

The Duntulm sauropod tracksite and environmental partitioning in Middle Jurassic dinosaurs on the Isle of Skye, Scotland

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Typescript received 20 September 2024; accepted in revised form 17 July 2026

Abstract: Dinosaur fossils from the Isle of Skye (Scotland, UK), particularly the abundant trace fossil record, provide a window into dinosaur evolution during the poorly known Middle Jurassic. Here we present a comprehensive description of the Duntulm tracksite from Cairidh Ghluimaig Bay, using aerial photography to provide whole site maps, catalogue the tracks, and identify trackways. The tracksite is located in rocks deposited in a shallow lagoonal environment and is dominated by small- to medium-sized (<75 cm) sauropod footprints spanning several preservation styles, from casts with details of toes to impressions with less distinct features. Several short, narrow-gauge trackways indicate that the sauropods were moving with a walking gait and the wide range of orientations of the trackways does not indicate any

gregarious behaviour. Sparse, isolated theropod footprints are also present along the Duntulm coastline. The abundance of sauropod footprints at this locality prompts an examination of the substrate preferences of Skye's dinosaurs. We surveyed all currently known dinosaur tracks from the island and statistically analysed the relationship of trackmaker with substrate. This analysis indicates that Skye's sauropods had a preference for lagoonal substrates whereas 'non-sauropod' dinosaurs (theropods, thyreophorans and ornithopods) are more abundant in subaerially exposed mudflats. We argue that this signal is robust, but this pattern can be further tested as more footprints are discovered on Skye.

Key words: dinosaur, footprint, Isle of Skye, sauropod.

DINOSAUR fossils are rare in Scotland. In 1995, Scottish-born palaeontologists Michael Benton and Neil Clark published two papers describing the first dinosaur bones from Scotland (Benton *et al.* 1995; Clark *et al.* 1995). Both the partial tibia of an Early Jurassic theropod (Benton *et al.* 1995) and the partial limb bone of a Middle Jurassic sauropod (Clark *et al.* 1995) came from the Isle of Skye. These body fossils complemented the island's emerging trace fossils record. Some of the island's dinosaur footprints were initially discovered by a Skye native, Dugald Ross, in the 1960s and a footprint first entered the scientific literature in the 1980s (Andrews

& Hudson 1984). Together, these body and trace fossils hinted that the Early–Middle Jurassic rocks of Skye would be fruitful for investigating dinosaur evolution during this time, a poorly sampled interval that was pivotal for the diversification of sauropods, theropods and thyreophorans (Serenó 1999; Weishampel *et al.* 2004; Benson *et al.* 2014; Benson 2018; Raven *et al.* 2023).

Over the past several decades, further fieldwork and research have elucidated the Jurassic faunas of Skye. In particular, Middle Jurassic rocks from the island preserve fossils from a diverse fauna, including salamanders, turtles, frogs, lizards, choristoderes, crocodilians, pterosaurs, tritylodonts and docodonts (Waldman & Savage 1972; Evans & Waldman 1996; Evans *et al.* 2006; Anquetin *et al.* 2009; Wills *et al.* 2014; Young *et al.* 2016; Panciroli

[†]Died 28 October 2025.

et al. 2017, 2019, 2020, 2022, 2024; Yi *et al.* 2017; Kean *et al.* 2021; Jagielska *et al.* 2022, 2023; Jones *et al.* 2022; Tałanda *et al.* 2022; Martin-Silverstone *et al.* 2023). Additionally, although the record remains sparse, the bones and teeth of sauropods and theropods (Clark *et al.* 1995; Liston 2004; Barrett 2006; Wills *et al.* 2014; Brusatte & Clark 2015; Clark & Gavin 2016; Young *et al.* 2019) and a fragmentary thyreophoran radius and ulna (Clark 2001) provide evidence for multiple clades of dinosaurs in the ecosystem. Skye's terrestrial vertebrate record is complemented by marine vertebrate fossils including ichthyosaurs, plesiosaurs, shark teeth and spines, and fish otoliths (Clark *et al.* 1993; Evans *et al.* 2006; Brusatte *et al.* 2015; Schwarzhans & Wakefield 2024).

Most of our knowledge of Skye's dinosaurs comes not from their bones, but from a burgeoning trace fossil record in the Great Estuarine Group: a paralic sequence of fluvio-deltaic and lagoonal deposits (Harris & Hudson 1980). Dinosaur footprints have been found both *ex situ* in loose blocks (Andrews & Hudson 1984; Clark & Barco Rodríguez 1998; Clark & Gavin 2016) and *in situ* on intertidal platforms (Clark *et al.* 2004, 2005; Marshall 2005; Brusatte *et al.* 2016; dePolo *et al.* 2018, 2020). These footprints can be attributed to sauropod (e.g. Brusatte *et al.* 2016), theropod (e.g. Clark *et al.* 2004), thyreophoran and putative ornithopod (dePolo *et al.* 2020) trackmakers and indicate that Skye was home to a diverse Middle Jurassic dinosaur community.

Footprints hold special value in understanding the ecology and environmental preferences of dinosaurs because, as sedimentary structures, they are intrinsically linked to their depositional environments (Lockley 1986). Unlike body fossils, which can be transported great distances away from the ecosystems where the animals were living, dinosaur footprints always preserve information about the environments inhabited (Thulborn 1990; Lockley & Meyer 2000). As such, footprints can provide fine-scale information about potential spatial partitioning between different dinosaurs in an ecosystem (e.g. Carvalho 2004).

Here, we present a comprehensive description of the largest known *in situ* dinosaur tracksite on Skye: Scotland's 'Dinosaur Disco', a sauropod-dominated tracksite on the coast below Duntulm Castle. An announcement and brief description was previously published (Brusatte *et al.* 2016), but lacked elements such as a site map to catalogue all of the tracks and group them into trackways. In the decade since its discovery, the Duntulm site has become a popular location for both tourists and student trips, hence the addition of more detailed information to the literature is desirable. Our current study builds upon the previous work and presents descriptive elements such as site maps and quantitative trackway parameters. Although the bulk of this descriptive work focuses upon

the main track-bearing platform, dinosaur footprints have also been found on other sedimentary horizons at this locality (Brusatte *et al.* 2016) and are touched upon here in brief. We then survey the dinosaur footprint record of the Isle of Skye, including several tracksites reported since the 2015 discovery of this site, to place Duntulm into a broader context and reflect on its implications for dinosaur ecology.

GEOLOGICAL SETTING

The Great Estuarine Group is a package of sedimentary rocks from paralic environments deposited in the Hebrides Basin from the latest Bajocian to Bathonian Stages of the Middle Jurassic (Harris & Hudson 1980). The Duntulm tracksite is found in the type section of the Duntulm Formation on the foreshore of Cairidh Ghlu-maig Bay on the Isle of Skye (*an t-Eilean Sgitheanach*) immediately to the south of the ruins of Duntulm Castle (Fig. 1). The Duntulm Formation (Great Estuarine Group, Inner Hebrides) is characterized by beds of oyster shells in a limestone matrix that are interbedded with thin beds of shale and sandstone (Harris & Hudson 1980). As a result, the Duntulm Formation is inferred to be

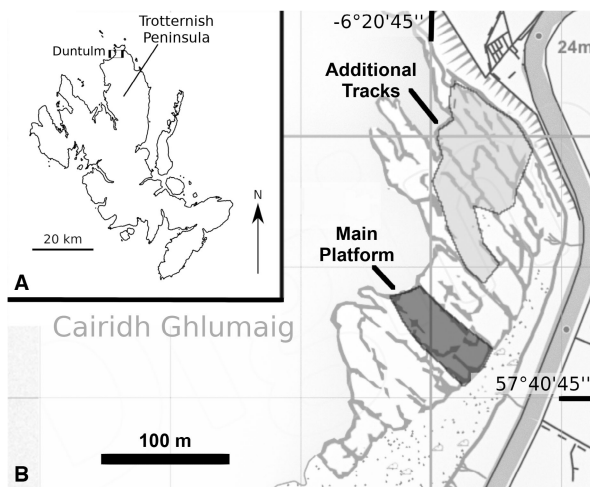


FIG. 1. Geographical location of the Duntulm tracksite on: A, the Isle of Skye; B, an Ordnance Survey basemap. The main track platform is shown in dark grey while the locations of additional track-bearing layers are light grey. Duntulm Castle is located immediately off the map view to the north and the road adjacent to the site is the A855. The vertical grid lines are oriented along the central meridian of the British National Grid (not strictly geographic north–south) but can be used as reasonable proxies for the north arrow at this location. Map generated in Edina Digimap © Crown copyright and database rights, 2017, Ordnance Survey (Digimap Licence) for educational use.

composed primarily of sediments from marine to brackish coastal lagoons (Andrews & Walton 1990).

The main track-bearing platform is composed of beds 34 and 35 of the Duntulm Formation (Brusatte *et al.* 2016; numbering system from Andrews & Walton 1990). These beds present two lithologies: bed 34 is a sandy limestone that preserves an oyster (*Praexogyra hebridica*) shell bank, and bed 35 is a hard calcareous sandstone that is resistant to weathering (Cox & Sumbler 2002; Brusatte *et al.* 2016).

Bed 34 belongs to Lithofacies 1 as defined by Andrews & Walton (1990) and its monotypic oyster shell banks are considered characteristic of the Duntulm Formation. Although the oyster shells show a strong orientation fabric (Fig. 2), they tend not to be in life position and, instead, lie in horizontal to sub-horizontal layers (Andrews & Walton 1990). The persistent articulation of the oysters and the presence of a fine-grained micritic matrix indicate that these sediments underwent only a modest degree of reworking by wave or tidal processes (Andrews & Walton 1990). Bed 35 belongs to Lithofacies 4 and is composed of sand that is likely to be derived from the delta-front environments that would have existed near the more marine lagoonal system (Andrews & Walton 1990).

In addition to *Praexogyra hebridica*, other fossils such as hybodont shark fin spines, fish jaws and teeth, and echinoid spines have been found in the Duntulm Formation (Andrews & Walton 1990; Brusatte *et al.* 2016). This brackish–marine faunal assemblage contrasts with the more freshwater-influenced assemblage of the underlying Valtos Sandstone Formation, which is often dominated

by bivalves such as *Neomiodon* (Harris & Hudson 1980; Andrews & Walton 1990).

METHODS

Track descriptions & measurements

The general terminology used to describe dinosaur footprints was drawn from Leonardi (1987), Thulborn (1990) and Marty (2008). We measured track length and width in the field and took all other measurements from field photographs using Image J 1.51k (Schneider *et al.* 2012) or from the scaled photogrammetric model of the site in CloudCompare v2.8.

For quadrupedal tracks, we measured the length and width of both the manus and pes (Fig. 3A) and qualitatively described features such as relief, sediment displacement rims and the shape of the digits (Marty 2008; Marty *et al.* 2010). When the anatomical orientations of the track could not be determined, we recorded long axis and short axis measurements.

The measurements of quadrupedal trackways were applied to both manus and pes impressions and include pace, stride, pace angulation, width of the angulation pattern, and progression (Fig. 3A; Thulborn 1990; Marty 2008). For all trackway measurements, we used the intersection of the length and width lines as the reference point between tracks (Leonardi 1987; Thulborn 1990; Marty 2008). Pace is the distance between two alternating tracks (i.e. right pes – left pes) and stride is the distance between two tracks made successively by the same foot



FIG. 2. The strongly oriented fabric of the oyster shell bed that composes bed 34 of the Duntulm Formation, demonstrating the sub-horizontal alignment among individual shells. The lens cap diameter is 5 cm.

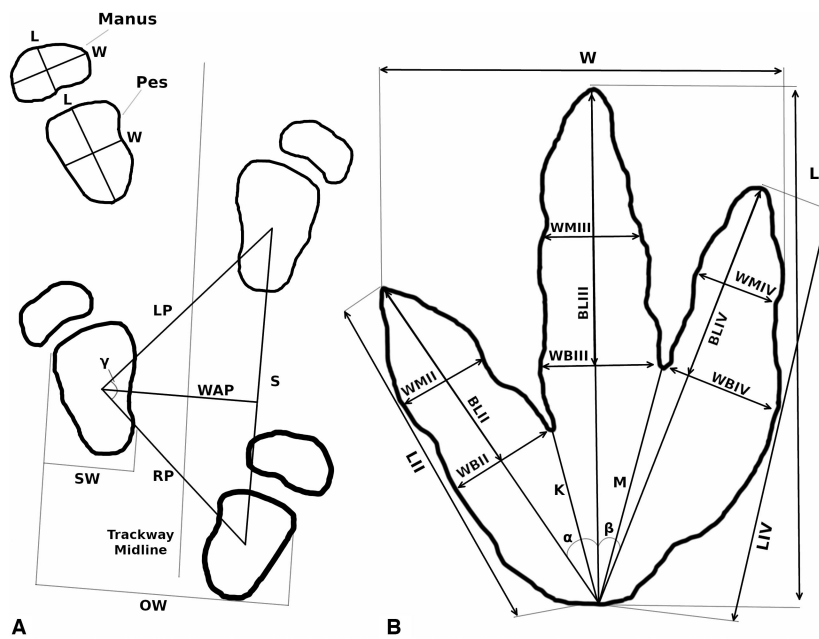


FIG. 3. The measurements for: A, quadrupedal tracks and trackways; B, tridactyl tracks. *Abbreviations:* quadrupedal tracks: L, length; W, width; quadrupedal trackways: γ , pace angulation; LP, left pace; OW, overall width; RP, right pace; S, stride; SW, side width; WAP, width of the pes angulation pattern; tridactyl tracks: α and β , interdigital angles between digits II–III and digits III–IV, respectively; BL, basal digital length (measured from the distal end of the digit to the basal digital line (the connection between the hypices)); K and M, heel–interdigital (hypex) distances; L, total track length (equivalent to the total length of digit III (LIII)); LII and LIV, total digital length (measured from the posterior margin of the heel); W, total track width; WB, basal digital width (measured along the basal digital line); WM, middle digital width.

