans Formation, Cape south coast, showing alternating manus and pes sets. Red arrows point to features inferred to represent faint digit tip traces that help orient the trackway. (**C**) Two trackways of *Musaltipes* from the Miocene Browns Park Formation, Colorado, also showing manus-pes sets (Lockley et al., 2007; Lockley and Milner, 2014). Heavy black arrows indicate pes tracks with toe traces. White arrows show direction of progression.

to have poorly preserved anteriorly situated toe traces. In some cases, in the mid-portion of the trackway, a single larger impression is apparent in the midline, rather than two separate impressions. No tail-drag impressions are apparent.

If the 12 pairs of tracks were interpreted as a series of 11 hind foot hops, then the mean length of each hop would be ~3.9 cm. However, if the discernable pattern of alternating widely and closely spaced tracks represents alternating manus and pes traces,

as we infer (see Discussion), then the closely spaced pairs (e.g., 5, 7, and 9 in Fig. 2B) represent manus traces that are not discernibly separated under the quality of preservation observed here, and the mean distance between corresponding points of these larger impressions is ∼7.5 cm. Therefore, the trackway configuration appears to reflect the characteristic reduced inter-track spacing between the manus impressions of a bounding gait compared with the wider spacing of pes tracks. Post-registration erosion of the tracks may contribute to the overlapping appearance of individual tracks. The present state of preservation may reflect the influence of both gait and erosion factors (see Discussion). By 2021, detail on the track-bearing surface had deteriorated significantly due to erosion.

An adjacent large block, with poorly defined bedding, contains a variety of infaunal burrows, ∼5 cm in diameter and as much as 50 cm in length (Fig. 3). Two loose slabs lie beside each other close to the high-tide mark, 310 m farther to the east of the trackway site. Branching burrows, ∼4 cm in diameter, with maximum length of 80 cm, form a complex pattern on the surface of the western slab. Several of these traces lead to the base of an unusual, raised feature that measured ∼25 × 20 cm, with a height of ∼12 cm (Fig. 4). Within months of its identification, this raised feature had partly disintegrated. On the eastern slab, similar burrows are exposed on the same layer. Part of this slab contains overlying layers exhibiting parallel bedding, and the burrow-containing bedding plane can be followed around the side of the slab, where burrows are evident in profile, to where another raised feature can be viewed in profile.

Arthropod traceway

The term 'arthropod traceway' is used here to describe a single, surface traceway, ∼25 cm long and between ∼3.0 cm and ∼4.5 cm wide (Fig. 5). The traceway has a morphological configuration that invites comparison with the bilaterally asymmetric arachnid (spider) ichnogenus *Octopodichnus*, which originally was described from Permian sand-dune facies by Gilmore (1927). This configuration includes a repetition of a distinctive quadripartite set of four regularly spaced traces (footprints) on each side (right and left) of the traceway. Each set of four traces in the case of the traceway described here is between 5.5 cm and 5.8 cm long, parallel to the traceway axis, and the spacing between corresponding points in consecutive sets (strides) is ∼9.0 cm. The traceway described here shows this regular configuration of quadripartite sets more clearly on one side than the other. The individual traces are round to oval and ∼1.0 cm in diameter.

The track-bearing dune facies surface was identified on loose slabs in an unstable rockfall area. By 2021, the surface could no longer be identified, presumably due to slumping of the slabs into the ocean.

DISCUSSION

Clearly the studied material, consisting of only one small-mammal trackway with probable associated burrows, and one spider traceway, is limited. However, it is significant from both ichnotaxonomic and facies perspectives. There is ample precedent in the paleoichnological literature for comparative analysis of similar mammal and spider trackways. The record of spider traceways goes back to the Paleozoic (Sadler 1993; Lockley and Hunt, 1995), whereas that of hopping mammaliform trackmakers only goes back to the mid Mesozoic (Casamiquela, 1961; de Valais,

2009). In the sections that follow, we briefly review the fossil track record of both groups, before discussing the ichnology, behavior, and facies preferences of extant representatives of these groups.

Fossil trackways of small mammals

The track record of small mammaliforms extends back to the Jurassic and includes a few trackways that indicate hopping or bounding behavior. The most celebrated examples come from Argentina where the oldest "true mammal" trackways were first reported from the Middle Jurassic La Matilde Formation as *Ameghinichnus patagonicus* (Casamiquela, 1961) and *A. manantialensis* (de Valais, 2009). These exceptionally well-preserved tracks, showing all digit traces in fine detail, reveal evidence of both bounding or hopping behavior, as well as alternating gaits. As noted by de Valais (2009), typical *Ameghinichnus* tracks have average footprint lengths and widths of 9.0 mm and 13.0 mm, respectively (L/W 0.7). Thus, they are similar in size to the tracks described here, but are wider.

Although there are reports of isolated mammal tracks from the Cretaceous, the only unambiguous trackway segment is that reported by Kim et al. (2017) from the Lower Cretaceous Jinju Formation of Korea. This trackway, named *Koreasaltipes jinjuensis*, reveals clear evidence of a small hopping or bounding animal that registered a trackway, symmetrical about the mid-line, with nine consecutive pairs of pes prints. The mean trackway width is 21.3 mm (range 19.0–24.0 mm). The mean hop distance was given as ∼4–5 times the pes length (= ∼4.0 cm), and pes tracks had a mean width (W) and length (L) of 4.76 mm and 8.06 mm, respectively, and thus, a mean L/W of 0.59 (Kim et al., 2017). Most tracks revealed anteriorly directed toe traces, some with extended toe-drag traces registered in a fine, cohesive mud. The Korean trackway is similar to the Cape south coast trackway with respect to the 'hopping' trackway configuration, but the individual tracks are smaller, relatively wider, and were registered in a quite different sedimentological substrate.

It is beyond the scope of this discussion to describe other isolated mammal tracks from the Cretaceous, such as *Schadipes crypticus* from the Maastrichtian of Colorado (Lockley and Foster, 2003), as well as unnamed tracks from the Lower Cretaceous of Maryland (Stanford et al., 2007), Tunisia (Contessi, 2013), and Angola (Marzola et al., 2014, 2015), the latter revealing isolated mammal tracks named *Catocapes angolanus* (Mateus et al., 2017). None of these tracks is comparable in size, individual track morphology, or trackway configuration, although the short, incomplete *Schadipes crypticus* segment shows ambiguous evidence of a hopping gait.

