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Research Article

Pleistocene aardvark (*Orycteropus afer*) burrow traces on South Africa's Cape coast

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Abstract

The aardvark (*Oryecteropus afer*) is a fossorial species with a widespread distribution across sub-Saharan Africa. It leaves distinctive tracks and traces of its presence, including large burrows. However, despite a substantial body fossil record, few trace fossils registered by aardvarks have been described. Its distribution range in southern Africa during historic and prehistoric times was probably broadly similar to that of today, with the addition of the currently submerged Palaeo-Agulhas Plain during much of the Pleistocene. Five new trace fossil sites have been identified in Pleistocene aeolianites on the Cape coast and are here interpreted with varying degrees of confidence as large burrows that were made by aardvarks. In addition, a possible aardvark tracksite has been identified. Together these add to the sparse paleoichnological evidence of aardvarks and add to the global ichnological record of large vertebrate burrows. While at this point the evidence does not warrant the proposal of new ichnotaxa, the findings may act to spur further identification of fossilized traces of aardvarks and other fossorial species on the Cape coast and beyond.

Keywords: Aardvark; aeolianite; paleosol; burrow; ichnology; Cape coast

Introduction

The aardvark, *Orycteropus afer*, also known as the antbear or erdvark, falls within the Order Tubulidentata and Family Orycteropodidae. 'Aardvark' is an Afrikaans term meaning 'earth-pig,' and the Latin binomial is translated as 'burrowing foot of Africa.' The Tubulidentata is the only mammalian order containing only a single extant species, although the genus *Orycteropus* contains several extinct species (Patterson, 1975; Lehmann, 2009).

Despite a widespread presence throughout sub-Saharan Africa (Shoshani et al., 1988), and a substantial body fossil record, the global trace fossil record attributed to Tubulidentata is extremely sparse, with only a single case known to us (Pickford, 2018). This is perhaps surprising, because burrows and other traces are distinctive features in landscapes in which extant aardvarks occur.

Ichnofossils can be classified on an ethological basis, as proposed by (Seilacher 1964). Classes that pertain to vertebrate ichnology include 'repichnia' (locomotory tracks and trackways), 'fodichnia' (feeding traces), and 'domichnia' (dwelling structures). The burrow traces described here most closely align with domichnia (and possibly fodichnia). Another category of relevance here is 'aedificichnia,' which includes termitaria.

Since inception of the Cape South Coast Ichnology Project in 2008, more than 350 Pleistocene vertebrate ichnosites have been documented on South Africa's Cape south coast within a 350-km stretch of coastline (Helm, 2023). Recent exploration on the Cape west coast (Helm et al., 2022), Cape southwest coast, and Cape east coast (Lockley et al., 2021; Helm et al., 2023a) has identified additional vertebrate ichnosites. The majority of ichnosites thus far described are vertebrate tracksites (repichnia). Exceptions involving domichnia and fodichnia include golden mole burrows (Helm et al., 2019; Lockley et al., 2021) and probable gerbil (*Gerbilliscus afra*) burrow traces (Lockley et al., 2022). Another exception is sand-swimming traces resembling those of the extant golden mole (genus *Eremitalpa*), which can be regarded as intermediate between repichnia and fodichnia (Lockley et al., 2021). Fossorial species and their Pleistocene burrows on this coastline were briefly reviewed by (Helm 2019), while coprolites that form another kind of trace fossil also have been reported from the Cape south coast (Helm et al., 2023b).

The earliest clear evidence of tetrapod burrows, attributed to lysorophians or amphibians, is from the early Permian from North America (Hembree et al., 2004). Vertebrate burrows from the Cenozoic have largely been attributed to mammals, mainly rodents, sloths, armadillos, and carnivorans. For example, (McDonough et al. 2000) reported in detail on armadillo burrows from South America and North America, while (Lopes et al. 2017) reported giant burrows from South America (as much as 2 m in diameter and attributed to ground sloths), and (Hunt et al.

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1983) described denning behavior of bear dogs in North America. In their comprehensive review of vertebrate burrow ichnology, (Melchor and Cardonatto, in press) noted the fossorial habits of the aardvark in Africa but did not discuss trace fossil evidence for this behavior.

Creatures inhabiting burrows can be divided into primary excavators (such as the aardvark), secondary modifiers, and simple occupants (Kinlaw, 1999). A distinction can also be made between the terms 'fossorial habit' and 'subterranean' (Melchor and Cardonatto, in press). In the former case, exemplified in southern Africa by the aardvark, a significant portion of the animal's life is spent outside its burrows, whereas in the latter case foraging either occurs underground or close to burrow entrances. In the Cape coastal context, the Cape dune mole rat (*Bathyergus suillus*) is an example of the 'subterranean' category.

The relative paucity of published work on Cape coast vertebrate burrow traces stands in contrast to the many vertebrate burrows associated with scratch marks reported from South Africa's Karoo region, preserved in Palaeozoic and Mesozoic deposits (see Bordy et al., 2023, for a review). One of six southern African geoheritage sites selected by (Bordy et al., 2023) is from the Lootsberg Pass in the Katberg Formation (Lower Triassic), and exhibits large, long burrows thought to have been dug by therapsids.

Nonetheless, fossilized vertebrate burrows are encountered relatively frequently on the Cape coast. Based on inventories of Pleistocene mammals in the regional body fossil record (Klein, 1976; Klein and Cruz-Uribe, 2000; Klein et al., 2007; Marean et al., 2014; Matthews et al., 2020), and comparing them with extant burrowing species (e.g., Stuart and Stuart, 2019), we have categorized these based on burrow diameter as (1) the smallest (3–5 cm in diameter) that are consistent with gerbil burrows (Muridae, probably *Gerbilliscus afra*); (2) those of medium size (6–7 cm in diameter) that are consistent with golden mole burrows (Afrosoricida, probably *Amblysomus* spp.); (3) burrows 10–16 cm in diameter that are consistent with those of the Cape dune mole rat (Bathyergidae, *Bathyergus suillus*), ground squirrels, the yellow mongoose (*Cynictis penicillata*), and the suricate (*Suricata suricatta*), although this last species prefers digging its colonial burrows in stony ground (Stuart and Stuart, 2019); (4) still larger burrows, 18–25 cm in diameter, that may have been dug by the springhare (*Pedetes capensis*); and (5) the largest (> 30 cm), which are consistent with aardvark burrows, although porcupine (*Hystrix africaeaustralis*) and carnivoran burrows are also considered, as described below.

The purpose of this article is to provide a first description of large burrows identified on the Cape coast (five sites, attributed with varying degrees of confidence to aardvarks) as well as a possible aardvark tracksite. The relevance of these findings for the global ichnology record is then considered.

Geological context

The deposits on the Cape coast that bear the aardvark Pleistocene trace fossils occur in cemented dunes (aeolianites), a rock type that is globally common in mid-latitude regions (Brooke, 2001). The trace fossils on South Africa's southwest coast and south coast occur in the Waenhuiskrans Formation of the Neogene–recent Bredasdorp Group (Malan, 1989). On the east coast, the correlate of the Waenhuiskrans Formation is the Nahoon Formation of the Algoa Group (Le Roux, 1989). Figure 1 provides a map of the Cape coast, and the burrow sites described herein.

The aeolianites are typically composed of medium- to fine-grained sand. Features such as distinctive crossbedding occur commonly, along with more massive deposits and paleosols, which are often laterally persistent. Quaternary tectonic activity has been reported as minimal along the Cape coast (Fleming et al., 1998). Aeolianite bedding-plane surfaces therefore lie at or close to the original angle of deposition, which is often the angle of repose of wind-blown sands (Roberts et al., 2013). The orientation, geometry, and archaeological and paleontological contents of these fossil dune systems make them sensitive paleoenvironmental indicators (Roberts et al., 2013).

The aeolianites within the present study region, from Walker Bay to Woody Cape, have been shown in previous works to date from Marine Isotope Stage (MIS) 11 at circa 400 ka (Roberts et al., 2012), through MIS 6 and MIS 5 (Roberts et al., 2008; Carr et al., 2010; Bateman et al., 2011; Cawthra et al., 2018; Helm et al., 2023c; van Tonder et al., 2024), to MIS 3 at circa 35 ka (Carr et al., 2019). The majority of aeolianites sampled thus far have been shown to date to between MIS 6 and MIS 5.

Methods

Global positioning system readings were obtained for the five burrow sites, using a handheld device. Locality data are reposited with the African Centre for Coastal Palaeoscience, to be made available to researchers upon request. Measured burrow dimensions in centimeters included maximum and minimum diameter and, where feasible, depth. Strike and dip measurements were recorded on adjacent surfaces for in situ sites.

Length, width, and depth of traces were measured for the possible aardvark tracksite. Photographs were taken for photogrammetric analysis (Matthews et al., 2016). Three-dimensional models were generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal length 4.5 mm; resolution 4000 × 3000; pixel size 1.56 × 1.56 um). The final images were rendered using CloudCompare (v.2.10-beta).

The sites were interpreted in the context of the local and regional stratigraphy and of any nearby trace fossils, body fossils, and fossilized plant material, using standard field techniques. Stratigraphic correlation to known dated sites was applied. Photographs were taken of all sites, along with videos where appropriate. A DJI Mini 2 drone with an inbuilt DJI camera/video was used to obtain additional images.

Results

The results from five burrow sites are presented, in order from west to east, followed by a description of the tracksite. Examples of Pleistocene termite or ant nests (representing the likely food source) from the region are then presented.

