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Stops and turns: Uncommonly preserved theropod locomotive behavior patterns in an Upper Cretaceous tracksite from Torotoro National Park, Bolivia

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A B S T R A C T

The Carreras Pampa tracksite from the Upper Maastrichtian of Bolivia preserves one of the world's largest concentrations of dinosaur trackways. Thus far, we have assigned all but a small number of these trackways to theropod trackmakers. With such a high concentration of trackways, the Carreras Pampa tracksite is an excellent place to find evidence of a diversity of uncommonly preserved dinosaur locomotive behaviors. To date, we have found four trackways with turns ranging from 44° to 84° and describe a fifth trackway with a turn of 38° that contains unusual features. Four trackways have been found that indicate the trackmaker was walking, stopped or paused, and then began walking again. One of the trackways that records a stop also shows evidence that the trackmaker was limping. Another trackway shows that the trackmaker made a sudden, abrupt change in its direction of movement, probably in response to an unknown obstacle, and then gradually returned to its original orientation. One series of fossil traces is reported that we believe is best interpreted as a crouching trace involving multiple tracks and tail traces. These tracks were made by theropods of various sizes, with track lengths ranging from 7.3 to 32.4 cm. These trackways show that a diversity of locomotive behavior patterns occurred during the formation of the Carreras Pampa tracksite.

1. Introduction

The majority of dinosaur trackways that have been described represent walking individuals following mostly straight paths. Thus, any trackways that deviate from this pattern are of interest because they indicate behavior that is not usually preserved at most tracksites. Lockley et al. (2021) reviewed dinosaur trackways that made significant changes in direction. While minor changes in direction are common, significant turns with changes in direction of 45° or more are rare. Of the trackways reviewed by Lockley et al. (2021), the majority were made by theropods and sauropods, with only one example of an ornithopod trackway making a turn of more than 45°. Intrinsic and extrinsic factors can influence the cause of significant changes in direction. However, determining the exact nature of those factors is difficult, if not impossible, due to the difficulty of determining the cause of behaviors solely from trackways. Another factor that influences the preservation of turns in trackways is the size of a given tracksite exposure. Large tracksites are more likely to register turns than small tracksites, thus, preservation of large outcrops is important for preserving evidence of turns (Lockley et al., 2021).

Examples of a dinosaur trackmaker stopping or pausing during normal progression and then continuing again are uncommon in the literature (Lee et al., 2022). This type of locomotive behavior is indicated by trackways that show the trackmaker placed its feet side-by-side or nearly side-by-side at some point along the path of a trackway (Weems, 2021). To our knowledge, there have been no reports of sauropod trackways indicating that the trackmaker stopped, limiting evidence for this type of behavior to bipedal dinosaurs. There has only been a small number of reports of trackways indicating this type of behavior since the first report in the United States by Hitchcock (1927). Often, in these reports, a trackway indicating that the trackmaker stopped is only one of many trackways described and does not receive significant attention in the paper. A notable exception is Weems (2021), who described many trackways indicating one or more stops from the Culpeper Quarry in Virginia, USA.

This paper aims to describe trackways from the Carreras Pampa tracksite in the Torotoro National Park (TTNP), Bolivia, that indicate uncommonly preserved dinosaur trackmaker behavior. We describe five trackways with one or more turns ranging from 38° to 84° and a trackway showing a sudden change in direction that we interpret as a dinosaur trying to avoid some unknown factor or obstacle. In addition to trackways showing changes in direction, we also describe four trackways that indicate the animal stopped or paused, placing both feet near each other and then began moving again. Finally, we described a series

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of tracks and tail traces that we believe are best described as a crouching trace of a theropod dinosaur. The trackways reported here highlight the uniqueness of the Carreras Pampa tracksite in preserving multiple examples of locomotive behavior that are uncommonly preserved elsewhere.

2. Geological setting

The sedimentation of Cretaceous formations in the Eastern Cordillera occurred in the Andean back-arc basin (Meyer et al., 2021). These Cretaceous formations compose the Puca Group, which overlies Paleozoic layers. One of the formations that form the Puca Group is the El Molino Formation, well-known for dinosaur tracks (Esperante et al., 2023; Meyer et al., 2018, 2021; Leonardi, 1981, 1989; Riguetti et al., 2021). The predominant facies of the El Molino Formation are mudstones or marls that are intercalated with thin, fine to coarse-grained limestones and very fine sandstones (Sempere et al., 1997). At the study site, the track-bearing unit is an ooid, ostracod-rich arenite. A thin, green layer of claystone overlies the track-bearing layer, and a red mudstone overlies the green claystone layer. Deposition of the El Molino Formation occurred in a lacustrine system; however, the degree and frequency of marine influence this system experienced has been disputed. Some have argued that this system was frequently in contact with marine waters due to marine transgressions (Gayet et al., 1993; Sempere, 1994). Others have proposed that connection with marine waters was less frequent and controlled by oscillations of water levels within the system (Camoin et al., 1997; Rouchy et al., 1993). The El Molino Formation was deposited between Maastrichtian and Paleocene times (Fink, 2002) and is equivalent to the Vilquechico Formation of Peru (Jaillard et al., 1993) and the Yacoraite Formation of Argentina (Cónsole-Gonella et al., 2017; Marquillas et al., 2011).

The Carreras Pampa tracksite comprises at least eight exposures (total exposure area of ~8,100 m) in close proximity labeled as sites 1–8 (Fig. 1C). Sites 1–3 are continuous with each other, with sites 1 and 2 containing the majority of the exposed tracksite surface. All the sites are composed of the same track-bearing surface of the same stratigraphic horizon. Ripple marks are preserved in the track-bearing surface, and track depths range from very shallow to very deep (0.5 cm – >15 cm), with large variations in depth occurring within the same trackway in some cases. These observations indicate that 1) the tracksite was covered with water at some point, but not while the tracks described below were formed, and 2) the substrate consistency varied across the tracksite for at least some of the track-forming interval resulting in tracks of varying depths within the same trackway. Almost all of the tracks at the Carreras Pampa tracksite are preserved as concave epireliefs, with a very small number preserved as convex epireliefs. In addition to tracks, multiple different forms of invertebrate bioturbation are preserved on the track-bearing surface. The trackways described here are from sites 1, 2, and 3 of the Carreras Pampa tracksite.