(Lockley 1991). Pace angulation (γ) marks the angle inscribed by two successive paces in a trackway (Marty 2008). The width of the angulation pattern (WA) is a measure of overall trackway width derived from an established reference point on alternating (right–left) tracks (Thulborn 1990) and can be calculated by applying the Pythagorean theorem to the pace and stride lengths (Marty 2008). The width of the angulation pattern can be determined for either manus (WAM) or pes (WAP) impressions. Progression derives from WAP and describes how far forward the trackmaker moved during a single footfall (Marty 2008). Here, we calculated progression only for the pes impressions of the trackways because manus impressions were present less frequently. We additionally measured the overall trackway length (from the heel of the first track to the toe of the last) and trackway orientation (a bearing measured relative to magnetic north).

Additionally, we calculated heteropody (the ratio of the areas of the manus and pes impressions) (Lockley *et al.* 1994a; Marty 2008). Finally, we calculated several ratios for understanding the gauge of the trackways. Sauri-pod trackways have been qualitatively divided into ‘wide gauge’ and ‘narrow gauge’ configurations (Farlow 1992). The first quantitative gauge metric used was the track

ratio (TR), which relates the side width of the tracks (SW) with the overall width of the trackway (OW) (Romano *et al.* 2007). Both SW and OW are measured perpendicular to the long axis of the trackway (i.e. the midline) (Fig. 3A). In context of the trackways examined here, we calculated the pes track ratio (PTR; Romano *et al.* 2007). PTRs $\leq 35\%$ denote wide gauge trackways, PTRs from 36% to 49% denote medium gauge trackways, and PTRs $\geq 50\%$ denote narrow gauge trackways (Romano *et al.* 2007). The second gauge metric used was the ratio of the width of the pes angulation (WAP) to the pes length (PL) (Marty 2008). Lower WAP/PL ratios describe narrower trackway gauges (Marty 2008).

For tridactyl tracks, we recorded: total track length (L), total track width (W), total digital length (LII and LIV), basal digital length (BL), basal digital width (WB), middle digital width (WM), the heel–interdigital (hypex) distances (K and M) and the interdigital angles between digits II and III, and digits III and IV (α and β) (Fig. 3B; Moratalla *et al.* 1988).

Deriving from reasoning detailed in Delgalvis (2015), we created qualitative criteria for assessing our level of confidence in the identification of sedimentary structures as dinosaur footprints. ‘Definite’ tracks are those that possess discernible toes, track-sized features associated

with highly localized sediment deformation, or track-sized features with a clear association or pattern. ‘Probable’ tracks are impressions or casts without the features of a definite track but with the same preservation style and general shape and size as a definite track. Probable tracks are often closely spatially associated with definite tracks. ‘Possible’ tracks (those with the lowest confidence) are track-shaped variations in how the track-bearing platform is weathering. Possible tracks sometimes show weakly localized sediment deformation and are often weakly associated with probable or definite tracks. In addition to the qualitative track confidence assessment, we assigned a preservation grade (Marchetti *et al.* 2019) to each footprint.

We divided both quadrupedal and bipedal tracks into previously established size classes (Marty 2008, table 2.2). We also estimated the possible hip height, speed and gait of the trackmakers. Acknowledging that size estimates in quadrupedal trackmakers are a point of on-going debate (Stevens *et al.* 2016), we estimated the hip height of both sauropod trackmakers and bipedal trackmakers using the general relationship proposed by Alexander (1976) linking track length to hip height through a scaling factor. Later studies for both sauropods (Tschopp *et al.* 2015) and bipedal dinosaurs (Henderson 2003) lend support to this classical estimate and suggest that morphometrics-based equations (e.g. Thulborn 1990) tend to overestimate hip height. We estimated the speed at which the dinosaurs were travelling using the equation of Alexander (1976). Due to large uncertainties underpinning its key assumptions, this equation should not be expected to yield strictly accurate speeds (Alexander 2006). Rather, it is used here to give a rough estimate and to begin reflecting in broad strokes on the locomotion and gait of the trackmaker. Gait can be further qualitatively described as walking or running (Thulborn 1989), with the points at which an animal transitions between gaits approximated by the ratio of stride length to hip height (Alexander 1976; Thulborn 1982, 1989). Stride length/hip height ratios lower than 2.0 indicate a walking gait (Thulborn 1982, 1989).

Aerial survey & photogrammetric models

We used two unmanned aerial vehicles (UAVs) to survey the main track-bearing platform at Duntulm. The first set-up was a custom hexacopter using a Tarot 680 pro airframe with a payload of a Sony A6000 (24 mp, 20 mm lens) camera oriented at nadir. The camera was run in aperture priority mode and relied on an external trigger from the UAV flight controller. After the shoreward third of the platform was surveyed with this set-up, we encountered technical difficulties and switched to a 3DR Iris+

quadcopter with a payload of a Canon S110 (12 mp) camera oriented at nadir. The Canon S110 cameras used CHDK (Canon Hacker Development Kit) firmware to support external triggering of the camera via the flight controller and greater control of the image exposure. We calculated our flight paths and triggering locations in Mission Planner v.1.3.41 and flew both UAVs using Pixhawk flight controllers running Arducopter 3.3 firmware operated from a ground control station communicating with the UAV over a 433 MHz telemetry link. In total, we flew six flights at 6 m above the ground surface.

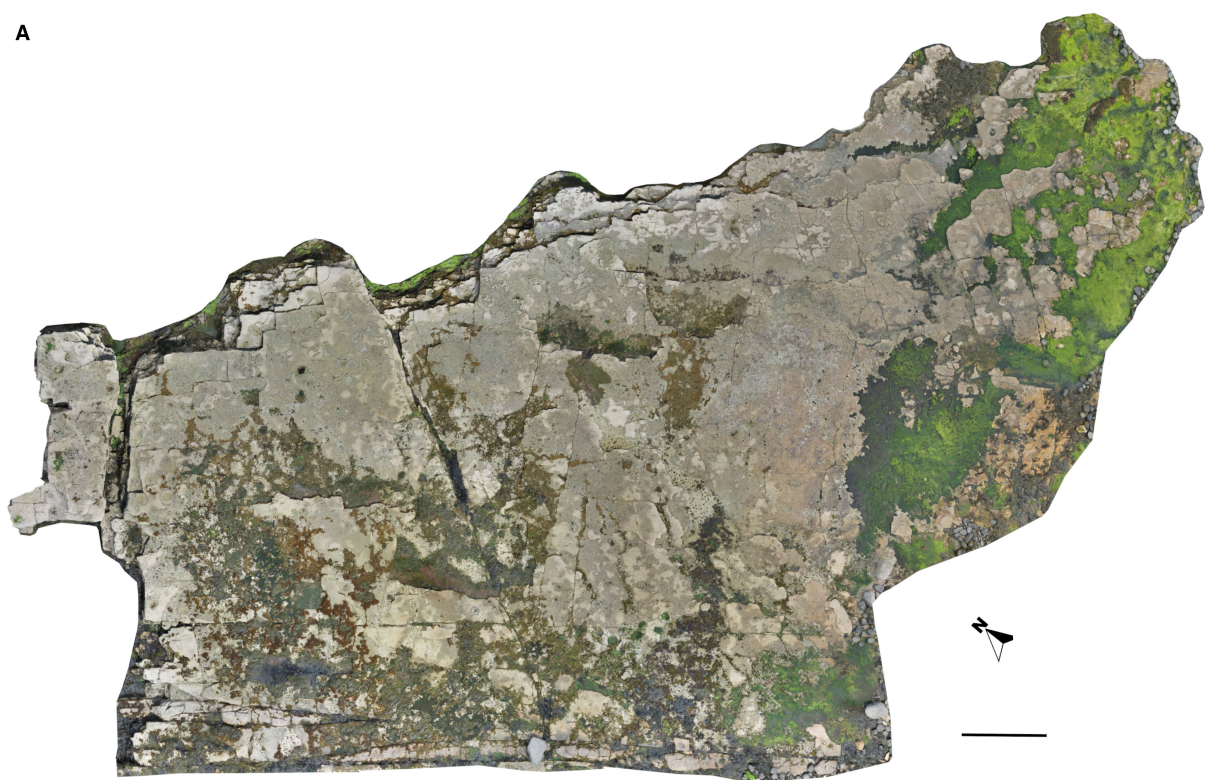
We constrained the photogrammetric model with ground control points (GCPs) from relative carrier phase GNSS (Global Navigation Satellite System) data collected with Leica GS10 receivers. We established a base station on the site and collected location data for c. 4 h. Individual GCPs were collected using a roving receiver (using a satellite cut-off angle of 10° above the horizon) and paired with the base station to resolve ambiguities. Data were post-processed in Leica GeoOffice 8.4 by pairing the base station to an established Ordnance Survey reference station. The reference station (Lochcarron – LCAR) was located c. 60 km away. Precise ephemeris data were downloaded from the International GNSS Service (IGS) (https://igs.org/data/#broadcast_ephemerides) on 10 April 2017. The estimated GCP position quality was c. 1 cm.

Photogrammetric models were constructed in Agisoft Metashape v1.8.4 (<https://www.agisoft.com>). In sum, 554 images were used to construct the Duntulm tracksite model. The calculated error for the GCPs in the model averaged to 2.10 cm, with 6.43 cm averaged error for the check points. The ground sampling resolution of the orthophoto was 2.58 mm/px.

SITE OVERVIEW

More than 150 tracks were identified on the main platform at Duntulm with at least 35 additional tracks located in stratigraphically older layers north of the main platform. An orthophoto of the main track-bearing platform generated from the photogrammetric model (Fig. 4A) was used as the base for several site maps (Figs 5–7). The main platform was divided into three sections (Fig. 4B) for site mapping due to the large lateral extent of the tracksite and the density of the footprints present. The main platform at Duntulm encompasses three definite trackways, two possible trackways, and a large scattering of isolated or weakly associated tracks including several manus–pes pairs. Some areas of the platform showed intensive sediment deformation, but no distinctive track boundaries or outlines. These areas are identifiable from aerial imagery by having a distinctive pockmarked aspect and being slightly more resistant to

A



B

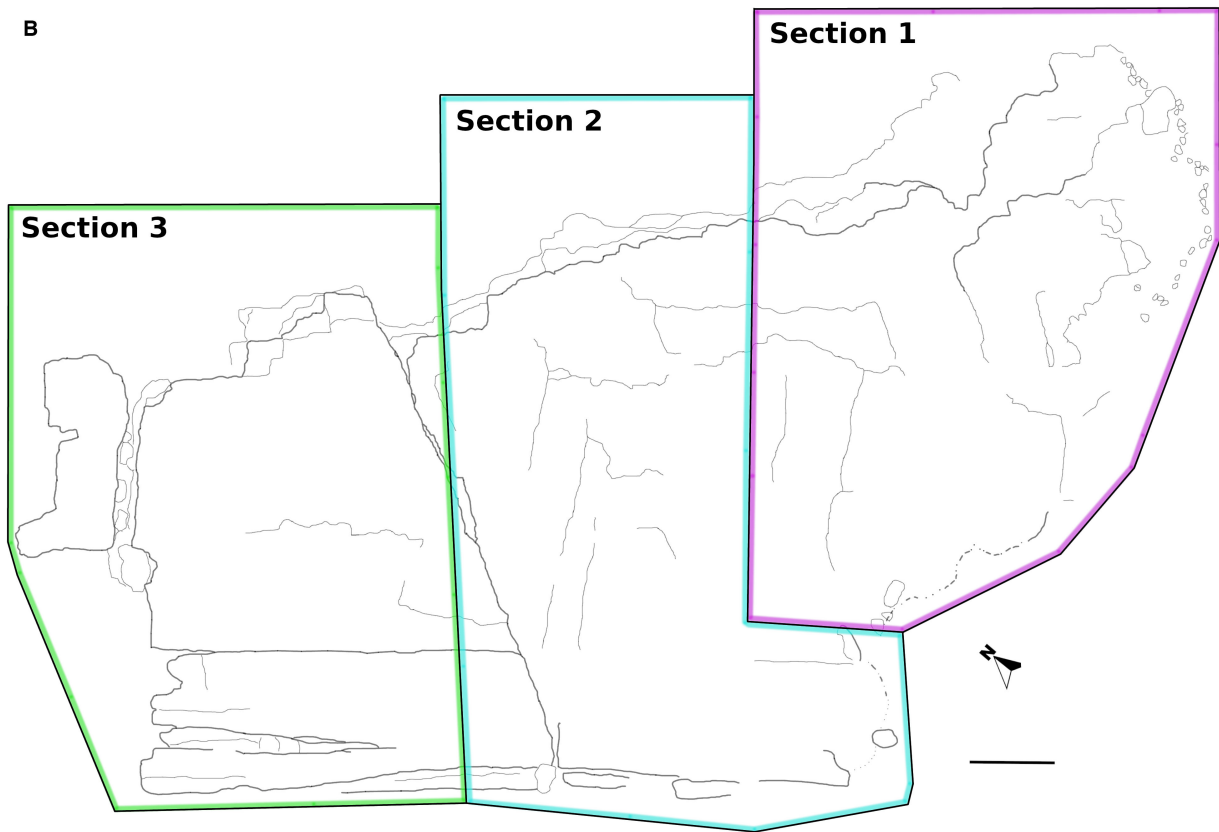


FIG. 4. The main track-bearing platform of the Duntulm tracksite: A, georeferenced orthophoto; B, sections used to subdivide the platform into smaller-scale site maps (shown in later figures), laid over a line drawing of the outcrop. At this scale, it is difficult to see individual tracks or trackways. Scale bars represent 5 m.

erosion and have been tentatively mapped as areas of dinoturbation in the site maps (Figs 6, 7).

MODES OF TRACK PRESERVATION

The main platform at Duntulm has two dominant styles of track preservation: casts, which lie on top of the bedding surfaces, and concave impressions pressed into the bedding plane. While both casts and impressions are scattered throughout the platform surface, some spatial patterns exist in terms of preservation style. Casts are the more prevalent type of preservation style in the most shoreward section of the platform (Section 1; Fig. 5), while impressions dominate the middle of the platform and its most seaward extent (Sections 2 and 3; Figs 6, 7).

