Pleistocene rhinoceros tracks from the Cape coast of South Africa

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Abstract
Ichnological sites have the potential to corroborate and complement the traditional body fossil record. Seven Pleistocene tracksites, attributed with varying degrees of confidence to rhinoceros trackmakers, have been identified on aeolianite surfaces on South Africa's Cape south coast. Thus far only one track has been assigned to a trackmaker species. In combination, these sites appear to provide the only reported fossil rhinoceros tracks from the middle and late Pleistocene. They thus form an important part of the global record.

Résumé
Les sites ichnologiques représentent des ressources à même de corroborer et d'enrichir les archives fossiles traditionnelles. Sept sites à empreintes datant du pléistocène, que l'on attribue, avec plus ou moins de certitude, à des rhinocéros, ont été identifiés sur des surfaces d'éolianite situées sur la côte sud du Cap, en Afrique du Sud. Jusqu'à présent, l'appartenance à une espèce n'a été confirmée que pour l'une de ces empreintes. Ces sites seraient les seules zones connues à disposer de traces de fossiles de rhinocéros datant du pléistocène moyen et supérieur. Ils constituent par conséquent une part importante des archives mondiales.

Introduction
The origins of rhinocerotoids can be traced though the body fossil record at least to the Eocene; the Family Rhinocerotidae includes five extant species and many extinct species (Prothero 1993, but see below for Oligocene records). Two species occur today in southern Africa, the black rhinoceros (*Diceros bicornis*) and the white rhinoceros (*Ceratotherium simum*). In southern Africa the rhinoceros body fossil record extends back to the Miocene (Avery 2019). The southern African Pleistocene rhinoceros body fossil record has been reviewed by Badenhorst et al. (2021).

The ichnology (trace fossil) record has the potential to complement the traditional body fossil record. There have been brief descriptions of Pleistocene rhinoceros tracks from South Africa's Cape south coast, as detailed below. At a global level, there are many such reports, and in 1965 Vyalov coined the term *Rhinoceripeda tasnadyi* for tracks from the lower Miocene (Lucas 2007). The first report of preserved rhinoceros tracks might be from southern Africa: Wilmer (1893) reported Holocene tracks of elephant and rhinoceros in the Walvis Bay area in what is now Namibia. The oldest track attributed to *Rhinoceripeda* appears to be from the Oligocene of France (Costeur et al. 2009). The record includes a Miocene example of ichnopathology (Belvedere et al.

