

Digging Sauropods: excavation behaviour or evidence for nest building? An example from the Late Cretaceous El Molino Formation (Maragua, Bolivia)

Christian A. Meyer¹, Jose Hugo Heymann², Edwin Chuca Ibarra³, Eddy Laura Flores⁴, Lara Sciscio^{5,6}

¹ *Departement of Environmental Sciences, University of Basel, CH4056 Basel, Switzerland*

² *Calle Grau 349, Sucre, Bolivia*

³ *Calle Brasil, Barrio alto San Juanillo “A”, Sucre, Bolivia*

⁴ *Av. Diagonal Jaime Mendoza, Barrio Villacopacabana, Sucre, Bolivia*

⁵ *JURASSICA Museum, Route de Fontenais 21, CH-2900 Porrentruy, Switzerland*

⁶ *Département des Géosciences, Université de Fribourg, Chemin du Musée 6, CH-1700 Fribourg, Switzerland*

<https://zoobank.org/221601FD-5B91-49D1-9858-E3E1DB2D281C>

Corresponding author: Christian A. Meyer (chris.meyer@unibas.ch)

Academic editor: Florian Witzmann ♦ Received 7 May 2026 ♦ Accepted 14 July 2026 ♦ Published 24 July 2026

Abstract

The Late Cretaceous deposits of Bolivia contain a diverse record of fossil vertebrate tracks. Extensive surfaces within the El Molino Formation (Maastrichtian) preserve evidence of diverse animal behaviour. Here, we report an unusual sedimentary structure from a titanosaurid track-bearing surface at the Mullurina Mayu locality (Maragua, Dep. Chuquisaca). The structure occurs within a massive claystone bed, interpreted as an overbank deposit, based on associated sedimentary structures and overlying units (i.e., desiccation cracks, caliche-bearing marls). The structure is a bowl-shaped depression, longer than wide (4.2×3.2 m), deeper internal basin (maximum depth of 60 cm), with a sharp coherent rim and an irregular margin. Along the basin walls, groups of parallel linear grooves (1 cm wide, interspace ~ 1.8 cm, length ~ 30 cm) occur within semi-circular depressions, showing two dominant orientations (NE-SW and ESE-WNW). Isolate broader scratches, interpreted as claw traces, occur on the basin floor. Several hypotheses are considered for the structure's formation, including scouring, weathering, to animal excavation, and nest construction. The absence of scour marks, tool marks, or weathering textures, combined with syn-sedimentary nature and distribution of the scratch-like traces, support a biogenic origin. The bundled grooves are interpreted as possible skin-slip striations produced by repeated foot movement in the soft sediment during excavation. Given the close association with titanosaurid trackways, we tentatively consider this as evidence of their digging and possible abandoned nest scrape.

Key Words

Digging behaviour, Late Cretaceous, Maastrichtian, nesting, Potosi Basin, South America, vertebrate tracks

Introduction

The Late Cretaceous deposits of Bolivia have long been known for their rich record of fossil vertebrate tracks (e.g. Leonardi 1984; Meyer et al. 2001, 2019). The El Molino Formation and coeval deposits of Peru and Argentina form a megatracksite with a surface area of 100 000 km² (Lockley

and Meyer 2022). Meyer et al. (2019) suggested that the palaeogeographic position of the main El Molino sites within the Potosi Basin are part of a seasonal migration route along the shoreline and deltas of an ancient lake system. The diverse El Molino track assemblage includes trackmakers ranging from ankylosaurids, small and large theropods, various titanosaurid sauropods, small birds,

and rare ornithopods (e.g., Leonardi 1984; Meyer et al. 2019; Riguetti et al. 2021; Esperante et al. 2024; Llampen Salinas 2024). These tracks provide evidence for herd behaviour in ankylosaurids and titanosaurids, as well as records of turning theropods and slipping ankylosaurs (Lockley et al. 2002; Meyer et al. 2018, 2025a, 2025b). The present paper reports on an unusual, potentially biogenic sedimentary structure, that occurs in association with titanosaurid tracks within a track-bearing package in the upper part of the Lower Member of the El Molino Formation. The study site lies within the Maragua Syncline, east of the constitutional capital of Bolivia, Sucre (Dep. Chuquisaca), at the Mullurina Mayu locality. The Mullurina Mayu palaeosurface displays several tens of sauropod tracks forming at least five trackways. The manus and pes are very well preserved with digit impressions, and this morphology can be confidently attributed to the ichnotaxon *Calorckosauripus lazari*, consistent with non-derived titanosaurids based on track morphology and the regional faunal context.

Geological setting

The Cretaceous of the Cordillera Oriental in Bolivia is primarily represented by the Puca Group (Kimmeridgian to Paleocene) which unconformably overlies Palaeozoic sedimentary rocks (Sempere et al. 1997). The Puca Group within the Potosi Basin is deposited in an under-filled, back-arc foreland basin formed by subduction along the western margin of the South American plate (Sempere et al. 1997; Tasistro-Hart et al. 2019). Today, however, Cretaceous rocks are found only as relicts in small, overthrust nappes or synclines. One notable structure is the Maragua syncline, a large bowl-shaped structure with a NW-SE trending axis that forms part of the Potosi Basin, exactly in the Betanzos-Ravelos syncline. The Puca Group is deposited across an angular unconformity that formed over the Jurassic La Puerta Formation, and deposition commences within the siliciclastic Chaunaca Formation. The overlying El Molino Formation can be divided into three members: Lower, Middle, and Upper, respectively (Sempere et al. 1997 and Fig. 1).

The Lower Member of the El Molino Formation has been dated between ~73 Ma to 67 Ma (Sempere et al. 1997). Sempere et al. (1997) placed the Cretaceous-Paleogene (K/Pg) boundary between the Middle and Upper Member, a lithostratigraphic boundary that was also regarded as coinciding with the K/Pg boundary by Tasistro-Hart et al. (2019) based on cyclostratigraphy and radiometric ages.

The depositional environment of the El Molino Formation has long been debated. Based on the presence of selachians and (estuarine) actinopterygian fishes, Gayet et al. (1991, 2001) and Sempere et al. (1997) favour fully marine conditions; however, Rouchy et al. (1993), based on stable isotopes and palynomorphs, prefer an almost continuous lacustrine system in Bolivia during the Late Cretaceous. Furthermore, the El Molino Formation

contains ostracods, gastropods, turtles, and catfishes, which support the ephemeral lacustrine basin model (e.g., Meyer et al. 2001; Meyer et al. 2019).