While impressions formed on both bed 34 (exposed primarily along the northern edge of the platform: the right side as one faces the sea) and bed 35, casts formed more frequently on bed 35. The casts in this case were deposited as an overlying bed (probably bed 36) infilled existing depressions. These infillings proved slightly more resistant than the surrounding rock and were later isolated during the process of erosion. A third, less common preservation mode exists as a combination of the two dominant styles where the remnants of a cast are found infilling a shallow impression. Although this relationship between the preservation styles is relatively rare, it demonstrates the intrinsic link between the two strongly: namely, that the casts of Duntulm were formed in pre-existing impressions. These occurrences indicate that tracks were formed on this platform during sequential periods of deposition and, thus, support the observation that multiple generations of dinosaurs travelled through the lagoon system exposed on the platform (Brusatte *et al.* 2016).

These modes of track preservation persist in additional track-bearing layers north of the main platform at Duntulm. Although footprints appear more sparsely distributed in these beds (which limits an assessment of the spatial distribution of preservation styles), these footprints are preserved predominantly as low-lying casts where the surrounding rock has not yet eroded and, occasionally, as shallow impressions. These stratigraphically lower layers tend to have a higher mud content, and sediment deformation around the casts tends to be more visible than in the limestone of the main platform.

These styles of track preservation (in addition to their location in the erosive environment of the modern intertidal zone) result in an overall low preservation grade (Marchetti *et al.* 2019) for the footprints. The majority of the footprints at the site have a morphological grade ranging from 0 to 1 (Table S1).

TRACK OBSERVATIONS & ICHNOTAXONOMY

Tracks & trackways

The main track-bearing platform at Duntulm is characterized by a large number of tracks ranging in completeness from casts preserving digits and heel pad impressions to less diagnostic negative relief ‘potholes’, to broken casts in shallow impressions (Table S1). In order to fully characterize the range of track presentation observed on the platform, we describe and discuss the three identified trackways, two possible trackways, two track groupings, and several isolated tracks with distinctive features on the main track-bearing platform. These descriptions will be synthesized into more generalized statements about the overall characteristics of the track assemblage on the platform.

Trackway 1 (Fig. 8; Table 1) is the most striking of the definite trackways present and is located on the western edge of the platform. It consists of 10 deep negative relief impressions ranging in shape from subcircular to sub-oval. No toe impressions or other fine details can be discerned in these tracks. The average track length is 67 cm (range, 56–86 cm) and the average track width is 59 cm (range, 50–76 cm). The trackway curves slightly through its progression so that the initial orientation is 160° and its final orientation is 130°. The stride and pace lengths throughout the trackway are regular with exceptions existing around the largest and shallowest impression (DUNT_88; possibly a composite track). Trackway 1 is a pes-only trackway with no distinctive manus impressions preserved. Trackway 1 is narrow gauge with individual footprints overlapping or immediately adjacent to the midline (Farlow 1992). This qualitative observation is supported quantitatively through both the WAP/PL ratio and the PTR (Table 1).

Although the trackway parameters and characteristics can be clearly defined for Trackway 1, the tracks themselves lack distinctive features. The direction of

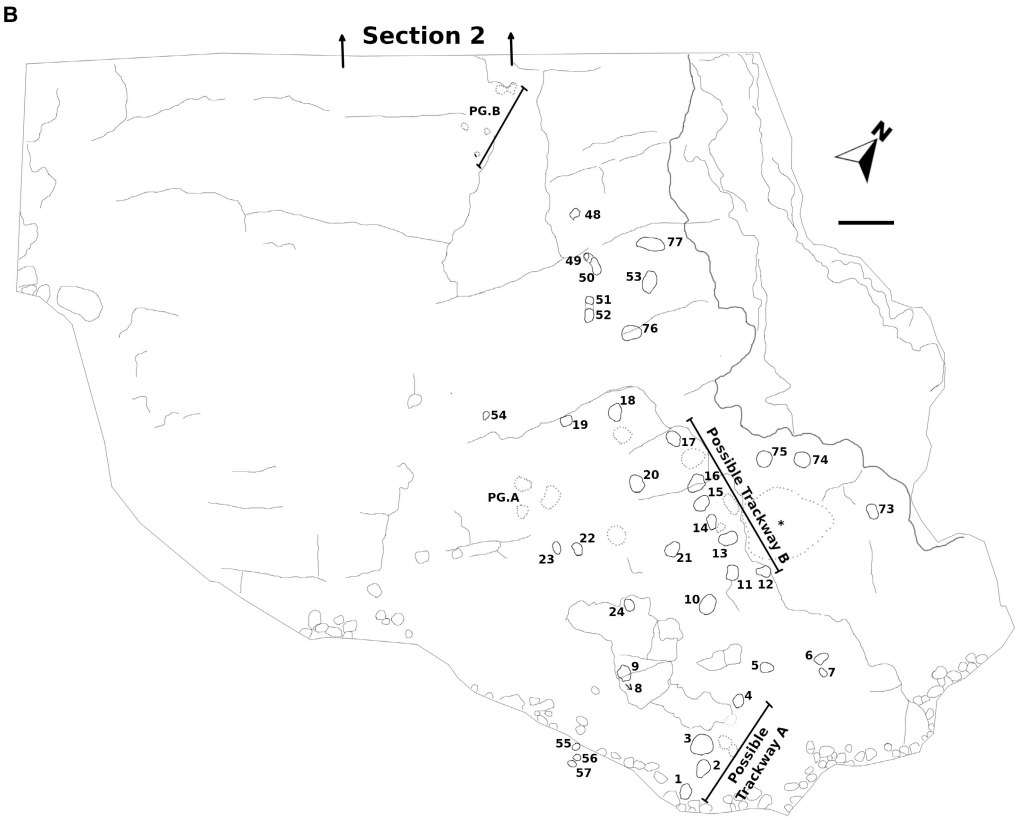
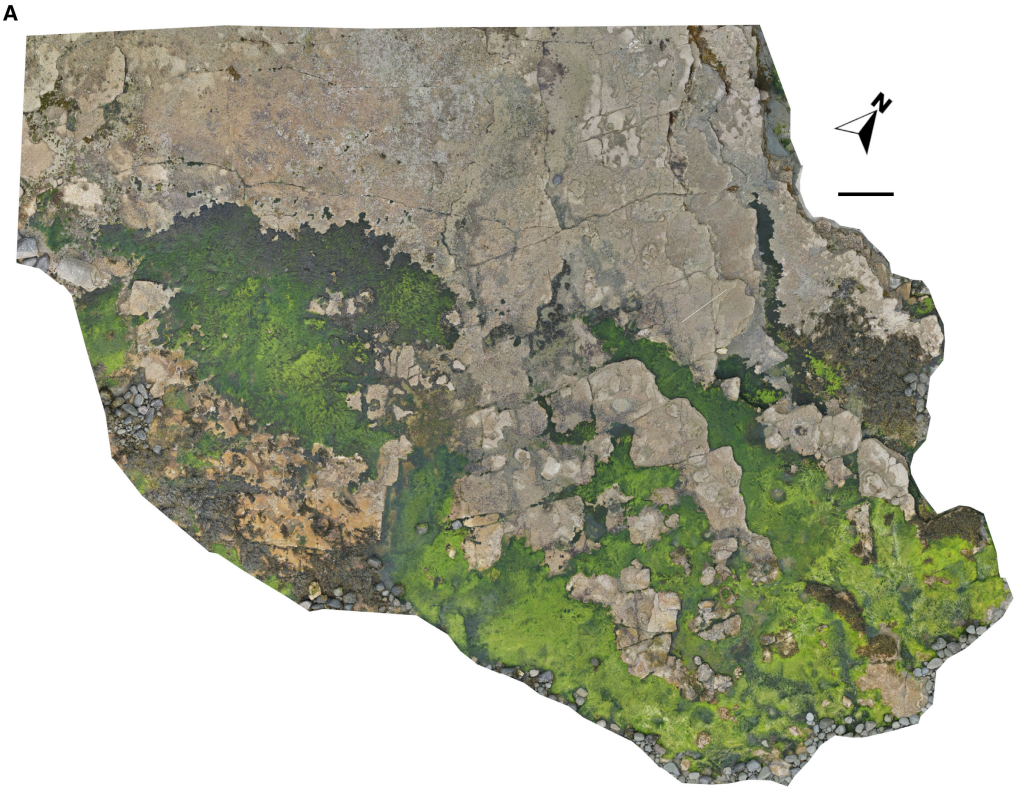


FIG. 5. Section 1 of the Duntulm tracksite: A, orthophoto; B, line drawing highlighting the locations of tracks and marking two possible trackways (A and B) and two groups of possible tracks (PG.A and PG.B). Section 1 is the most shoreward section on the Duntulm platform. * denotes a scattering of rounded impressions (possible footprints?) submerged among the weeds along a stepped portion of the platform. Scale bars represent 2 m.

progression of the trackway is possibly to the southwest as the more elongated impressions tend to widen slightly in that direction. In the more distinctive tracks at the site where toes are preserved, a general pattern of widening towards the anterior of the track is observed.

Trackway 2 (Fig. 9; Table 1) occurs adjacent to Trackway 1. The bearing lines of these two trackways cross each other. Trackway 2 is short, consisting of four definite positive relief tracks and a possible impression along the line of progression. The tracks are preserved as reddish-brown weathering, low-lying positive relief casts. These casts are heavily affected by limpet scarring and have a pockmarked appearance. The impressions that the casts infill are visible around the edges of some of the casts, along with small sediment deformation rims (particularly in the case of the manus–pes pair). The tracks are elongate and widen anteriorly. The lateral margins of the pes tracks curve inward towards the trackway midline with the inner margin more concave than the straighter outer margin. No distinctive toe or heel impressions are preserved in the casts. Trackway measurements proved difficult to assess in the case of this particular trackway. The gauge of the trackway was not quantitatively assessed, but is qualitatively observed to be narrow, with the tracks overlapping the midline of the trackway. This trackway is notable for the unique preservation style of the casts and for the overlapping relationship between the manus–pes pair. This overlap between the manus and the pes is unique among the clear pairs observed on the track-bearing platform.

Trackway 3 (Fig. 10; Table 1) represents the final definite trackway on the main platform. The trackway is composed of five deep pes impressions with no associated manus tracks. The tracks are sub-oval to elongate and widen anteriorly. The width of the tracks tapers to a curved posterior margin while the anterior margin is more flattened. The average length of the tracks is 52 cm and the average width is 39 cm. The pace lengths throughout the short section of trackway preserved are systematically irregular, with the left pace length (average 1.96 m) consistently *c.* 50 cm longer than the right pace length (average 1.41 m). This mismatch between pace lengths suggests that the individual may have been walking with a slightly uneven gait, although the trackway is too short for this inference to be made confidently. Previous studies of a similar mismatch in pace length in bipedal and quadrupedal trackways suggest that these

irregular gaits may be the result of limping due to injury (Dantas *et al.* 1994; Lockley *et al.* 1994b; Ishigaki & Lockley 2010; Razzolini *et al.* 2016). The WAP/PL ratio and the PTR both indicate that the trackway has a slightly wider gauge than Trackway 1, edging into the medium–narrow range. We speculate that the slightly wider gauge of this trackway results from the same factors that caused the uneven gait of the individual.

Two other, possible trackways exist at the site, but lack the clear relationships between the individual tracks of Trackways 1–3. Both possible trackways are informative in understanding the overall character of the Duntulm tracksite and will be described here in brief.

Possible Trackway A (Fig. 11; Table 1) is located on the most shoreward portion of the platform and appears to emerge from the wave-washed boulders along the platform edge. This short track association consists of four definite tracks (three positive relief and one negative relief impression) and two probable tracks (one impression and one cast). The most distinctive track is the second one in the line of progression (DUNT_02). It is a slightly broken pes cast and is notable because it clearly shows a sub-triangular shape (broadening anteriorly) and preserves four partial anteriorly directed digit impressions along the slightly postero-laterally sloped anterior margin. The track has weak entaxy, with digit I the most anteriorly located and digit IV the most posteriorly located. The track association appears narrow gauge with tracks touching and, indeed, overstepping the midline. The WAP/PL ratio and PTR support this inference.

Possible Trackway B (Fig. 12) represents a striking series of positive relief casts along the northern edge of the most shoreward step of the main platform (Section 1; Fig. 5). These casts preserve more fine detail, particularly of the digits, than tracks anywhere else on the platform (Brusatte *et al.* 2016, fig. 3). While the linear arrangement of these casts led Brusatte *et al.* (2016) to consider that they were associated into a trackway, a closer examination of the orientations of the tracks and the relative distribution of manus and pes prints calls that interpretation into question. Even allowing for the outward rotation expected of sauropod tracks, the angles that the long axes of the tracks make to the apparent midline (*c.* 90°) are not consistent with postural expectations for these animals. Furthermore, the orientation of the toes of the tracks challenges expectations. The way in which the toes point, with successive tracks sometimes being oriented in nearly