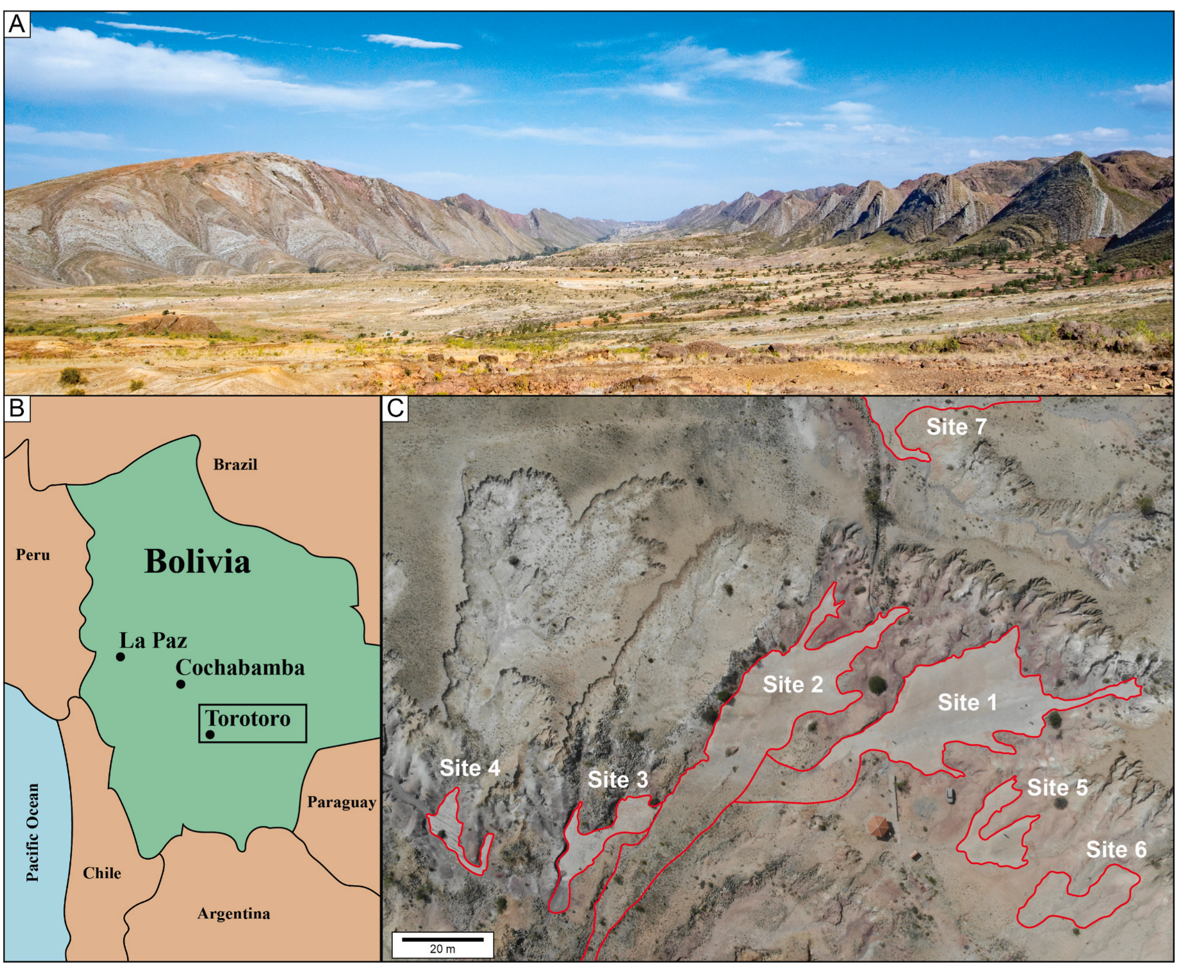

Fig. 1. (A) View of the Torotoro syncline in which the study site is located. This view is looking towards the southeast. (B) Map of Bolivia showing the location of Torotoro. (C) Map of the sites at the Carreras Pampa tracksite. Sites 1–3 are continuous with each other, with sites 1 and 2 representing most of the exposed surface area. All sites represent the same track-bearing unit.

3. Material and methods

Each trackway was named as part of a study of all the trackways at the Carreras Pampa tracksite, and we used the same names in the present study, except for the crouching trace which we gave a unique name following the same naming pattern. These names are composed of first the year in which data for the trackway was collected, then the site in which the trackway was located, and finally the trackway number. All the tracks included in the present study are preserved as concave epireliefs. The tracksite surface was swept clean, and tracks were cleaned out in preparation for measuring and photographing the tracks and trackways. We measured all tracks for footprint length (FL), footprint width (FW), anterior triangle length (ATL), interdigital angles (αII-III and αIII-IV), pace length (PL), and stride length (SL). We used rulers, tape measures, and digital angle finders to record these data. We followed Lockley (2009) and Thulborn (1990) for these measurements, with the exception that we measured FW from the tip of digit II to the tip of digit IV, as this was the most efficient way to measure FW. We measured anterior triangle length using the tip of digits rather than digit pads, as pad impressions are not preserved in these tracks. In some instances, we could not complete all measurements for a given track because of deformation, the track being stepped on by another track, or other reasons. We calculated pace angulation (PANG) following Thulborn (1990). We calculated height at hip (h) using FL*4 (Alexander, 1976; Henderson, 2003). An advantage of calculating h in this way is that it gives relatively conservative speed estimates for the trackmakers (Navarro-Lorbés et al., 2021). For estimating the gaits of trackmakers, we used the principle that for bipedal dinosaurs, the transition from walking to running occurs when the ratio of SL/h exceeds 2.0 (Alexander, 1976; Navarro-Lorbés et al., 2021; Ruiz and Torices, 2013). We calculated the speeds of the trackmakers following Alexander (1976).

We used a Canon 7D Mark II camera with a Canon EF 24–70 mm lens to photograph the tracks and trackways. We took photographs to create panoramas by mounting the camera on a monopod held at ~2 m with the camera pointed down at a 90° angle relative to the track-bearing surface. These photographs were then made into panoramas using the software PTGui Pro (v. 12.21). Lockley et al. (2021) used change in azimuth direction and tortuosity to describe the turns of dinosaur trackways. Both are used in the present study. Tortuosity is calculated by dividing the direct length (DL) between the start and end points of a trackway segment by the total length (TL) of the same segment (DL/TL). We measured the TL of trackways in the field. We used the software ImageJ (v. 2.1.0/1.53c) to measure the DL of trackways from panoramas of the trackways. We used a Brunton compass to measure the orientations of trackways in the field. We created photogrammetric models using a separate series of photos from those taken for panoramas and the software MetaShape (v. 1.7.5). We then imported the models into Meshlab (v. 2022.02) for rotating to the XY plane. Finally, we added scale bars and created false-color depth maps using ParaView (v. 5.10.0).

4. Descriptions of trackways

The tracks described here are all true tracks with one possible exception (T22-1-102 L25). Several lines of evidence support that the Carreras Pampa tracksite layer is the surface that the dinosaurs walked on: 1) dinosaur swim traces occur in the same layer as the other tracks (described in another publication being prepared), 2) expulsion rims are preserved in walking tracks and swim traces, 3) fossil bird tracks and very small theropod tracks are preserved in the same layer (described in other publications being prepared), 4) ripple marks are present in the trackbearing layer and in some instances are stepped on by tracks or cut through by swim traces, 5) the absence of deformation in the green claystone or red mudstone that are directly above the trackbearing surface, 6) the occurrence of rosette-like invertebrate burrows within tracks (these burrows form rosette-like structures on the surface of a bed, and if those occur inside the impression of a track, it means that the impression is that of a true track on the original surface where the dinosaurs walked).

The usefulness of preservation scales to describe and compare dinosaur tracks has been questioned (Gatesy and Falkingham, 2017). However, the use of simple scales can still be useful. The preservation of tracks at the Carreras Pampa tracksite can vary considerably within individual trackways. For the trackways described in this study, all have tracks that range from 1 to 2 on the scale proposed by Belvedere and Farlow (2016).

4.1. Turning trackways

4.1.1. Trackway T21-1-44

Trackway T21-1-44 (Fig. 2A) consists of 67 tracks, including two missing (R5 and L21). It was made by a theropod with an average FL of 24.9 cm and an estimated height at the hip of 99.6 cm. The beginning of the trackway (R1–L4) has a northeastern bearing of 71° before making a 7° turn to the left (new bearing of 64°) and continuing straight from tracks L4 to L16. Between tracks L16 to L17, the trackway makes a 44° turn to the left with a new bearing of 24° after the turn. After this turn, the trackway makes several more, smaller changes in direction with turns ranging from 4° to 19°. The two strides involved in the turn are reduced compared to the ones before and after, showing that the trackmaker slowed down to make the turn and then sped up again to its original walking speed of an estimated 5.6 km/h. The total length of the measured trackway section (R9–L23), including the turn, is 22.1 m, and the direct length is 20.5 m, giving this section of the trackway a DL/TL tortuosity value of 0.93.