Turning to the Cenozoic record of trackways of small mammals, we again find very few examples of clearly defined trackways of hopping, rodent-sized animals. The formally defined ichnotaxa are named as *Musaltipes occidens* and *M. longidigitus* from the Cenozoic (Miocene) of Colorado and Utah, respectively (Lockley and Milner, 2014). The former ichnospecies occurs in an aeolian sandstone and is represented by symmetrical trackways revealing multiple pes pairs as 'hop' traces occurring in association with well-preserved arthropod trackways. Both ichnospecies reveal sub-optimal preservation, with individual tracks showing only indistinct digit traces. *Musaltipes occidens* is ∼2.5 cm long and 1.25 cm wide (L/W ∼2.0), and *M. longidigitus* is about half this size (L 1.2 cm, W 0.8 cm: L/W ∼0.67), with hop lengths between ∼6.0 cm and 8.0 cm. In many respects, as discussed below, ichnogenus *Musaltipes*, named to connote a hopping

Figure 3. Burrows on a rock surface adjacent to the small-mammal tracksite.


Figure 4. Branching burrow traces on a surface 310 m to the east of the small-mammal tracksite, leading to an unusual raised feature that is interpreted here as a debris mound at the entrance to Cape gerbil burrows.

mouse, is the only fossil trackway similar to the Cape south coast example with respect to facies association, quality of preservation, size, age, and trackway configuration.

Few other small-mammal tracks are of significance with respect to the present study because they are not preserved as trackways and, given the poor preservation in many cases, offer few useful points of comparison. Lockley et al. (2021) recently described *Musvestigium minutus* from the Cenozoic of

Colorado, which was named on the basis of a short trackway segment indicating an alternating gait. These authors also reviewed some of the small-mammal ichnotaxa reported from elsewhere in the Cenozoic (e.g., by Sarjeant and Langston, 1994). They also cited reports of unnamed Miocene tracks of hopping mammals from Miocene volcaniclastic sequences in Washington State (Kaler, 1998). No other Cenozoic tracks of small mammals invite comparison with the Cape south coast trackway.
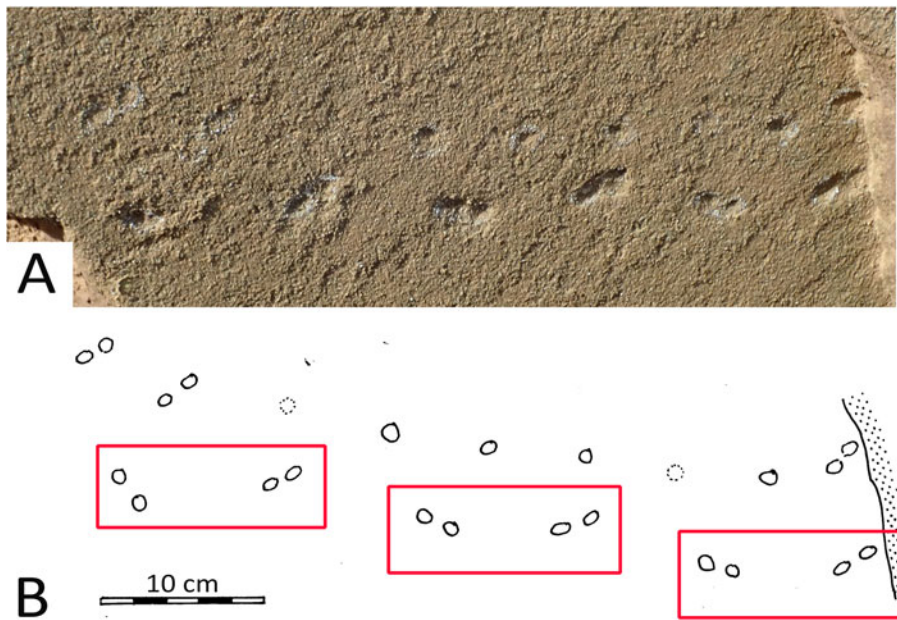
Figure 5. Photo (**A**) and line drawing (**B**) of presumed arachnid (spider) traceway from Pleistocene dune facies of the Cape south coast. Repeat pattern of quadripartite sets (red boxes) suggest a spider and identification of the traceway as *Octopodichnus*. Probable direction of progression was from left to right. See text for details.

Thus, in summary, there are only two Mesozoic trackways of small hopping mammals (*Ameghinichnus* and *Koreasaltipes*) that are comparable to the South African trackway. Likewise, there are only two Cenozoic trackways (*Musalipes occidens* and *M. longidigitus*) that are comparable and would tentatively allow us to label the South African trackway as cf. *Musaltipes*. All other aforementioned ichnotaxa and track morphotypes are based on isolated tracks or small trackway segments with different individual track morphologies and trackway configurations.

Fossil traceways of arachnids

As discussed below, fossil traceways and other traces of arthropods have a long geological range, and are too numerous to mention (Buatois and Mángano, 2018). However, limiting our discussion to traceways attributed to large arachnids, particularly spiders, constrains comparative analysis to a much smaller set of traces, reviewed here, especially if we limit our focus to *Octopodichnus* and similar traces. A review of the available literature informs us that almost all occurrences are associated with dune facies, ranging in age from Permian to the present. In the following brief sections, we outline the stratigraphic distribution of *Octopodichnus* and compare traceway morphology with that of the Cape south coast traceway.

Paleozoic arachnid traceways have been known at least since the 1920s, and are widespread and appear typical of the dune facies (Fig. 6). The type specimen of *Octopodichnius didactylus* originates from the Coconino Sandstone of Arizona (Gilmore, 1927; Brady, 1947; Sadler, 1993), and the ichnogenus is also known from other Permian dune deposits, including the De Chelly Sandstone of Arizona (Sadler, 1993), the Lyons Sandstone of Colorado (Lockley and Hunt, 1995), and the Weber Sandstone of Utah (Chure et al., 2014a). In the three examples shown in Figure 6, the diagnostic *Octopodichnus* configuration is shown, where the traceway is asymmetric about the mid-line, with alternating quadripartite sets of four tracks in an 'L'-shaped configuration. Note also that the traceways are quite wide: ~8.0 cm in type *O. didactylus* and 6.0–9.0 cm in the examples shown in Figure 6. In well-preserved examples, the individual

tracks show tarsal spine traces that bifurcate in the direction of anterior progression (hence the ichnospecies name *O. didactylus*). This reveals that typically the longer portion of the 'L' configuration, with two tracks situated anterior of the L's inflection point, is oriented antero-medially, whereas the shorter portion is marked by one postero-medially situated track. This configuration helps to identify the direction of progression when tarsal spine traces are not preserved. However, it should be noted that this L-shaped configuration may vary depending on the progression of the tracemaker, as in the case of *Octopodichnus raymondi* named by Sadler (1993, fig. 7).