Site 1 is located on the Cape southwest coast, north of the community of Die Kelders in the coastal stretch of the Walker Bay Nature Reserve. Three large sub-circular or elliptical cavities were noted in a single horizon within in situ aeolianite deposits in a track-rich area. They are described here from left to right as viewed in Figure 2A. Their centers are separated by distances of 220 cm and 135 cm. The left cavity measures 35 cm in maximum width and height, and has a depth of 70 cm. The middle cavity has a maximum width of 40 cm, maximum height of 43 cm, and depth of 230 cm. The right cavity has a maximum width of 30 cm, maximum height of 43 cm, and depth of 140 cm. From the distal end of the right cavity, two smaller tunnels connect with the surface

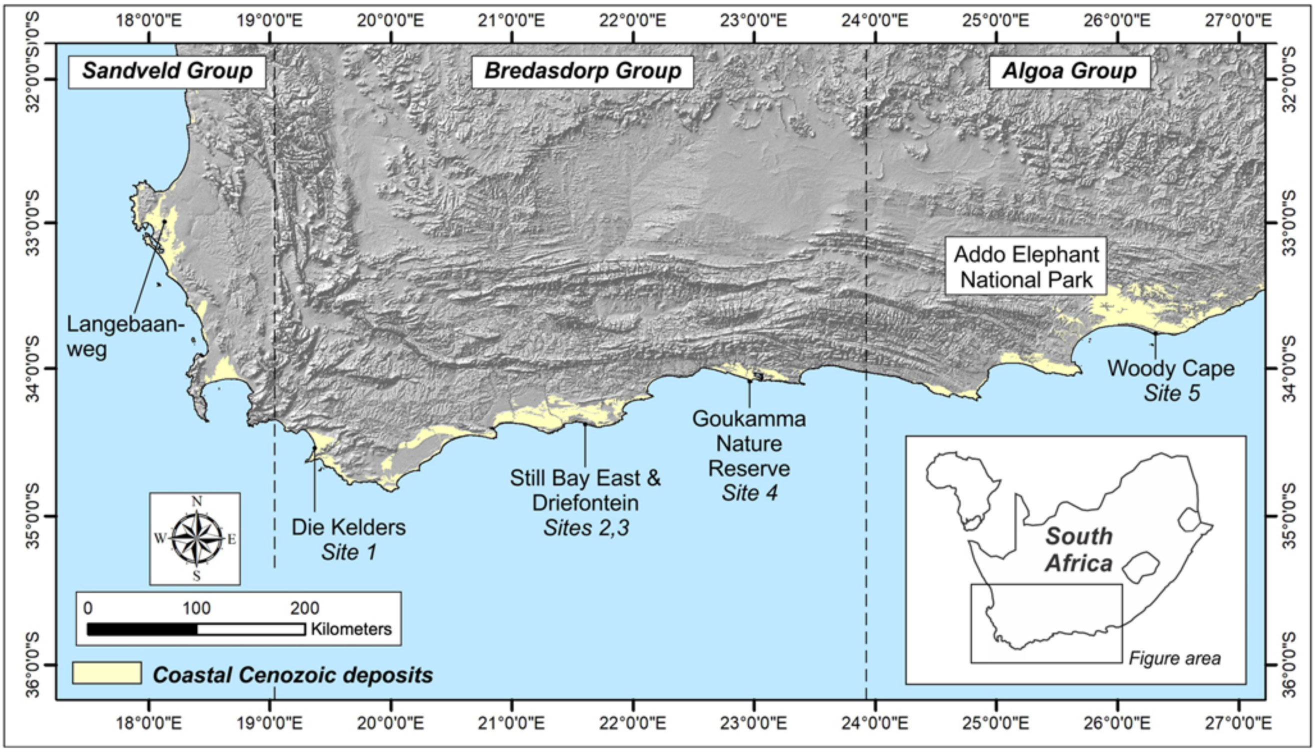

Figure 1. Map of the Cape coast, showing the extent of coastal Cenozoic deposits and the burrow sites described. The possible aardvark tracksite is situated between Site 2 and Site 3.

above. One measures 35 × 28 cm, with a length of 100 cm. The second measures 20 × 20 cm, with a length of 180 cm (Fig. 2B). Proximal to the entrance to the middle cavity is a raised feature, ~ 50 × 30 × 18 cm in size, that exhibits bedding planes and is attached to the underlying aeolianite surface (Fig. 2C). A link to a drone video of Site 1 is provided as supplementary information. A 60-cm long infilled burrow with a diameter of 18 cm was noted in a loose slab in the intertidal area 1 km to the north (Fig. 2D).

Site 2 is located near Still Bay on the Cape south coast, ~3 km east of the mouth of the Goukou River. The area has been dubbed 'Burrow Bay' due to the profusion of burrow cavities, mostly ~10 cm in diameter, in the bioturbated deposits. Two of these, located within in situ, bioturbated aeolianites, are larger and sub-circular (Fig. 3). Unfortunately, they have been affected by considerable wind and water erosion, and the eastern feature in particular is severely eroded. The western example measures 35 cm in height and width, and 52 cm in depth. The eastern example is harder to measure accurately, but has an approximate width of 35 cm and an approximate height of 33 cm. The absence of any claw scratch features might be related to the amount of erosion that has occurred in the walls. A link to a drone video of the Site 2 area is provided as supplementary information.

Site 3 is located 11 km east of Site 2, in the track-rich area known as Driefontein. Three mostly sub-circular, in situ structures, slightly irregular and fully infilled, were identified within a paleosol at the base of 60-m-high aeolianite cliffs (Fig. 4). From west to east, they were separated by 80 cm and 120 cm. The diameter of the central feature was ~50 cm. The shape of the eastern feature appeared slightly elliptical, with a horizontal diameter of 50 cm and a vertical diameter of 38 cm. The paleosol contained fossilized fragments of the snails *Achatina zebra* and *Tropidophora* sp. Subsequent to discovery of the site, a substantial rockfall has covered it. This is evident in the drone video of Site 3, which is provided as supplementary information.

Site 4 is situated in a track-rich area in the Goukamma Nature Reserve on the Cape south coast, and was identified by one of our mentors, the late Dave Roberts, in 2014. A loose aeolianite block that had come to rest near the high tide mark, at the foot of coastal aeolianite cliffs, exhibited what appeared to be a large, infilled burrow that ended in a larger chamber (Fig. 5A). When the site was revisited early in 2024 the loose block was almost completely covered by a deep layer of sand, which had to be excavated, although later in 2024 the area had been scoured free of sand.

The width of the burrow was ~30 cm, and the chamber width was ~50 cm. Maximum length that could be measured, including the chamber, was 70 cm. The aeolianite bedding was interrupted by the infilled feature. The surface contained at least two sub-parallel ridges, each ~1.5 cm in diameter, and 2–5 cm apart (Fig. 5B, C). In another area of the surface, two fine, sub-parallel, curvilinear ridges were noted, 5–6 cm in length, less than 0.5 cm in diameter, and ~2 cm apart from each other (Fig. 5D). Photogrammetry details and a link to a drone video of the Site 4 area are provided as supplementary information.

Site 5 is situated within the Woody Cape section of the Addo Elephant National Park, where a remote stretch of coastal aeolianites of the Nahoon Formation extends for 10 km, forming cliffs that rise to 40 m above mean sea level (Fig. 6A). The cliffs are capped with Holocene sands, and landward of the cliff tops lies the 15,000 ha Alexandria dune field. The aeolianite bedding planes are fairly level, laterally persistent, and calcified in places, suggesting ancient paleo-aquifers. Storm surges and spring tides batter the cliffs, which subsequently are in slow retreat. Aeolianite layers alternate with paleosols, which contain land snail fossils (*Achatina*

Figure 2. (A) White arrows indicate three large burrows within the same horizon at Site 1; black arrow indicates the infill feature shown in (C); scale bar = 10 cm. (B) One of the smaller tunnels linking the right cavity with the surface above; scale bar = 10 cm. (C) The purported infill feature, showing bedding planes, situated proximal to the entrance to the middle cavity – the middle and right cavities can be seen behind this feature; scale bar = 10 cm. (D) An infilled burrow, 18 cm in diameter, one km north of Site 1; scale bars = 10 cm.

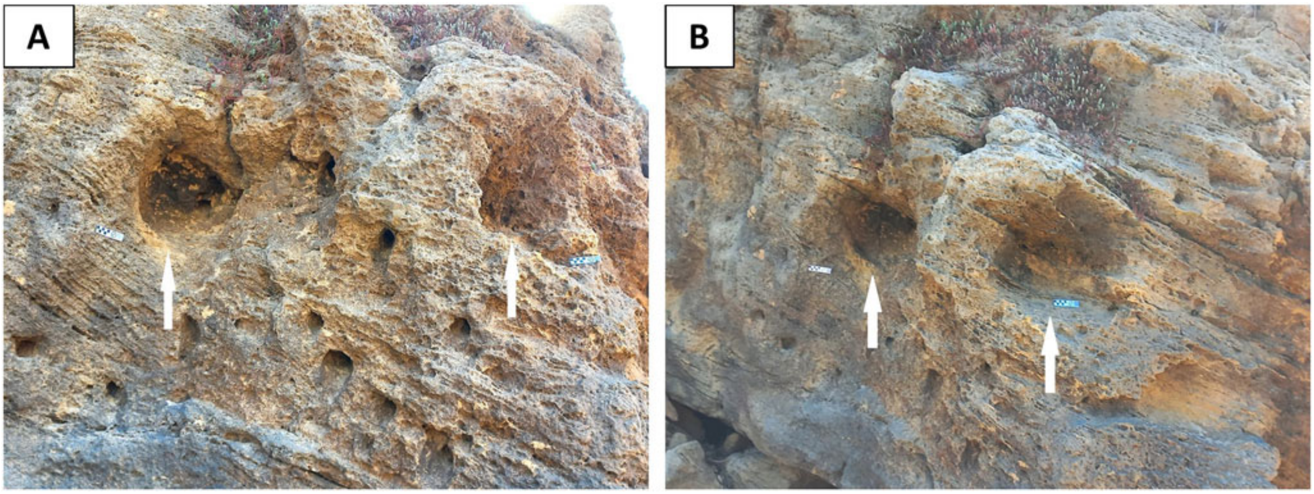

Figure 3. (A, B) Arrows indicate the two large burrow cavities at Site 2; numerous smaller burrow cavities are also present; scale bars = 10 cm.

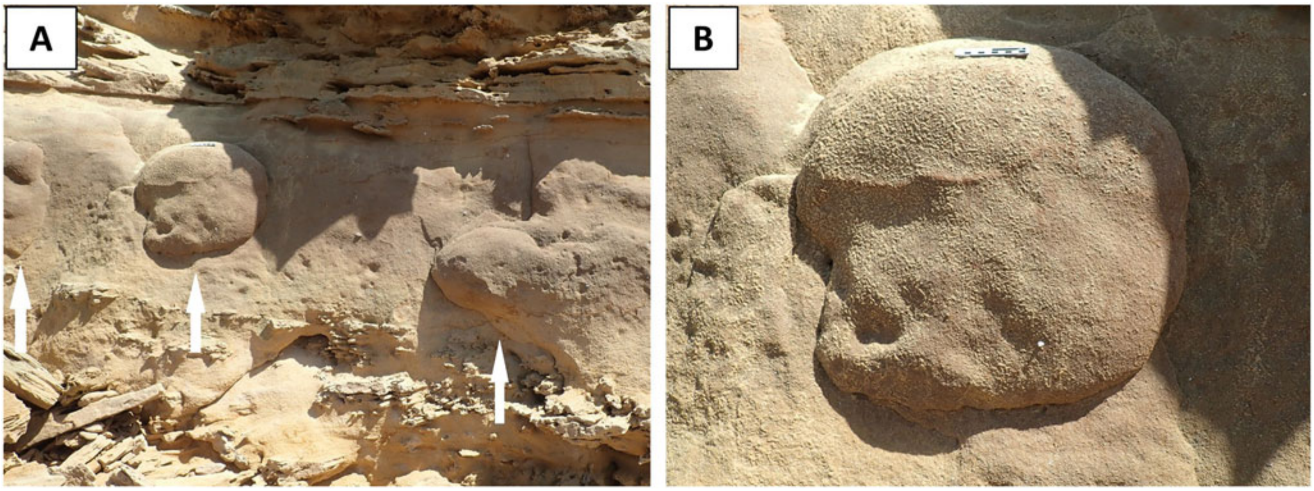

Figure 4. (A) Arrows indicate three infilled probable aardvark burrows at Site 3; (B) the central probable aardvark burrow at Site 3. Scale bars = 10 cm.