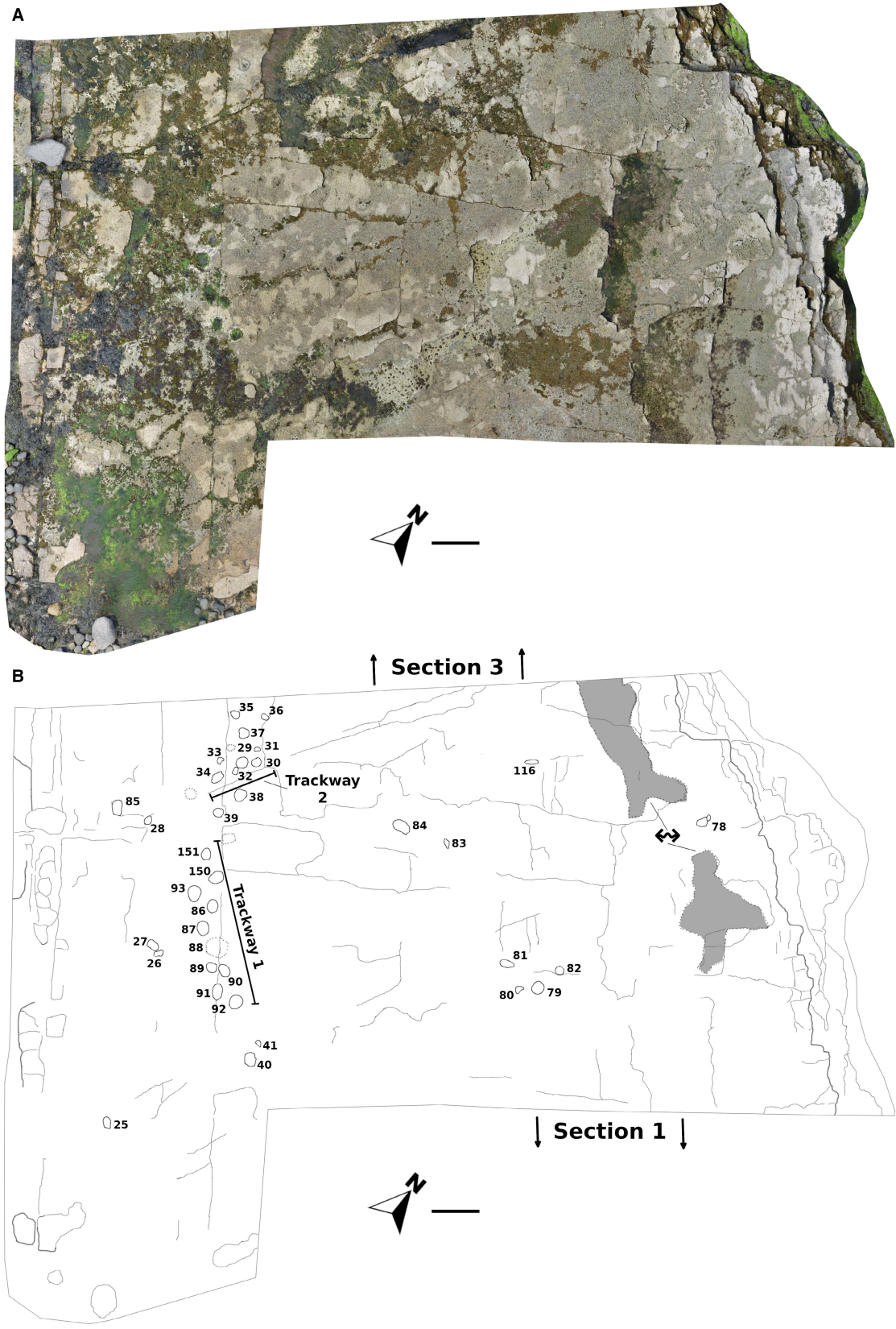


FIG. 6. Section 2 of the Duntulm tracksite: A, orthophoto; B, line drawing showing two distinctive trackways and a scattering of additional positive relief casts. ↔ and grey shading denote disrupted areas of the track-bearing surface, which are interpreted as dino-turbation. This section is bound along its southwestern edge by a large volcanic intrusion. Scale bars represent 2 m.

identical directions, would work well if the tracksite lived up to its nickname and the sauropod was performing a disco step, but is not consistent with alternating paces.

These observations demonstrate that Possible Trackway B is not a true trackway representing the motion of a single individual (*contra* Brusatte *et al.* 2016). Instead, the similarity in preservation styles and apparent linearity in the arrangement of the casts is postulated to result from Possible Trackway B's location along the upper edge of a step in the bedding planes and from bedding plane-scale influences on the quality of track preservation. Indeed, the preservation style of the dinosaur footprints on the most shoreward portion of the platform, with distinctive casts common, and sporadic large deep impressions, is unique for the tracksite. The rest of the main track-bearing platform is located at least 5 cm lower stratigraphically and the dominant preservation style shifts to shallow impressions and lower relief, poorly preserved casts. It is possible that the shoreward nature of this section means that it undergoes the least amount of tidal weathering, and hence the infilling casts have not yet been obliterated.

Track Grouping I (Fig. 13A, B) and Track Grouping II (Fig. 13C, D) are the most equivocal track groupings described from the Duntulm platform. However, despite their poorly defined association, these tracks highlight several additional aspects of the Duntulm site. Both track groupings consist of shallow (*c.* 3 cm deep) negative relief impressions with gently sloping (low amplitude) edges. These individual tracks are mainly discernible because of the water that pools in them at low tide, but a few are deep enough to support the dense and brightly coloured seaweed often seen in the negative relief impressions of definite trackways (Trackways 1 and 3). Track Grouping I spans two horizons, with DUNT_42–DUNT_45 located in the layer above the other tracks in this grouping.

The shallow, sloping edges and lack of fine detail in the impressions comprising these track groupings indicates that they are potentially undertracks that formed below the original surface on which the dinosaur was walking (Lockley 1991; Allen 1997; Milàn & Bromley 2006). Although simulations of the effects of erosion on track shape suggest that, if tracks are not preserved in laminated rocks, they are more likely to be eroded surface tracks than true undertracks (Henderson 2006), trampling by sauropods in other lagoonal systems shows distinct propagation of undertracks through thicker beds (Thulborn 2012). Zones of deformation are similarly observed

in the more massive limestone of bed 34 of the main track-bearing platform at Duntulm (Brusatte *et al.* 2016, fig. 4). Additionally, the tracks of these groupings are slightly larger on average than the deeper, more steep-sided tracks of Trackway 3 immediately adjacent to them on the main platform (Table S1; particularly DUNT_42–DUNT_45 of Track Grouping I). This under-track inference becomes important when contextualized with the information that the lower level of both Track Grouping I and Track Grouping II occurs in the same sedimentary horizon as Trackway 3's deep tracks. These differences in track depth and amplitude of the margins in adjacent areas of the same stratigraphic horizon provide a further indicator of the presence of multiple generations of dinosaurs in the lagoonal environment of Duntulm. This repeated occupation of Duntulm's lagoons over time is further indicated by the presence of DUNT_121 as a cast infilling an impression adjacent to Track Grouping I. The cast is formed from the same horizon that bears the shallow impressions of the grouping, while the impression it fills is located on a lower horizon.

Analysis of the recognizable trackways, track associations and track groupings on the main track-bearing platform at Duntulm shows that there is remarkable consistency in both track and trackway characters, with the trackways generally being narrow gauge and possessing sub-circular to sub-oval pes tracks that widen anteriorly (Fig. 14A–F). Interestingly, the pes-only trackways at Duntulm are exclusively negative relief, while the positive relief trackway (preserved as a series of low-lying casts and impressions rather than solely impressions) contains both pes tracks and a possible manus track.

In addition to the track presentations observed in the definite and possible trackways at the site, another distinctive track presentation is observed on the main track-bearing platform (Fig. 15). In this presentation (represented by DUNT_49 and DUNT_50; Fig. 15A, B), a single large, elongated, positive relief cast formed as a composite of a closely associated manus and pes. The pes is sub-oval with evidence of displacement rims along the posterior margin on the track-bearing platform (below the level of the cast). The anterior margin of the pes is obscured by the disturbed sediment around the manus. The manus is sub-rectangular with roughly straight anterior and posterior margins. The manus cast appears to be located stratigraphically 'higher' in the composite cast than its corresponding pes (Fig. 15E). This preservation style is similarly seen in tracks DUNT_51 and DUNT_52

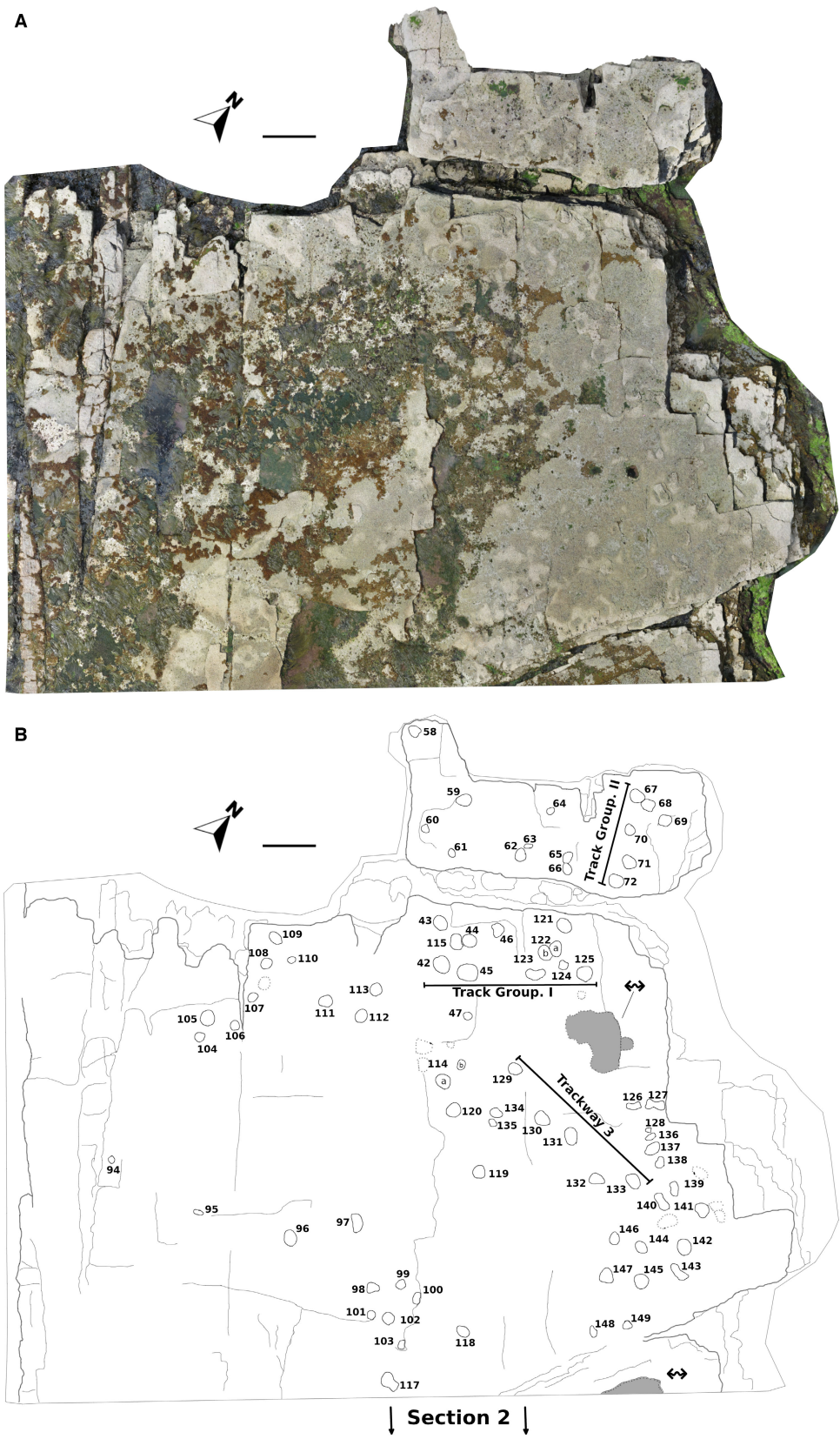


FIG. 7. Section 3 of the Duntulm tracksite: A, orthophoto; B, line drawing of the most seaward section of the main track-bearing platform. This section of the platform is notable for its high track density and contains Trackway 3 and Track Grouping I and II. ~ and grey shading denote disrupted areas of the track-bearing surface, which are interpreted as dinoturbation. Scale bars represent 2 m.

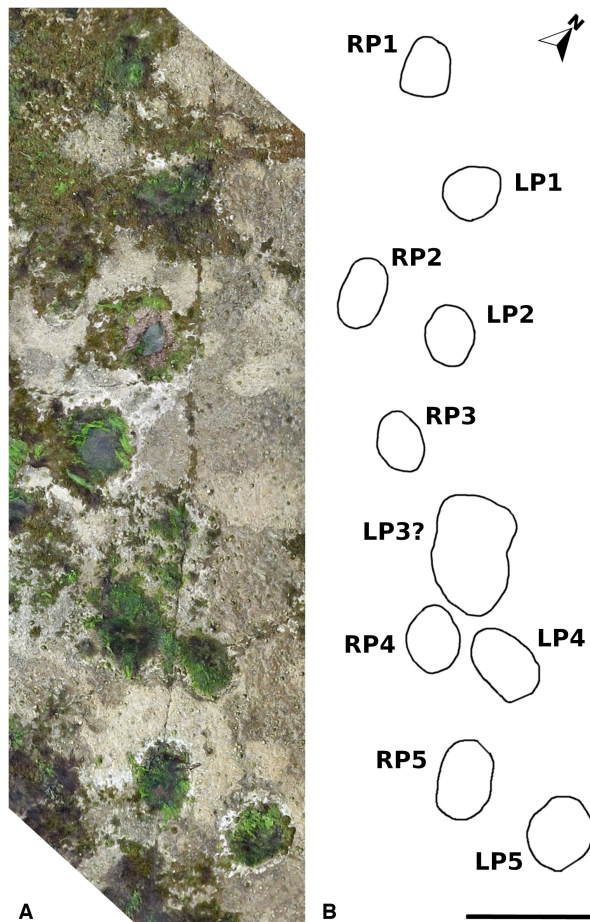


FIG. 8. Trackway 1 shown as: A, an orthophoto; B, a line drawing. It is the longest trackway at the site and is composed of 10 impressions. These impressions do not preserve fine details of the tracks. The line of progression of the trackway proceeds from the top of the image to the bottom. Abbreviations: LP, left pes; RP, right pes. Scale bar represents 1 m.

(Fig. 15C, D), and, in this latter case, the anterior widening of the pes observed across the track-bearing platform is seen more clearly. Manus–pes pairs preserved in this fashion tend to have a less pronounced heteropody than that observed with other positive relief manus–pes pairs on the platform. A final track presentation style can be found lower in the section in the beds exposed north of the main track-bearing platform (Fig. 14G, H). Lower in the stratigraphy, the sauropod footprints tend to be preserved casts that have not yet weathered out of the surrounding cast-forming sediments. The track margins are

visible, particularly along breaks in the platforms, but the overall relief of the tracks is low. Additionally, as seen on the main track-bearing platform, some footprints are present as shallow impressions.

In summary, with some variations arising from preservation style and completeness, Duntulm's quadrupedal footprints exhibit broadly similar track morphologies. The manus prints range from a half-circle with a convex anterior margin and an almost straight posterior to a more ellipsoidal feature with the same marginal curves and a pronounced medial claw (pollex). The pes prints range in shape from sub-circular to elongated and tend to widen anteriorly. This widening results in some tracks being sub-triangular in overall shape. Additionally, the elongated pes tracks tend to present with the outer edge of the pes curved less than the sometimes strikingly concave margin of the inner edge.