Maragua tracksites

In the Maragua syncline, several dinosaur tracksites have been reported and which broadly occupy the same stratigraphic package in the uppermost part of the Lower Member of the El Molino Formation (Lockley et al. 2002; Meyer et al. 2019; Riguetti et al. 2021). Lockley et al. (2002) thoroughly documented the Humaca site (Fig. 1A) which provides evidence of a herd of eleven (subadult) titanosaurids (av. 45 cm pes length) and small theropods (12–30 cm pes length) in the uppermost part of the Lower Member the El Molino Formation (*contra* Lockley et al. 2002 and Meyer et al. 2019). The Niñu Mayu site (Fig. 1A) has yielded tracks of cf. *Tetrapodosaurus* attributed to small nodosaurid ankylosaurs based on manus morphology (Riguetti et al. 2021), a large theropod trackway, and tracks of large titanosaurids (ca. 80 cm pes length; larger than at Humaca and our Mullurina Mayu site). Several other sites are known but currently remain undocumented in the area.

Herein, we report on a track surface within this area, which is located at Mullurina Mayu (Quechua for “arc-shaped river”) at 3450 m.a.s.l., 5.6 km WNW of the small village of Maragua, 23 km west of Sucre (19°03'46.96"S, 65°28'51.61"W, Distrito 8; Departamento de Chuquisaca), Bolivia (Fig. 1). It is situated 450 m east of the Niñu Mayu locality (19°03'58.88"S, 65°28'43.97"W; 3434 m.a.s.l.), reported by Riguetti et al. (2021), and 2.25 km northeast of the Humaca locality (19°04'40.81"S, 65°27'58.97"W 3179 m.a.s.l.) described by Lockley et al. (2002).

Methods

A short (~3 m) section was logged across the Mullurina Mayu track-bearing horizons (Fig. 1C) following standard field protocols (Miall 2006), and microfacies was determined using a hand lens. Sampling of rocks for further analysis is currently not allowed. The lower part of the depression had to be cleaned and accumulated sand had to be removed. For accurate documentation, precise measurements, and description of the traces we followed the guidelines of Mallison and Wings (2014) and Falkingham et al. (2018). Furthermore, close overhead photographs were taken with a drone (DJI Mavic Air 3S) in November 2025, post-flight treatment of the pictures was performed in AIRMAGIC (1.0). Detailed photographs of the traces on the wall were captured with a Leica D-Lux 6. Photogrammetric models were created using AGISOFT METASHAPE PRO (v 2.1.2). The isolation of the tracks and the structure, the refined orientation, and the false-colour depth maps of all models were produced in CLOUDCOMPARE (v. 2.13) and PHOTOSCAN (v. 5.13.1).