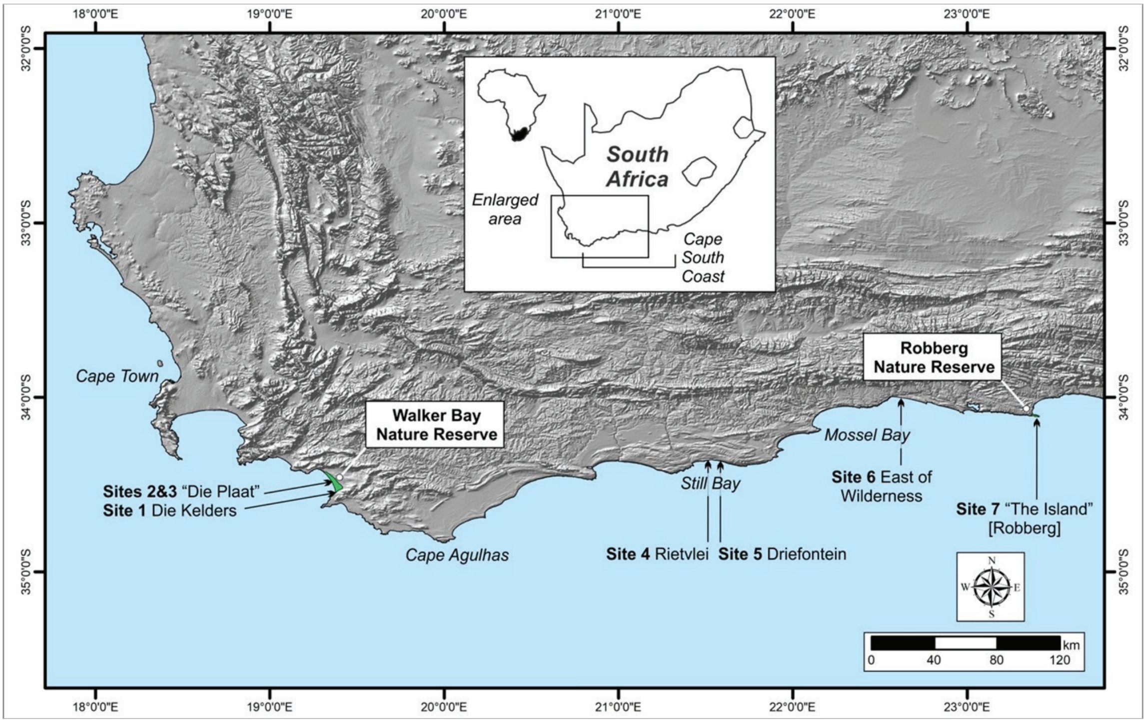

Figure 1. Map of South Africa's south Cape coast, showing the sites mentioned in the text.

2025). The African record includes the Pliocene site of Laetoli in Tanzania (Musiba et al. 2008) and the early Pleistocene site of Ileret in Kenya (Roach et al. 2016; 2018). A middle Pleistocene track assemblage at Swanscombe in the United Kingdom contains 'probable' rhinoceros tracks (Sutcliffe 1985; Davis 1996).

Through the Cape South Coast Ichnology Project, more than 350 vertebrate Pleistocene tracksites have been identified along 350 km of South African coastline (Helm 2023). The sites containing tracks attributed to rhinoceros trackmakers are described here (Fig. 1). All occur in aeolianites (cemented dunes) of the Waenhuiskrans Formation. Sites were measured and photographed, including for photogrammetric analysis where appropriate (Matthews et al. 2016). 3D models were generated with Agisoft MetaShape Professional (v. 1.0.4) using an Olympus TG-5 camera (focal length 4.5 mm; resolution 4000 x 3000; pixel size 1.56 x 1.56 um). The final images were rendered using CloudCompare (v.2.10-beta). Locality information is reposited in the African Centre for Coastal Palaeoscience, to be made available to researchers upon request.

Rhinoceros track morphology

Well-preserved extant rhinoceros tracks, exhibiting high anatomical fidelity, are readily identifiable through a combination of track size and tridactyl form with distinctive digit impressions, and are identifiable to species level (Liebenberg 2000; Stuart and Stuart 2019; Van den Heever et al. 2024). When tracks of the black rhinoceros (*Diceros bicornis*) and the white rhinoceros (*Ceratotherium simum*) are compared, those of the black rhinoceros are slightly smaller, the medial and lateral digit impressions are relatively smaller, and the lateral digit impression has a relatively more posterior location. In addition, the indentation in the posterior margin is relatively less in black rhinoceros tracks (Liebenberg 2000; Stuart and Stuart 2019; Van den Heever et al. 2024).

A caveat exists if the tracks were registered in a soft, unconsolidated sandy substrate, as the two central digit impressions of a hippopotamus (*Hippopotamus amphibius*) track may appear to fuse, in which case a tridactyl track pattern resembling that of a rhinoceros track might result (Van den Heever et al. 2024). In addition, confusion may exist between juvenile elephant tracks and poorly-preserved rhinoceros tracks that do not display obvious digit impressions. Figure 2 illustrates

Figure 2. (a) A track of a white rhinoceros; scale bar = 18.5 cm; (b) a track of a black rhinoceros; scale bar = 18.5 cm; (c) a well-preserved hippopotamus track. (d) A hippopotamus track registered in a sandy substrate, in which the two central digit impressions are partially fused, causing it to resemble a rhinoceros track. © Alex Van den Heever.

typical tracks of black rhinoceros, white rhinoceros and hippopotamus, as well as a track in which the central digit impressions in a hippopotamus track partially fuse and thus create confusion.

Sites attributed to rhinoceros trackmakers on the Cape coast

Seven possible rhinoceros tracksites have been identified. They are described here from the perspective of traversing the coastline from west to east. In each case, our estimate of the likelihood of a rhinoceros trackmaker is expressed.

Site 1

On the coastline north of Die Kelders in the Walker Bay Nature Reserve, a single track with maximum length of 23 cm and maximum width of 19 cm exhibited tridactyl morphology (Helm et al. 2024—their Site 23, fig. 9C). It was located on a loose slab on the beach. Favouring the interpretation of a rhinoceros track were the apparently bifid heel outline and plausible impressions of the medial and lateral digits. However, the central digit impression appeared less rounded than expected, and 'off-centre' (Fig. 3). We view this as a probable, but not definite, rhinoceros track.