4.1.2. Trackway T22-2-207

Trackway T22-2-207 (Fig. 2B) consists of 30 tracks, including three missing (L10, L11 and R14). It was made by a theropod with an average FL of 18.0 cm and an estimated height at the hip of 72.0 cm, walking with an estimated speed of 6.8 km/h. The beginning of the trackway (R1–R2) has a bearing of 259° before making a turn to the right of 34° to a new bearing of 225° between tracks L2 and R4. The trackway then makes a 64° turn back to the left from tracks L4 to R8 with a final bearing of 289°. The trackway is covered between tracks R8 and L8 by an area of overlying sediment. The rest of the trackway on the other side of the overlying sediment (L8–R16) follows a straight path. The total length of the turning section (R1– R8) is 9.3 m, and the direct length is 8.4 m, giving a DL/TL tortuosity value of 0.90.

4.1.3. Trackway T22-3-10

Trackway T22-3-10 (Fig. 2D) consists of 23 tracks, with a portion of the final part of the trackway covered by overlying rocks and sediment that could not be removed. The first section contains 21 tracks, with only two tracks on the other side of the overlying sediment. It was made by a theropod with an average FL of 32.3 cm and an estimated height at the hip of 1.3 m, walking with an estimated speed of 4.1 km/h. The beginning portion of the trackway (R1–L5) has a bearing of 253° before making a 38° turn to the right with a new bearing of 291°. There is a reduction in stride length in the two strides leading up to the turning point with the final stride between tracks L4 and L5 being longer, suggesting that the trackmaker slowed down just before making the turn. In most trackways at the site, left and right tracks are relatively aligned with each other and in line with the midline of the trackway. However, the individual orientations of tracks in T22-3-10 before the turn show an unusual pattern of right tracks being rotated to the right with orientations ranging from 260° to 279°, while left tracks have orientations that range from 243° to 249° and are relatively in line with the direction of the trackway. Track L5 has an orientation of 264°, but track R6 is already oriented in the direction of the rest of the trackway (291°), suggesting that the trackmaker made a relatively sharp turn in only two steps.

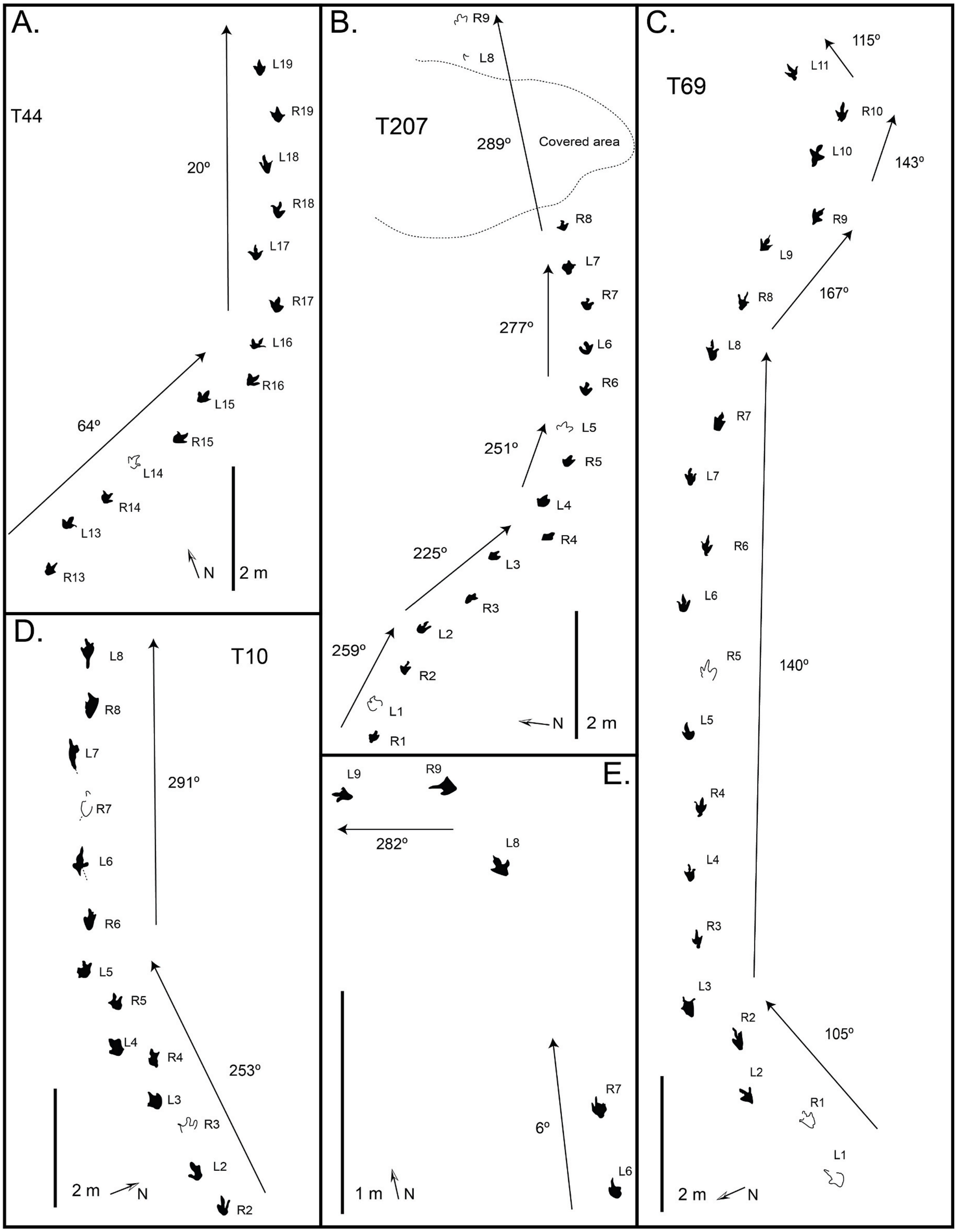

Fig. 2. Outlines of trackways making turns. (A) Trackway T21-1-44 making a left turn of 44°. The average track length is 25 cm. (B) Trackway T22-2-207 making a left turn of 64°. The average track length is 18 cm. (C) Trackway T22-3-69 that contains multiple turns ranging from 27° to 52°. The average track length is 27 cm. (D) Trackway T22-3-10 making a right turn of 38° transitioning from relatively shallow to very deep tracks. The average track length is 32 cm. (E) Trackway T23-4-98 making a left turn of 84°. The average track length is 8 cm. Arrows next to scale bars are oriented towards north for each trackway. Tracks that are not filled with color are not preserved with a complete track border. R = right foot, L = left foot, and number indicates track number.

Multiple aspects of the trackway are different before and after the turn. The average depth of tracks before the turn (4.3 cm) is approximately half that of those after the turn (7.9 cm). The two tracks on the other side of the overlying sediment are shallower again, indicating that the substrate consistency changed back to being firmer in that area of the tracksite when this trackway was made. Multiple tail traces are associated with tracks after the turn, but no tail traces are present before the turn. This difference is likely due to the increased depth of tracks after the turn (work in progress). The average TW before the turn is 36.3 cm, and after the turn, the average TW is 15.5 cm, possibly also due to the increased depth of tracks. The total length of the trackway (not including the two tracks beyond the overlying sediment) is 15.1 m, and the direct length is 14.1 m, giving a DL/TL tortuosity value of 0.93.