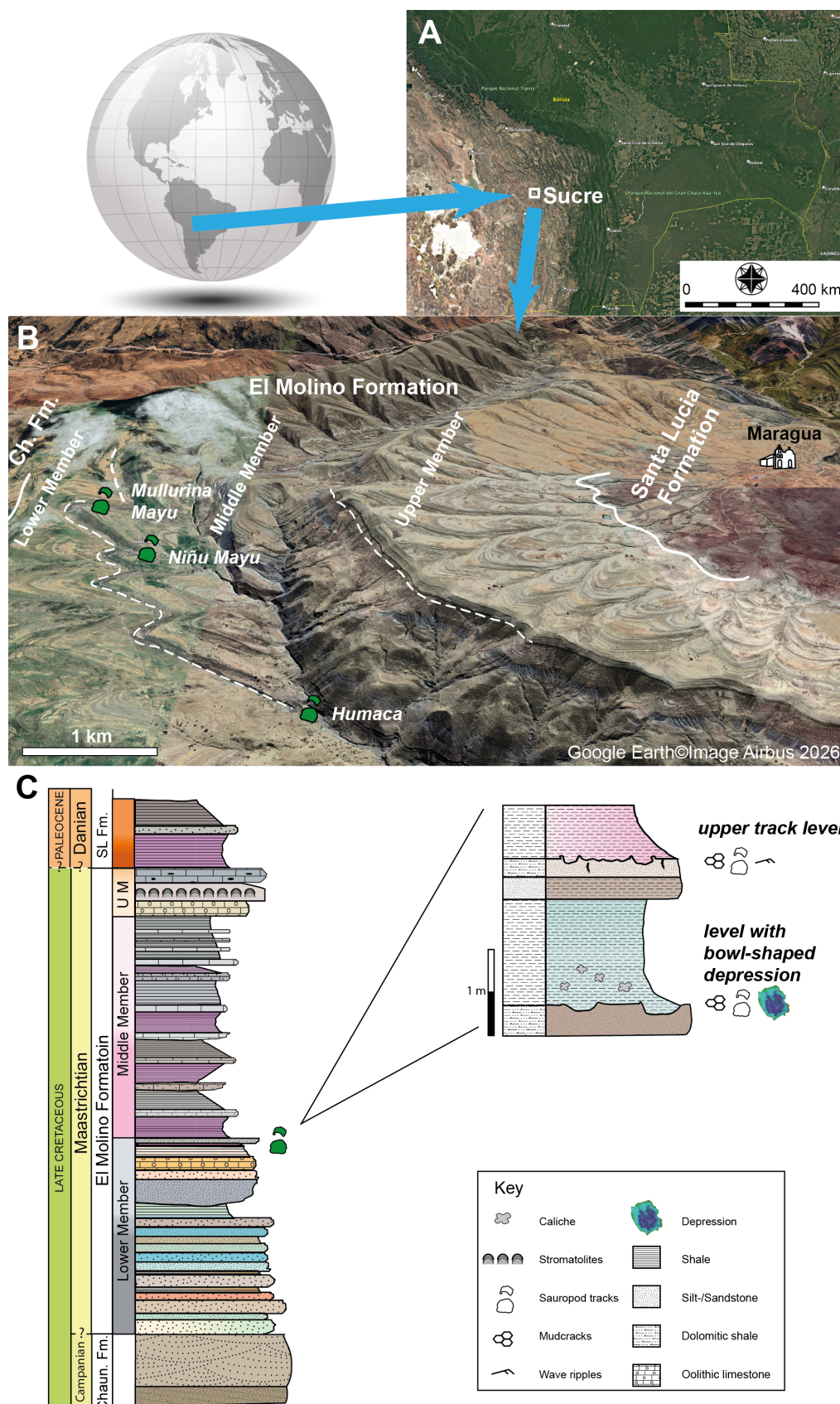


Figure 1. Location and stratigraphy of the Mullurina Mayu site. **A.** Geographic location of Bolivia and the Maragua syncline region in white box; **B.** Detailed map of the Mullurina Mayu, Niñu Mayu and Humaca locality in relation to the underlying (Chauca Fm.) and overlying (Santa Lucia Fm.) formations; **C.** Overall stratigraphic section of the Lower Member, El Molino Formation, with inset showing the detailed section of the Mullurina Mayu track- and depression-bearing horizon (colours correspond to true rock colours in the outcrop). Map Data © 2026 Google Earth.

Results

As of September 2025, a total of 522 m² of the Mullurina Mayu palaeosurface is exposed, featuring at least four sauropod trackways (Fig. 2). Based on our field observations, all these surfaces occur within the same package of a siliciclastic sequence in the uppermost part of the Lower Member of the El Molino Formation. The sediments of the respective surfaces are claystones with some silt content, show desiccation cracks, and are carbonate-free, rather than limestones as stated by Riguetti et al. (2021) for the Niñu Mayu locality. The structure (bowl-shaped depression) occurs within a massive, cemented claystone, which is infilled and overlain by a thick marl with pedogenic features (caliche, Figs 1C, 2).

Sauropod tracks

The sauropod trackways consist of manus-pes couplets, with the preserved pes preserved as an elongated depression visible posterior to the manus impression. Although the overall dimension of the pes is unknown, similar specimens from the higher level, 1.5 m above (see Fig. 2) average 56 cm in length and 49 cm in width. The manus is half-moon shaped, averaging 41 cm in width and

20 cm in length. Soft sediment deformation features are associated with manus impressions near the depression described below (Figs 4, 5). While digit impressions on the current surface are poorly defined, many well-preserved tracks with digit impressions are visible on the higher surface (Fig. 3, heteropody index = 0.3). Data from these trackways indicate an average stride of 1.7 m and a gleno-acetabular distance of ~1.8 m. One measurement from the level with the depression indicates a slightly higher gleno-acetabular distance (~2–2.2 m) while stride varies between 1.8 and 2 m.

Bowl-shaped depression

Towards the western part of the surface, a single, relatively deep, bowl-shaped depression is cut into the palaeosurface. The length along the dip of the strata is 4.2 m, the width along the strike is 3.2 m, and the maximum depth is ~60 cm. The complete surface area is 12 m² (Figs 2, 3). There is a relatively sharp rim (break in slope) and a deeper inner “basin” which shows two longitudinal trough-like structures at the western end (Fig. 4D–G). The margin is frayed, irregular in shape, and has scalloped edges (Fig. 5). Several areas show groups of parallel, linear grooves at the margin of the depression, which appear to be bound to what seem to be semi-circular impressions



Figure 2. Field views of the Mullurina Mayu palaeosurface and bowl-shaped depression. **A.** Oblique view of the lower part of the surface from the east, showing the general extent of the exposed palaeosurface. People for scale indicate with a box; **B.** Close-up view of the bowl-shaped depression and trackway association; **C.** Aerial view showing titanosaurid trackways and the position of the bowl-shaped depression.