Figure 3. The single Site 1 probable rhinoceros track; scale bar = 10 cm.

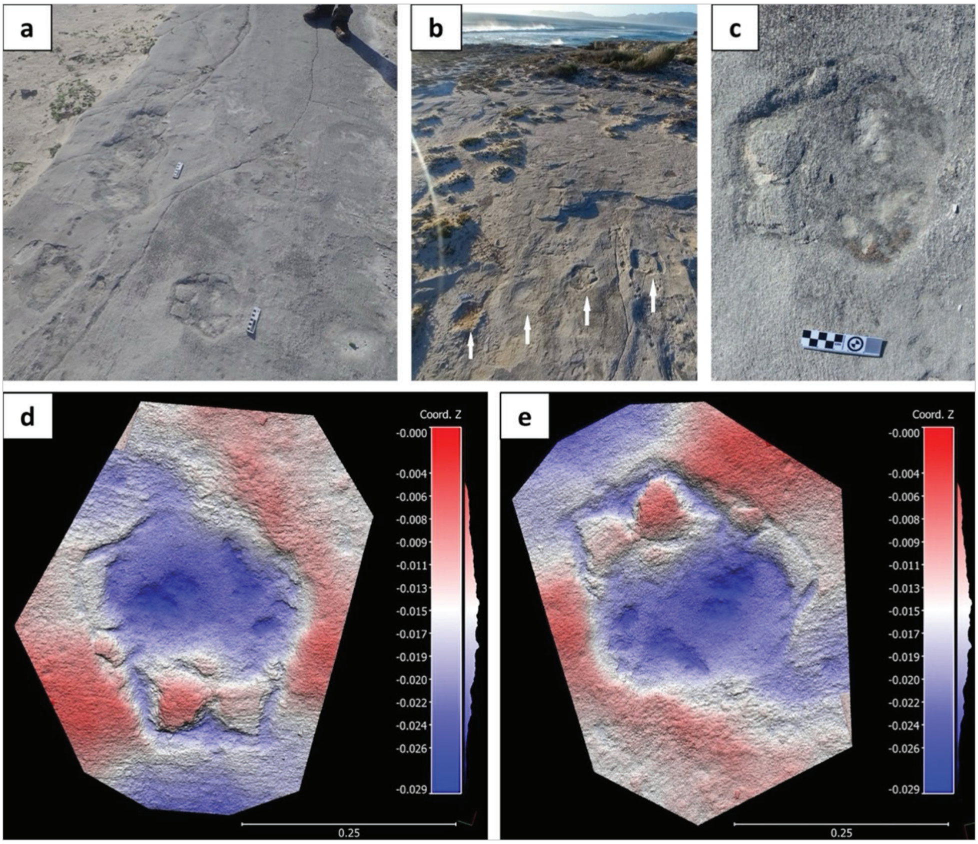

Figure 4. (a) When first examined, a trackway was not obvious; scale bars = 10 cm. (b) Late-afternoon sunlight allowed the trackway to be visualised; the tracks are indicated by arrows. (c) The best-preserved track at Site 2; scale bar = 10 cm. (d) 3D model of the best-preserved track at Site 2, with north-south orientation. (e) 3D model of the track shown in (c) and (d) Here with a south-north orientation. Horizontal and vertical scales are in metres. Both a rhinoceros and a hippopotamus could have made the tracks, making either option equally possible.

Site 2

Site 2 was reported as a possible hippopotamus tracksite (Helm et al. 2024 – their Site 17, fig. 7D). It was reanalysed by members of our research team (now including San Master Trackers) in 2025 under different lighting conditions, following removal of surrounding sand and vegetation to expose a larger track-bearing area. These efforts resulted in the identification of a trackway comprising at least four large, evenly spaced tracks (Fig. 4b). The north-south axis of the trackway could be determined, but no clues (e.g., displacement rims) were present that might indicate the direction of travel. Other tracks of similar size were present in the immediate vicinity. Maximum length of the best-preserved track was 27 cm, and maximum width was also 27 cm (Fig. 4c). Depending on the inferred direction of travel (from north to south or from south to north), it either exhibited a bifid heel impression and a typical 'cloverleaf' pattern suggestive of a rhinoceros trackmaker (Fig. 4d), or possible tetradactyl morphology suggestive of a hippopotamus trackmaker (Fig. 4e). A consistent pace length of 67 cm was measured. We consider the two possibilities to be equally plausible.