Mesozoic *Octopodichnus* have mostly been reported from the Lower Jurassic Navajo, Nugget, and Aztec sandstones of the western USA (Faul and Roberts, 1951; Rainforth and Lockley 1996a, b; Lockley et al., 2011; Chure et al., 2014b; Rowland et al., 2014), and from the Jurassic–Cretaceous Botucatu Formation of Brazil (Buck et al., 2017). As shown in Figure 7, in some cases, *Octopodichnus* traceways indicate that both left and right sets of footprints failed to register completely. This appears to have been the case on the Cape south coast traceway (Fig. 5), which may reflect progression across a slope (e.g., in contour-parallel direction where left and right footprints might exert differential pressures on the substrate).

Lockley et al. (2007) reported that the aforementioned trackways of small hopping mammals from the Miocene of Colorado (Lockley and Milner, 2014) were commonly associated with arthropod surface traceways, including at least two identified as cf. *Octopodichus* (Lockley et al., 2007, fig. 8). This observation means that *Octopodichnus* has been reported in association with mammal or mammaloid tracks in dune facies ichnocoenoses from the Paleozoic (Permian), Mesozoic (Jurassic and Cretaceous), and Cenozoic (Miocene), as well as from the Pleistocene sites reported here (see discussion below).

Trackway and burrow interpretation

In a bounding gait, the hind legs provide the propulsion for pushing the tracemaker off the ground and forwards (Van den Heever et al., 2017). The tracemaker lands on the two front feet, which are usually smaller than the hind feet, and the manus tracks are
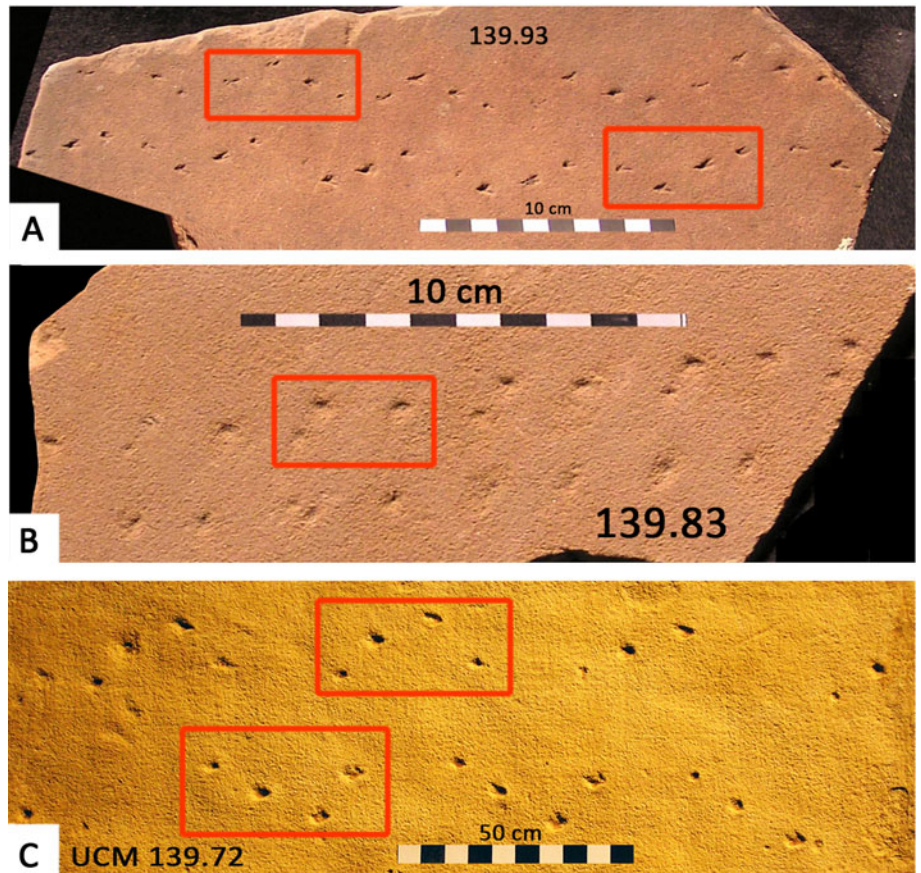
Figure 6. (**A–C**) Permian *Octopodichnus* from University of Colorado Museum (UCM) collections. (**A**) and (**B**) (UCM 139.93 and 139.83, respectively) from the Coconino Sandstone of Arizona. (**C**) *Octopodichnus* (UCM 139.72) from the De Chelly Sandstone of Arizona (from Lockley et al., 2007). Note 'L'-shaped quadripartite track sets (red boxes). Note also that some individual tracks show tarsal spine traces that bifurcate in the direction of forward progression. Thus, traceway 139.93 indicates progression to the right and 139.72 to the left. See text for details.

thus situated closer to each other and close to the midline of the trackway. The hind legs then follow, over and around the front feet, landing ahead of them, farther apart from each other than in the case of the front feet, and farther from the midline. The push-off phase by the hind feet then initiates another bounding cycle. Such configurations, as detailed by Liebenberg (2000), Stuart and Stuart (2019), and Van den Heever et al. (2017), are consistent with the features present in the trackway described here, and suggest the front feet landing close enough to each other that the impressions they created coalesced into a single larger depression on three occasions, in 'pairs' 5, 7, and 9 in Figure 2. Such a configuration is clearly seen in the Miocene trackway (*M. occidens*) from Colorado. The alternative (less parsimonious) interpretation is of a hopping gait in which the distance between hindfoot track pairs happened to vary.

Extant small mammals capable of registering tracks on Cape south coast dunes of the size described here, with a bounding gait pattern, include gerbils and mice. Both may walk with an alternating gait, run, or employ a hopping or bounding gait. Identifying small-rodent tracks to trackmaker species in the field is difficult. However, gerbils, as a rule, indulge much more frequently in bounding, and are considered the most likely trackmaker group for the trackway described here (e.g., the extant and common Cape gerbil, *Gerbilliscus afra*). The most commonly encountered mouse in the region is the four-striped grass mouse (*Rhabdomys pumilio*), and is a plausible, albeit less likely candidate trackmaker species. Figure 8A illustrates *G. afra* in the process of registering a bounding gait pattern in sand, and Figure 8B depicts a bounding gait pattern of an extant small mammal from the Cape south coast.

The measured length of 7.5 cm between corresponding points on tracks pairs 5, 7, and 9 in Figure 2 is short for a pace length in a bounding gait pattern. Pace length in bounding gaits increases with trackmaker velocity, and sets of four tracks become spread farther apart at higher velocities (two manus tracks posteriorly, and two pes tracks ahead of them). Figure 9A illustrates the typical pattern in snow, and corresponds closely to the pattern reported for *M. occidens* trackways from the Miocene of Colorado (Fig. 2C) (Lockley et al., 2007; Lockley and Milner, 2014). The even spacing noted in the described trackway may represent a slow bounding gait. Alternatively, it may conceivably represent the superimposition of one trackway on another, which fortuitously (but less parsimoniously) has resulted in even spacing of the tracks—a possibility that we consider unlikely. Small mammals regularly re-use their paths, and such a phenomenon may be encountered in extant small-mammal trackways that exhibit bounding gaits.