Although the turn in this trackway is less than 45°, we include this trackway because of the unusual behavior it suggests. This trackway is the only one we have observed at the Carreras Pampa tracksite, where the left and right tracks are not relatively aligned with each other. When viewing this trackway in the field, it is immediately apparent that the right tracks are rotated to the right, out of line with the trackway. This is especially true for the first three right tracks in the trackway. Another seemingly unusual aspect of this trackway is the difference between the track depths before and after the turn, notably that the trackmaker continued to walk after the turn even though it was sinking deeper into the substrate. Animals typically choose the most energy-efficient path when moving through an environment, and sinking into the substrate is energetically costly (Shepard et al., 2013). Thus, the reason for the change in direction must have been worth the higher energy cost. Finally, the average TW after the turn is less than half the average TW before the turn, suggesting that narrowing of the trackway width was probably needed due to the mechanics of walking in soft sediment.

4.1.4. Trackway T22-3-69

Trackway T22-3-69 (Fig. 2C) consists of 21 tracks. It was made by a theropod with an average FL of 27.2 cm and an estimated height at hip of 1.1 m. The beginning portion of the trackway (L1–L3) has a bearing of 105°. The first turn occurs between tracks L3 and R3, turning 35° to the right and resulting in a new bearing of 140° between tracks R3 and L8. Another turn to the right of 27° occurs between tracks L8 and R8, resulting in a new bearing of 167° for tracks R8 to R9. At this point, the trackway makes a tight turn back to the left of 52° with a final bearing of 115° before being covered by rocks and sediment that could not be removed. The trackmaker was walking for the length of the trackway with an estimated speed during the straight section of the trackway (R3–L8) of 7.8 km/h. However, there are considerable reductions in the length of strides in the turning parts of the trackway, showing that the trackmaker slowed down while turning but sped up when walking in a straight line. The total length of the trackway is 17.6 m, and the direct length is 16.4 m, giving a DL/TL tortuosity value of 0.93.

4.1.5. Trackway T23-4-98

Trackway T23-4-98 (Fig. 2E) consists of 18 tracks including four which are missing (L2, R5, L7, and R8). It was made by a theropod with an average FL of 7.7 cm and an estimated height at hip of 30.9 cm. Most of the trackway (R1–L7) has a bearing of 6°. Tracks L7 and R8 are missing due to a large crack in the track-bearing surface. Track L8 is rotated to the left and is followed by tracks R9 and L9, which have a bearing of 282°. This represents a turn of 84° to the left. With tracks L7 and R8 missing, we cannot know if there was a reduction in speed just before the turn. However, the last stride before the turn (R6–R7) has a length of 64.5 cm, and the stride in the turn (L8–L9) has a length of 64.1 cm, suggesting that the trackmaker did not slow down much, if at all, before making the turn. Despite a lengthy search under optimal lighting conditions, no tracks could be found beyond track L9, the most likely scenario being that the substrate was harder after track L9, and the trackmaker was too light-weight to leave tracks. This characteristic of tracks seeming to vanish suddenly has been observed in other trackways consisting of small tracks at the Carreras Pampa tracksite. The estimated gait of the trackmaker (the ratio of SL/h) is 2.1. Alexander (1976) and Ruiz and Torices (2013) considered SL/h ratios of 2.0 or more to indicate a running gate. Thus, this trackmaker was probably running, but it was probably a slow run since the SL/h ratio is just over the minimum for a running gait. The trackmaker was running at an estimated speed of 5.3 km/h. The total length of the trackway is 5.7 m, and the direct length is 5.3 m, giving a DL/TL tortuosity value of 0.93.

4.2. Trackways with stops

4.2.1. Trackway T22-1-102

Trackway T22-1-102 (Fig. 3) consists of 59 tracks. It was made by a theropod with an average FL of 29.7 cm and an estimated height at the hip of 1.2 m. The total trackway length is 47.2 m. The trackway follows a relatively straight path oriented north (0°). Stride lengths in this trackway are highly variable, ranging from 84 cm to 194 cm. Throughout the trackway, R-L paces have an average length of 93 cm, whereas L-R paces have an average length of 80 cm, indicating that the animal was limping (Lockley et al., 1994). Lockley et al. (1994) stated that short paces precede foot placement on the injured side; thus, in this trackway, there was probably an injury on the right side of the trackmaker. However, the tracks have a normal morphology, suggesting that the injury was not to the foot of the trackmaker. In addition to showing a limping gate, this trackway also preserves a stopping point. Tracks L25 and R26 are placed side-by-side, close together. Track L25 is very shallow, but track R26 is very deep. Other trackways at the tracksite contain a range of shallow and deep tracks, showing considerable variation in substrate consistency across different areas of the tracksite. Despite the significant difference in depth between the two tracks that are placed closely together, we believe track L25 is a part of this trackway because there is no other trackway in this area of the tracksite that it could belong to, it is a similar size to tracks in this trackway, and it is oriented in the same direction as the rest of the trackway. The large difference in how tracks L25 and R26 are preserved could also have resulted from L25 being part of some other trackway. However, no other trackway was found in this area that L25 could belong to. We also do not believe track L25 is an undertrack from an overlying layer due to the lines of evidence described above. Even if track L25 does not belong to this trackway, the trackmaker must have either stopped or taken a much shorter stride in this area of the trackway, because the alternating pattern of right and left tracks switches at the point of track R26. This necessitates a stop, a short stride, or a hop on one foot (which is the least likely possibility).

The tracks before the stopping point are shallower than those following the stopping point. The last two strides leading up to the stopping point show a reduction in length from an average of 186 cm (for the last five strides leading up to where strides begin to shorten) to 143 cm for the last stride into the stop. The first stride after the stopping point is very short (84 cm), probably due to the trackmaker's foot sinking deeply at the stopping point. After this initial step, the stride lengths increase again to an average of 159 cm, but stride lengths continued to show variation as in the rest of the trackway. We interpret this trackway as made by a theropod walking and most likely limping due to an injury on the right side. The trackmaker consistently varied its speed throughout the trackway and stopped for an unknown amount of time before continuing again.

4.2.2. Trackway T22-1-56

Trackway T22-1-56 (Fig. 4A) consists of 21 tracks. It was made by a theropod with an average FL of 30.7 cm and an estimated height at the hip of 1.2 m. The total trackway length is 25.8 m. A bank of overlying sediment separates the first two tracks from the rest of the trackway. The trackway continues on the other side of the bank, following a relatively straight path oriented towards the southeast (129°) from tracks R2 to L5. Track R6 is turned to the right and is immediately followed by tracks L6 and R7, which are placed near each other, with R7 slightly ahead of L6. These tracks have an orientation of 161°, which represents a turn of 32° to the right. Tracks L7 to R11 have an orientation of 134°, representing a turn back to the left of 27°. Following a short acceleration period after the stop, the dinosaur continued at the same speed it was initially walking at (8.6 km/h).