The Site 2 tracks were preserved in epirelief, in situ, on 'Die Plaat', a relatively level series of aeolianite palaeosurfaces located just inland of the coast. While Die Plaat contains genuine tracks, it presents challenges. In many areas it is encrusted with calcrete, which may be hard to distinguish from aeolianite. Furthermore, rounded or oval depressions that form in calcrete may resemble vertebrate tracks. Caution is advised, and long trackways provide one indication that pseudotracks are not being visualised, following the 'ten paleoichnological commandments' of Sarjeant (1989).

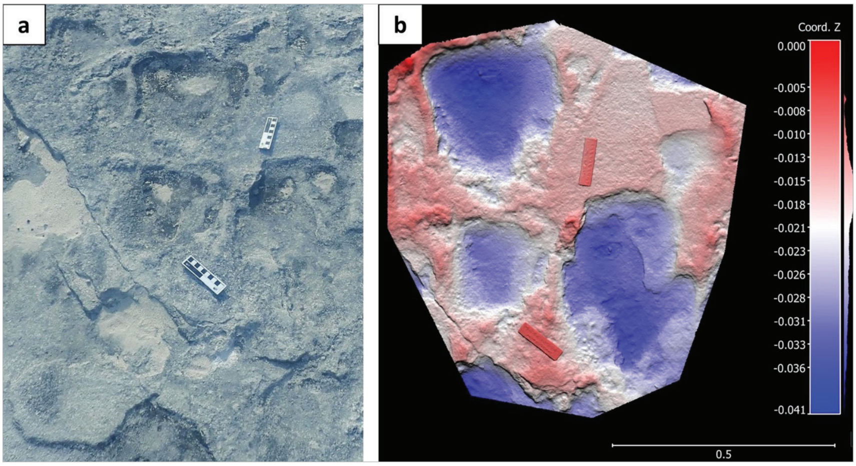

Figure 5. (a) These are purported rhinoceros tracks at Site 3; scale bars = 10 cm. (b) 3D model of the Site 3 tracks—the middle track is seen in (a) Horizontal and vertical scales are in metres.

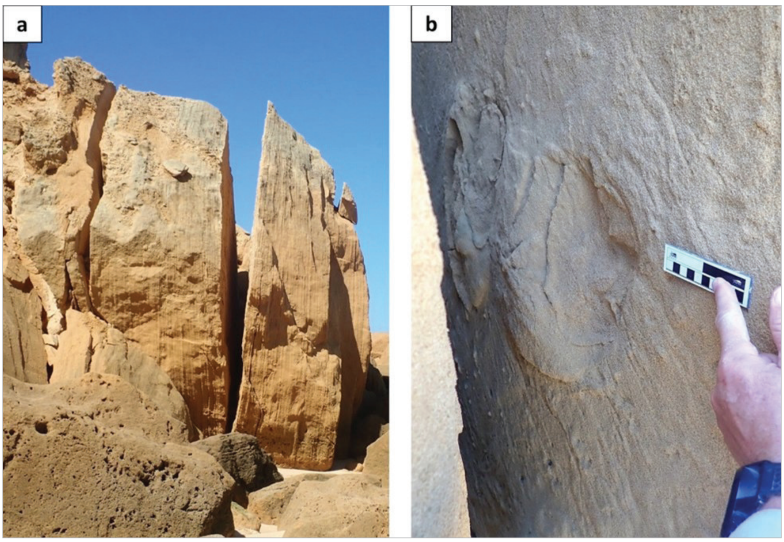

Figure 6. (a) The large, split fallen block at Site 4. (b) One of the tracks in the gap in the split rock at Site 4; scale bar = 10 cm.

Site 3

Site 3 is also situated on Die Plaat in the Walker Bay Nature Reserve, as reported in Helm et al. (2024— their Site 3, figs 2D and 2E). Several large depressions, 30–40 cm in length, occurred in a linear pattern beside and on a 4WD track (Fig. 5). While the quality of preservation was poor, irregularities in their outlines were detectable, and we consider a rhinoceros origin likely.