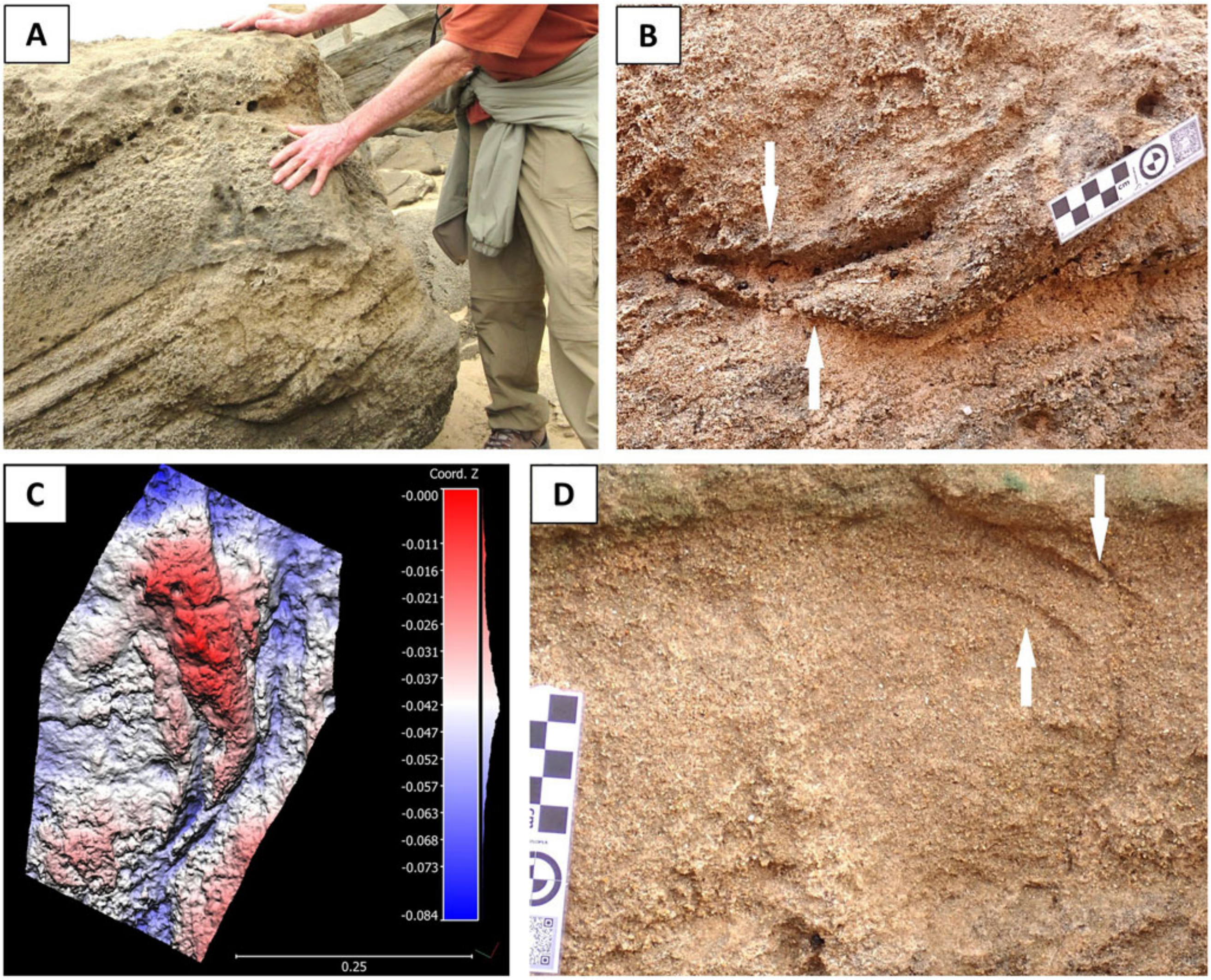

Figure 5. (A) Probable aardvark burrow at Site 4 in the Goukamma Nature Reserve in 2014; adult male human hand for scale. (B) Arrows indicate probable aardvark claw scratch casts; scale bar = 10 cm. (C) 3D photogrammetry model of the probable aardvark claw scratch casts; horizontal and vertical scales are in meters. (D) Arrows indicate curvilinear features that probably represent smaller claw scratch casts; scale bar = 10 cm.

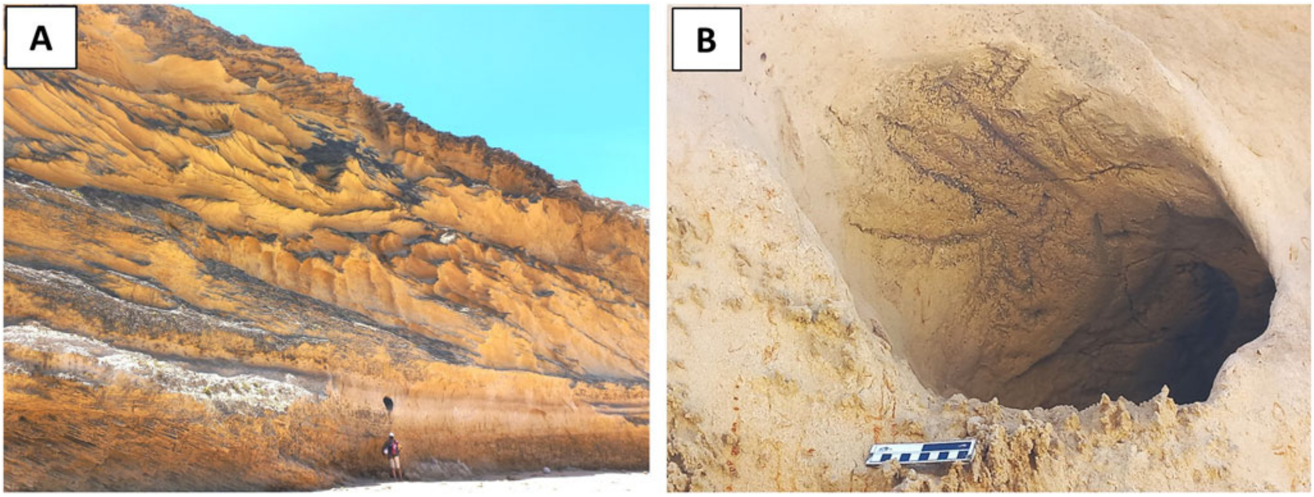

Figure 6. (A) The burrow cavity at Site 5 lies just above the head of the human figure, towards the bottom of high coastal aeolianite cliffs. (B) The Site 5 burrow cavity, showing claw scratch marks; scale bar = 10 cm.

zebra). The burrow site occurs in a paleosol at the bottom of the cliffs.

The burrow (Fig. 6B) is situated approximately 2.5 m above the beach at the foot of the cliffs and extends gently upwards in a northeasterly direction. It is sub-circular in cross section, with a diameter of ∼50 cm, and contains no infill. A prominent feature is a set of at least three sub-parallel grooves in the burrow wall. The height of the burrow above the beach made it impossible to measure the distance between the grooves directly, but they appear to be ∼7 cm apart from each other. During the process of burrow documentation, an Egyptian goose (*Alopochen aegyptiaca*), which had been residing within it, suddenly and unexpectedly emerged. The elevation above the beach level and the presence of an Egyptian goose that may have been nesting precluded accurate measurement of burrow depth. A link to a drone video of Site 5 is provided as supplementary information.

A possible aardvark tracksite

The tracksite is located approximately 3 km east of Site 2 and 8 km west of Site 3, where the coastal section of the Geelkrans Nature Reserve (to the west) abuts the Bosbokfortein Private Nature Reserve (to the east). It occurs on the surface of a loose aeolianite slab that came to rest at the base of the cliffs. The features on the surface are preserved in hyporelief (Fig. 7). The possible aardvark track is tridactyl—the three digit casts are slightly splayed, and the two digit casts on the right (Fig. 7C) exhibit a slight lateral convexity. As viewed in Figure 7C, the digit cast on the left of the image is less distinct than the other two digit casts, and has a maximum length of 6 cm and a maximum width of 4 cm. The middle digit cast has a maximum length of 6.5 and a maximum width of 3 cm. The digit cast on the right of the image has a maximum length of 7.5 cm and a maximum width of 3 cm. The distance between the left and middle casts is ∼7.5 cm, and between the middle and right casts is ∼6.5 cm. The maximum height of the casts is ∼2 cm. Photogrammetry details are provided as supplementary information.

As shown in Figure 7A, further features are apparent on the surface. While these remain enigmatic, they may be related to the tridactyl track. One of these features exhibits sub-parallel grooves and ridges that are in broad alignment with the orientation of the tridactyl track. If this indeed represents a short, poorly preserved trackway segment, then a ‘pace length’ of 27 cm is evident.

Termite and ant traces

Given that the preferred diet of the aardvark consists of termites and ants, we note the presence of three sites on the Cape coast where traces of these invertebrates are identified, providing (circumstantial) evidence that the coastal dune systems were likely suitable aardvark habitats. Roberts et al. (2008, fig. 8B) reported ‘fossil termite nests’ in a paleosol in the Driefontein area east of Still Bay. One of us (ASC) has identified a fossilized termitarium or ant nest in sandy deposits on the west coast (Fig. 8A), while at Arniston, on the south coast, a structure measuring 24 cm in maximum height and width was identified in an in situ aeolianite layer (Fig. 8B). It resembles either a fossilized ant nest or termite nest. Middle Pleistocene termitaria have also been reported from Calitzdorp in the Little Karoo, ∼100 km north of the modern coastline (Abrahams et al., 2024; Muir et al., 2024).

Discussion

Aardvark habits and traces

Aardvarks leave clear signs of their presence (Gutteridge and Liebenberg, 2021). Consideration of the habits and attributes of extant aardvarks, coupled with a review of the traces they create, enable an understanding of the type of evidence potentially preserved in the paleoichnology record.