Identification of quadrupedal trackmaker

The presence of several manus–pes pairs at the site and the overall shape character of the tracks indicates that the majority of the footprints at Duntulm came from a quadrupedal trackmaker. One clade of saurischians (sauropods) and several clades of ornithischians (thyreophorans, ceratopsians and hadrosaurs) have achieved quadrupedality in their evolutionary history (Maidment & Barrett 2012; Barrett & Maidment 2017). Of these clades, two are known from the Isle of Skye: sauropods (dePolo *et al.* 2018) and thyreophorans (specifically, stegosaurs indicated by *Deltapodus* tracks; dePolo *et al.* 2020). The footprints at Duntulm have been previously interpreted as arising from sauropod trackmakers (Brusatte *et al.* 2016). However, it is difficult to distinguish between sauropod and thyreophoran tracks when distinctive morphological features such as digit impressions are not preserved (Castanera *et al.* 2024). Therefore we will evaluate, in brief, whether these footprints are likely to derive from a stegosaurian trackmaker.

Deltapodus footprints were originally described from Yorkshire, UK (Whyte & Romano 1994) and are attributed to stegosaurs (Whyte & Romano 2001; Lockley *et al.* 2017; dePolo *et al.* 2020). The pes of *Deltapodus* is characterized by a generally symmetrical, subtriangular outline broadening from a narrower heel to a maximum width near the anterior margin (Whyte & Romano 2001). The *Deltapodus* pes is tridactyl and mesaxonic with blunt

TABLE 1. Average trackway measurements at the Duntulm tracksite.

	TL (m)	Bearing (°) [†]	S (m)	P (m)	γ (°)	WAP (m)	WAP/PL [‡]	PTR (%)
Trackway 1	7.09	Curved	1.40	0.92	94	0.67	1.01	53
Trackway 2	3.41	190	1.22	0.85	—	—	—	—
Trackway 3	7.03	270	3.05	Variable	137	0.83	1.6	48
Possible Trackway A	4.30	355	1.37	0.87	131	0.32	0.6	53

See Table S2 for step-by-step tabulation of stride values. [†]Relative to magnetic north; [‡]dimensionless ratio. Trackway 2 stride averaged from right pes tracks and pace length averaged from left manus pace and right pes pace. γ, pace angulation; P, pace length; PTR, pes trackway ratio; S, stride length; TL, trackway length; WAP, width of pes angulation pattern.

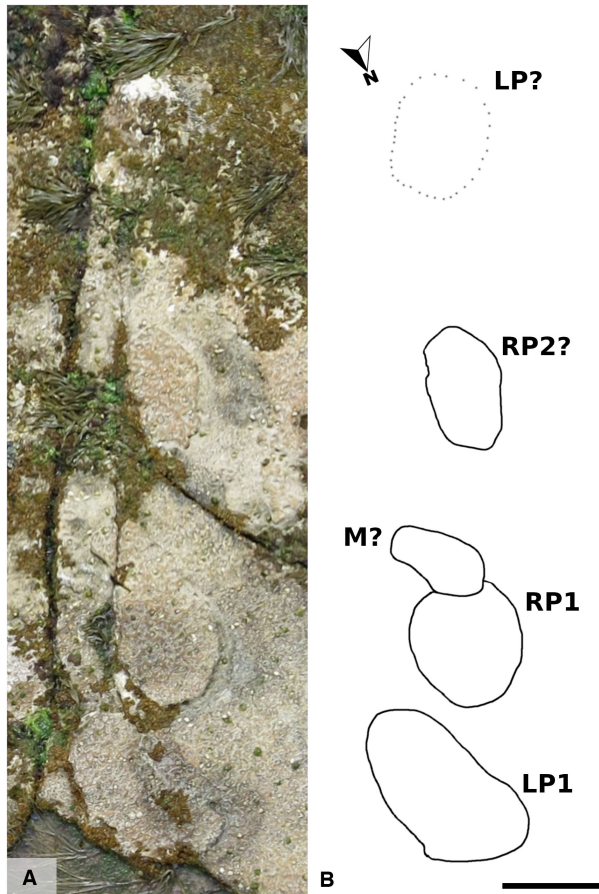


FIG. 9. Trackway 2 shown as: A, an orthophoto; B, a line drawing. These tracks are the shortest trackway on the Duntulm main platform. Although the alternating pattern is less clear than in other trackways, the distinctive preservation style of the tracks enables them to be associated. *Abbreviations:* LP, left pes; M, manus; RP, right pes. Scale bar represents 50 cm.

digits along the anterior edge of the footprint. Both the medial and lateral margins of the pes are generally straight with minimal curvature (Whyte & Romano 2001). The manus impression of *Deltapodus* is generally crescentic in shape (Whyte & Romano 2001), with variable development of the pollex, from pronounced in

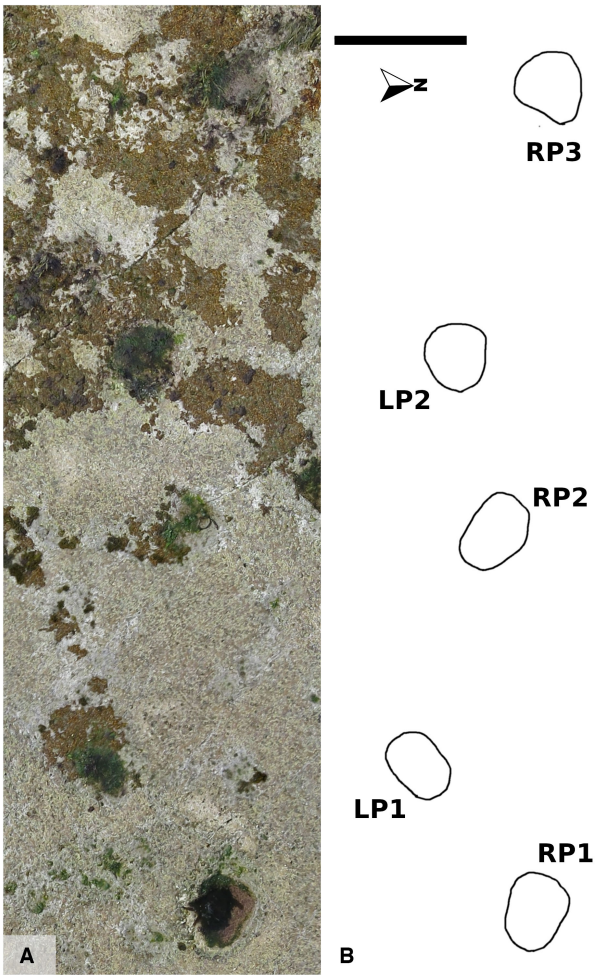


FIG. 10. Trackway 3 shown as: A, an orthophoto; B, a line drawing. This short trackway is composed of five impressions and hints at an unusual gait in the trackmaker. The right pace is notably shorter than the left pace and could indicate that the sauropod was limping. *Abbreviations:* LP, left pes; RP, right pes. Scale bar represents 1 m.

D. brodericki and *D. curriei* to absent in *D. ibericus* (Xing *et al.* 2013; Castanera *et al.* 2024).

While their preservation grade is generally low and their overall shapes are variable, the Duntulm footprints

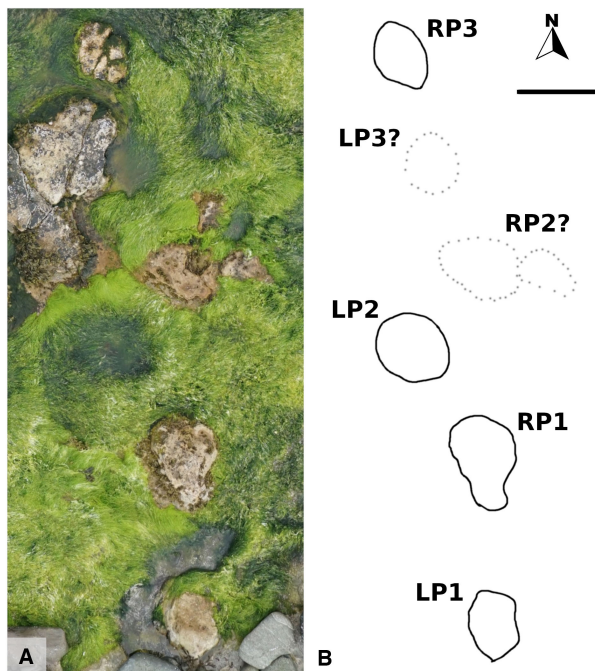


FIG. 11. Possible Trackway A shown as: A, an orthophoto; B, a line drawing. The solid black outlines denote definite tracks (DUNT_01–DUNT_04) and the dashed grey outlines indicate possible tracks. Possible Trackway A has a very narrow gauge, with the tracks overstepping the midline in some cases. Abbreviations: LP, left pes; RP, right pes. Scale bar represents 50 cm.

differ from *Deltapodus* in the following ways: (1) sub-oval to elongated footprints typically have curved internal and external margins resulting in an overall asymmetrical outline of the impression; and (2) in the rare cases where digits are preserved, pes impressions have four digits (Brusatte *et al.* 2016, fig. 3a, e). Manus measurements also support the inference of a sauropod trackmaker. Seven clear manus tracks are known from the main track-bearing platform at Duntulm. L/W ratios of these tracks average to 0.68. These ratios are higher than the L/W ratios observed for the manus of Iberian specimens of *Deltapodus* (<0.5) and are more consistent with the >0.65 threshold reported for sauropod manus impressions (Castanera *et al.* 2024).

Additionally, there is a notable size difference between the Duntulm footprints and the range expected for *Deltapodus*. The majority of *Deltapodus* footprints from Yorkshire have lengths between 25 and 50 cm (Whyte *et al.* 2007), and *Deltapodus* footprints from Teruel Province of the Iberian Peninsula are less than 55 cm long (Castanera *et al.* 2024). Although there is indeed an overlap in size range between the largest *Deltapodus* footprints and Duntulm's smaller subcircular to sub-oval footprints, there are dozens of individual tracks at Duntulm with lengths greater than 60 cm, with some even reaching

longer than 75 cm (Table S1). This size range provides strong support for referring these footprints to a sauropod trackmaker. Additionally, the known *Deltapodus* footprints from the Isle of Skye fall on the lower side of the size range of that known for *Deltapodus* (<25 cm in length; dePolo *et al.* 2020).

To sum up, despite their generally low preservation grade, we lack proof of a thyreophoran affinity for these tracks. The overall track shape and size and both general morphology and manus measurements are more consistent with sauropod trackmakers. The sauropod tracks at this locality typically fall into the small to medium size class (Marty 2008).

Sauropod ichnotaxonomy & trackmakers

The Duntulm sauropod tracks consistently form narrow gauge trackways and are therefore inconsistent with wide gauge Middle Jurassic ichnotaxa such as *Polyonyx* (Santos *et al.* 2009) and *Occitanopodus* (Moreau *et al.* 2020). They similarly lack the wide gauge trackway characteristic and outward claw rotation of *Brontopodus* (Lockley *et al.* 1994a). While the Duntulm prints are consistent with the majority of the characteristics of *Parabrontopodus* (narrow trackway, elongated pes with a length of c. 50–90 cm and semicircular manus), the toes of the Duntulm prints are anteriorly directed (Lockley *et al.* 1994a). As originally noted by Brusatte *et al.* (2016), on the basis of their narrow gauge trackway, crescent-shaped manus impressions and anteriorly directed toes, the Duntulm tracks are most similar to the ichnogenus *Breviparopus* (Dutuit & Ouazzou 1980; Ishigaki 1989, fig. 5). Additionally, the manus–pes pairs (Fig. 16) have moderate to high heteropody with an average ratio of 1:1.25 (range, 1:1.17 to 1:2.98). This value is less extreme than the 1:3.6 of the Moroccan tracks used to diagnose *Breviparopus* (Dutuit & Ouazzou 1980; Marty *et al.* 2010), but remains qualitatively consistent with the pronounced heteropody of this ichnogenus. The orientation of the toes along the anterior edge of the footprints at this site is also similar to unnamed sauropod tracks described from the Big Horn Basin of Wyoming (Platt & Hasiotis 2006, fig. 4) and *Breviparopus*-like tracks from the Cleveland Basin, Yorkshire (Romano *et al.* 1999, fig. 3B). While the Duntulm footprints are *Breviparopus*-like, we refrain from making a formal ichnotaxonomic assignment of these tracks due to the generally poor preservation and indistinct track features at the locality.