The capacity for track detail to be registered is greater in finer-grained substrates. High-quality small-mammal tracks are therefore more likely to be encountered in substrates of silt, mud, or snow. Figure 9B illustrates this phenomenon in snow (cf., Lockley and Milner, 2014, fig. 9). In the Cape south coast context, silty Pleistocene lagoonal deposits, reflecting depositional quiescence, have greater potential to record fine ichnological detail (i.e., better quality of preservation), but these are underrepresented on this coast compared to paleodune and paleobeach environments.

The dimensions (3–5 cm diameter) of the burrows (Fig. 3) on the loose block adjacent to the small-mammal tracksite are consistent with gerbil burrows or small golden mole burrows,
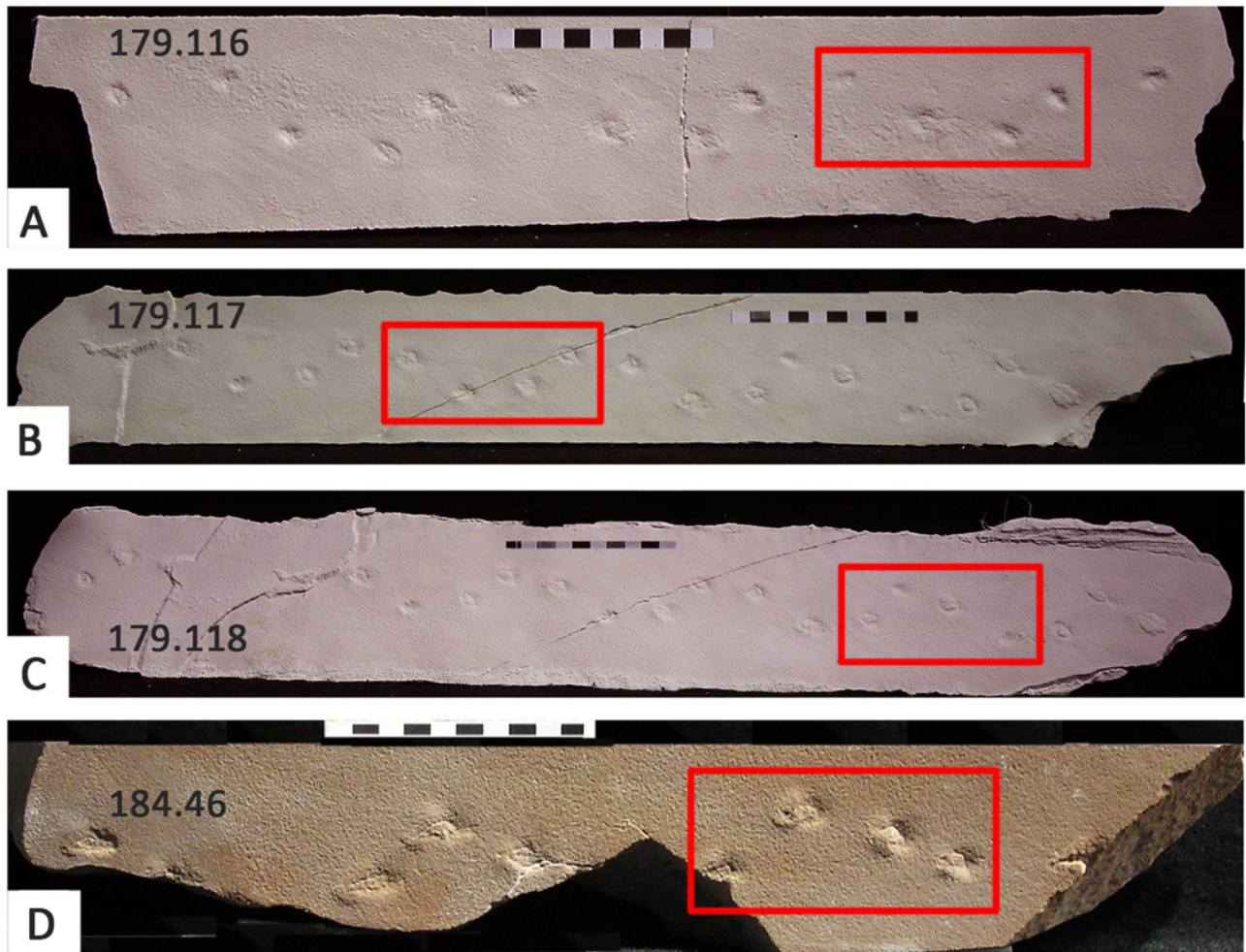
Figure 7. Four examples of partial *Octopodichnus* from the Nugget Sandstone of Idaho, showing characteristic quadripartite track sets (red boxes). UCM 179.116–118 are replicas, UCM 184.46 is an original specimen. Note that in all cases, only one side of the traceway is preserved. Compare with Figure 5 and Lockley et al. (2011, figs. 7, 8). See text for details.

among extant fossorial species (Stuart and Stuart, 2019). In contrast, the two adjacent loose slabs at the burrow site 310 m to the east (Fig. 4) provide substantially more evidence of a gerbil origin —gerbils create mounds of debris adjacent to their tunnels (Fig. 10), which is consistent with the size of the raised features noted at this site (Stuart and Stuart, 2019; Nigel Bennett and Chris Faulkes, pers. comm., 2021). These observations suggest that evidence of such mounds might be found in the fossil record, in addition to the Cape south coast example (Fig. 4). Indeed, in studies of Middle Jurassic burrows attributable to mammals, Loope (2006, fig. 7C; 2008, fig. 7D) illustrated kangaroo rat burrows and mounds that are very similar to those illustrated here (Figs. 3, 4). As noted below, tetrapod burrows of mammal/mammaloid affinity have been reported from various Lower Jurassic aeolian deposits (Lucas, 2006). The disintegration of the raised feature, interpreted here as a debris mound, serves as a reminder of the ephemeral nature of Cape south coast trace fossil sites, and the need for frequent coastal surveys, in particular after rockfall events and storm surges.

In a study of micromammal remains from fossil and archaeological sites from the Cape south coast from MIS 9 through MIS 1, Matthews et al. (2020) reported remains of *G. afra* from all sites, and it remains a common denizen of the region in sandy soils. In combination, the various features identified at the tracksite and burrow sites therefore strongly suggest various forms of gerbil activity, and contribute to a sparse global record of such features.