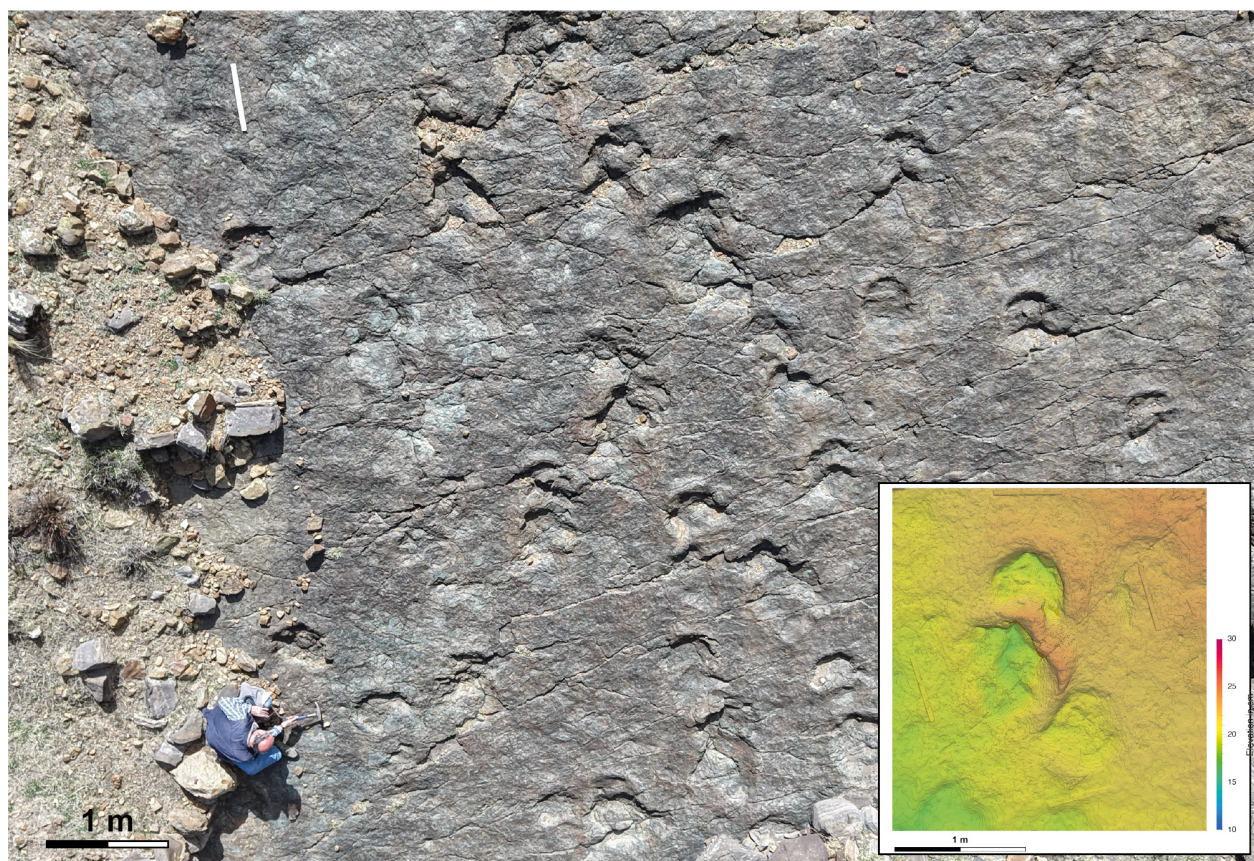


Figure 3. Mullurina Mayu aerial view of higher surface with titanosaurid trackways. 3D model of a manus-pes set.

(Figs 4, 5). The bundles of linear grooves (1 cm wide) are confined to these impressions (width 23–28 cm) and have an average interspace (between scratches) of 1.8 cm (Fig. 6). There are six to seven parallel grooves per bundle (impression) with a maximum length of 30 cm in transverse section; they are hummocky-shaped in section. Furthermore, there are isolated broad single scratches that seem to be claw marks (length 5–10 cm, width 2 cm; Fig. 6D). Soft sediment deformation features (sediment bulges, sediment collapse) are associated with the impressions and scratch bundles.

Discussion

The titanosaurid trackways described from the Mullurina Mayu align, both in size and morphology, closely with those described from nearby sites at Humaca (Lockley et al. 2002) and Cal Orck'o (Meyer et al. 2018). All of these sites are situated in the uppermost part of the Lower Member, which we could confirm during our last visit to these sites. Based on manus morphology and manus-pes configuration, they are assigned to *Calorckosauripus lazari* Meyer et al. 2018, which is attributed to non-derived titanosaurid sauropods. Currently, no titanosaurid sauropod body fossils are known from the Maragua syncline or the Lower Member of the El Molino Formation, although titanosaurids are known from coeval records in Argentina

(e.g. Lacovara et al. 2014). Considering the size of the Mullurina Mayu tracks (FL ~56 cm), these are intermediate in size between those documented at Humaca (FL: ~40–50 cm; Lockley et al. 2002) and smaller than those from the Ninu Mayu site (FL: ~80–100 cm; Riguetti et al. 2021), suggesting that, like at Humaca, these trackmakers are smaller, possibly younger, subadult individuals.

The unusual Mullurina Mayu bowl-like structure associated with the *Calorckosauripus* trackways, may be explained by either abiotic processes (i.e., erosional, hydrodynamic, or weathering-related), or by biogenic activity. It is incised into a massive, siltstone/ claystone interpreted as an overbank or levee deposit based on its lateral extent and associated with overlaying caliche-bearing marls with indication of subaerial exposure (desiccation cracks; Fig. 1). To evaluate the potential means of Mullurina Mayu “bowl” formation, several hypotheses are discussed below against the observed morphology, internal sedimentary fabric, and stratigraphic context.

Abiotic hypotheses

The irregular Mullurina Mayu bowl-like structure could be explained as a feature, such as a pothole or a large scour, within a fluvial setting. A scour would form on the surface due to high-velocity, sediment-laden