Site 4

In the Rietvlei area, east of Still Bay, a large block has fallen from overlying cliffs and come to rest at the upper end of the beach (Helm 2023). It has split down its centre along a bedding plane (Fig. 6a). Peering into the resulting narrow gap, six large tracks are evident, preserved in epirelief on one side and in hyporelief on the other. Because the gap is so small, the tracks cannot be viewed adequately, but measure ~20 cm x 16 cm in maximum dimensions, with digit impressions and natural casts evident (Fig. 6b). Although a rhinoceros origin is consistent with the findings, a confident identification is currently not possible.

Figure 7. The single Site 6 track; scale bars = 10 cm.

Site 5

Further east, in the Driefontein area, a single track was attributed to a possible rhinoceros trackmaker, although the 'heel' portion appeared deeper and longer than expected (Helm et al. 2020). Unless this is a composite track, the probability of a rhinoceros origin is relatively low. The track was of interest because the rock surface was thought also to contain tracks of elephant (*Loxodonta africana*), the extinct long-horned buffalo (Syncerus antiquus) and the extinct giant Cape zebra (*Equus capensis*). Maximum length of 24 cm and maximum width of 20 cm were recorded (Fig. 7).

Site 6

East of Wilderness, two trackways, containing a total of twelve tracks, were noted in situ in epirelief (Helm 2023). Maximum length of ~24 cm, maximum width of ~20 cm, and pace length of 65–70 cm were recorded (Fig. 8). The tracks would have been registered in soft sand, with a resulting lack of morphological detail. This makes it impossible to confidently attribute the tracks to family level, although the trackmaker was probably a rhinoceros or hippopotamus. Subsequent visits to the site aimed at performing photogrammetric analysis were unsuccessful, as the area was covered by metres-deep beach sand.

Site 7

Trackways preserved in hyporelief on the ceiling of a tunnel on The Island in the Robberg Nature Reserve provide the best example of rhinoceros tracks reported until now from the Cape coast (Helm et al. 2019). The tracks occur in hyporelief on a truncation surface and are only accessible during very low tides. The tracks are being eroded by wave action. Two rhinoceros trackways are present, with a total of at least six tracks (Fig. 9). Mean track length of 23.4 cm and mean track width of 23.2 cm were recorded. One track in particular (the middle track in Figure 9b) exhibited the track morphology of a rhinoceros, probably a black rhinoceros: the lateral digit impression was relatively small and was located relatively far from the central digit impression (Liebenberg 2000; Stuart and Stuart 2019; Van den Heever et al. 2024). In one case, a track pointed in the opposite direction, indicating a trail that had been used in two directions.

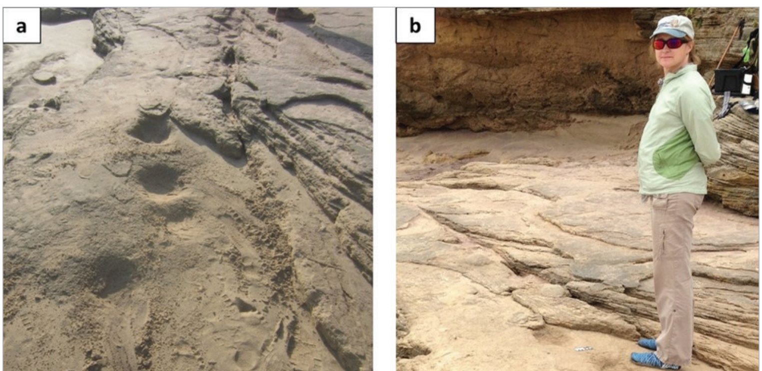

Figure 8. One of the Site 6 trackways; a person is included, for scale.