Aardvarks (Fig. 9A) are seldom-seen, nocturnal, solitary creatures, weighing as much as 65 kg (Gutteridge and Liebenberg, 2021). Distinctive anatomical features include a long snout (often referred to as ‘pig-like,’ e.g., Liebenberg, 2000), large ears (often referred to as ‘donkey-like,’ e.g., Liebenberg, 2000), and a long, thick, tapering tail (Shoshani et al., 1988). Other physical attributes include a stocky body, short neck, and arched back (Shoshani et al., 1988). Sturdy legs and feet with long, robust claws are characteristic. The forelimbs are short and particularly powerful, allowing for subterranean digging at great speed (van den Heever et al., 2017; Walker 2018). Melton (1976) reported that a 1-m-long burrow could be dug within five minutes. Stuart and Stuart (2019)

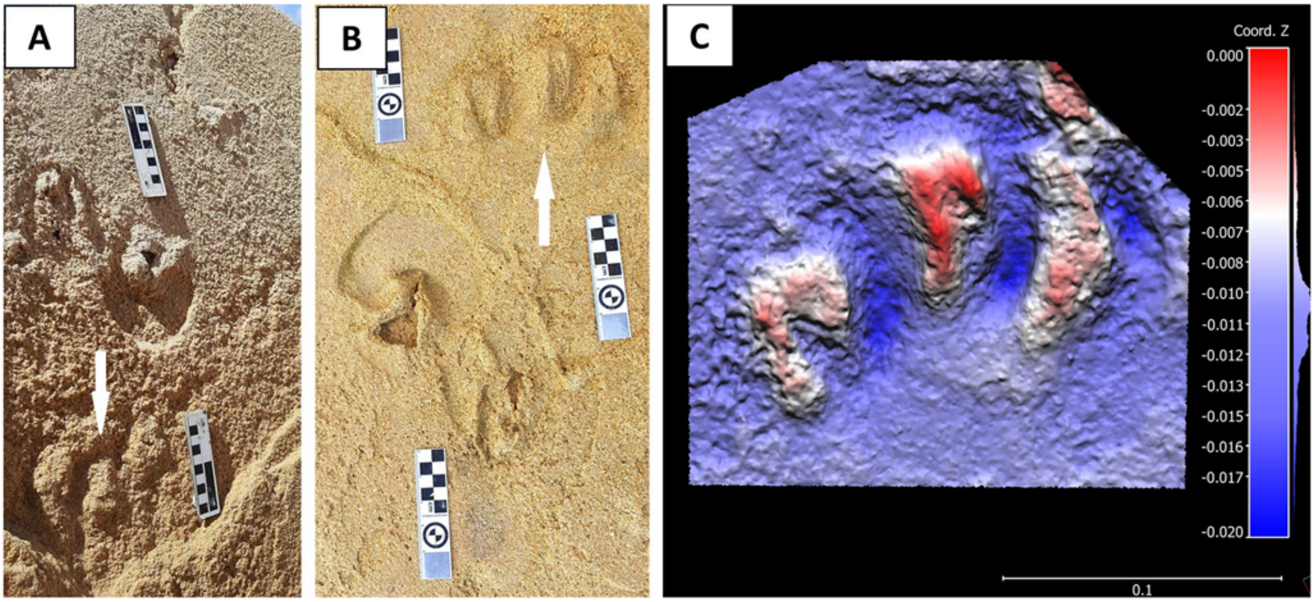

Figure 7. (A) Track-bearing surface in sunshine; image reproduced with permission from Richard Webb. The tridactyl track is indicated by an arrow; scale bars = 10 cm. (B) Track-bearing surface in shadow. The tridactyl track is indicated by an arrow; scale bars = 10 cm. (C) 3D photogrammetry model of the tridactyl track; horizontal and vertical scales are in meters.

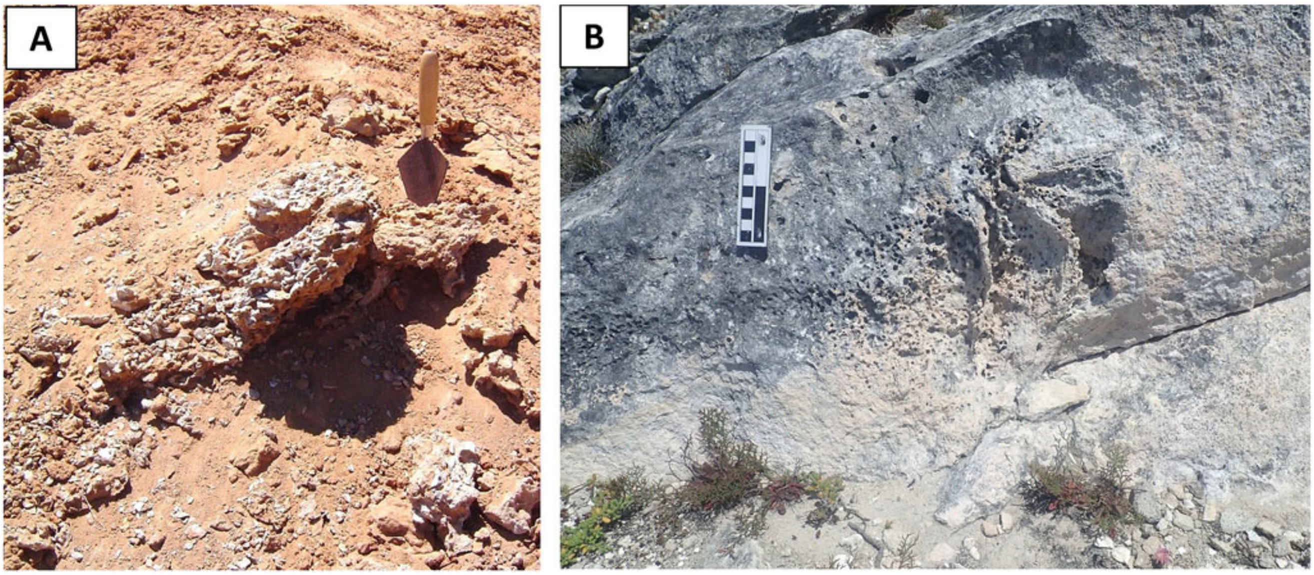

Figure 8. (A) Fossilized termitarium or ant nest on the west coast north of Lambert's Bay; trowel for scale, with width of 5 cm. (B) Ant or termite nest in an aeolianite deposit at Arniston; scale bar = 10 cm.

referred to the aardvark as the 'master digger' and noted that it occurs anywhere in sub-Saharan Africa where its preferred diet of termites and ants is available.

Southern African tracking guides indicate that aardvark tracks (Fig. 9B) are distinctive and readily recognizable (Liebenberg, 2000; van den Heever et al., 2017; Walker, 2018; Stuart and Stuart, 2019; Gutteridge and Liebenberg, 2021). Four toes are present on the forefoot, and five toes on the hindfoot. The resulting tracks, ~8–10 cm long, are typically tridactyl and show three long toes ending (in well-preserved cases) in claws on both the slightly smaller front feet and slightly larger hind feet (Stuart and Stuart, 2019). Occasionally, in soft substrates, impressions of claw V on the front foot and claws I and V on the hind foot may be registered; the hind foot is usually placed behind the forefoot impression, although it may be partially superimposed on it in an imperfect direct register (van den Heever et al., 2017). A tail drag may be evident in soft substrates. Illustrations in the above-mentioned tracking guidebooks indicate that the outer digit impression of the hindfoot (digit IV), and to a lesser extent the middle digit impression (digit III), display an outward convexity. These features are not obvious in forefoot tracks.

However, burrows (Fig. 9C), rather than tracks, are the most characteristic element of aardvark traces. Stuart and Stuart (2019) described large burrows with an entrance measuring 50–80 cm in diameter, with deep grooves in the burrow walls created by the massive claws on the aardvark's foot (Fig. 9D). Use of the tail as

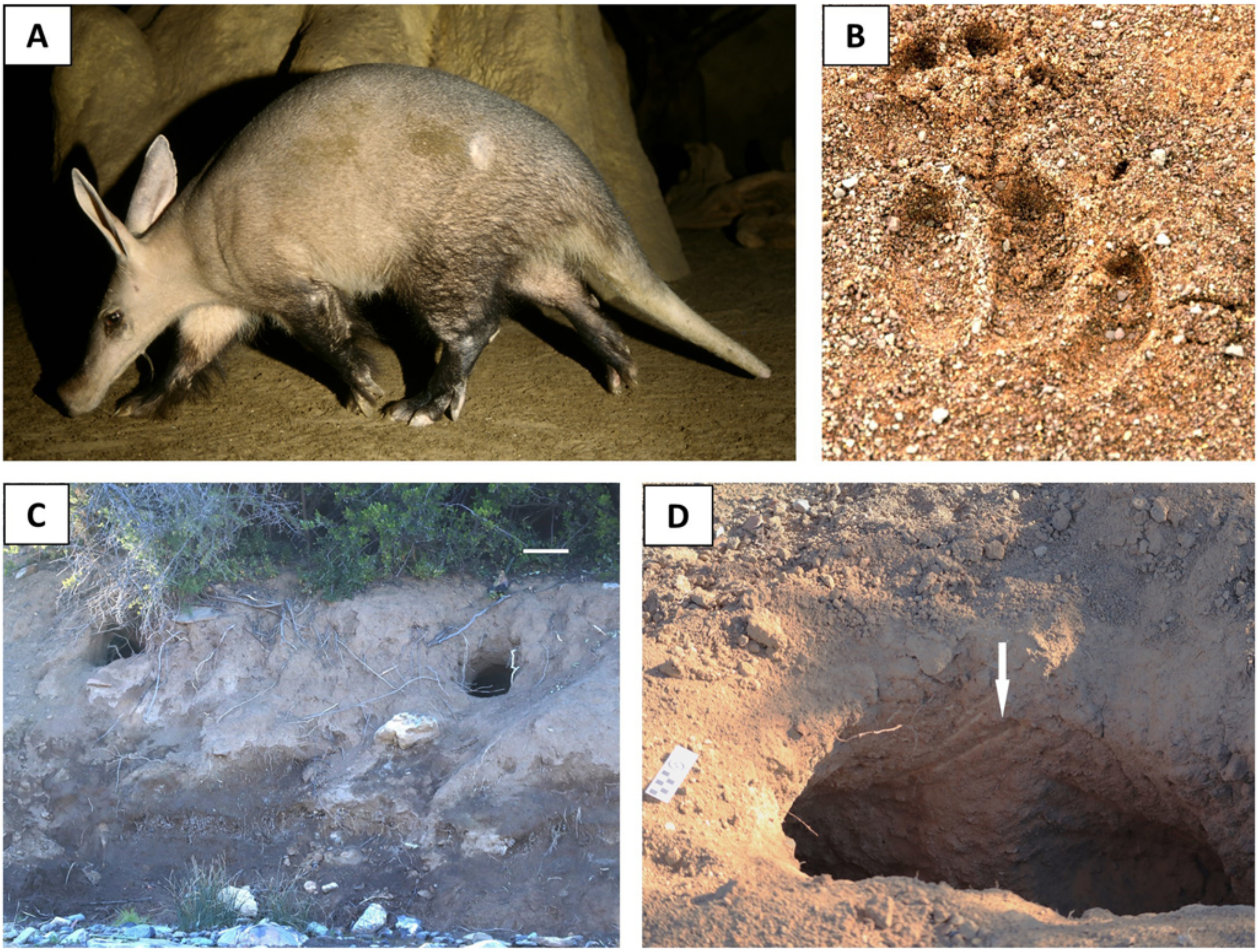

Figure 9. (A) The aardvark, *Orycteropus afer*. (B) An aardvark track, showing the distinctive tridactyl morphology; typical aardvark tracks are ~8–10 cm in length. (C) Two adjacent aardvark burrows in the Karoo region of South Africa, in a pattern resembling the findings at sites 1, 2, and 3; scale bar = 10 cm. (D) An aardvark burrow in the Karoo region of South Africa, with an arrow indicating claw scratch marks in a pattern resembling the findings at sites 4 and 5; horizontal white scale = 50 cm. Images (A) and (B) reproduced with permission from Mathilde Stuart.

a support when digging was noted, resulting in a wedge-shaped impression in the soil.