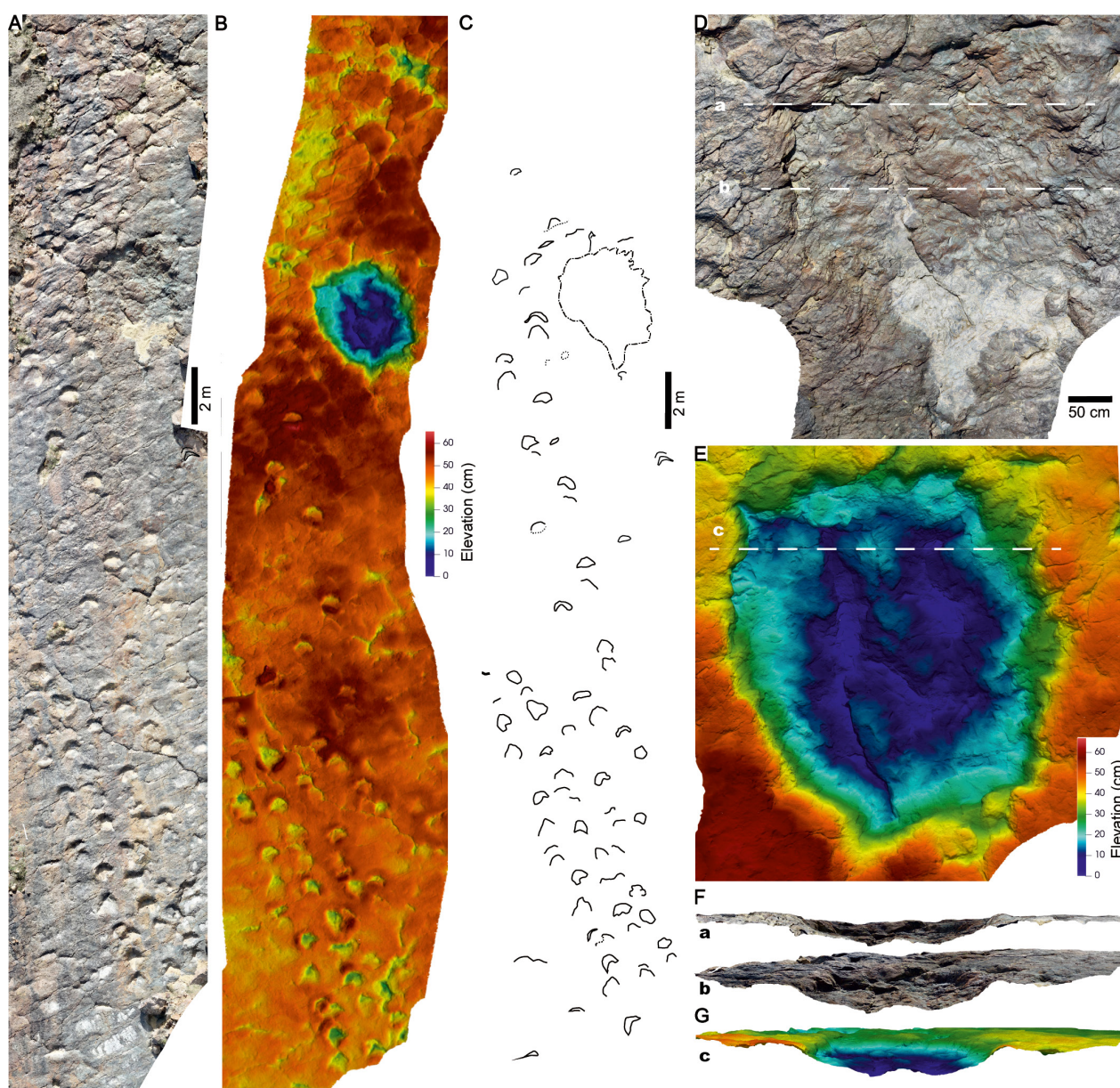


Figure 4. Mullurina Mayu palaeosurface. **A.** Aerial view with titanosaurid tracks; **B.** False-colour depth map of the palaeosurface; **C.** Outline illustration showing the spatial relationship between the depression and titanosaurid trackways indicated and depression outlined (stippled line); **D–E.** Aerial view of bowl-shaped depression as shown in (A–C) and false colour depth map; **F.** Median plane(s) from west-east across the bowl-shaped depression (transsect a, b in D). **(G)** False colour depth map of median plane cross section. (transsect c in E).

flow over the semi-cohesive palaeosurface, producing erosional sole marks (which include scours and gutter casts; Miall 2006). These features are characterised by U-, V-, or rectangular cross-sections and are commonly elongate and asymmetric in plane view. Diagnostic criteria would include smooth or locally polished walls, tool marks, and a geometry that indicates unidirectional flow. In our case, the bowl-like morphology in planform, rim, and syn-sedimentary internal structures is inconsistent with flow-parallel, elongate structures typical of hydraulic scouring. We observe no scouring, tool marks, or polished surfaces on any part of the palaeosurface.

Additionally, the structure can be compared to a weathering pit (panhole) that forms during water pooling and repeated physical or chemical weathering (Udomsak et al. 2021; Timms 2021). In this case, we would expect to see textures consistent with weathering and no internal bedding disturbance. Typically, panhole pits occur as multiples on the same surface and within a similar size range (Timms 2021), which does not align with the singular bowl nor its overall morphology, which displays syn-sedimentary features rather than secondary weathering. Furthermore, no comparable pits have been identified on the same surface, and the structure's morphology falls outside the size range typical of panhole associations (e. g. 2 m by 1 m).



Figure 5. Textured model of the bowl-shaped depression in aerial view. Asterisks mark semicircular impressions that contain bundles of parallel grooves illustrated in Fig. 6. Scale bar: 50 cm.

Biogenic Origin: evidence from sauropod skin traces

A biogenic process of formation for the Mullurina Mayu depression is supported by the presence of grouped, parallel grooves (several confined to defined areas; Figs 5, 6) along the basin walls, together with isolated, single scratch-like marks on the basin floor, which are interpreted as ungual traces. Associated titanosaurid trackways and the size and morphology of the scratch traces make the most parsimonious interpretation that a sauropod was involved in the formation and/or modification of this basin-like structure (Fig. 6). Additionally, sauropod tracks (manus impressions) can be seen near the basin margin (Figs 2, 4, 6).

The most directly comparable example for the scratch-like parallel grooves comes from Late Cretaceous titanosaur track soft tissue traces (Nemegt Formation, Mongolia; Bell et al. 2025), in which both the manus and pes show evidence of parallel striae (scale scratch lines; Bell et al. 2025; Fig. 7C–F) created by keratinised scales during foot movement in the sediment. The width and interspacing of scale scratch lines vary alongside variations in scale size, morphology and geometry. In the manus of the Nemegt trackmaker, the diameter of the scales scratch lines is ~10–12 mm, with interstitial area width of 2–7 mm. The low relief smooth/hummocky, large scales grade into pyramidal or spur-like scales at the palmar margins (Bell et al. 2025). Similar bundling of parallel grooves (scale scratch lines) within the walls and floor of a 3D sauropod manus impression cast (e.g., Late Jurassic, Milàn et al. 2005) provides evidence of manus

movement. In other latest Maastrichtian titanosaurian skin traces (southern Pyrenees), sub-rounded pentagonal and hexagonal polygons (11–16 mm in diameter) are arranged in rosettes in the manus (Fondevilla et al. 2017) when impressed.

In the Nemegt pes (Fig. 7C, D), Bell et al. (2025) measure scratch line diameters between ~2–3 mm at the margin of digit I, which increase to ~10 mm in digits IV and V, with the posteromedial area of the heel preserving the widest scratch lines at ~20 mm ending in polygonal skin impressions. The Mullurina Mayu parallel striae traces are ~10 mm wide, with an interspacing distance of ~18 mm. These are comparable to the scale scratch lines from the Nemegt titanosaurid traces (~20 mm around the heel, 2–10 mm around digits; Bell et al. 2025) in the mid-foot to distal digital scales. In addition to the presence of scratch lines, the Mullurina Mayu traces occur in semi-circular depressions and exhibit two main orientations. They are inconsistent with a single direction of movement. The multidirectional striae bundles are interpreted as produced by repeated foot movements around the margin of the bowl depression. These differ from the previously outlined skin impressions associated with locomotion. The traces in the depression show evidence of scraping or scratch digging. Bell et al. (2025) discuss the Mongolian titanosaurid pedal ungual traces, and estimated them to represent only 10–13% of the ungual protruding from the fleshy cuticle, they have hypothesised that scratch digging is possible for pedal digit functionality. Bonnan (2005) was one of the first to come up with this possibility. This is supported by Cretaceous nesting structures (see below; Chiappe et al. 2004; Vila et al. 2010).