We interpret this trackway as being made by a theropod dinosaur that was walking and came to a pause rather than a stop for an indefinite amount of time, since the position of tracks L6 and R7 indicate that the

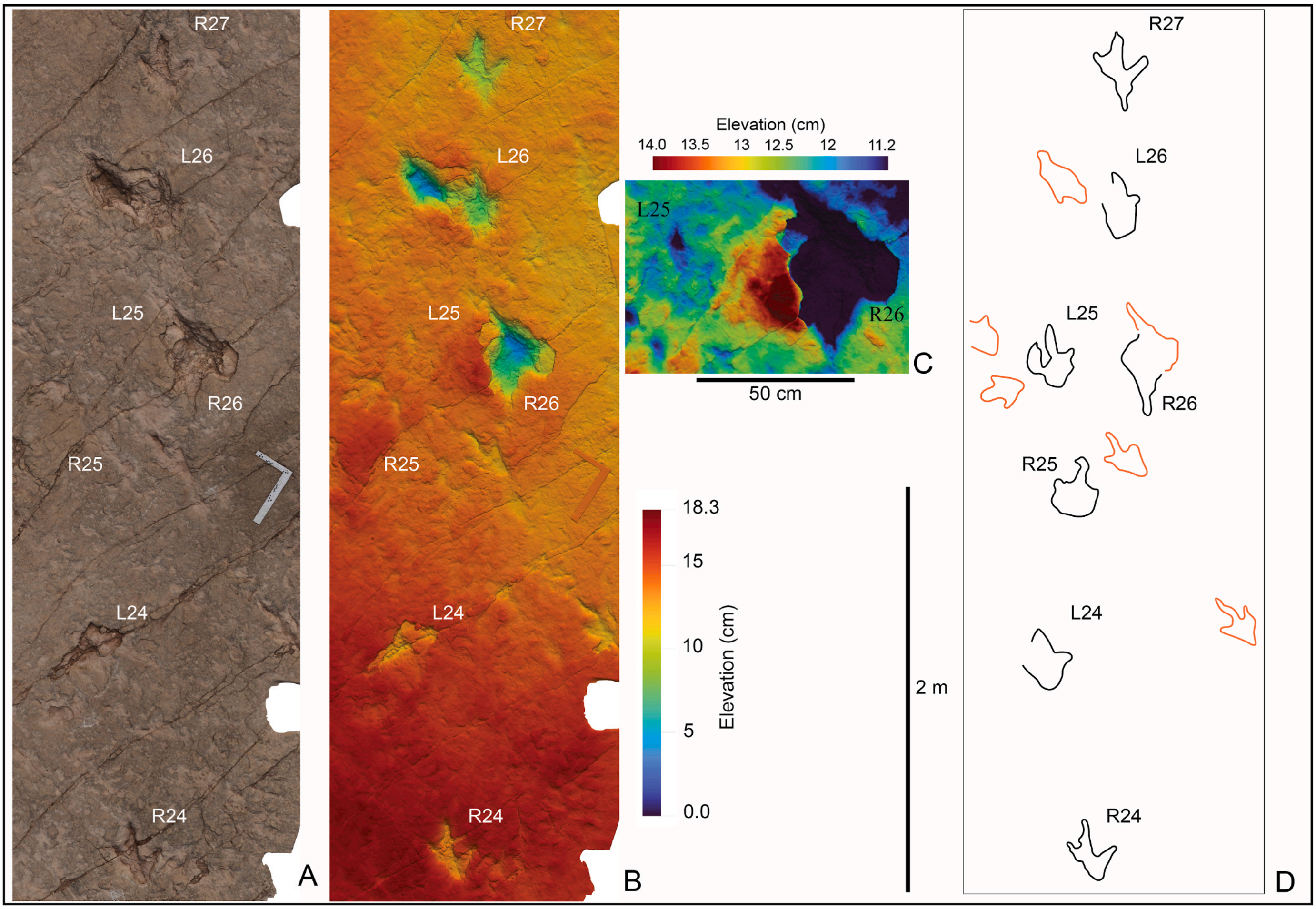

Fig. 3. Stopping point within trackway T22-1-102. (A) Orthophoto of the section of trackway T22-1-102 that contains the stopping point. (B) False-color depth map of the same section of the trackway. (C) False-color depth map showing an enlarged view of the stopping point. The elevation range was reduced compared to B to show track L25 better, which is much shallower than track R26. (D) Outline drawing of the trackway section. Tracks belonging to trackway T22-1-102 are outlined in black and other tracks in the area are outlined in red. R = right foot, L = left foot, and number indicates track number.

posture of the trackmaker would not have been as stable compared to placing the feet directly side-by-side (Weems, 2021). The stop immediately follows a 32° turn to the right, with the trackway continuing back to the left following a direction close to the original orientation of the trackway leading up to the stopping point. A possible explanation is that immediately following the turn, something made the dinosaur stop and decide to follow its original path rather than continue on its new orientation.

4.2.3. *Trackway T22-2-234*

Trackway T22-2-234 (Fig. 4B) consists of 56 tracks. It was made by a theropod with an average FL of 26.2 cm and an estimated height at the hip of 1.0 m. The trackway follows a relatively straight path, making several minor changes in direction of 12° or less. The beginning of the trackway (R1–L7) follows a typical pattern of alternating right and left tracks. Tracks R8 and L8 are placed near each other, with L8 slightly ahead of R8. The remaining part of the trackway (R9–L28) continues to follow a regular pattern of alternating right and left tracks. The last three strides before the stopping point show a reduction in stride length from an average of 180 cm (for the strides from R1 to R6) to 127 cm for the last stride into the stopping point (L7–L8). Following the stop, there is an increase in stride length from the first stride following the stop (R8–R9) of 112 cm to an average of 177 cm for the rest of the exposed trackway. The trackmaker was walking at an estimated speed of 7.1 km/h, slowed down and stopped or paused, then accelerated and continued walking at an estimated speed of 6.9 km/h for the rest of the trackway.

4.2.4. *Trackway T23-4-139*

Trackway T23-4-139 (Fig. 4C) consists of 15 tracks including one which is missing (L7). It was made by a theropod with an average FL of 7.3 cm and an estimated height at the hip of 29.2 cm. Tracks R2, L2, and R3 are clustered closely, with the right tracks slightly ahead and behind track L2 but with track R3 more closely associated with track L2. The first stride of the trackway (R1–R2) is 44.4 cm long, and the stride into the stop (R2–R3) is 12.4 cm long. The first stride after the stopping point is 22.1 cm long, with the remaining strides in the trackway ranging from 36.0 to 40.1 cm in length. After this cluster of tracks, the trackway proceeds in a typical alternating pattern until track R8 after which more tracks could not be found. Most tracks in this trackway are only partial, with four (L3, R4, L4, and R7) only consisting of a trace of the tip of digit III. The trackmaker was walking at an estimated speed of 2.3 km/h.

We interpret this trackway as made by a walking theropod that stopped at the point of tracks L2 and R3. Without more tracks in the first portion of the trackway, we cannot know what the average SL was before the last few strides leading into the stopping point. However, the available data suggest a considerable reduction in SL, indicating a significant reduction in speed before stopping. We could not locate additional tracks at the beginning or end of this trackway despite a lengthy search under optimal lighting conditions. As noted earlier, other trackways consisting of small tracks at the Carreras Pampa tracksite also seemingly disappear. We believe this is due to the varying substrate consistency during track formation and that these small trackmakers were too lightweight to leave tracks in areas with firmer substrate.