Aardvark burrows may be used as permanent burrows, temporary refuges, and burrows made while foraging (Shoshani et al., 1988; Liebenberg, 2000). A typical feeding sign is a hole dug into the side of a termite mound (Stuart and Stuart, 2019). Such holes may be deep enough to cover the aardvark completely or may be shallower and only large enough to cover the animal's head (Shoshani et al., 1988). Temporary refuges tend to be shallow, but may run underground for meters (Liebenberg, 2000). Permanent burrows, in which aardvarks reside and bear young, are more complex and tend to be deeper, with multiple tunnels and several entrances. (Melton 1976) reported that the entrance, measuring 40–50 cm in diameter, was often the narrowest part of the burrow, and that terminal chambers were as much as a meter in diameter, large enough to enable the aardvark to turn around. Burrow lengths of 5–8 meters, with smaller cavities and compartments leading off from the main chamber, have been reported by (van den Heever et al. 2017) . Mounds of excavated material may accumulate beside the burrow entrance.

Use by other animals of burrows that have been abandoned by aardvarks is a common theme. (Stuart and Stuart 2019) noted that warthogs (*Phacochoerus africanus*) occupy and modify holes dug by aardvarks, and that while porcupines (*Hystrix africaeaustralis*) may excavate their own burrows, they may also use and modify aardvark burrows. These species fall within the 'secondary modifier' category of (Kinlaw 1999). In addition, (van den Heever et al. 2017) noted that disused burrows may be used by wild dogs, hyenas, honey badgers, snakes, and birds. These fall into the 'simple occupant' category of (Kinlaw 1999).

Aardvark scat is seldom encountered by modern trackers, as droppings tend to be covered up or buried beneath excavated soil (van den Heever et al., 2017; Walker, 2018). However, aardvark scat is distinctive, being composed of soil impregnated with the heads of termites and ants (Stuart and Stuart, 2019). As such, aardvark coprolites might be readily identifiable.

In summary, traces of aardvarks that could be sought in the fossil record include tracks, tail impressions, feeding traces, burrows, and coprolites. Of these, burrows are probably the most obvious and may be the easiest to identify. An ideal case might involve a feeding burrow within a termitarium, complete with claw-scrape impressions, tracks, and an adjacent wedge-shaped tail impression.

Despite all these possibilities, it appears that until now, only a single, undated case of probable aardvark burrows has been reported. This was from Simanya, on the south bank of the Kavango River in northern Namibia, where Pickford (2018, Fig. 7) described an infilled ovoid feature as much as a meter in diameter. The purported burrow penetrated poorly consolidated, pale, nodular sand and silt. The infill was formed by dark gray clayey-silty soil and fragments of the subjacent rock. The lowest portion of the burrow appeared V-shaped, suggesting modification by a porcupine or other secondary modifier.

The regional record

The historic and prehistoric distributions of aardvarks in the Western Cape and Eastern Cape provinces were extensive. Evidence includes reports of travelers and early naturalists, place names, traditional names, and the rock art record. In addition, during much of the Pleistocene the vast Palaeo-Agulhas Plain (Cleghorn et al., 2020), most of which is currently submerged, was exposed south of the modern coastline and would have provided substantial extra habitat. Sites 1–4 would have been located at the margin of the Palaeo-Agulhas Plain, and there is no reason to think that the aardvark would not have utilized this habitat.

Skead (1987), in his monumental work on the historical distribution of mammals in the Cape Province, disclosed that aardvark records had largely been overlooked because of the species' widespread distribution, leading to the assumption that the historic distribution range was similar to that of the present. Numerous references were noted, many of them pertaining to the dangers to horses and riders, or to wagons and carts, through unexpected encounters with aardvark burrows. Given the prevalence of termite mounds, it was concluded that aardvarks could have occurred 'almost anywhere.'

A description by the missionary (Latrobe 1818, p. 310) provides an example from the Mamre area of the Western Cape Province in 1816. In describing the risk of injury from burrows adjacent to the dwelling of a blind chief, he commented: "These singular creatures are about as large as a common pig. They have a long snout, long sharp claws, very little hair, and a rough skin. Their food is the ants, and probably other insects." This leaves no doubt as to the identity of the burrower.

(Möller 2017) quoted reports of names for the aardvark in a variety of San, Khoikhoi, Nama, and Korana languages, as well as place names, which in the Western Cape included 'Beervlei,' an Afrikaans translation of an original San term. Such records confirm the widespread distribution of the aardvark and how indigenous peoples were familiar with it.

Although depictions of aardvark are relatively rare in the rock art record, they have been recorded from at least four sites in the Western Cape Province. Aardvark paintings from Cloete's Pass in the Little Karoo (Fig. 10A) were reproduced as the frontispiece in a rock art book (Rust, 2012), and a probable aardvark image is reported from Sevilla in the Cederberg (Fig. 10B) (Andrew Paterson, personal communication, 11 May 2024). A painting depicting a possible aardvark was reported by (Helm et al. 2024a) from a Western Cape site south of the Langeberg, in close proximity to an image that might represent flying termites. The juxtaposition was regarded as potentially significant, given the dietary preferences of the aardvark. Finally, probable aardvark images from the Leeublad site in the Kammanassie Mountains in the Little Karoo are provided as Figure S1 in supplementary information. Together, these images further confirm the regional existence of aardvarks and awareness of their presence by local inhabitants, although the precise dating of San rock art can be challenging, and in certain areas such rock art was still being created in the late nineteenth century. A potential age estimate for regional rock of at least 2000 years has been provided (Deacon and Deacon, 1999), while in some areas southern African rock art may be as old as 27,000 years BP (Lewis-Williams and Challis, 2011).

The body fossil record

The earliest known aardvark is dated to circa 19 ka (Pickford, 2019), although it has been suggested that the Tubulidentata appeared in Africa during the Paleocene (Patterson, 1975). In southern Africa, the aardvark fossil record extends back to the Miocene, with reports of the genera *Amphiorycteropus* and *Orycteropus* from southern Namibia (Pickford, 1996, 2003, 2008; Avery, 2019), and a Pliocene record from northern Namibia (Pickford et al., 2016). Aardvarks of undetermined genera and species were reported from Early Pliocene deposits of the Sandveld Group at Langebaanweg, in the Western Cape Province near the west coast (Hendey, 1981). (Pickford 2005) suggested that they were compatible in size and most morphological details to *Orycteropus afer*. These are therefore the earliest fossils attributed to this species, and the extant lineage may have evolved in southern Africa (Pickford, 2005).

The Pleistocene and Holocene record of *O. afer* in southern Africa is extensive, with the type specimen being recorded by Pallas in 1766 from the Cape of Good Hope (Avery, 2019). Pleistocene records from the Western Cape or Eastern Cape include Eland's Bay Cave, Klasies River, Nelson Bay Cave, and Sea Harvest, while Holocene records include Nelson Bay Cave and Oudepost 1. For example, the species has been recorded in Later Stone Age archaeological deposits at Elands Bay Cave (Klein et al., 2007), Pleistocene deposits at Elands Bay Cave (Klein and Cruz-Uribe, 1987), and in layers dating to 10–9 ka in Nelson Bay Cave near Plettenberg Bay (Klein, 1972) in the Western Cape Province. *Orycteropus afer* has been documented in Pleistocene deposits in the Eastern Cape Province at Klasies River (Klein, 1976). However, following excavations of Middle Stone Age and Later Stone Age deposits at Die Kelders 1 Cave near Site 1, and despite an extensive list of mammalian fauna, no aardvark records were reported (Klein and Cruz-Uribe, 2000).

Differential diagnosis

In formulating a differential diagnosis for the burrow traces described here, a first question relates to any possible non-burrow explanation for the noted features. While clear claw scratch marks in the walls make a burrow identification essentially unequivocal, large tubular cavities also could have a botanical origin and could represent areas where substantial roots once existed. Indeed, rhizoliths (Klappa, 1980; Durand et al., 2018) are a common feature in Cape coastal aeolianites and sometimes in paleosols. However, in our experience, rhizoliths usually can be distinguished by examining the appearance of the surrounding rock, which typically appears altered due to chemical interaction with the organic plant matter. If a burrow is examined in longitudinal section, it may be possible to distinguish it from a rhizolith by the tendency of rhizoliths to taper if exposed for a sufficiently long distance; however, the purported aardvark burrows described here happen to occur predominantly in cross section. Nonetheless, we contend that the features at the sites described are inconsistent with rhizoliths.