The sauropod trackmakers at Duntulm stood between 2 and 3 m high at the hip. All velocity estimates from the trackways (Table 2) indicated a walking gait, with Trackmaker 1 appearing particularly ponderous with a low progression between steps. The progression of Trackway 3

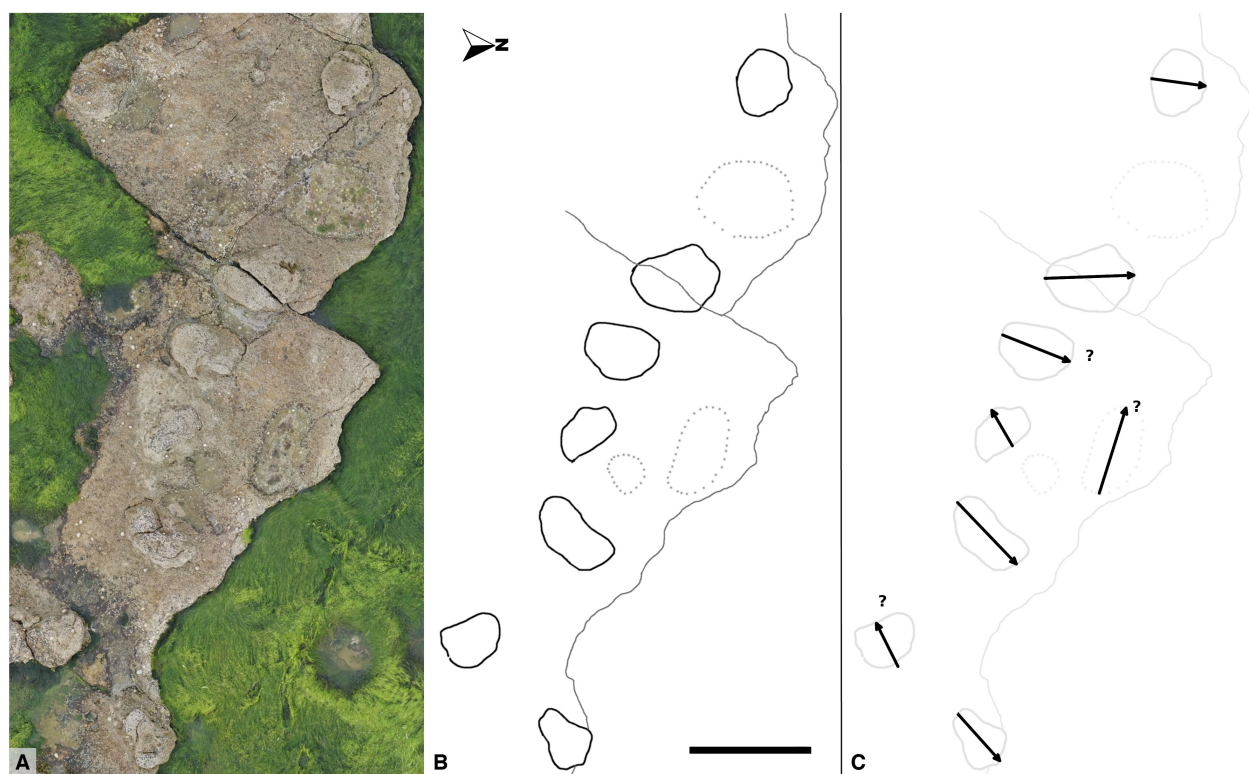


FIG. 12. Possible Trackway B shown as: A, an orthophoto; B, a line drawing showing the linear arrangement of these predominantly positive relief casts. C, arrows show the orientation of the track implied by either the remains of toes or the anterior widening of the pes. This inconsistent orientation indicates that Possible Trackway B is not a true trackway. Scale bar represents 1 m.

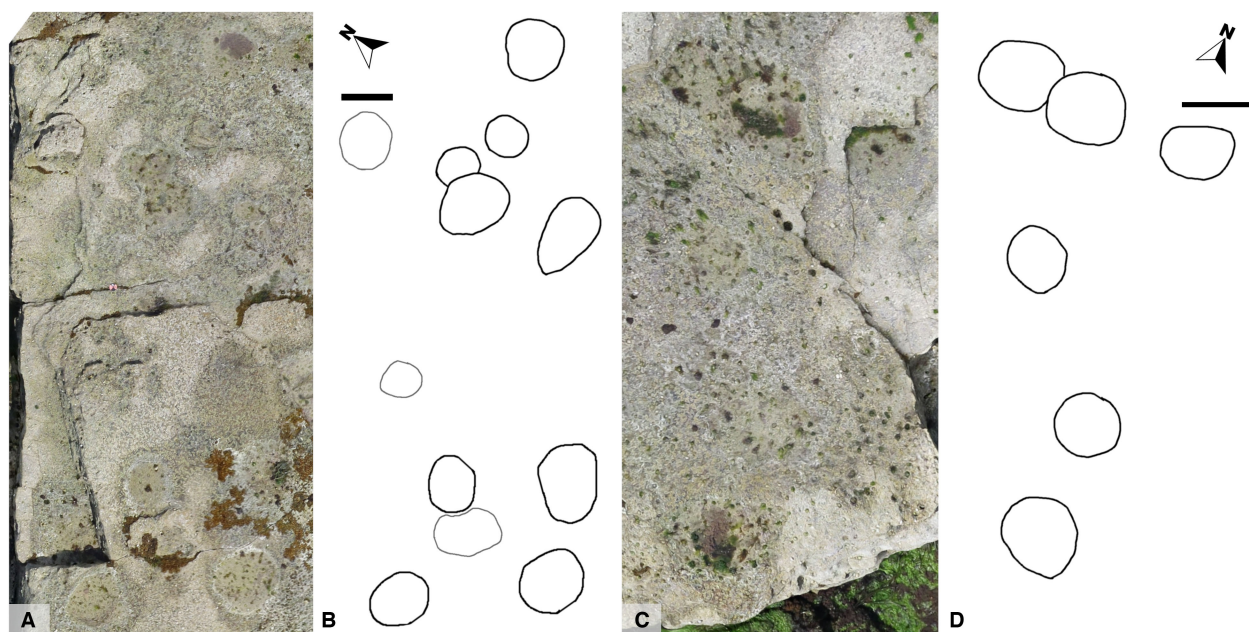


FIG. 13. Orthophotos and line drawings of Track Grouping I (A, B) and Track Grouping II (C, D) showing the spatial relationships of these track associations. Both of these groups of shallow impressions are located along the most seaward edge of the main track platform. Scale bars represent 50 cm.

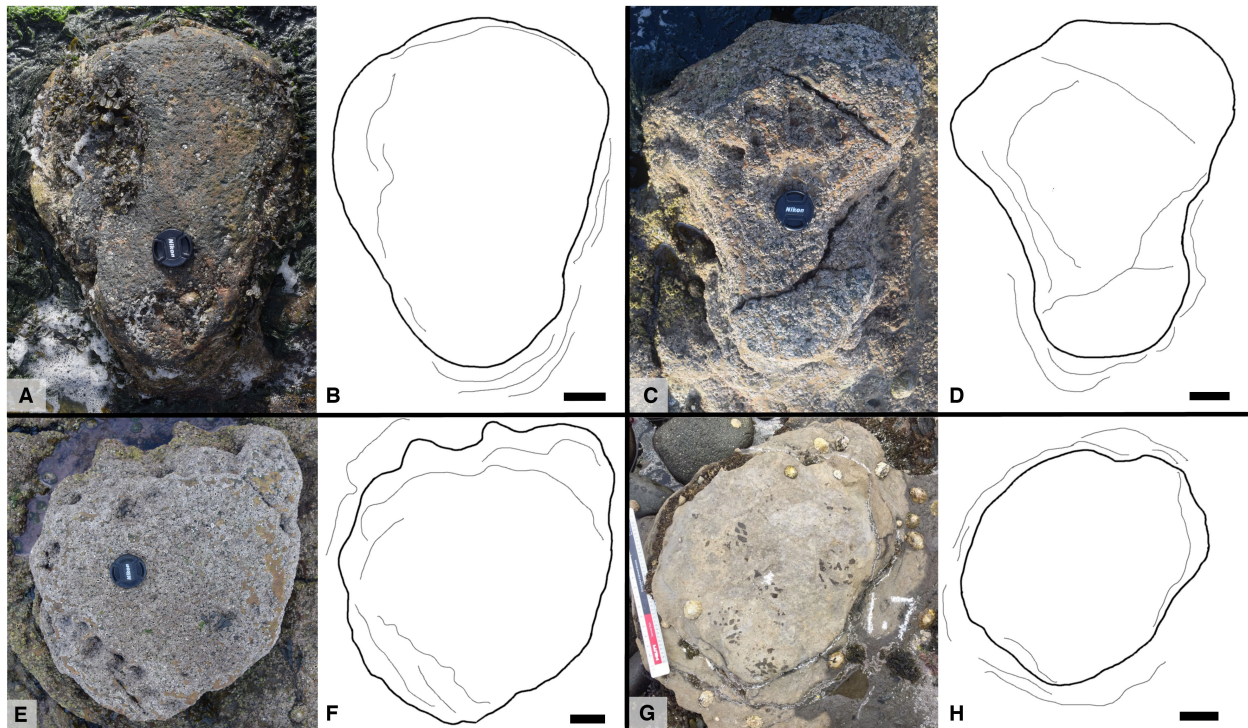


FIG. 14. Several examples of the sauropod tracks seen on the main track-bearing platform at Duntulm (A–F) and in the stratigraphically older layers to the north (G, H). DUNT_05 (A, B), DUNT_12 (C, D), and DUNT_17 (E, F) show the range in pes shape from elongated (sub-oval) to subcircular with the tracks widening anteriorly in each case. DUNT_T1.7 (G, H) shows a preservation style in which the cast has not yet fully weathered out of the surrounding sedimentary layer. The lens cap diameter is 5 cm. Scale bars represent: 5 cm (B, D, F); 10 cm (H).

varied based on whether the individual was pushing off the right foot (1.14 m) or the left foot (1.78 m). This variable progression reflects an uneven gait and hints at the animal possibly limping. Interestingly, despite this uneven gait, Trackmaker 3 is estimated to be moving the most quickly of these trackmakers. In general, trackway estimates for the Duntulm sauropods indicate that these animals were moving slowly through their environment.

Tridactyl tracks

A single, definite large tridactyl track (DUNT_08) is preserved as a low, positive relief cast on the main track-bearing platform. DUNT_08 (Fig. 17A, B; Table 3) is tridactyl and mesaxonic with extremely narrow toes that taper to points. The left toe is more poorly preserved than the right toe. The posterior margin of the track tapers to a U-shaped, narrow heel. The central digit has a sigmoidal sinuosity that is probably related to the movement of the foot through the substrate (Falkingham & Gatesy 2014). The track does not preserve any fine morphological details such as phalangeal pads. Due to its length (39.3 cm), characteristics of the toes, the

interdigital angles and the shape of the heel, this track is likely to be associated with a large theropod trackmaker.

Another, similarly preserved tridactyl footprint (DUNT_T3.3; Fig. 17C, D; Table 3) was observed in the outcrops of the Duntulm formation north of the main track-bearing platform (stratigraphically lower). As with DUNT_08, this track is preserved as a low, positive relief cast. DUNT_T3.3 is tridactyl and mesaxonic with narrow digits. The right toe is more poorly preserved than the left toe and appears as a shallow impression rather than the infilling cast. The posterior margin of DUNT_T3.3 is narrower and tapers to a V shape. This posterior margin may reflect a partial metatarsal pad (Lallensack *et al.* 2022, fig. 3). As with DUNT_08, DUNT_T3.3 (L = 31.0 cm) is likely to be associated with a large theropod trackmaker. Several other, more poorly preserved tridactyl footprints that generally conformed to the track characteristics of DUNT_08 and DUNT_T3.3 were observed in these more northerly outcrops of the Duntulm Formation.

Additional support for the theropod affinity of these tracks can be found by comparing their track parameters to Moratalla *et al.*'s (1988) threshold values (Table 4). Although these tracks can be confidently interpreted as belonging to a theropod trackmaker, their preservation

grade of 1 (Marchetti *et al.* 2019) does not support assignment to a more specific ichnotype.

The estimated hip height of the theropod trackmaker on the main platform is 157 cm, and for the trackmaker in the stratigraphically lower layers it is 124 cm. Thus,

despite these tracks being large for a bipedal trackmaker, the theropods present at Duntulm paled in size in comparison with the sauropod trackmakers. Tridactyl tracks are extremely sparse at this locality, with only a single one present among the dense sauropod traces of the main



FIG. 15. Track preservation style in which manus–pes pairs are linked together by the sediment deformation that occurred while the trackmaker was walking. This sediment deformation has protected the shape of the tracks as they are preserved as casts. Field photographs (A, C) and line drawings (B, D) of DUNT_49–DUNT_50 and DUNT_51–DUNT_52, respectively. A field photograph (E) of DUNT_49–DUNT_50 shows the higher elevation of the manus cast above the pes cast. The lens cap diameter is 5 cm. Scale bars represent 5 cm.

FIG. 16. The variability in relative size of the manus–pes pairs at Duntulm illustrated by DUNT_6 and DUNT_7 (A, B), DUNT_26 and DUNT_27 (C, D) and DUNT_40 and DUNT_41 (E, F). In all cases, the pes is larger than the manus, but the manus ranges from around three-quarters the size of the pes (DUNT_26–DUNT_27) to less than a quarter the size of the pes (DUNT_40–DUNT_41). The lens cap diameter is 5 cm. Scale bars represent 5 cm.

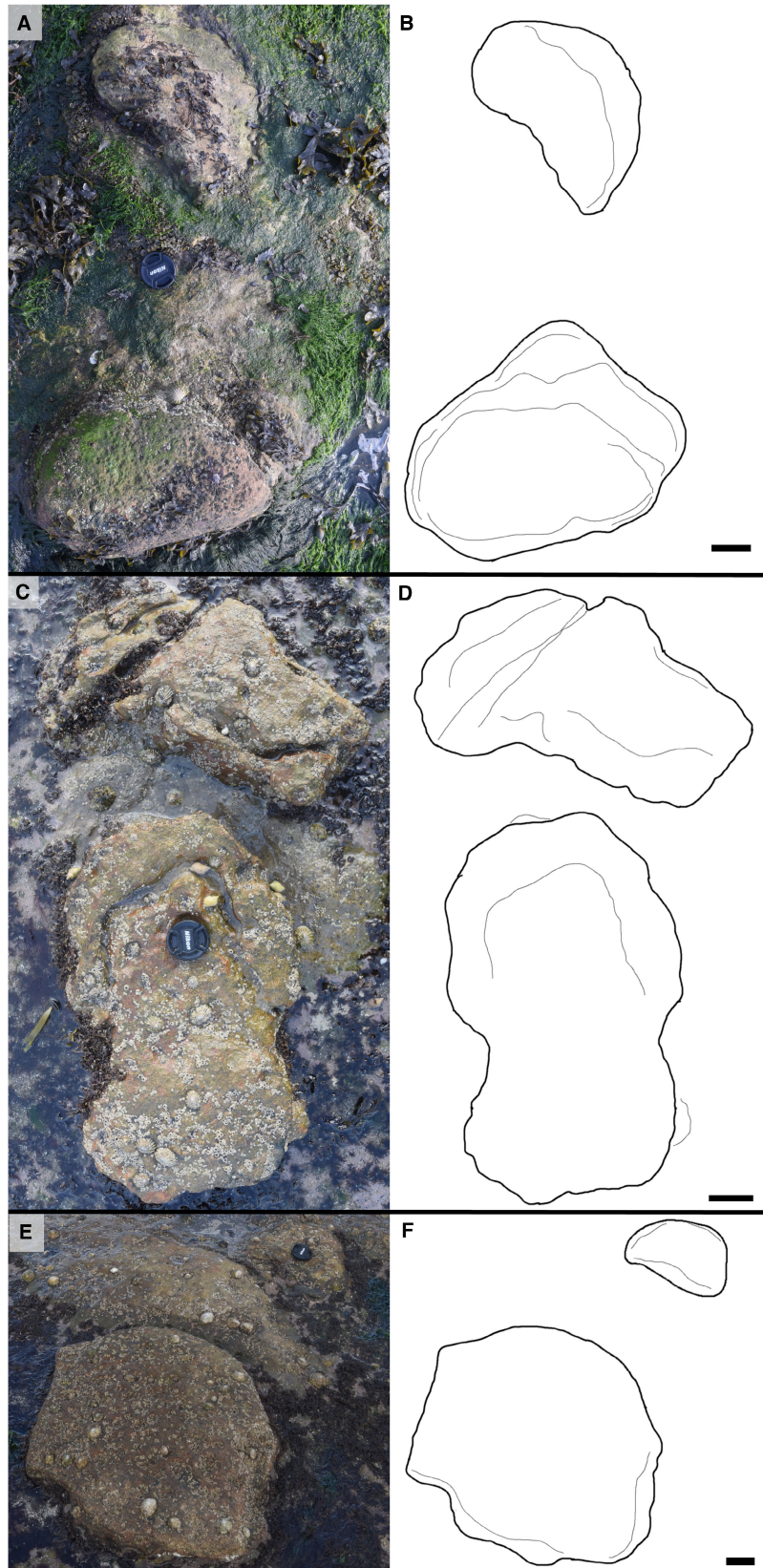


TABLE 2. Speed estimates, gait, and progression for Duntulm trackways.