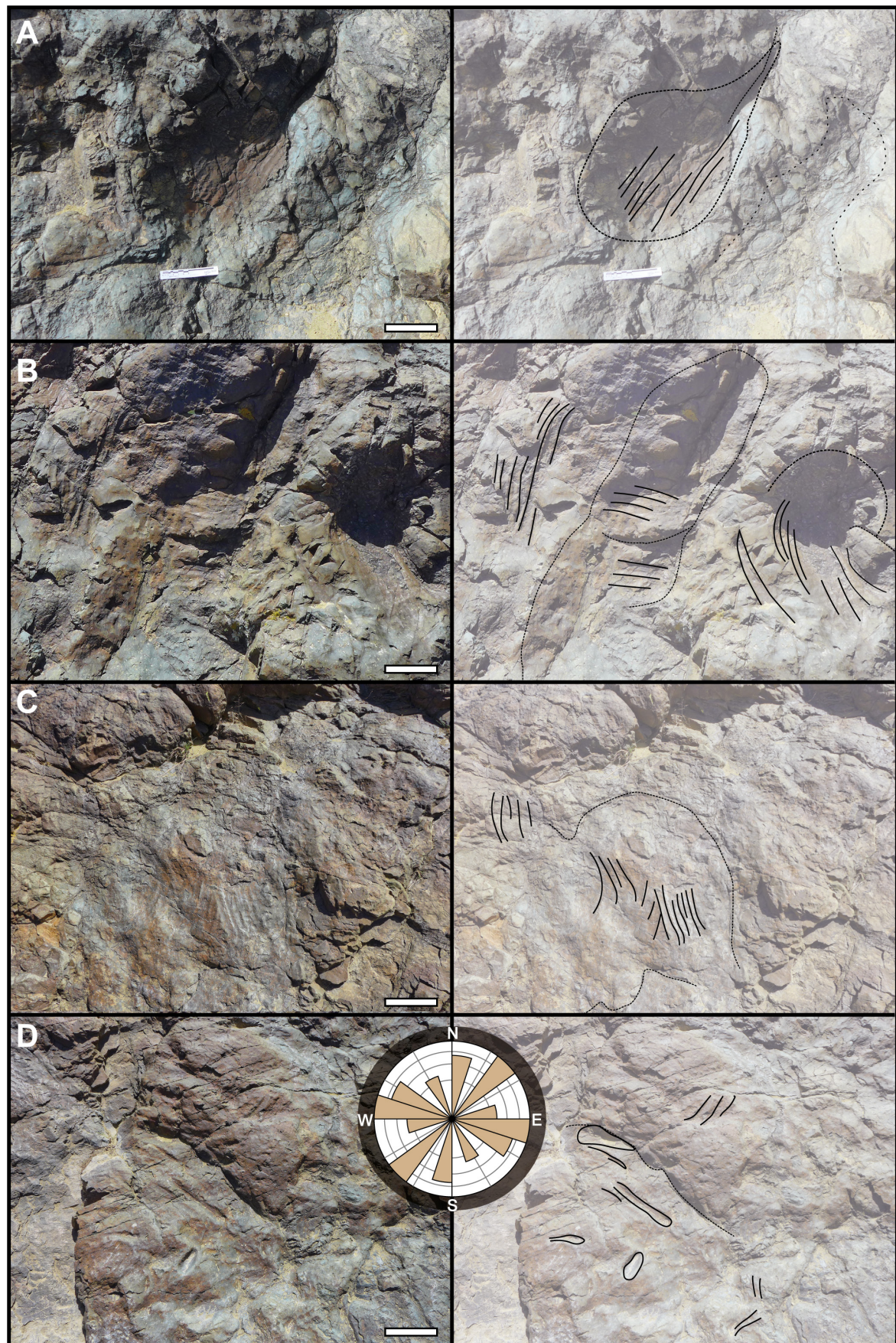


Figure 6. Bundle-like scratch traces within the depression and their orientations. Solid lines indicate scratch-like marks. Dotted lines indicate the boundaries around some of these scratch traces. Note also soft sediment deformation. Rose diagram indicates scratch directions ($n = 17$). Scale bars: 10 cm.

Possible structures

We hypothesise that the Mullurina Mayu bowl-like depression may represent the following, in order from most to least likely:

A dinoturbation basin like a trampled watering hole. In contemporary semi-arid settings, topographic low points retain standing water and serve as congregation points for animal visitation (Jarman 1972). Continuous trampling compacts and deforms the substrate, while scraping and slipping behaviour introduces grooves and irregular surface textures. Periodic quiet-water inundation deposit fine-grained laminated sediment between trampling events, recording episodic activity. This model predicts a substrate with compaction structures, scratch or slip grooves, and interbedded fine-grained laminae reflecting alternating wet and dry phases. However, at Mullurina Mayu, both the underlying substrate and infill lack lamination (structureless, no interbedding), which contradicts the hypothesis of repeated trampling cycles. Pedogenesis indicators in the overlying bed suggest prolonged subaerial exposure, consistent with a single low-energy event rather than episodic ponding. Moreover, sauropod tracks do not show a congregation point or trampling near the basin.

Geophagy: A dinoturbation basin for mineral mining or water. Geophagy, the ingestion of substrate for minerals, by large herbivores such as elephants (Jarman 1972) is one possible explanation for the creation of the depression. The present substrate does not contain any traces of minerals (except quartz and mica), therefore we can likely exclude geophagy. Mammals are also known to excavate holes to reach the water table and for purifying drinking water (Ramey et al. 2013). This could be another avenue for the creation of the structure; however, it is hard to prove or disprove either of these assumptions.

An attempt at a nest scrape (Chiappe et al. 2004). Trackmakers are known to excavate a shallow to moderately deep pit-like structure for egg-laying (Varicchio et al. 1997; Grellet-Tinner et al. 2006; Chiappe et al. 2004; Dhiman et al. 2023). Chiappe et al. (2004) has documented pit-like structures used for egg-laying by sauropods. Morphologically, these show some similarity with the Mullurina Mayu depression. Chiappe et al. (2004) suggest 4 criteria for recognising such a structure: (a) presence of eggs/eggshell/juvenile body fossils in the depression; (b) depression truncates primary stratification; (c) elevated rim of displaced sediment around the depression, and (d) contrasting infill. Vila et al. (2009, 2010) reported dinosaur nests from the Late Cretaceous of Spain and concluded that the structures were excavated by the hind feet of the sauropods. The Mullurina Mayu depression shows two of these features (truncation and infill differs from host substrate). There are no repeated basin-like or nest-like structures (i.e., no evidence of communal nesting behaviours).