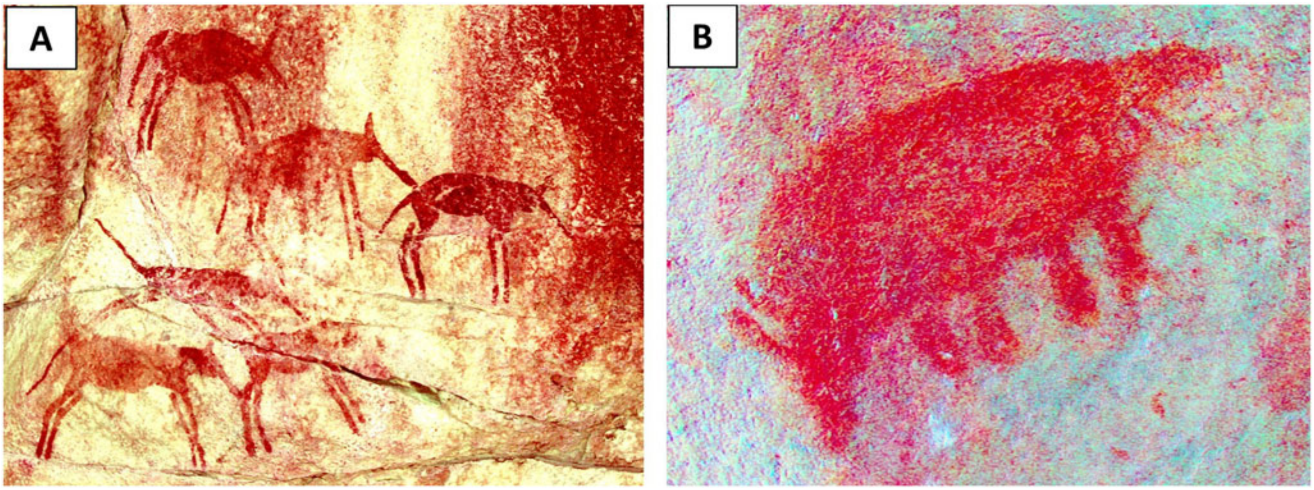

Figure 10. (A) San rock art of aardvarks from Cloete's Pass in the Western Cape Province, reproduced with permission from Renée Rust. (B) San rock art of a probable aardvark from the Cederberg in the Western Cape Province, reproduced with permission from Andrew Paterson.

The Cape porcupine (*Hystrix africaeaustralis*), the largest rodent in Africa (van den Heever et al., 2017), also digs, and therefore needs to be considered. (Gutteridge and Liebenberg 2021) noted that the porcupine is a 'prolific digger,' and will dig to reach its food of roots and bulbs. They further noted that Cape porcupine burrows are V-shaped (something that is confirmed in our experience) and can be large, with smooth upper walls due to abrasion from quills (van den Heever et al., 2017). (Walker 2018) noted that the porcupine frequents disused aardvark burrows or holes that it has dug itself. It may live singly or in a group in a burrow, which has usually been taken over from an aardvark (van den Heever et al., 2017). (Stuart and Stuart 2019) described 'feeding holes,' which may contain claw marks in the walls, although never as large as those left by aardvarks (also confirmed in our experience). It is evident, then, that porcupines use aardvark burrows and create feeding holes, and when they do create their own burrows, there are no reports of them being as complex or substantial as those of aardvarks. Furthermore, the burrows are V-shaped in cross section, in contrast to the more circular shape of aardvark burrows. Porcupines are therefore unlikely candidates for the creation of any of the large fossilized burrows identified here.

Among regional extant carnivorans, jackals are discussed below and the African wild dog (*Lycaon pictus*) is not a burrower. Some fox species dig burrows. Among southern African species, the bat-eared fox (*Otocyon megalotis*) uses aardvark burrows (van den Heever et al., 2017) or modifies burrows of the yellow mongoose, and on occasion may dig its own burrow; it frequently digs feeding holes, but these seldom exceed 7 cm in diameter (Stuart and Stuart, 2019). The Cape fox (*Vulpes chama*), in contrast, is a more regular burrow digger, although it too occupies the burrows of other animals such as the yellow mongoose or springhare (van den Heever et al., 2017). However, both species are small, slender carnivorans, with tracks less than 4 cm in length, compared with ∼5.5 cm for jackals and 8–10 cm for the aardvark (Stuart and Stuart, 2019). They do not excavate burrows as large as those of aardvarks and are therefore also excluded.

Jackals and warthogs are sometimes thought of as burrowers, but this relates to their habit of occupying disused aardvark burrows (Walker; 2018; Gutteridge and Liebenberg, 2021). Likewise, the aardwolf (*Proteles cristatus*) does not dig its own burrows but occupies those of aardvarks and springhares (van den Heever et al., 2017).

The springhare (*Pedetes capensis*) can be excluded on grounds of burrow diameter. Although these rodents certainly occurred in the Cape in historic times (Skead, 1987), and there is no reason to think that the Pleistocene distribution range was dissimilar, their burrows are substantially smaller in diameter than those of the aardvark. (Stuart and Stuart 2019) reported burrow diameters of 18–25 cm for this species.

It is not possible to disprove the possibility that an extinct fossorial species, as yet undocumented in the body fossil record, might have created the burrow traces. However, given the extensive, well-documented regional body fossil record (Avery, 2019), this appears to be extremely unlikely.

A final question pertains to the age of the burrow at Site 5. Even if it is accepted as an aardvark burrow, the age of 126 ± 8 ka relates to the basal aeolianite layer, not the paleosol in which the burrow occurs. Furthermore, the burrow may have been dug some time after the paleosol horizon was established. If this is a matter of a few decades or even a few thousand years, it would not be significant, but could it have been dug much more recently, say within the last thousand years? We think the likelihood of such a possibility is remote, given the beach setting and the high aeolianite cliffs that occur above the burrow. Aardvarks are subsurface burrowers and have not been reported burrowing into cliff faces. This possibility can therefore be excluded.

In summary, there is no evidence to support the likelihood of any of the fossilized burrow traces reported here to have been made by anything other than aardvarks. We are confident in identifying aardvarks as the burrow makers, although the certainty of this conclusion varies from site to site.

With respect to the possible aardvark track, (van den Heever et al. 2017) noted that aardvark tracks can be confused with those of warthog (*Phacochoerus africanus*) or bushpig (*Potamochoerus larvatus*), or when two partially overlapping medium-sized antelope hoof prints are registered beside each other. All three of these alternative trackmakers register didactyl tracks, and the tridactyl morphology evident at the tracksite, coupled with the absence of any other tracks of warthogs, bushpigs, or antelope, increase the likelihood that the track was registered by an aardvark. Although the track is slightly shorter than the typical, reported size range, comparison with the track morphology (Fig. 9B) establishes the close resemblance to the tracks of modern aardvarks.

Optically stimulated luminescence dating

Over the last two decades, sites on the Cape coast have been dated through optically stimulated luminescence (OSL) studies, with more than 100 ages now published for aeolianite deposits. Initial studies (e.g., Roberts et al., 2008; Carr et al., 2010; Bateman et al., 2011; Cawthra et al., 2018; Jacobs et al., 2020) were followed by our own OSL dating work focused on ichnofossil-bearing sites (e.g., Helm et al., 2023b, 2023c, 2023d, 2024b). For the latter work, each sample was assigned a code beginning with 'Leic'. While none of the sites described herein has been dated directly, they can be compared with nearby dated sites, thus an approximation of their ages can be obtained. A caveat is that aeolianite exposures on much of the Cape coast exhibit extensive crossbedding and a lack of lateral persistence. Other than being able to conclude in broad terms that sites at the base of aeolianite cliffs are older than those towards the top of the cliffs, this limits the accuracy of any conclusions if sites are not directly dated. Paleosols, by way of contrast, may exhibit more lateral persistence (e.g., Roberts et al., 2008) and may thus provide more accuracy in this regard.

At Site 1 an OSL age of 76 ± 5 ka was obtained ∼40 m to the north and from the same elevation Leic23004, (Helm et al., 2024b). Although the burrow site and sampling site are from the same elevation, it cannot be assumed that they are from the same unit or layer.

At Site 2 the closest site dated using OSL (Leic21008) lies 6 km to the east, where an age of 134 ± 9 ka was obtained (Helm et al., 2023d). The distance of 6 km unfortunately limits the usefulness of this result.

At Site 3 the closest site dated though our OSL dating project (Leic20024) lies 300 m to the west, where an age of 109 ± 9 ka was obtained (Helm et al., 2023c), while an age range of 140 ± 8 ka to 91 ± 5 ka was previously obtained from a sampled section spanning the full thickness of the cliff exposure at a site 100 m to the west (Roberts et al., 2008). The Site 3 paleosol containing the possible aardvark burrows is laterally persistent and appears to be the same as 'P1' in (Roberts et al. 2008); the ages obtained therein from sediments above and below this layer (DF05/2/1, 2/2, and 2/3) allow some narrowing of this age range to circa 126–114 ka.

At Site 4 the closest dated site (Leic20025) lies 1.1 km to the east, where an age of 78 ± 5 ka was obtained (Helm et al., 2023b). This is a typical result for this stretch of the Goukamma coastline. Finally, in the region of Site 5, the basal unit has been dated (Leic22025) through OSL to 126 ± 8 ka (van Tonder et al., 2024), a period with a comparable climate and sea-level to the present.

As discussed above, the limitations imposed by the difficulties in aeolianite stratigraphic correlation and the distances of the OSL sampling sites from the purported burrow sites are acknowledged. Nonetheless, the results are consistent with others obtained from, for example, the Goukamma region and the area east of Still Bay, and more generally in terms of the dominance of MIS 5 ages that are reported for the seaward-most aeolianite deposits (Bateman et al., 2011). Of these results, the age range estimate of circa 126–114 ka for Site 3 is regarded as the most reliable, given the stratigraphic inferences that can be made.

Review of the sites

The five burrow sites most likely span an age range from circa 134–76 ka, potentially representing MIS Stage 6 through 5a. During this time period, sea level would have varied from ∼110 m lower than the current mean sea level during the MIS 6–5e transition, to 6–8 m higher than the current mean sea level during the MIS 5e high-stand, to ∼45 m lower than the current mean sea level during MIS 5a (Spratt and Lisiecki, 2016).

Burrow site 1, comprising three sub-circular or elliptical cavities from a single horizon, may represent part of an aardvark burrow complex seen in cross section with the preservation of short tunnels. The two tunnels that connect from the right cavity to the overlying surface may represent part of the burrow complex, although one of them is small. It can also be postulated that storm surges may have eroded this cavity and exploited lines of weakness at its distal end to create 'blowholes.' The raised feature close to the entrance of the middle cavity is intriguing. The presence of bedding planes within it makes it unlikely that it represents the remains of a mound of excavated material beside the burrow entrance. A more likely explanation is that it represents part of the infill from an extension of a burrow. The infilled trace (1 km to the north), 18 cm in diameter, is small for an aardvark burrow and large for a mole rat burrow and may represent a springhare burrow.

Burrow site 2, comprising two sub-circular cavities, is similar to Site 1, and may represent part of an aardvark burrow complex in cross section, with the preservation of short tunnels.

Burrow site 3, containing three circular or elliptical features in a paleosol, may also represent an aardvark burrow complex in cross section. In this case, each feature is infilled. The associated snail fossils are typical of regional paleosols from the Pleistocene.

Burrow site 4 provides an example of a burrow trace that is not evident only in cross section. The infilled burrow is essentially a natural cast, and the large sub-parallel ridges in the cast of the chamber wall may represent infilled claw scratch casts. The smaller, shallower sub-parallel ridges, separated by 2 cm, may also be claw scratch casts, but may have been registered by a juvenile aardvark or by a secondary modifier.