	Avg. PL (cm)	H (cm)	Velocity (A) (m/s)	Velocity (B) (km/h)	S/H	Gait	Progression (cm)
Trackmaker 1	67	268	0.43	1.6	0.52	Walking	0.63
Trackmaker 2	54.5	218	0.44	1.6	0.55	Walking	—
Trackmaker 3	52	208	2.14	7.7	1.47	Walking	Variable
Trackmaker A	53	212	0.55	2.0	0.65	Walking	0.81

The progression was not calculated for Trackmaker 2 because it was not possible to measure the width of angulation of the pes from the trackway. The length of DUNT_02 was used as the pes length for Trackmaker A calculations because the margins of the cast were clear. H, hip height; PL, pes length; S, stride length.

track-bearing platform and several isolated traces observed lower in the stratigraphy.

DISCUSSION

Implications for sauropod behaviour

Breviparopus-like sauropod tracks and narrow gauge trackways dominate the main platform at Duntulm. The lines of progression (orientations) of the trackways cross-cut one another and none exhibit any parallelism in orientation or close association (Table 1; Fig. 18). Therefore, despite the large number of tracks present at Duntulm, no definitive evidence of gregarious behaviour is observed. Additionally, the sauropods do not seem to have been constrained by local topography in the lagoonal environment in which they travelled. This lack of observable grouping behaviour between individuals is also seen at other *in situ* tracksites on Skye (dePolo *et al.* 2018, 2020). Additionally, although the Duntulm trackways are sparser and substantially shorter, the combination of straight (e.g. Trackway 3) and curving (e.g. Trackway 1) trackways is similar to that observed in the Galinha track-site in Portugal and interpreted as evidencing milling behaviour (Santos *et al.* 2009; Castanera *et al.* 2014). These interpretations are consistent with those presented in the initial brief description of the site (Brusatte *et al.* 2016), but here are supported by our site maps and trackway measurements that enable us to clearly map tracks to different sedimentary horizons and to distinguish trackways.

Evaluation of environmental partitioning hypothesis

One of the most notable aspects of the Duntulm tracksite is the preservation of the majority of the tracks in an oyster shell-bank, which led Brusatte *et al.* (2016) to interpret the sauropod trackmakers as regularly walking through Skye's shallow lagoons over multiple generations. If correct, this interpretation implies a possible

environmental preference for Skye's sauropod dinosaurs. This idea was presented as a hypothesis by Brusatte *et al.* (2016), and here we test it further.

The sediments of the Great Estuarine Group span a paralic sedimentary sequence ranging from fluvio-deltaic to lagoonal sediments (Harris & Hudson 1980). More specifically, these rocks were deposited in a dynamic coastal environment that included a series of partially protected lagoons separated by sandy deltas (Harris & Hudson 1980; Hudson & Andrews 1987), subaerially exposed mudflats (Hudson 1983) and thin layers of marine sediments (Barron *et al.* 2012).

Skye's dinosaur footprints are predominantly found in two types of depositional environment in the Great Estuarine Group: nearshore lagoons and subaerially exposed mudflats. Examination of the relationship between the depositional environment in which the footprints were found and the inferred trackmaker reveals an apparent pattern. *In situ* sauropod footprints such as those at Duntulm are also found in lagoonal sediments at Brothers' Point (dePolo *et al.* 2018). In both cases, sauropod traces dominate the assemblage. In contrast, the sites preserving sediments that were once subaerially exposed (as indicated by the presence of desiccation cracks on the track-bearing surface) preserve much more diverse ichnoassemblages of small to large theropods, possible ornithopods and small thyreophorans (e.g. dePolo *et al.* 2020). Qualitatively, it appears that different clades of dinosaurs on Skye demonstrated preferences for the substrate on which they walked.

Here, we statistically tested this hypothesis by creating a dataset of the tracks surveyed in this study and all tracks previously described from the Isle of Skye (Andrews & Hudson 1984; Clark & Barco Rodríguez 1998; Clark *et al.* 2004, 2005; Marshall 2005; Clark & Gavin 2016; dePolo *et al.* 2018, 2020). The key assumptions underlying the dataset were: (1) that the dinosaur tracks were formed independently of one another unless a clear association could be demonstrated (i.e. trackway or manus–pes pair); (2) that subaerial mudflats would be recognized by the positive identification of desiccation cracks on the track-bearing surface; and (3) that dinosaur

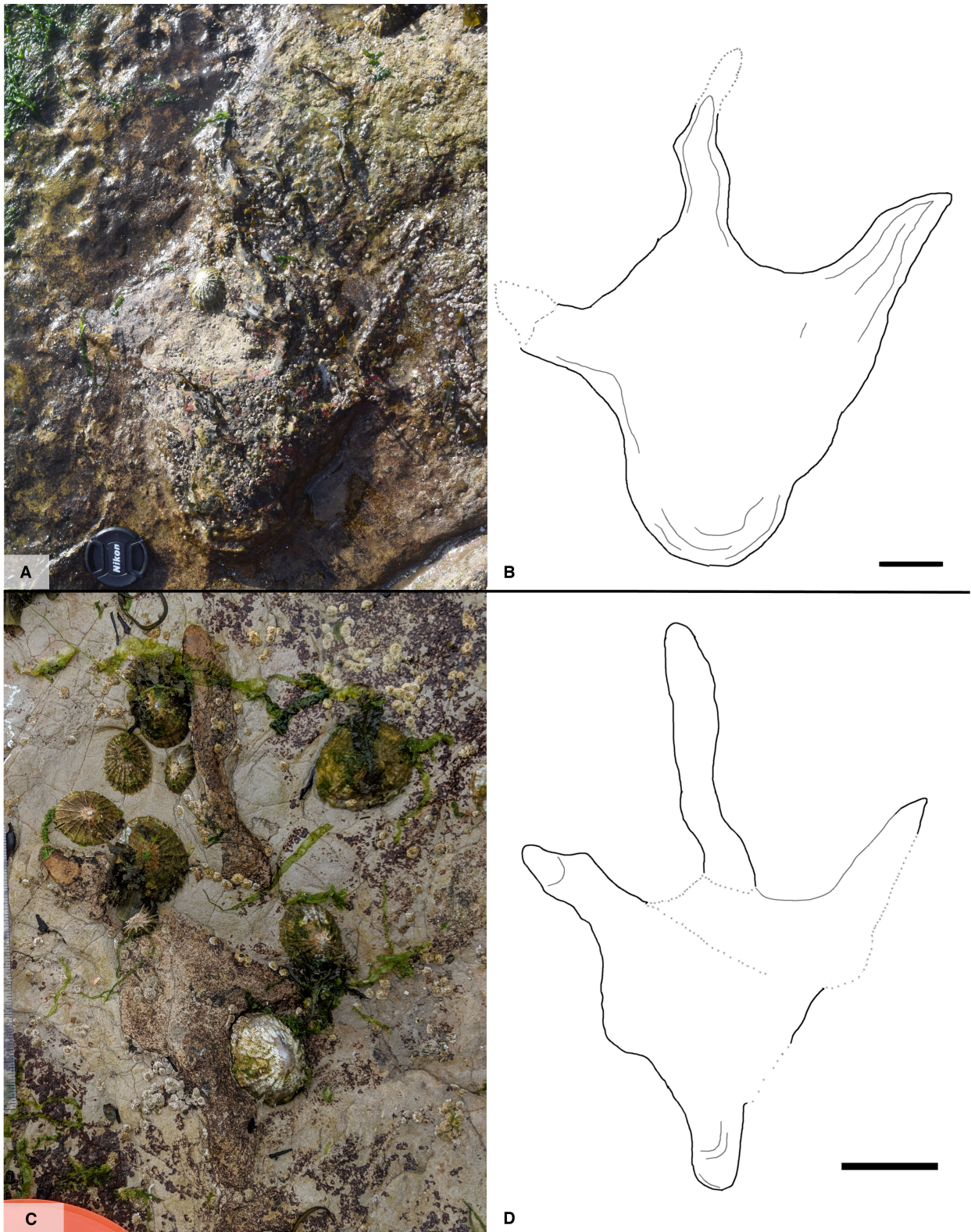


FIG. 17. Tridactyl footprints at Duntulm represented by photographs and line drawings of: A–B, DUNT_08; C–D, DUNT_T3.3. In both cases, these tridactyl tracks exhibit the narrow toes and tapering heels that are more consistent with a theropod trackmaker. The lens cap diameter is 5 cm. Scale bars represent 5 cm.

TABLE 3. The track measurements of DUNT_08 and DUNT_T3.3 (see Fig. 3 for abbreviations).

ID	L (cm)	W (cm)	K (cm)	M (cm)	BL2 (cm)	BL3 (cm)	BL4 (cm)	LII (cm)	LIII (cm)	LIV (cm)	WBII (cm)	WBIII (cm)	WBIV (cm)	WMII (cm)	WMIII (cm)	WMIV (cm)	α (°)	β (°)
DUNT_08	39.3	36.4	24.2	14.7	11.0	14.4	14.9	31.0	39.3	34.7	4.5	6.8	3.8	2.7	2.8	3.3	36.9	31.2
DUNT_T3.3	31.0	22.1	15.6	–	6.5	14.7	9.9	21.5	31.0	23.9	2.5	2.8	–	1.7	1.5	–	24.9	32.5

Some measurements of DUNT_T3.3 could not be taken because of the poor preservation of the right digit.

tracks reported from loose blocks along the coast would be included only if depositional environment could be determined from those blocks. The tracks were characterized by ichnotype and divided into groups based on trackmaker and on depositional environment. Two trackmaker groups (sauropod and non-sauropod) and two depositional environments (lagoon and subaerial mudflat) were defined.

Although the non-sauropod category could potentially be subdivided further into theropod, ornithopod and thyreophoran trackmakers, we have elected to maintain the broader category for two reasons. Most critically, in the case of tridactyl footprints, it is difficult to distinguish between theropod and ornithopod trackmakers (Moratalla *et al.* 1988; Lockley 2009; Lallensack *et al.* 2016, 2020). Additionally, when subdividing inferred non-sauropod trackmakers into specific clades, the number of tracks in each category becomes too low to place much confidence in the statistical analysis. For example, when inferred stegosaur footprints from Skye are tabulated, the trackway from which the majority of these footprints are known collapses into a single occurrence (dePolo *et al.* 2020), and only four independent thyreophoran track occurrences can be reported for the island. The aggregation of these different trackmakers in the non-sauropod category was the best way to ensure that the observed substrate preferences could be rigorously interrogated statistically. We recognize that our methods are a coarse approach to this question and should be treated as an exploratory framework that can be continually updated and tested as Skye's dinosaur track record improves.

We also evaluated the tracks based upon a varying confidence scale, with the most conservative track count including only definite tracks for which it was possible to clearly determine whether the trackmaker was a sauropod or a non-sauropod. Our least conservative track counts included both definite tracks and probable tracks. The track counts for both the most conservative confidence and the least conservative confidence are summarized in Table 5.

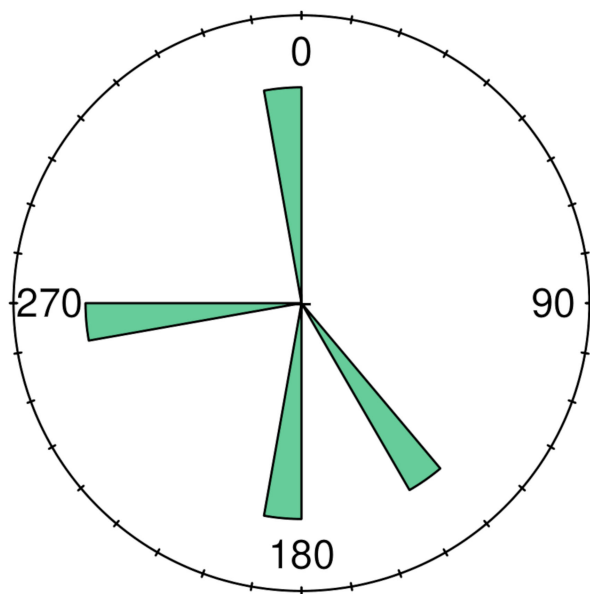
We used a chi-squared test for categorical variables to assess these track groupings. The null hypothesis tested was 'different dinosaur track groups do not preferentially occur in different substrates'. Another framing of the null hypothesis is 'environmental partitioning does not exist between different dinosaur groups'.

Table 6 lists the expected values in each category if the null hypothesis of no substrate preference among Skye's dinosaurs is true. Given that all of the expected frequencies are above a threshold value of 10, no Yates correction for continuity was applied for the chi-squared test. Table 7 lists the chi-squared value for each track grouping and the resultant probabilities.

TABLE 4. Theropod vs ornithopod affinities for tridactyl footprints at Duntulm (see Fig. 3 for abbreviations).