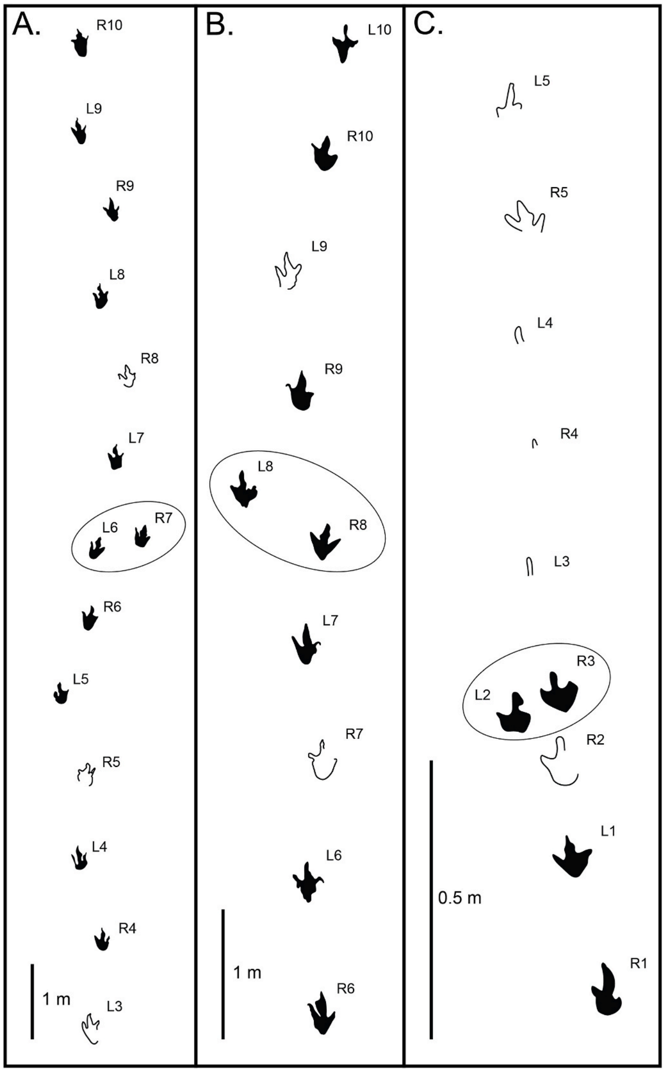

Fig. 4. Outlines of trackways with stopping or pausing points (circled). (A) Trackway T22-1-56 with a pausing point between tracks L6 and R7. The pausing point immediately follows a turn to the right of 32°, then turns back to the left 27°. The average track length is 30.7 cm. (B) Trackway T22-2-234 with a stopping or pausing point between tracks R8 and L8. The stop occurs within a straight section of the trackway. The average track length is 26.2 cm. (C) Trackway T23-4-139 with a stopping point between tracks L2 and R3. The average track length is 7.3 cm. Tracks that are not filled with color are not preserved with a complete track border. R = right foot, L = left foot, and number indicates track number.

Thulborn (1990) discussed similar traces as having been formed when there was insufficient force to produce a track when the entire foot was in contact with the ground. However, during the kick-off phase of the step cycle, the entire body weight would have been transferred to just the toes, and this, combined with the push-off force, was enough to leave a trace of the digit tips (Fig. 5). Another possibility is that this trackway represents a small theropod dinosaur entering a body of water. The average orientation of most ripple marks we have measured at the site is 280°. This trackway is oriented 0°, thus, the trackmaker was heading perpendicular to the preserved ripple marks and may have been walking towards a shore line. The transition from tracks with normal morphology to tracks only preserving the tips of digits may indicate a transition from normal walking to subaqueous locomotion. If this was the case, the stopping point probably would have been at or just past the shoreline. However, we have not found any sedimentological evidence of a shoreline being present within the exposure of the Carreras Pampa

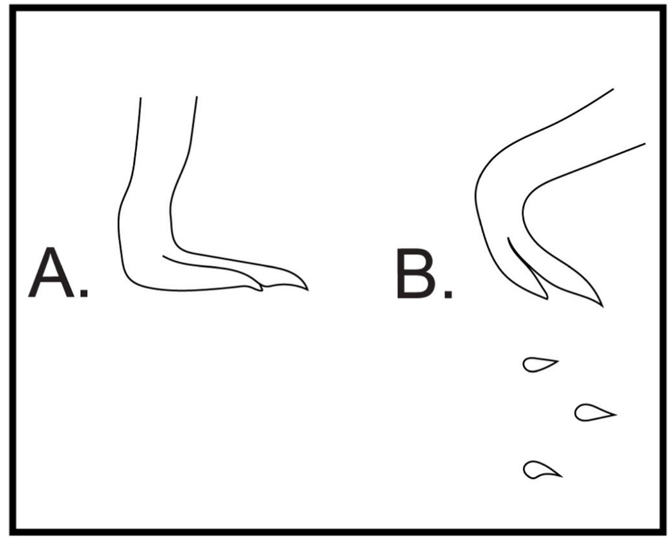

Fig. 5. Illustration of how digit tip traces may have formed. (A) When the entire foot is placed on the ground, the weight is distributed across the entire foot and no impression is formed. (B) During the kick-off phase, all the weight is transferred to the toes resulting in traces of just the digit tips. Redrawn from Thulborn (1990).

tracksite.

4.3. Trackway with a sudden change in direction

4.3.1. Trackway T22-1-126

Trackway T22-1-126 (Fig. 6) consists of 58 tracks with a total length of 57.4 m. This trackway was made by a theropod with an average FL of 29.2 cm and an estimated height at the hip of 1.2 m. The first part of the trackway (R1–R11) has a bearing of 224°. At track R11, the trackway makes a sudden change in direction, turning 11° to the right for two paces oriented towards 235°. The trackway then gradually turns 36° to the left between tracks L12 to L16, with the final part of this turn bearing 199°. The trackway then turns back to the right and straightens out, bearing 217° from track R17 to track L24. The final section of this trackway has a bearing of 225° between track R25 and track L29. The three strides involved in the sudden change in direction (L10–L11, R11–R12, and L11–L12) are reduced from an average of 1.99 m before the change in direction to 1.84 m, 1.83 m, and 1.74 m, respectively. As the trackway turns back to the left, the stride lengths increase again to an average of 2.02 m for the rest of the trackway. There is also a tail trace or toe drag associated with the sudden change in direction between tracks R10 and L10. However, the morphology of this groove is very similar to that of other tail traces at the site (describe in a manuscript being prepared for publication elsewhere).

We believe that the sudden change in direction recorded in this trackway resulted from the trackmaker trying to avoid some unknown factor or obstacle. The change in direction is abrupt and only occurs for two paces before the trackway begins returning to its original orientation. The sections of the trackway before and after the sudden change in direction have very similar orientations, suggesting that the trackmaker made an intentional effort to return to its original orientation. Track R13 had a substantial expulsion rim along the right side of the track, indicating that the trackmaker pushed off towards the left with considerable force, potentially to get back to its original orientation as soon as possible after making the abrupt change in direction. The trackmaker slowed down as it moved to the right, probably due to changing directions so quickly. We interpret the associated tail trace as the result of this reduction in speed, as some dinosaur tail traces are interpreted as having been caused by a backward rotation of the body when slowing down (Platt and Hasiotis, 2008). We cannot know what the trackmaker