Invertebrate trace fossils are common on Cape south coast Pleistocene paleosurfaces, but their analysis, description, and consideration of paleoenvironmental significance are in their infancy. The arthropod traceway described here illustrates the potential of this field for future study, especially as it relates to the interpretation of ichnofacies (Bautois and Mángano, 2011).

The two large extant spider groups on the Cape south coast capable of registering traces of the size described here are the rain spiders (family Sparassidae, e.g., *Palystes superciliosus*) and the baboon spiders (family Theraphosidae). Stuart and Stuart (2019, p. 216) noted that "generally, you will find only the trails of large spiders, and then only in the finest of substrates," and they also stated, in relation to the baboon spider, that "the spread of the legs… results in a wide straddle in the trail." Likewise, Van den Heever et al. (2017, p. 298) noted that "spider footprints are represented by faint lines or dots which can be seen only in perfectly soft substrate." Figure 11 depicts a traceway of a baboon spider registered in sand, and a cast of a rain spider from the Cape south coast.

These neoichnological observations raise interesting questions about the preservation of spider and other arthropod traceways in
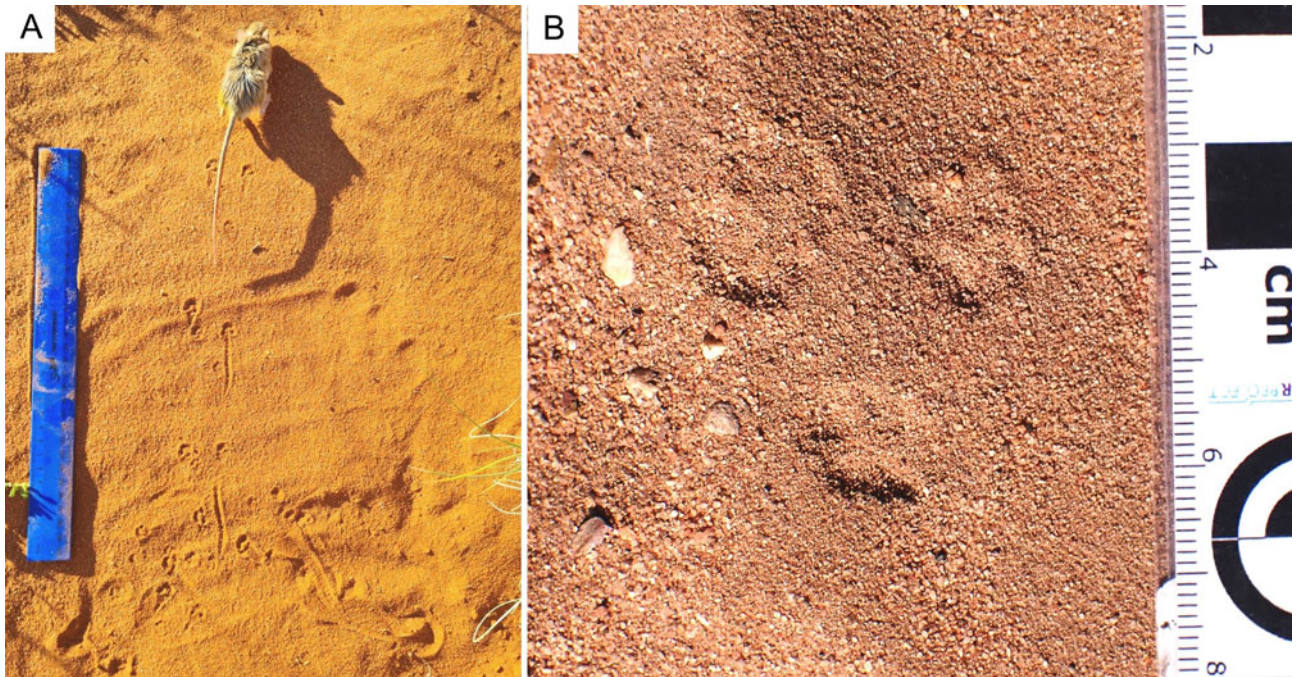
Figure 8. (**A**) Cape gerbil (*Gerbilliscus afra*) registering a bounding-gait trackway, which includes short tail-drag impressions; scale bar = 30 cm. (**B**) Bounding gait pattern of an extant small mammal on the Cape south coast, in which the front-foot impressions have coalesced into single depressions, behind the paired hind-foot impressions; scale is in cm and mm.
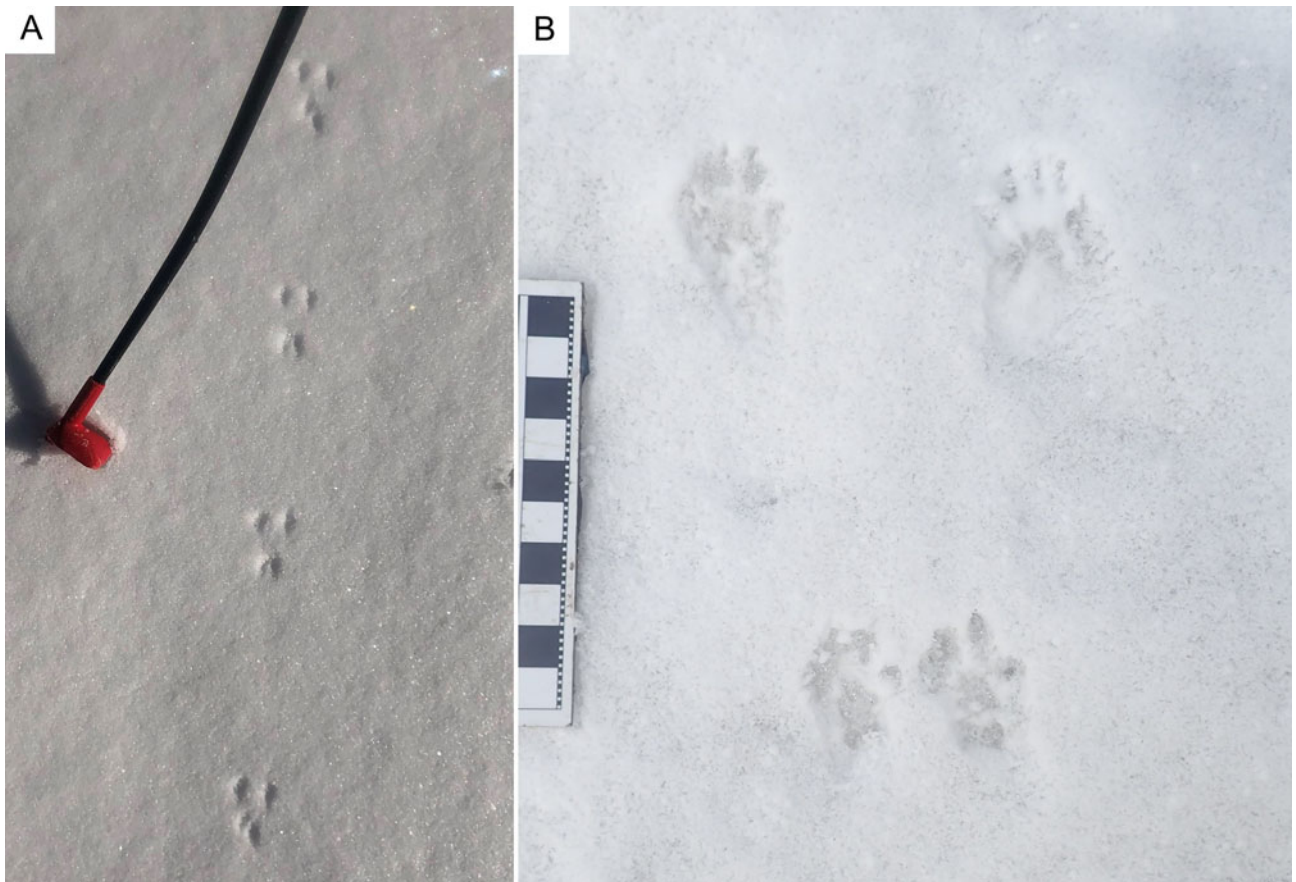
Figure 9. (**A**) Bounding gait pattern of a small mammal, registered in snow in British Columbia; (length of red base of ski pole = 5 cm; mean pace length = 20 cm). (**B**) Small-mammal tracks made by *Tamiasciurus hudsonicus* in snow in British Columbia, illustrating the level of detail that can be preserved in a fine-grained substrate; scale bar = 10 cm.