Burrow site 5 provides the most compelling evidence of an aardvark burrow, seen both in cross section with a sub-circular shape, and for some distance as a hollow burrow with sub-parallel claw scratch marks on the wall.

In summary, three of the sites are cavities and two sites are infilled burrows. At three sites more than one burrow feature is present, and at two sites only one burrow is present. In two cases claw scratch marks are present in the wall, highly likely at Site 5 as sub-parallel grooves, and more equivocally at Site 4 as sub-parallel ridges as part of a burrow cast. Two sites occur in paleosols (the other three occur in aeolianites) and one feature is interpreted as a chamber. Sites 4 and 5, with what we interpret as claw scratch marks, provide the strongest evidence. Sites 1, 2, and 3, presenting as tubular features (cavities and tunnels, or infilled) with a sub-circular appearance in cross section, suggest aardvark burrows but with less certainty.

The possible aardvark tracksite contains one relatively well-preserved track and an enigmatic feature containing linear elements that follow the same orientation as the well-preserved tridactyl track. The track bears a close resemblance to the tracks of modern aardvarks, but in the absence of a definite trackway attribution to an aardvark, the trackmaker attribution is tentative. If this is an aardvark track, and noting that the track is preserved in hyporelief, the outward convexity evident in two of the digit casts suggests that it was probably registered by a left hindfoot. If this interpretation is correct, it would be the first aardvark track in the global ichnology record.

Ichnotaxonomy

A comprehensive global summary on fossilized vertebrate burrows was provided by (Melchor and Cardonatto in press). Aligning this with the findings described here allows for an enhanced perspective on the relevance of aardvark burrows in the global record, and the potential for assigning an ichnotaxon to aardvark burrows. Criteria established to aid in the identification of vertebrate burrows, and potentially for assignment to an ichnotaxon (Lucas et al., 2006; Cardonatto and Melchor, 2021), apart from being a subcylindrical structure of approximately uniform diameter, include (1) the overall burrow size (at least 3–5 cm in diameter), along with the architecture and morphology of the burrow system and the ramp inclination; (2) the presence/absence of chambers and their location and contents; (3) surface ornamentation, if present (e.g., near-parallel grooves in the wall or ridges on burrow casts, including the pattern, number, and dimensions of claw/tooth traces); (4) infill, if present, that often contrasts with the surrounding rock; (5) cutting through sedimentary structures, often at a low angle to what would have been the horizontal at the time of deposition; and (6) occurrence in a continental succession, and often in a paleosol.

(Melchor and Cardonatto in press) indicated that there are 15 vertebrate-burrow ichnogenera and 23 vertebrate-burrow ichnospecies that are "available," and 6 ichnogenera and 7 ichnospecies that are "unavailable," (e.g., nomina dubia). The findings thus far identified at the five Cape coast sites, while allowing for an identification of fossilized aardvark burrows, do not yet meet the criteria for assignment to an existing ichnotaxon or the erection of a novel ichnotaxon. Indeed, (Melchor and Cardonatto in press) rely heavily on neoichnology for an understanding of burrow morphology and characteristics, whereas paleoichnology should provide the criteria for such assignment. Comparison with the extensive documentation of armadillo burrows from the Americas (McDonough et al., 2000, and references therein) and the role of neoichnology (Cardonatto and Melchor, 2023) may prove fruitful. The findings described herein are therefore regarded as preliminary in nature, pending further dedicated exploration of suitable deposits, and the features described are not yet assigned to an ichnotaxon. Likewise, aardvark tracks are distinctive, and identification of an unequivocal aardvark trackway would allow for the proposal of a new ichnotaxon.

Conclusions

The sites described do not represent range extensions for the aardvark and thus do not provide new information on the distribution range of the species, and do not have novel paleo-environmental implications (i.e., the implication is that MIS 5 conditions on the Cape south coast remained firmly within the wide environment range occupied by modern aardvarks). Nonetheless, the sites aid in understanding of the Quaternary Period in Africa by filling a substantial gap in the trace fossil record, and through independently confirming the body fossil record. The sites also offer an explanation for the presence of aardvark images within the rock art record—clearly the species was readily observed by occupants of this region in the Holocene (and perhaps also in the Pleistocene) and in the historical period.

The ichnosites described here contribute to the southern African ichnological record, in particular with respect to Pleistocene vertebrate burrows. They also contribute meaningfully to the global record, as the aardvark is the archetypal 'master digger' throughout much of the African continent. Aardvark traces are such conspicuous features of suitable present-day environments that, if they were absent from the trace-fossil record, this would have required explanation. While the relative incompleteness of the findings (and resulting absence of a proposal for a novel ichnotaxon) is acknowledged, they might lead to increased awareness of such traces and subsequent further discoveries. Furthermore, Pleistocene vertebrate burrows with smaller dimensions, such as those made by springhares and mole rats, might receive further attention and publication.

While the five purported burrow sites and the possible tracksite have limitations, in combination they provide an emerging picture of the Pleistocene ichnological activities of the aardvark. In so doing, the ichnosites complement both the body fossil record and the neoichnological record, and they contribute to a growing body of ichnological data that offer the potential (independently of faunal remains from archaeological contexts) to reconstruct in even more detail the ecosystems and paleoenvironments of this region during MIS 5.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/qua.2024.48.

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References

Abrahams, M., Muir, R.A., Jacobs, R., Harris, H., 2024. The termite's guide to building a long-lasting home. In: Quick, L.J., Ntsondwa, A. (Eds.), *Proceedings of the XXIV Biennial Congress of the Southern African Society for Quaternary Research (SASQUA), Cango Valley*, South Africa, 19–24 May, 2024, pp. 41–42.

Avery, D.M., 2019. *A Fossil History of Southern African Land Mammals*. Cambridge University Press, Cambridge, UK.

Bateman, M.D., Carr, A.S., Dunajko, A.C., Holmes, P.J., Roberts, D.L., Mclaren, S.J., Bryant, R.J., *et al.* 2011. The evolution of coastal barrier systems: a case study of the middle–late Pleistocene Wilderness barriers, South Africa. *Quaternary Science Reviews* **30**, 63–81.

Bordy, E.M., Smith, R.M., Choiniere, J.N., Rubidge, B.S., 2023. Selected Karoo geoheritage sites of palaeontological significance in South Africa and Lesotho. *Geological Society, London, Special Publications* **543**, 431–446. https://doi.org/10.1144/SP543-2022-202.

Brooke, B., 2001, The distribution of carbonate eolianite. *Earth-Science Reviews* **55**, 35–164.

Cardonatto, M.C., Melchor, R.N., 2021. Environmental influence on burrow system features of a colonial and fossorial rodent. Implications for interpreting fossil tetrapod burrows. *Palaios* **36**, 225–245.

Cardonatto, M.C., Melchor, R.N., 2023. Neoichnology of armadillos: keys for the paleoecological and behavioral interpretation of fossil tetrapod burrows. *Palaios* **38**, 57–75.

Carr, A.S., Bateman, M.D., Roberts, D.L., Murray-Wallace, C.V., Jacobs, Z., Holmes, P.J., 2010. The last interglacial sea-level high stand on the southern Cape coastline of South Africa. *Quaternary Research* **73**, 351–363.

Carr, A.S., Bateman, M.D., Cawthra, H.C., Sealy, J., 2019, First evidence for onshore marine isotope stage 3 aeolianite formation on the southern Cape coastline of South Africa. *Marine Geology* **407**, 1–15.

Cawthra, H.C., Jacobs, Z., Compton, J.S., Fisher, E.C., Karkanas, P., Marean, C.W., 2018, Depositional and sea-level history from MIS 6 (Termination II) to MIS 3 on the southern continental shelf of South Africa. *Quaternary Science Reviews* **181**, 156–172.

Cleghorn, N., Potts, A.J., Cawthra, H.C., 2020. Preface to the Palaeo-Agulhas Plain Special Issue. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The

Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. *Quaternary Science Reviews* **235**, 2–6.

Deacon, H.J., Deacon, J., 1999. *Human Beginnings in South Africa: Uncovering the Secrets of the Stone Age*. David Philip Publishers, Cape Town.

Durand, N., Monger, H.C., Canti, M.G., Verrecchia, E.P., 2018. Calcium carbonate features. In: Stoops, G., Marcelino, V., Mees, F. (Eds.), *Interpretation of Micromorphological Features of Soils and Regoliths*, Second Edition. Elsevier, Amsterdam, pp. 205–258.

Fleming, K., Johnston, P., Zwartz, D., Yokoyama, Y., Lambeck, K., Chappell, J., 1998. Refining the eustatic sea-level curve since the Last Glacial Maximum using far- and intermediate-field sites. *Earth and Planetary Science Letters* **163**, 327–342.

Gutteridge, L., Liebenberg, L., 2021. *Mammals of Southern Africa and their Tracks and Signs*. Jacana Media, Johannesburg.

Helm, C.W., 2023. Pleistocene Vertebrate Trace Fossils from the Cape South Coast of South Africa: Inferences and Implications. Ph.D. thesis, Nelson Mandela University, Gqeberha, South Africa. http://hdl.handle.net/10948/60589.

Helm, C.W., Cawthra, H.C., Hattingh, R., Hattingh, S., McCrea, R.T., Thesen, G.H.H., 2019. Pleistocene trace fossils of Robberg Nature Reserve. *Palaeontologia Africana* **54**, 36–47.

Helm, C.W., Cawthra, H.C., De Vynck, J.C., Hattingh, R., Lockley, M.G., 2022. Possible Pleistocene hominin tracks from South Africa's west coast. *South African Journal of Science* **118**(1/2), 11842.

Helm, C.W., Lockley, M.G., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Rust, R., Stear, W. *et al.*, 2023a. Possible shod-hominin tracks on South Africa's Cape coast. *Ichnos* **30**, 79–97.

Helm, C.W., Bamford, M.K., Carr, A.C., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Quick, L.J. *et al.*, 2023b. Coprolites in cemented Pleistocene deposits on the Cape south coast of South Africa. *Journal of Coastal Research* **39**, 221–233.

Helm, C.W., Carr, A.S., Lockley, M.G., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Stear, W., 2023c. Dating the Pleistocene hominin ichnosites on South Africa's Cape south coast. *Ichnos* **30**, 49–68.

Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Lockley, M.G., Stear, W. *et al.*, 2023d. Large Pleistocene tortoise tracks on the Cape south coast of South Africa. *Quaternary Research* **112**, 93–110.

Helm, C.W., Paterson, A., Rust, R., 2024a. The first known painting of the African rail? *Rock Art Research* **41**, 146–154.

Helm, C.W., Carr, A.S., Cawthra, H.C., De Vynck, J.C., 2024b. Late Pleistocene vertebrate trace fossils of the Walker Bay Nature Reserve. *Palaeontologia Africana* **58**, 37–52. https://hdl.handle.net/10539/42923.