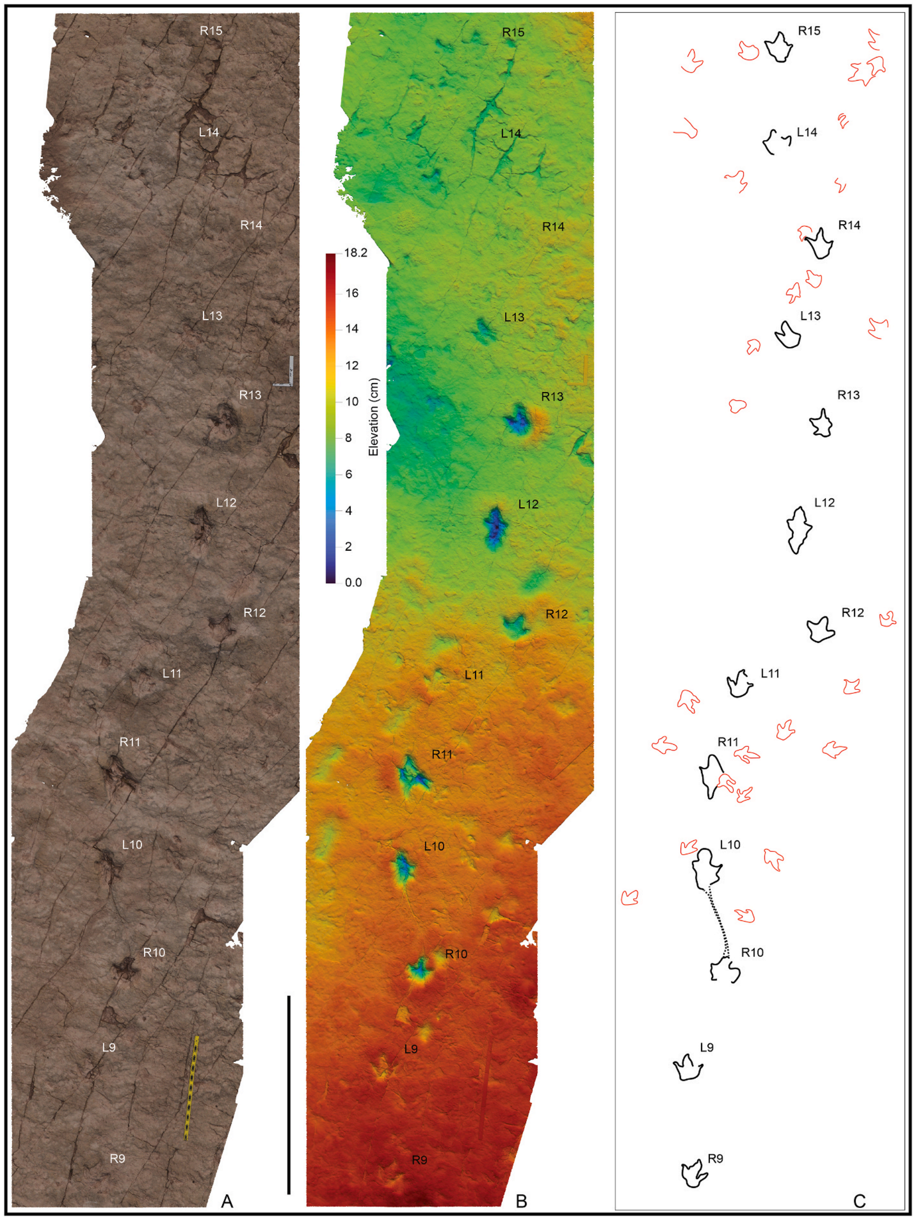

Fig. 6. Section of trackway T22-1-126 showing an abrupt move to the right and gradual return to the left. (A) Orthophoto of trackway section. (B) False-color depth map of trackway section. (C) Outline drawing of trackway section. Tracks belonging to trackway T22-1-126 are outlined in black and other tracks in the area are outlined in red. The dotted line between tracks R10 and L10 represents a toe drag or tail trace. The scale bar is 2 m. R = right foot, L = left foot, and number indicates track number.

was trying to avoid; however, due to the abrupt change in direction, we hypothesize that the trackmaker was trying to avoid a moving object and not a stationary one, possibly another dinosaur.

4.4. Possible crouching trace

4.4.1. Trackway T23-1-4

Trackway T23-1-4 (Fig. 7) consists of 53 tracks. It was made by a theropod with an average FL of 28.2 cm and an estimated height at the hip of 1.1 m. The trackway follows a relatively straight path across the site with an orientation of 197°. Between tracks L7 and L9, the trackway contains multiple unusual features. Track L7 has a regular morphology for theropod tracks at the Carreras Pampa tracksite. In the approximate location for the next track (R8), the surface is too disturbed by multiple tracks to identify an R8 track for this trackway confidently. Track L8 is rotated to the left compared to the trackway leading up to this section. This track has an elongate metatarsal mark, and the total length of the track and elongate mark is 54.2 cm. Behind this track and in line with it is a tail trace measuring 33.2 cm long and 0.9 cm wide at the center. This tail trace presents as a thin groove in the surface of the tracksite that curves at the posterior end and has a small expulsion rim at the posterior tip. There is also a small ridge built up towards the midline of the trackway along the first third of its length. Just to the right of track L8 and slightly ahead of it is a potential track R9. We say this is a potential track because its preservation is different compared to the other tracks in this trackway. All of the other tracks are preserved as depressions into the trackbearing surface, however, this potential track is slightly raised up from the surface. Even though there is a difference in preservation, we are hesitant to eliminate this as a possible track because there appears to be an outline of digits II and IV and a heel. This is especially evident when looking at the depth map. There is also what appears to be the first part of digit III (although the tip of digit III is not preserved) and

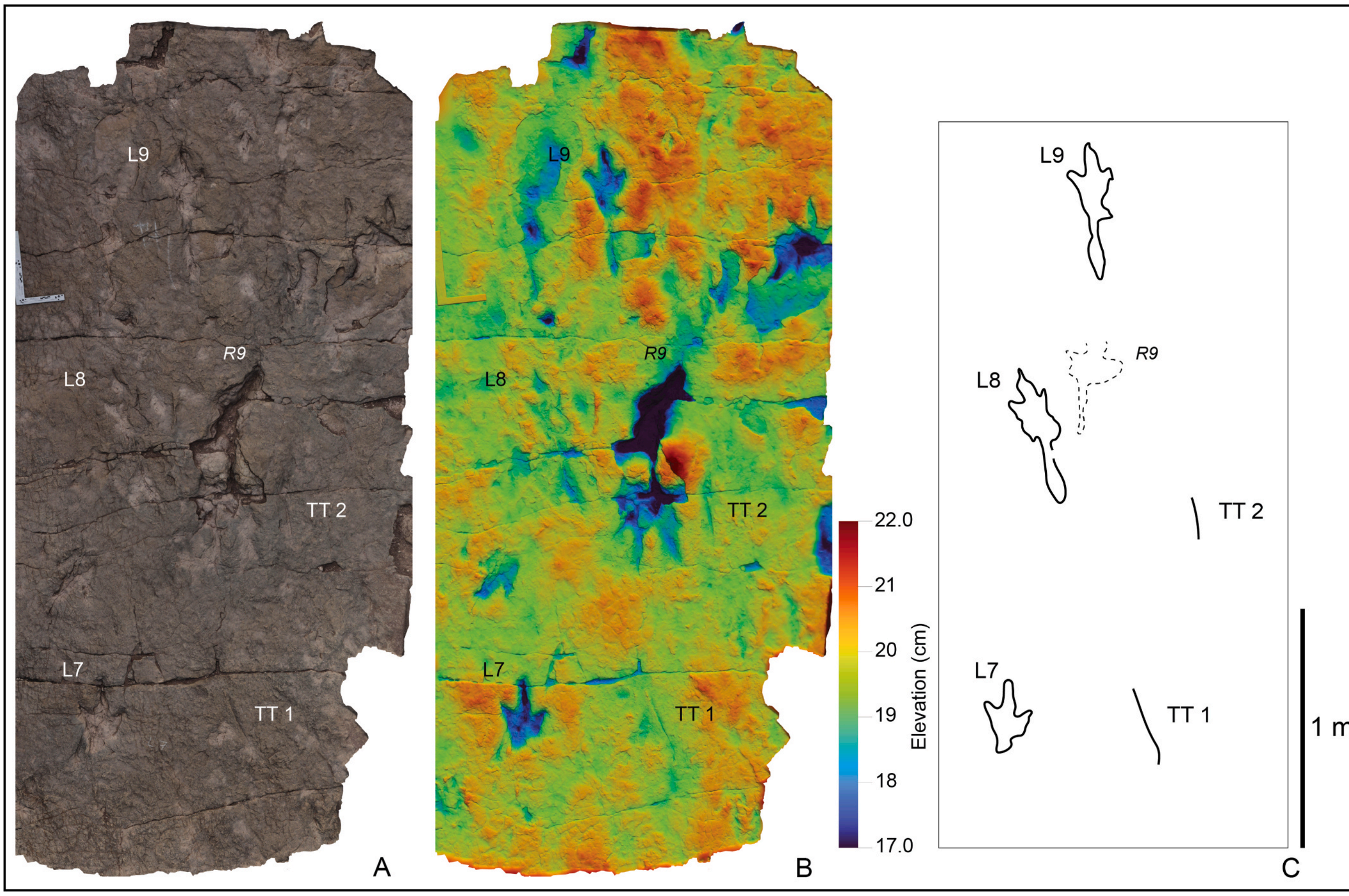

Fig. 7. Section of trackway T23-1-4 consisting of a series of tracks and tail traces we interpret as a potential crouching trace. (A) Orthophoto of trackway section. (B) False-color depth map of this section of the trackway. (C) Outline drawing of the trackway section. Track R9 is outlined with a dotted line because the preservation does not match the rest of the trackway, but the track is where we expect R9 for this trackway to be. Therefore, we consider it a possible track R9. TT 1 = tail trace 1, TT 2 = tail trace 2. R = right foot, L = left foot, and number indicates track number.