A less likely hypothesis is a mal-formed, lek-like display scrape area (Lockley et al. 2016; Buntin et al. 2025). In this case, the structure would show repeated, long, scratch-like grooves that create a depression within the sediment,

which can be ascribed to the ichnogenus *Ostendichnus*. *Ostendichnus* is characterised by an oval-shaped depression separated by a central ridge, bisecting the structure into two parallel troughs with internally parallel and longitudinal grooves (scratch marks). This trace has been linked to theropod dinosaurs, indicating areas for nesting or display behaviours (courtship) (Lockley et al. 2016; Buntin et al. 2025). The Mullurina Mayu bowl-like structure doesn't show any of the characteristics of *Ostendichnus* and therefore is unlikely to represent a lek-type trace.

Preferred Interpretation

Of the hypotheses evaluated, abiotic formation is considered least consistent with the syn-sedimentary nature, scratch-like traces, and bowl morphology of the structure. Among biogenic interpretations, the dinoturbation basin and nest scrape remain the most morphologically plausible, though neither can be confirmed without more detailed study and the presence of more concrete examples. The scratch traces are comparable to skin-slip impressions documented for both the manus and the pes of sauropods (e.g., Milàn et al. 2005; Fondevilla et al. 2017; Paik et al. 2017; Bell et al. 2025; Fig. 7).

Nesting behaviours

Sauropod nesting and reproductive biology is poorly understood from the fossil record (Chiappe et al. 2004), and the unknown ontogenetic stage of the Mullurina Mayu trackmakers makes interpretations complicated. We have assumed, based on size, that these tracks represent subadults, while acknowledging that track size alone is not a direct proxy for ontogenetic stage. However, adjacent sites within the same sedimentary package show large pes tracks (Niñu Mayu, pes length: >80 cm). Nonetheless, if assuming abandoned nesting for our depression, subadult titanosaurid sauropods could be capable of reproductive behaviour because sexual maturity is reached before maximum body size (Curry Rogers and Erickson 2005).

It is also possible that the Mullurina Mayu depression represents the activity of another animal. For instance, longirostrine crocodyliforms are known from the Bolivian Late Cretaceous (e.g., Jouve et al. 2021) and Late Cretaceous notosuchian crocodyliforms from Brazil are known to produce egg clutches in nests, preserved *in situ*, in floodplain mudstones (Paixão et al. 2026) while eggshell microstructure, i.e., oospecies *Bauruoolithus*, indicate burial-style nesting (Oliveira et al. 2011) consistent with crocodyliforms. No crocodyliform tracks are currently known in Bolivia, and in the absence of other evidence (*in situ* egg clutches/eggshells), a crocodyliform origin is considered less likely. Although the overall dimension of the Mullurina Mayu structure does show some geometric overlaps with modern crocodile hole nests (Table 1), it is considerably larger than those of