Hembree, D.I., Martin, L.D., Hasiotis, S.T., 2004. Amphibian burrows and ephemeral ponds of the lower Permian Speiser Shale, Kansas: evidence for seasonality in the midcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology* **203**, 127–152.

Hendey, Q.B., 1981. Palaeoecology of the late Tertiary fossil occurrences in 'E' Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum* **84**, 1–104.

Hunt, R.M.J., Xiang-Xu, X.U.E., Kaufman, J., 1983. Miocene burrows of extinct bear dogs: indication of early denning behavior of large mammalian carnivores. *Science* **221**, 364–366.

Jacobs, Z., Jones, B.G., Cawthra, H.C., Henshilwood, C.S., Roberts, R.G., 2020. The chronological, sedimentary and environmental context for the archaeological deposits at Blombos Cave, South Africa. In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. *Quaternary Science Reviews* **235**, 105850. https://doi.org/10.1016/j.quascirev.2019.07.032.

Kinlaw, A., 1999. A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments* **41**, 127–145.

Klappa, C.F., 1980. Rhizoliths in terrestrial carbonates: classification, recognition, genesis and significance. *Sedimentology* **27**, 613–629.

Klein, R.G., 1972. The Late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and environmental and cultural change. *Quaternary Research* **2**, 135–142.

Klein, R.G., 1976. The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. *South African Archaeological Bulletin* **31**, 75–98.

Klein, R.G., Cruz-Uribe, K., 1987. Large mammal and tortoise bones from Elands Bay Cave and nearby sites, Western Cape Province, South Africa. In: Parkington, J., Hall, M. (Eds.), *Papers in the Prehistory of the Western Cape, South Africa*. Archaeopress, Oxford, UK, pp. 132–163.

Klein, R.G., Cruz-Uribe, K., 2000. Middle and later Stone Age large mammal and tortoise remains from Die Kelders Cave 1, Western Cape Province, South Africa. *Journal of Human Evolution* **38**, 169–195.

Klein, R.G., Avery, G., Cruz-Uribe, K., Steele, T.E., 2007. The mammalian fauna associated with an archaic hominin skullcap and later Acheulean artifacts at Elandsfontein, Western Cape Province, South Africa. *Journal of Human Evolution* **52**, 164–186.

Latrobe, C.I., 1818. *Journal of a Visit to South Africa in 1815, and 1816*. L.B. Seely, London.

Lehmann, T., 2009. Phylogeny and systematics of the Orycteropodidae (Mammalia, Tubulidentata). *Zoological Journal of the Linnean Society* **155**, 649–702.

Le Roux, F.G., 1989. *Lithostratigraphy of the Nahoon Formation (Algoa Group)*. South African Committee for Stratigraphy (SACS), Lithostratigraphic Series 9. Department of Mineral and Energy Affairs, Pretoria, South Africa.

Lewis-Williams, D., Challis, S., 2011. *Deciphering Ancient Minds: The Mystery of San Bushman Rock Art*. Thames and Hudson, London.

Liebenberg, L., 2000. *A Photographic Guide to Tracks and Tracking in Southern Africa*. Struik Publishers, Cape Town.

Lockley, M.G., Helm, C.W., Cawthra, H.C., De Vynck, J.C., Perrin, M.R., 2021. Pleistocene golden mole and 'sand-swimming' trace fossils from the Cape coast of South Africa. *Quaternary Research* **101**, 169–186.

Lockley, M.G., Helm, C.W., Cawthra, H.C., De Vynck, J.C., Dixon, M.G., Venter, J.A., 2022. Pleistocene small-mammal and arthropod trackways from the Cape south coast of South Africa. *Quaternary Research* **107**, 178–192.

Lopes, R.P., Frank, H.T., Buchmann, F.S.deC, Caron, F., 2017. *Megaichnus* igen. nov.: giant paleoburrows attributed to extinct Cenozoic mammals from South America. *Ichnos* **24**, 133–145.

Lucas, S.G., Gobetz, K.E., Odier, G.P., McCormick, T., Egan, C., 2006. Tetrapod burrows from the Lower Jurassic Navajo Sandstone, southeast Utah. *New Mexico Museum of Natural History and Science Bulletin* **37**, 147–154.

Malan, J.A., 1989. *Lithostratigraphy of the Waenhuiskrans Formation (Bredasdorp Group)*. South African Committee for Stratigraphy (SACS), Lithostratigraphic Series 9. Department of Mineral and Energy Affairs, Pretoria, South Africa

Marean, C.W., Cawthra, H.C., Cowling, R.M., Esler, K.J., Fisher, E., Milewski, A., Potts, A.J. *et al.*, 2014. Stone Age people in a changing South African Greater Cape Floristic region. In: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region*. Oxford University Press, Oxford, UK, pp. 164–199.

Matthews, N.A., Noble, T.A., Breithaupt, B.H., 2016. Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), *Dinosaur Tracks: The Next Steps*. Indiana University Press, Bloomington, Indiana, pp. 28–55.

Matthews, T., Marean, C.W., Cleghorn, N., 2020. Past and present distributions and community evolution of Muridae and Soricidae from MIS 9 to MIS 1 on the edge of the Palaeo-Agulhas Plain (south coast, South Africa). In: Cleghorn, N., Potts, A.J., Cawthra, H.C. (Eds.), The Palaeo-Agulhas Plain: A Lost World and Extinct Ecosystem. *Quaternary Science Reviews* **235**, 105774. https://doi.org/10.1016/j.quascirev.2019.05.026.

McDonough, C.M., DeLaney, M.A., Le, P.Q., Blackmore, M.S., Loughry, W.J., 2000. Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America. *Revista de BioIogía Tropical* **48**, 109–120.

Melchor, R.N., Cardonatto, M.C., In press. Vertebrate burrows. In: Lucas, S.G., Klein, H., Hunt, A.P. (Eds.), *Vertebrate Ichnology*. Elsevier.

Melton, D.A., 1976. The biology of aardvark (Tubulidentata-Orycteropodidae). *Mammal Review* **6**, 75–88.

Möller, L.A., 2017. *Of the Same Breath: Indigenous Animal and Place Names*. Sun Media, Bloemfontein, South Africa.

Muir, R.A., Abrahams, M., Hadebe, G., 2024. Geomorphologic, stratigraphic, and temporal context of middle Pleistocene termitaria near Calitzdorp, South Africa. In: Quick, L.J., Ntsondwa, A. (Eds.), *Proceedings of the XXIV Biennial Congress of the Southern African Society for Quaternary Research (SASQUA), Cango Valley*, South Africa, 19–24 May, 2024. p. 41.

Patterson, B., 1975. The fossil aardvarks (Mammalia: Tubulidentata). *Bulletin of the Museum of Comparative Zoology* **147**, 185–237.

Pickford, M., 1996. Tubulidentata (Mammalia) from the middle and upper Miocene of southern Namibia. *Comptes Rendus de l' Académie des Sciences de Paris, Sciences de la Terre et des Planètes* **322**, 805–810.

Pickford, M., 2003. Minute species of *Orycteropus* from the early Middle Miocene at Arrisdrift, Namibia. *Memoirs of the Geological Survey of Namibia* **19**, 195–198.

Pickford, M., 2005. *Orycteropus* (Tubulidentata, Mammalia) from Langebaanweg and Baard's Quarry, Early Pliocene of South Africa. *Comptes Rendus Paléovol* **4**, 715–726.

Pickford, M., 2008. Tubulidentata from the northern Sperrgebiet, Namibia. *Memoirs of the Geological Survey of Namibia* **20**, 311–313.

Pickford, M., 2018. Piping, a geomorphological process relevant to African palaeontology and archaeology: sedimentary, taphonomic and biostratigraphic implications. *Communications of the Geological Survey of Namibia* **20**, 59–86.

Pickford, M., 2019. Orycteropodidae (Tubulidentata, Mammalia) from the Early Miocene of Napak, Uganda. *Münchner Geowissenschaftliche Abhandlungen* **47**, 1–101.

Pickford, M., Mocke, H., Ségalen, L., Senut, B., 2016. Update of the Pliocene fauna of the Ekuma Valley, Etosha, Namibia. *Communications of the Geological Survey of Namibia* **17**, 115–144.

Roberts, D.L., Bateman, M.D., Murray-Wallace, C.V., Carr, A.S., Holmes, P.J., 2008. Last Interglacial fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **257**, 261–279.

Roberts, D.L., Karkanas, P., Jacobs, Z., Marean, C.W., Roberts, R.G., 2012. Melting ice sheets 400,000 yr ago raised sea level by 13 m: past analogue for future trends. *Earth and Planetary Science Letters* **357–358**, 226–237.

Roberts, D.L., Cawthra, H.C., Musekiwa, C., 2013. Dynamics of late Cenozoic aeolian deposition along the South African coast: a record of evolving climate and ecosystems. In: Martini, I.P., Wanless, H.R. (Eds.), *Sedimentary Coastal Zones from High to Low Latitudes: Similarities and Differences*. Special Publication of the Geological Society of London **388**, 353–387.

Rust, R., 2012. *Water, Stone and Legend: Rock Art of the Klein Karoo*. Struik Travel and Heritage, Cape Town.

Seilacher, A., 1964. Sedimentological classification and nomenclature of trace fossils. *Sedimentology* **3**, 253–256.

Shoshani, J., Goldman, C.A., Thewissen, J.G.M., 1988. *Orycteropus afer*. *Mammalian Species* **300**, 1–8. https://doi.org/10.2307/3503996.

Skead, C.J., 1987. *Historical Mammal Incidence in the Cape Province Vol. I. Western Cape and Northern Cape. Vol. II. Eastern Cape, Ciskei and Transkei*. Chief Directorate, Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, Cape Town.

Spratt, R.M., Lisiecki, L.E., 2016. A late Pleistocene sea level stack. *Climate of the Past* **12**, 1079–1092.

Stuart, C., Stuart, T., 2019. *A Field Guide to the Tracks and Signs of Southern and East African Wildlife*. Struik Nature, Cape Town.

van den Heever, A., Mhlongo, R., Benadie, K., 2017. *Tracker Manual – a Practical Guide to Animal Tracking in Southern Africa*. Struik Nature, Cape Town.

van Tonder, M., Cawthra, H.C., de Vynck, J.C., 2024. The ichnology, archeology and geology of Pleistocene sequences in the Woody Cape Nature Reserve, Eastern Cape, South Africa. In: Quick, L.J., Ntsondwa, A. (Eds.), *Proceedings of the XXIV Biennial Congress of the Southern African Society for Quaternary Research (SASQUA)*, Cango Valley, South Africa, 19–24 May, 2024. p. 50.

Walker, C., 2018. *Signs of the Wild: A Field Guide to the Spoor & Signs of the Mammals of Southern Africa*. Struik Nature, Cape Town.