Figure 10. Debris mound beside the entrance to a *Gerbilliscus afra* burrow in a sandy, grass-covered setting (entrance hole is 5–7 cm in diameter); reproduced with permission from Chris and Mathilde Stuart.
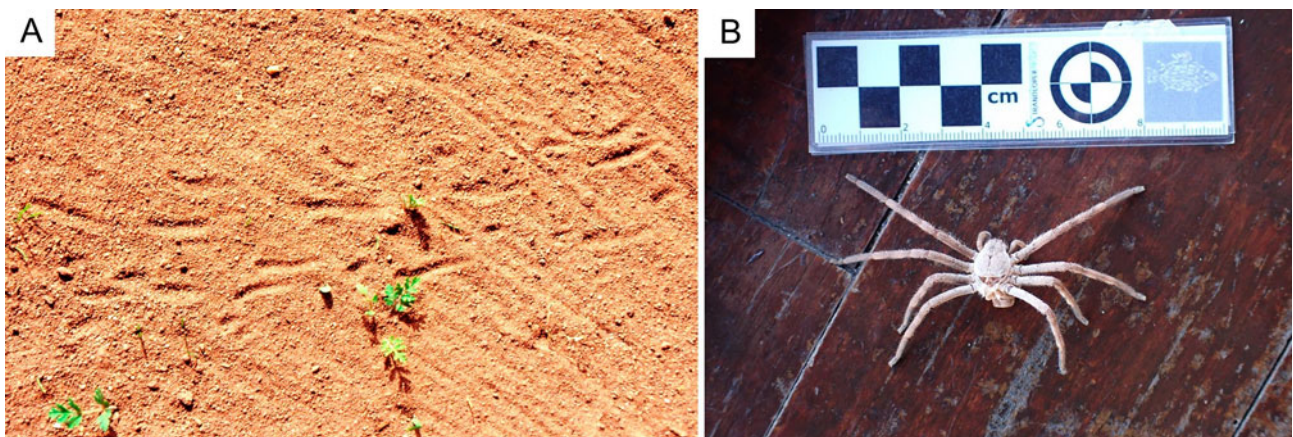

Figure 11. (**A**) Baboon spider traceway from South Africa; reproduced with permission from Chris and Mathilde Stuart. (**B**) Cast of rain spider from the Cape south coast; scale bar = 10 cm.

dune sediments. Firstly, most dune deposits consist predominantly of fine-grained, well-sorted sand, as noted in previous citations to Paleozoic through Mesozoic and Cenozoic facies. Thus, as noted by Stuart and Stuart (2019), these substrates are suitable for registration and preservation of small tracks. However, given that dune deposits are often in dynamic, wind-induced motion and ostensibly dry, it is not obvious how well-preserved spider tracks, in some cases with tarsal spine traces (Fig. 6), might be preserved. Based on the work of Milàn and Bromley (2006), Milàn and Loope (2007, p. 383) stated that "Experiments with track formation in different horizontal substrates, including dry sand, damp sand, and wet sand, demonstrate that totally dry sand is a bad medium to preserve true tracks." One possibility is that the dunes were wet, dampened by dew or mist. How such moistening of coastal dunes facilitates registration of high-quality arthropod traces is vividly illustrated in documentaries, such as Creatures of the Namib Desert (National Geographic Society, 1978). Once wetted, sand may quickly induce the growth of interstitial microbial (cyanobacterial) networks, which bind sand grains and enhance the preservation of traces. Seilacher (2008, p. 256) cited *Octopodichnus* from Permian dune faces of Arizona as a specific example of trackways in "moist dune surfaces … stabilized by the 'bioglue' of microbial grain envelopes."