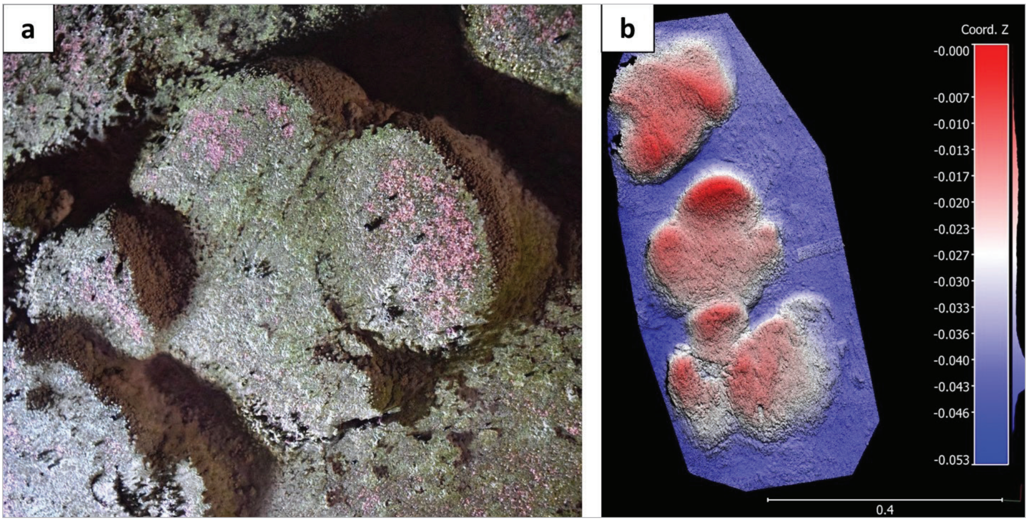

Figure 9. (a): The best-preserved track at Site 7—direction of travel is from left to right. (b) 3D model of one of the Site 7 trackways—the middle track is seen in; (a) and is attributed to a rhinoceros trackmaker, probably a black rhinoceros; horizontal and vertical scales are in metres.

Discussion and Conclusions

In the abovementioned examples, the trackways at Site 7 are confidently attributed to a rhinoceros trackmaker. Tracks at the other sites are interpreted as possible or probable rhinoceros tracks with varying levels of confidence or illustrate the confusion that can arise between rhinoceros- and hippopotamus tracks. We suggest that all reported rhinoceros tracks from Africa Musiba et al. 2008; Roach et al. 2016; 2018) be subjected to scrutiny to ensure that the possibility of a hippopotamus trackmaker has been excluded.

Site 1 and Site 5 only contain single tracks, whereas a trackway clearly provides more morphological clues. Time will tell whether the tracks at Site 4 were registered by a rhinoceros when the split in the large block opens up. The tracks would all have been registered in unconsolidated dune sand, a substrate that may contribute to less-than-optimal morphological preservation. The relatively coarse-grained size of dune sand may be another contributing factor, as fine-grained substrates typically allow for the preservation of finer track detail.

Distinguishing between the tracks of the two rhinoceros species presents more of a challenge. Enough evidence is present at Site 7 to suggest a black rhinoceros trackmaker, but identification to species level is not possible at the other sites.

The black rhinoceros was historically more common than the white rhinoceros in the south-western Cape and has been recorded more often in the Pleistocene body fossil record (Avery 2019; Badenhorst et al. 2021). Distinguishing between tracks of these two species has paleoecological implications, given their different feeding niches (Skinner and Chimimba 2005).

Sites 1, 2 and 3 all occur within the Walker Bay Nature Reserve. These three sites lie close to the archaeological site of Die Kelders 1 Cave (Klipgat Cave). Klein and Cruz-Uribe (2000) recorded the remains of black rhinoceros in the cave, as well as many rhinoceros bones that could not be identified to species level. This site has yielded the majority of Pleistocene rhinoceros remains from the coastal Western Cape and Eastern Cape (Badenhorst et al. 2021). As the database of rhinoceros tracksites from the Cape south coast expands, it may be possible to identify the trackmaker to species level in more cases, and thus corroborate or complement the body fossil record.

Dating through optically stimulated luminescence (OSL) suggests that the Walker Bay Nature Reserve sites are close to 76 ± 5 ka in age (Helm et al. 2024). Sites 4 and 5 lie within kilometres of a section dated through OSL to an age range of 140 ± 8 ka and 91 ± 4.6 ka (Roberts et al. 2008). Deposits in the general region of Site 6 have been dated to 131 ± 7 ka and 133 ka ± 7 ka (Bateman et al. 2011). Dating samples obtained adjacent to Site 7 yielded an age range of 56 ± 5 ka to 43 ± 4 ka (Helm et al. 2019).

The tracksites thus appear to date to a range between marine isotope stage (MIS) 6 and MIS 3. They appear to be the only rhinoceros tracksites thus far reported from the late Pleistocene. As such, they form an important part of the global rhinoceros palaeontological record.

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