a raised metatarsal mark. This track is also in line with the rest of the trackway and we did not find any other trackway it could belong to. However, we do acknowledge that the tracksite in this area has been trampled by multiple trackways and thus we cannot eliminate the possibility that track R9 belongs to another trackway which has been mostly destroyed in this area. We did not measure the total length of this potential track because digit III is missing, and thus, the length would not have been comparable to other tracks. Track L9, also has an elongate metatarsal mark and a total length (including elongate mark) of 54.2 cm. This track is rotated to the left, but not as far as track L8. Behind this track and in line with it is a second tail trace measuring 22.1 cm long and 1.9 cm wide at the center. This tail trace presents as a thin, straight groove in the tracksite surface. Tracks return to a normal morphology, starting with track R9. Before this section, the beginning of the trackway has an average SL of 1.86 m. The stride between L7 and L8 measures 1.27 m long, thus showing a reduction in speed in this part of the trackway.

We present the following interpretation of this series of traces. The trackmaker of this trackway was walking normally until the section of the trackway containing tracks L7–R9. We believe that the trackmaker rotated its body to the left and placed its right foot (R8) in line with track L8, although, without a clear R8 track, we cannot know for certain. The trackmaker then crouched down, causing the metatarsi and tail to contact the substrate. It appears the trackmaker then stepped forward with its right foot, forming the potential track R9, and then stepped forward again with its left foot (L9) while being crouched or crouching down after completing these steps, as track L9 is shallow but has a metatarsal mark. At this point (when track L9 was formed), the tail of the trackmaker made contact with the substrate a second time. At track R10, the trackmaker resumed normal walking and proceeded for the rest of the trackway.

This series of traces shares some similarities with the resting trace from Utah described by Milner et al. (2009). Both resting traces show multiple shallow tracks with elongated metatarsal marks and a tail trace in line with the tracks at the point where the trackmaker crouched down. However, the resting trace in Utah revealed that the left and right feet were next to each other and oriented parallel to each other while the trackmaker crouched down. The crouching trace was also aligned with the rest of the trackway. The possible crouching trace presented here shows that the feet were rotated considerably out of line with the rest of the trackway when the trackmaker crouched down and that the feet may not have been directly next to each other, although we cannot know this for certain. The crouching trace in Utah also preserved impressions of the ischial callosity, which we did not find in the traces presented here. While the series of traces presented here only share some similarities with the Utah resting trace, we believe that a trackmaker crouching down is the best explanation for this series of traces.

5. Discussion

Trackmaker behaviors could have resulted from many factors, including intrinsic and extrinsic factors (Lockley et al., 2021). While we cannot know what caused the various locomotive behaviors at the Carreras Pampa tracksite, some trackways reveal more than others. For example, trackway T22-1-126 (Fig. 6) is a case that strongly supports an extrinsic factor influencing a trackmaker's movement. The change in direction is abrupt and accompanied by a slight reduction in speed. We believe this trackway may have resulted from the trackmaker avoiding another dinosaur at the site. A sudden change in direction rather than a gradual change supports that the trackmaker was avoiding a mobile object rather than a stationary one and was almost certainly reacting to an extrinsic rather than an intrinsic factor. There are far too many trackways in this area of the tracksite to hypothesize which one may have been interacting with T22-1-126. Most trackways at the site have orientations towards the north to northwest or the southeast. Thus, since trackway T22-1-126 is moving almost perpendicular to the majority of trackways, it may have been avoiding another trackmaker moving in one of these two primary directions. We do not know how many individual trackmakers contributed to the tracks at the Carreras Pampa tracksite, but the large number of trackways suggests a high number of individuals. This trackway suggests that, at times, multiple dinosaurs were present at the site concurrently and that interactions between them occurred. It is possible that the trackways recording turns or stops may have also been in response to other dinosaurs in the area.

We believe the trackways with stopping points suggest that both intrinsic and extrinsic factors influenced the trackmakers to stop. Trackway T22-1-56 indicates a sudden stop immediately following a turn to the right. After the stopping point, the trackway turns immediately back to the left towards its original orientation. These trackway attributes could indicate that an extrinsic factor was affecting the trackmaker to turn back towards its original direction of travel. The large reduction in stride lengths occurring just after the turn before the stopping point also supports a more abrupt stop that could have been in reaction to some extrinsic factor. In contrast to trackway T22-1-56, trackway T22-2-234 shows a stop preceded by a more gradual reduction in speed occurring in the middle of a straight section of the trackway. This potentially indicates an intrinsic factor producing the stop, as the trackmaker had time to slow down before stopping and did not change direction before or after the stop.

The Carreras Pampa tracksite preserves a diversity of dinosaur locomotive behaviors, highlighting the usefulness of tracks in understanding dinosaur behavior. With a total area of approximately 8,100 m^2, the tracksite also reinforces the observation of Lockley et al. (2021) that larger tracksites have a better chance of preserving abnormal behavior and that deviations from relatively straight walking are rare. Out of 978 trackways discovered at the Carreras Pampa tracksite thus far, only three make changes in direction of more than 45° and only four have stopping points, representing 0.3% and 0.4% of the total trackways, respectively. Thus, the Carreras Pampa tracksite is an excellent example of the rarity of preserving dinosaur locomotive patterns outside of relatively straight walking in the track record. The diversity and rarity of dinosaur behaviors preserved at the Carreras Pampa tracksite, including tail dragging and swim traces (work in progress), highlight the importance of this tracksite as one of the premiere tracksites in the world.

6. Conclusions

Most dinosaur trackways reported in the literature indicate that the trackmaker was walking in a relatively straight line. Significant deviations from this pattern are rare. The Carreras Pampa tracksite preserves 11 trackways that indicate a diversity of uncommonly preserved locomotive behaviors. All the trackways described here belonged to theropod trackmakers, with size estimates ranging from 29.2 cm to 1.3 m at the hip. Three trackways with changes in direction of 45° or more are reported. A fourth trackway that makes a turn of 44° is also described. Four trackways show stopping or pausing points, with trackways indicating both sudden stops and more gradual reductions in speed before the stop. One trackway shows a sudden change in direction followed by a gradual return to the trackway's original orientation, which we interpret as a trackmaker trying to avoid a mobile obstacle, probably another dinosaur. Finally, a series of traces is interpreted as a possible crouching theropod trace. This work highlights the importance of the Carreras Pampa tracksite both in terms of the total number of trackways and because of the rarity and diversity of dinosaur behaviors preserved there.

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CRediT authorship contribution statement

J.A. McLarty: Writing – original draft, Visualization, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **R. Esperante:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix ASupplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2024.105011.

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