Track parameters	Threshold values and probability that the track is either theropod or ornithopod	DUNT_08	DUNT_T3.3
L/W	80.0% Theropod > 1.25 > Ornithopod 88.2%	1.08	1.4
L/K	70.5% Theropod > 2.00 > Ornithopod 88.0%	1.62	2.0
L/M	65.0% Theropod > 2.00 > Ornithopod 90.7%	2.67	—
BL2/WMII	76.1% Theropod > 2.00 > Ornithopod 97.4%	4.07	3.8
BL3/WMIII	72.7% Theropod > 2.20 > Ornithopod 97.7%	5.14	9.8
BL4/WMIV	76.1% Theropod > 2.00 > Ornithopod 97.6%	4.52	—
LII/WBII	84.6% Theropod > 3.75 > Ornithopod 90.2%	6.89	8.6
LIII/WBIII	70.6% Theropod > 4.00 > Ornithopod 91.5%	5.78	11.1
LIV/WBIV	73.7% Theropod > 3.75 > Ornithopod 93.4%	9.13	—

All track parameters for DUNT_T3.3 demonstrated a theropod affinity. The majority of the track parameters assessed for DUNT_08 demonstrated a strong theropod affinity. The two values that suggested an ornithopod affinity (L/W and L/K) may have been affected by the poor preservation quality of the distal ends of digit III.

**FIG. 18.** Rose diagram of the trackway bearings at Duntulm, showing that there is no preferential orientation in their lines of progression. There is no evidence of either gregarious behaviour among the sauropods or a topographic constraint on their movement.

For both the most conservative track groupings and the least conservative track groupings, the null hypothesis was strongly rejected ($p < 0.0001$). Both track groupings were also assessed using Fisher's exact probability test with similar results ($p < 0.0001$ in both cases). As with the chi-squared test, the null hypothesis is rejected. The consistent rejection of the null hypothesis demonstrates that the qualitative relationship observed between depositional environment and inferred trackmaker is statistically significant. Non-sauropod tracks are more commonly found on subaerially exposed mudflats while sauropod

TABLE 5. Two-way values of Skye's trackmakers and substrates.

	Most conservative track totals		Least conservative track totals	
	Lagoon	Subaerial mudflat	Lagoon	Subaerial mudflat
Sauropod	73	0	154	0
Non-sauropod	20	53	21	74

The most conservative table counted only definite tracks with a clear trackmaker affinity while the least conservative track totals included possible tracks with an inferred trackmaker affinity.

TABLE 6. Expected values of Skye's trackmakers and substrates.

	Expected most conservative track totals		Expected least conservative track totals	
	Lagoon	Subaerial mudflat	Lagoon	Subaerial mudflat
Sauropod	47	26	108	46
Non-sauropod	47	26	67	28

Chi-squared testing of categorical variables relies on the estimation of what the distribution of the variable counts should be if the null hypothesis is true. The expected values diverged quite strikingly from the observed, particularly with regard to the number of sauropod tracks expected in mudflat environments.

tracks are, currently, exclusively found in lagoonal sediments. These trends indicate that the different dinosaur groups may have mostly kept to different places in the marginal coastal system and therefore engaged in environmental partitioning.

TABLE 7. Chi-squared values and probabilities for Skye trackmakers and substrates.

	Most conservative track totals	Least conservative track totals
χ^2	83.20	170.68
d.f.	1	1
p-value	7.40×10^{-20}	5.25×10^{-39}

The chi-squared test results remained robust when the number of sauropod tracks was substantially decreased and the number of non-sauropod tracks substantially increased in the lagoons (Tables S4–S7). This sensitivity analysis was conducted to reflect the low preservation grade of footprints in these depositional environments. Many footprints at Duntulm and Brothers' Point lacked clear diagnostic features but were assessed as belonging to sauropods because they had the same general shape and size of more distinctive tracks. Varying the relative numbers of sauropod and non-sauropod tracks in lagoonal environments showed that, even if half of Skye's sauropod tracks have been misidentified and should be reclassified as deriving from non-sauropod trackmakers, the statistical significance of the observed trend between substrate and trackmakers is preserved.

This robustness of the statistical result arises from the complete lack of sauropod tracks in clearly subaerially exposed environments. The absence of sauropods in these environments is more easily ascertained than the identity of some of the more weathered tracks at Duntulm and Brothers' Point and thus, these observed values can be treated with more confidence. Although there is always the potential of additional tracksite discoveries changing the character of the dataset, the strong statistical support for a relationship between the trackmaker and the substrate seems robust after this sensitivity testing.

We posit that this pattern in the Skye footprints reflects a behavioural signal among these different dinosaur groups. We express additional confidence in that interpretation by performing a thought experiment on an alternative hypothesis for the observed track distribution. This alternative hypothesis argues that the observed distribution may not result from different dinosaurs occupying different micro-environments in the coastal setting, but from differences in track preservation potential in different substrates. The preservation hypothesis acknowledges the statistical significance of the distribution of different track types across different depositional environments but is critical of the inference of environmental partitioning.

The sauropod dominance in lagoonal track assemblages could arise, not because of sauropods being more abundant, but because the tracks of smaller animals are less

likely to be preserved in that setting. Smaller-bodied animals will begin to float at shallower water depths than the larger-bodied sauropods, which would reduce the opportunity to leave footprints in the submerged substrate. Indeed, a size bias in the sparse tridactyl footprints preserved in lagoonal settings (Clark *et al.* 2004; dePolo *et al.* 2018) towards larger tracks might lend ancillary support to this hypothesis. This framing illustrates that all dinosaur clades could be present in lagoonal environments even if one cannot conclusively demonstrate their presence using the positive proof of footprints.

This preservation argument weakens, however, when examining the track assemblages in the mudflats. To date, on the Isle of Skye, no sauropod footprints have been found at dinosaur tracksites preserving a subaerially exposed mudflat. Subaerial mudflats capture a wide variety of track shapes and sizes, ranging from thyreophoran trackways (dePolo *et al.* 2020), to tiny (<10 cm long) to large (*c.* 40 cm) size classes of tridactyl footprints (e.g. Clark *et al.* 2005; dePolo *et al.* 2020). No clear formation mechanism exists for excluding the registration of sauropod footprints from substrates suitable for both large tridactyl trackmakers and smaller trackmakers. Additionally, we would expect post-registration erasure mechanisms such as erosion to preferentially remove the smaller and shallower footprints first. If no sauropod tracks are preserved, then it can be reasonably inferred that this absence truly reflects an absence of sauropods in that locality during the formation of the other tracks rather than a preservational bias. This is not to say that Skye's sauropods never walked on the subaerially exposed mudflats. Rather, if they did, they did it so rarely compared with other contemporaneous dinosaurs that we have yet to find evidence for it, evidence that we should be able to see in the track assemblages preserved on these mudflats.

In summary, there is a statistically significant relationship between trackmakers and substrate on the Isle of Skye and this pattern cannot wholly be rationalized by invoking biases in track preservation. While we cannot be confident that smaller dinosaurs were absent from Skye's lagoons, on the basis on the available evidence, we can see that, to our current knowledge, sauropods are absent from subaerially exposed mudflats. We, therefore, argue that Skye's sauropods preferred the submerged lagoonal substrates to those of the subaerially exposed mudflats. This preferred substrate gives an insight into how different dinosaur clades in this dynamic coastal ecosystem might have partitioned their micro-environments.

The frequent appearance of sauropod footprints in coastal and marginal marine settings has been noted for several decades, with the definition of the *Brontopodus* ichnofacies underpinned by the association of sauropod footprints with marine carbonate platforms (Lockley 1991; Lockley *et al.* 1994c). Although a total-evidence dataset of

body and trace fossils for Cretaceous dinosaurs suggested a preference for inland, terrestrial environments for sauropods (Butler & Barrett 2008), this tension can be resolved by the later insight that different sauropod clades may have frequented different environments. Specifically, it appears that, while titanosaurs (the predominant sauropods in the Cretaceous) preferred inland environments, more primitive sauropods with narrow gauge trackways frequented coastal settings such as carbonate platforms (Mannion & Upchurch 2010). Despite this broad pattern of apparent environmental preference, titanosaur tracks are known from carbonate platforms and other marginal marine settings (e.g. Marmi *et al.* 2014; Console-Gonella *et al.* 2017; Díaz-Martínez *et al.* 2018). In the case of Cretaceous South America, it has been suggested that titanosaurs may have been using these marginal environments as migration pathways rather than preferentially inhabiting them (Meyer *et al.* 2021; Tomaselli *et al.* 2021). The hypothesis of a migration corridor is not currently testable in the context of Skye's more primitive (non-neosauropod) sauropod trackmakers in large part due to the limited spatial exposures of the island's tracksites. Furthermore, the patterns we observe on Skye relate to fine-scale differences between individual substrates (*sensu* Lyson & Longrich 2011) rather than the overall island's palaeogeographical context. At the level of detail of most other studies of sauropod environmental preferences, all of Skye's depositional environments would be considered 'coastal' or 'marginal marine' and the fine-scale environmental partitioning we are suggesting here would be collapsed into that broader category. Ultimately, regardless of the scale of the analysis, the myriad descriptions of sauropods in these lagoonal and coastal environments (e.g. Pittman 1989; Meyer & Pittman 1994; Day *et al.* 2004; Nicosia *et al.* 2007; Navarrete *et al.* 2014; Moreau *et al.* 2020; and Butler *et al.* 2024) suggest that these behemoths habitually passed through these settings. In light of this evidence, Skye's sauropods are consistent with the emergent global pattern of sauropods frequenting these marginal environments.

CONCLUSION

Since Mike Benton's description of one of Scotland's first dinosaur bones in 1995, our knowledge of dinosaurs from the Isle of Skye has increased, largely through the discovery of numerous dinosaur tracksites. The main platform of the Duntulm tracksite is the most extensive *in situ* dinosaur tracksite known from the Isle of Skye. The rocks composing the site were deposited in a shallow water, lagoonal environment. This interpretation is supported by both the carbonate sedimentology and by the invertebrate fossils present (e.g. echinoids). We mapped more than

150 tracks from this site, the vast majority of which were sauropod tracks similar to the ichnogenus *Breviparopus*. The trackways we observed had a narrow gauge and did not show any parallelism or other signs of gregarious behaviour, although one hints at a dinosaur walking with an uneven gait. The presence of tracks on multiple stratigraphic layers with a variety of preservation styles gives credence to the inference that multiple generations of individuals occupied this lagoonal system.

Additionally, our synthesis of all published dinosaur footprints from the Isle of Skye allowed for statistical analysis of behaviour in dinosaur communities in this coastal environment. On Skye, sauropods preferred lagoonal environments while other dinosaur clades could be more commonly found on shore, in subaerially exposed mudflats. This study highlights one of the qualities of a dinosaur footprint that is pivotal to its value to palaeontology: it is intrinsically linked to the ecosystem in which the dinosaur was living.

Acknowledgements. We write this paper in commemoration of Mike Benton's distinguished career in research, teaching, mentorship and public engagement. Mike has been a long-time colleague, friend and mentor to many of us. Three of us (SLB, TJC and DF) were educated in the University of Bristol's Palaeobiology MScR programme that Mike developed. Mike was SLB's Master's supervisor, and provided invaluable support and advice, inspiring SLB to write the types of popular science palaeontology books that Mike pioneered. Later, SLB moved from the USA to Mike's native Scotland and established a research lab at the University of Edinburgh. PEDP wrote this paper as part of her MScR thesis (dePolo 2017) at the University of Edinburgh (in the MScR programme developed by SLB with inspiration from his time in Bristol). Mike, SLB and PEDP are three generations of an academic lineage, which has helped Scotland become the locus of Jurassic dinosaur research. Sláinte Mhath, Mike!

The Duntulm site was discovered in the spring of 2015 by SLB and TJC during the PalAlba consortium's annual fieldwork on the Isle of Skye, which included DF, MW and DAR as team members, along with Hong-yu Yi and Shaena Montanari. Additional footprints in slightly older stratigraphic horizons were documented by the University of Edinburgh's 2018–2019 MScR in Palaeontology and Geobiology cohort (Will Foster, Kim Kean, Pei-Chen Kuo, Will Newton and Jules Walter), and undergraduate Dan Marke. We also thank Moji Ogunkanmi, Rachel Bartlett and Michela Johnson for fieldwork assistance, and Sarah McGrory and Colin MacFadyen of Scottish National Heritage for arranging collection and sampling permission. Minor Loan 1080 from the NERC Geophysical Equipment Facility supported the use of GNSS survey equipment at the site. PEDP's MScR work was supported by a student award from the Association of Women Geoscientists (AWG). Fieldwork funding was provided by the National Geographic Society (GEFNE185-16) and a Philip Leverhulme Prize (awarded to SLB), and by Derek and Maureen Moss, Richard Devereira, the Edinburgh Zoo, the Royal Zoological Society of Scotland and the Edinburgh Geological Society. This is PalAlba Publication Number 16.

We are grateful to Diego Castanera and an anonymous referee for constructive reviews that improved the quality of this manuscript, and to Sally Thomas for additional editorial comments.

Author contributions. **Conceptualization** SL Brusatte (SLB), TJ Challands (TJC), PE dePolo (PEdP); **Investigation** PEdP, SLB, TJC, D Foffa (DF), M Williamson (MW), NDL Clark (NDLC), DA Ross (DAR), TJ Wade (TJW); **Resources** DAR, TJW; **Supervision** SLB, TJC; **Visualization** PEdP; **Writing – Original Draft Preparation** PEdP; **Writing – Review & Editing** PEdP, SLB, TJC, DF, MW, NDLC, DAR, TJW.

DATA ARCHIVING STATEMENT

Data for this study including photogrammetric models (both of the whole tracksite and of subsampled sections), high-resolution orthophotos, and the underlying photo-sets and GNSS coordinates are available on Dryad at: <https://doi.org/10.5061/dryad.j3tx95xv6>

Editor. Emily Rayfield

SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.70116>):

Appendix S1. Track and trackway measurements and characteristics (Tables S1, S2), brief geological context of the Great Estuarine Group (Fig. S1), details of trackmaker and substrate characterization, and sensitivity tests of the environmental partitioning hypothesis (Tables S4–S9).

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