Ichnocoenoses and ichnofacies

There is a growing literature on terrestrial invertebrate and vertebrate (tetrapod) ichnocoenoses and ichnofacies (for a brief introduction to vertebrate/tetrapod ichnocoenoses and ichnofacies concepts, see Lockley et al., 1994; Hunt and Lucas, 2007, 2016; and Buatois and Mángano, 2011). These ichnocoenoses are defined, albeit somewhat loosely, as recurrent associations of trace fossils representative of once extant biological communities, which are usually facies related (given biological communities' preferences for certain paleoenvironments, depositional systems, and or ecosystems). According to Hunt and Lucas (2007, 2016), multiple tetrapod ichnocoenoses from similar terrestrial facies (e.g., the Paleozoic, Mesozoic, and Cenozoic dune facies examples
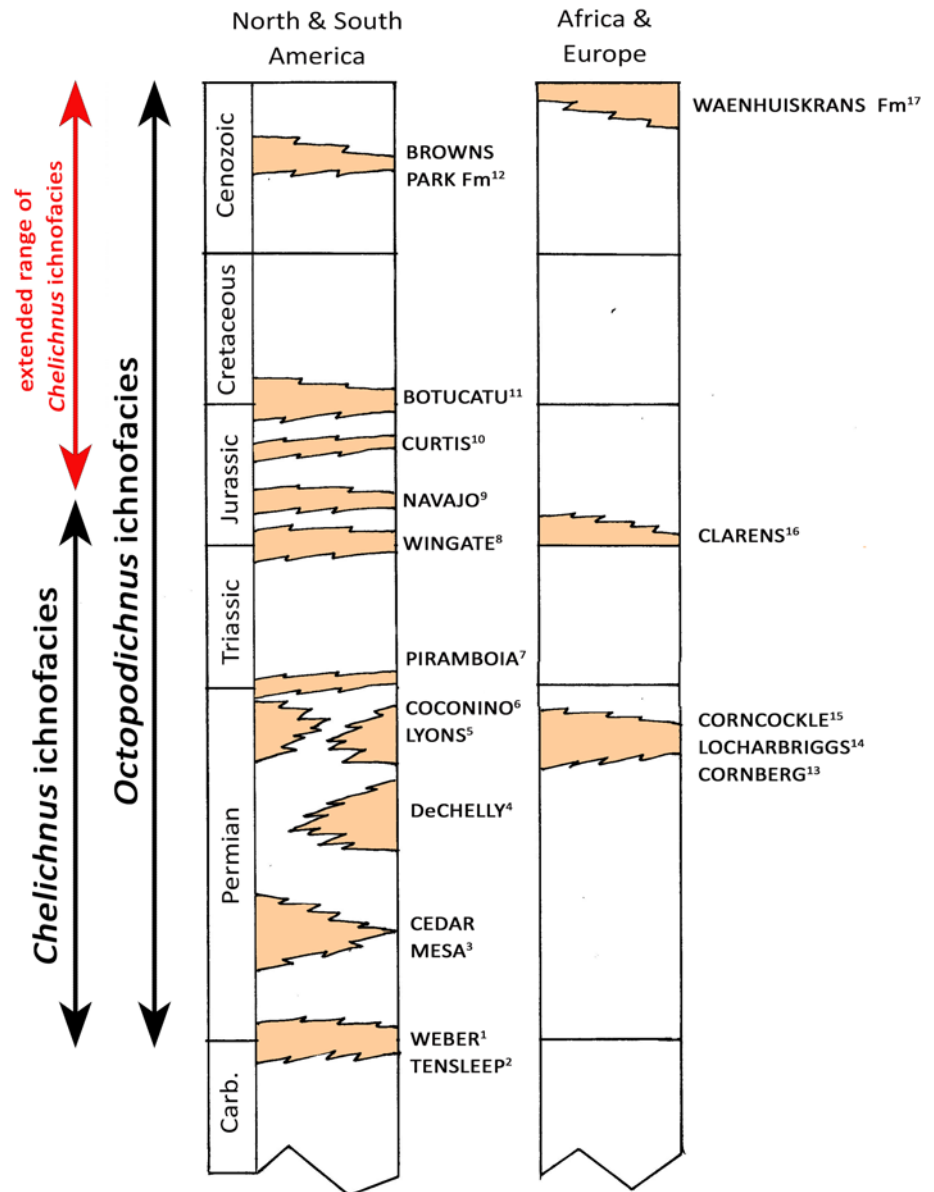
Figure 12. Generalized stratigraphic column showing better-known dune deposits that have yielded mammal/mammaloid and arachnid track assemblages (or ichnocoenoses) attributed to or potentially attributable to the *Chelichnus* and *Octopodichnus* ichnofacies. Possible extended range of *Chelichnus* ichnofacies shown with red arrow. Superscript numbers 1–17 with formation names refer to original or secondary sources as follows 1: Chure et al. (2014a); 2–6, 8, 9: Lockley and Hunt (1995) or Hunt and Lucas (2007, 2016, and references therein); 7, 14, 15: Francischini et al. (2018); 10: Lockley (2021); 11: Buck et al. (2017); 12: Lockley et al. (2007); 13: Haubold et al. (1995); 16: Raath and Yates (2005); 17: this study. The inference that the Curtis Formation dune facies ichnofauna represents the *Chelichnus* ichnofacies is questionable.

given here) can be grouped into a single global or archetypal ichnofacies, as is the usual procedure in the study of marine ichnofacies. Thus, Hunt and Lucas (2007, 2016) subsumed the Permian and Jurassic dune facies ichnocoenoses into the *Chelichnus* ichnofacies, which they described as "recurrent in dune faces of eolian environments," but they stated that it only "extends from the early Permian to the Early Jurassic" (Hunt and Lucas, 2016, p. 240). This is not disputed as a starting point for further discussion, but is elaborated below.

Lockley et al. (2007, p. 59) had noted that the Miocene dune assemblages reveal "a distinctive facies-controlled small mammal and arthropod-dominated track assemblage representative of the *Chelichnus* ichnofacies […] also the first example of this ichnofacies reported from the Cenozoic." The notion that this ichnofacies might be extended beyond the Early Jurassic was further discussed by Krapovickas et al. (2016) in a comprehensive review of the ichnology of aeolian environments. In a recent report on a Late Jurassic dune tetrapod ichnocoenosis from the coastal dune facies of the Moab Member of the Curtis Formation in eastern

Utah, the ichnocoenosis from that unit may not be attributable to the *Chelichnus* ichnofacies (see Lockley, 2021, for cautious use of the label ?*Chelichnus* ichnofacies). This uncertainty is in part due to the invertebrate and tetrapod components of the ichnocoenosis as well as the sedimentary facies, which lack both *Octopodichnus* and recognizable small-mammal tracks (Hunt and Lucas, 2016; Lockley, 2021).

It is somewhat of an impediment to full understanding of terrestrial ichnofacies that invertebrate and vertebrate (tetrapod) ichnofacies have too often been studied and defined separately. In fact, there is debate as to whether their definition can or should follow the same guidelines (Hunt and Lucas, 2007, 2016; Lockley, 2007; Santi and Nicosia, 2008), given that vertebrates are more mobile and evolved more rapidly. Fortunately, there is general agreement that there is close correspondence between invertebrate and vertebrate ichnofacies from dune settings. This was stated succinctly by Krapovickas et al. (2016, p. 63), who noted that "…numerous authors highlighted the concurrent characteristics of the eolian trace-fossil assemblages in the …

contrasting *Chelichnus*, *Octopodichnus*, and *Entradichnus* ichnofacies and suggested the integration of these separate models (e.g. Buatois and Mángano, 2011; Ekdale and Bromley, 2012; Krapovickas et al., 2010, 2016). Originally, Hunt and Lucas (2007) emphasized the close correspondence between the *Octopodichnus* and *Chelichnus* ichnofacies (Hunt and Lucas, 2007, p. 67). This same idea was already stated by Lockley et al. (1994) in the original definition of the *Chelichnus* ichnofacies where the authors indicated the common correspondence between *Laoporus* (=*Chelichnus*) and invertebrate trace fossils, such as *Octopodichnus* and *Paleohelcura*."

Hunt and Lucas (2016, p. 238), "regard the '*Entradaichnus* ichnofacies' as a synonym of the *Scoyenia* ichnofacies." This implies it has no obvious relationship to the *Octopodichnus* ichnofacies. As reviewed by Lockley (2021, p. 15), "a label like '*Chelichnus-Octopodichnus* ichnofacies [as] a natural combination (Lockley, 2004)… would allow naming of ichnofacies based on full integration of both vertebrate and invertebrate ichnofaunal evidence." In other words, "the separate invertebrate (*Octopodichnus*) and vertebrate (*Chelichnus*) ichnofacies names for the same eolian or dune ichnofacies" had been proposed for ichnofaunas already recognized as "entirely co-extensive" (Lockley 2007, p. 51).

In short, the dune facies ichnofaunas are among those that most frequently show consistent similarities between their invertebrate and vertebrate traces from site to site, particularly with respect to the co-occurrence of mammaliform and arachnid surface trails. This is possibly due to the low diversity and ease of identification of many dune ichnofaunas. For this reason, it is tempting to simply conclude that dune ichnofaunas represent a single broadly defined ichnofacies ranging in age from Paleozoic to Recent. However, as the Late Jurassic Moab Member ichnocoenosis indicates, not all dune ichnocoenoses are the same (Lockley, 2021) (see, for example, Marchetti et al., 2019b, who identified a higher ichnofaunal diversity on some Permian dune substrates). Thus, too broad, if not oversimplified, categorizations mean it is difficult, or at least unsatisfactory, to define overarching or 'archetypal' ichnofacies in detail based only on invertebrate or vertebrate components, not least because they have generally been defined independently by those working separately on vertebrate or invertebrate ichnofaunas. Another complicating factor is that there is persuasive evidence that some infaunal burrows created by mammals, or mammaliform tracemakers, are attributable to the same groups (?species) as the makers of surface trackways, as noted above. Burrowing invertebrates, including spiders, also make surface traceways.

Presently, given that the *Chelichnus* ichnofacies sensu Hunt and Lucas (2007, 2016) is defined on the basis of tetrapod tracks as limited to the Permian through Lower Jurassic, and the *Octopodichnus* ichnofacies, also defined by various authors (see Krapovickas et al., 2016) as ranging from Permian to Recent, we are left to ponder the relationships and appropriate ichnocoenoses and ichnofacies labels applicable to Cretaceous through Cenozoic dune ichnofaunas. For example, Peixoto et al. (2020) noted that the occurrence of traceways like *Octopodichus* helps trace continuity between Paleozoic and post-Paleozoic ichnofaunas, at least in the sense of the eponymous *Octopodichnus* ichnofacies, when regarded as an 'invertebrate' ichnofacies recognized independently of tetrapod traces. The extent to which different ichnofaunas, including their tetrapod components, might be considered representative of different dune/desert paleoenvironments (e.g., with different precipitation regimes) is open to discussion, as

noted by Krapovickas et al. (2016), and naturally involves wide-ranging and complex consideration of paleoenvironmental and paleobiological evolution in space and time (e.g., Buatois and Mángano, 2011). Moreover, the Cape south coast coastal dune ichnofaunas discussed here exemplify such complexity—more than one ichnocoenosis (or ichnofacies) may be represented and challenging to identify, as in the case of interpreting the small-mammal and spider surface trails on the one hand, and, on the other, their relationship 'within' coastal dune facies replete with very different large-animal traces and infaunal burrows. Moreover, there are obvious differences between coastal dune ichnofaunas and those associated with large ergs deposited in arid continental interior deserts.

It is outside the scope of this contribution to opine, definitively, as to how various invertebrate and vertebrate ichnoassemblages, ichnocoenoses, and ichnofacies and their distributions in space and time should be categorized and labeled. However, what can be confidently stated is that it is already recognized that dune facies are host to mammal/mammaloid and arachnid trackway assemblages, and variously labeled ichnocoenoses include the Permian *Chelichnus* and longer-ranging *Octopodichnus* ichnocoenoses, subsumed in the eponymous *Chelichnus* and *Octopodichnus* ichnofacies, respectively. At the time of writing, the *Octopodichnus* ichnofacies is ostensibly recognized from the Permian to Recent (Lockley et al., 1994; Lockley, 2004; Hunt and Lucas, 2007; Krapovickas et al., 2016; Peixoto et al., 2020), an inference consistent with the Waenhuiskrans Formation assemblage reported here (Fig. 12). However, to date, the *Chelichnus* ichnofacies, with its component *Chelichnus* and *Brasilichnium* ichnocoenoses, has been reported to range from Permian to Lower Jurassic (Hunt and Lucas, 2016). Given the aforementioned co-occurrence of an assemblage of mammal (*Musaltipes*) and arthropod (including *Octopodichnus*) trackways, already identified as representative of the *Chelichnus* ichnofacies (Lockley et al., 2007), as well as the present report of a very similar co-occurrence in the Pleistocene Waenhuiskrans Formation, a case can be made for inferring an extended temporal range for the *Chelichnus* ichnofacies to the Recent (Fig. 12). Also as noted, the obvious relationship between mammalian/mammaliform trackways and burrows adds a biological/ichnological signal that supports this interpretation.

CONCLUSIONS

Large-vertebrate Pleistocene tracksites on the Cape south coast have led to significant paleoenvironmental inferences. Expanding this field of study to smaller-vertebrate and invertebrate trackmakers, such as the small-rodent trackway (and associated burrows) and arthropod (spider) traceway described here, adds to the diversity of trackmaking taxa represented. Such evidence has the dual value of (1) demonstrating that small-animal traces can be preserved and (2) opening a discussion of the paleoecology, which is highly convergent with the literature on both invertebrate and vertebrate ichnofacies. Thus, the presence of mammal tracks (cf., *Musaltipes*) made by bounding rodents, and spider tracks (*Octopodichnus*) similar to those found in Miocene dune deposits, suggests we can recognize, in the Pleistocene, both the *Chelichnus* and *Octopodichnus* ichnofacies, as defined by vertebrate and invertebrate ichnologists, respectively. The temporal range of the *Chelichus* ichnofacies, formerly identified in Permian through Early Jurassic dune deposits, is thereby a candidate for extension through the Cenozoic. While

the presence of small-mammal tracks in dune facies is a characteristic signal of the *Chelichnus* ichnofacies, until now the presence of burrows (Paleozoic through Cenozoic) attributed to these same mammal and mammaliform trackmakers has not been explicitly cited as evidence in support of such ichnofacies schema. Such additional ichnnological evidence is pertinent to the description and definition of ichnocoeonoses and ichnofacies, and should be included.

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