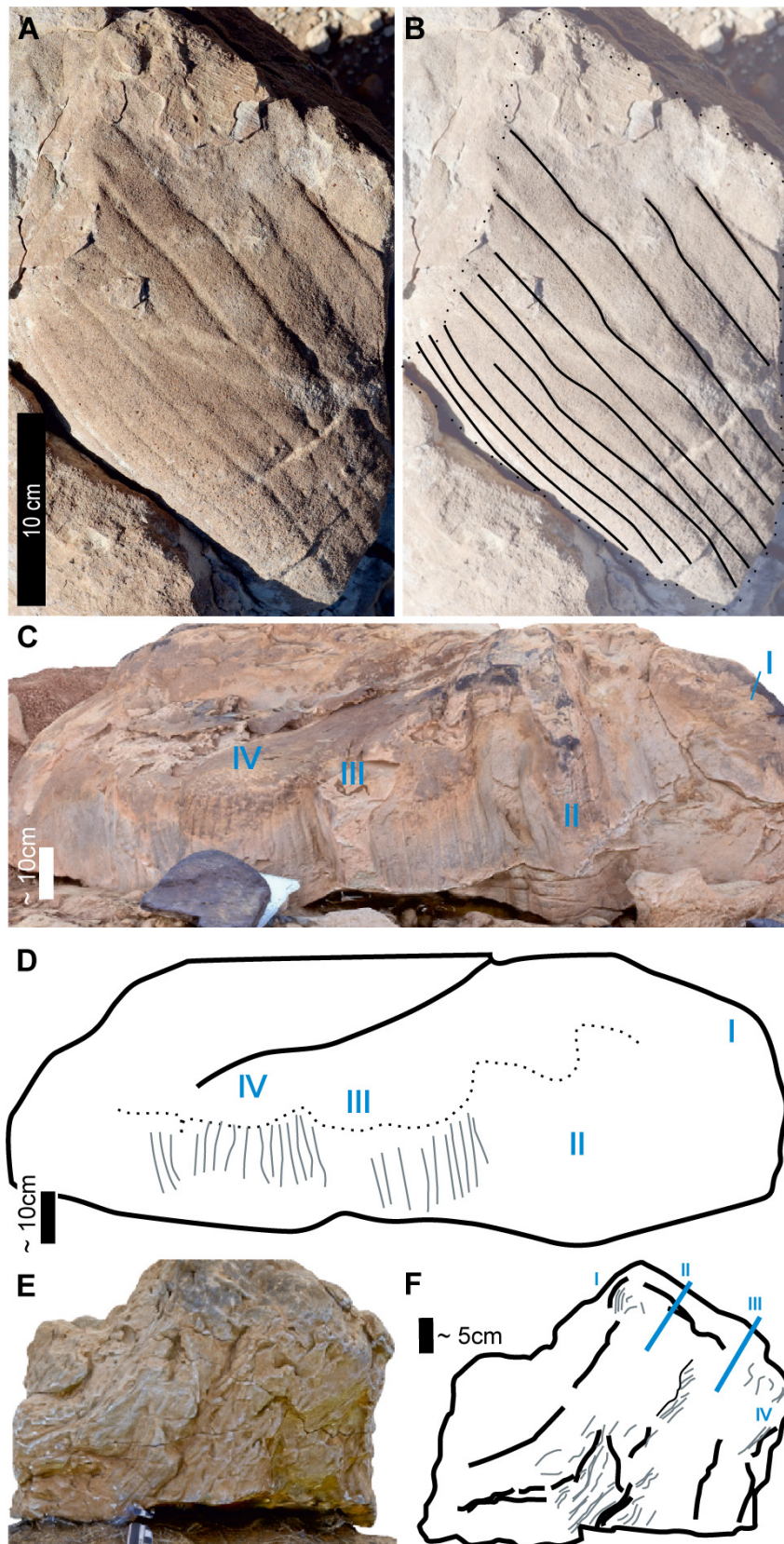


Figure 7. Skin scratch traces preserved in sauropod tracks. **A.** Impressions of skin drag marks (pes) from the Purgatoire tracksite (USA; Late Jurassic); **B–F.** Cretaceous titanosaurid skin scratch traces from the Nemegt Formation, adapted from Bell et al. (2025) and associated supplementary materials; **B.** Nemegt pes 3D model, taken from Bell et al. (2025) supplementary material and annotated with digit impressions I–IV following Bell et al. (2025, fig. 4); **D.** Outline trace of skin scratch impressions (grey), pes outline in solid or stippled line; **E.** Nemegt manus 3D model, taken from Bell et al. (2025) supplementary material, with **F.** outline trace adapted per Bell et al. (2025, fig. 2), with digits indicated in blue along with direction of movement (blue lines).

Table 1. Comparison of Mullurina Mayu structure and titanosaurid nests with those of modern crocodiles.

Depression feature	<i>Crocodylus niloticus</i> Modha 1967	Titanosaur nest (cf. Chiappe et al. 2004)	Mullurina Mayu structure
Dimensions	subcircular burrow opening: 23–75 cm × 21–50 cm; Egg chamber: 25–48 cm × 20–40 cm	1–1.4 m	4.2 × 3.2 m
Depth	~20–50 cm	10–18 cm	Max 60 cm
Shape	Oblique burrow with wide opening, narrows to a neck leading to a wider chamber where eggs are deposited	Bowl to kidney-shaped	Bowl
Evidence of excavation	Yes	Yes	Yes
Rim	?	Clear rim (bulge)	Clear rim (no bulge)
Infill	Sediment collapse (covered eggs)	Contrasting infill (did not bury eggs)	Contrasting infill

known crocodyliform nest chambers (modern hole-nests; Modha 1967; and fossil clutch size; Paixão et al. 2026). Moreover, the size and geometry of the scratch trace bundles, confined within oval depressions, along the basin walls, are more consistent with the geometry and sizing of sauropod pes movement than with crocodyli-form limb actions.

Conclusion

We document an unusual compound trace-sediment structure (Fig. 8) formed on a levee/overbank palaeosurface within the Lower Member of the El Molino Formation at Mullurina Mayu, preserved in close spatial association with titanosaurid trackways (*Calorckosauripus lazari*). The depression is bowl-shaped, 4.2 m × 3.2 m, with a maximum

depth of 60 cm and truncates the primary stratification (claystone) and is infilled by massive caliche-bearing marls showing pedogenic overprinting. The latter indicates a single low-energy event followed by drying.

We consider a biogenic explanation for the formation of the depression most likely given the presence of scratch and claw traces on the walls and floor of the depression. Bonnan (2005) was one of the first who came forward with a scratch digging hypothesis in sauropods. The morphology and arrangement of bundled grooves (scale scratch lines) is known from several sites where sauropod tracks have been preserved (e.g., Milàn et al. 2005; Bell et al. 2025). Thus, in our view the most parsimonious explanation of the bundled grooves, along with their multidirectional orientation, is the result of repeated foot movement around the edge and within the bowl-like depression by sauropods. Among our biotic hypothesis for



Figure 8. Artistic reconstruction of the Mullurina Mayu bowl-shaped depression during the Late Cretaceous, depicting the probable tracemakers responsible for the *Calorckosauripus* trackways and possibly the bowl-shaped depression. Illustration by Joshua Knüppe (commissioned 2025).

basin formation, abandoned nesting is plausible given the cutting of the primary sediment and the basin walls (i.e., Chiappe et al. 2004; Dhiman et al. 2023). However, in the absence of other indicators (i.e., eggs, traces of eggshells), sauropod nesting behaviour is tentatively linked.

Acknowledgements

We would like to express our gratitude to the local Ayllus for granting access to the site. Funding support for the senior author provided by Professional Palaeo Consulting (Switzerland) is gratefully acknowledged. We thank Joshua Knüppe for his skilful palaeoartistic reconstruction, commissioned by the senior author at the 2025 annual meeting of the European Association of Vertebrate Palaeontologist (EAVP) in Kraków, Poland. We also thank Jens Lallensack and Bell Phil for their constructive comments which have improved the quality of the manuscript.

References

- Bell PR, Woodruff DC, Nguyen K, Mainbayar B, Currie PJ (2025) Remarkable soft tissue anatomy recorded in titanosaur (Sauropoda) tracks from the latest Cretaceous of Mongolia. *Zoological Journal of the Linnean Society* 204. <https://doi.org/10.1093/zoolinnean/zlaaf053>
- Bonnan MF (2005) Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny. In: Carpenter K, Tidwell V (Eds) *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Bloomington, IN: Indiana University Press, 346–380.
- Buntin RC, Mokslestad T, Matthews NA, Breithaupt B, Murphey PC, Kapinos I, Noffke N (2025) A new theropod dinosaur lek in the Cretaceous Dakota Sandstone (Dinosaur Ridge, Colorado, USA). *Cretaceous Research*, 176 pp. <https://doi.org/10.1016/j.cretres.2025.106176>
- Chiappe LM, Schmitt JG, Jackson FR, Garrido A, Grellet-Tinner G (2004) Nest structure for sauropods: Sedimentary criteria for recognition of dinosaur nesting traces. *Palaios* 19: 89–95. [https://doi.org/10.1669/0883-1351\(2004\)019<0089:NSFSSC>2.0.CO;2](https://doi.org/10.1669/0883-1351(2004)019<0089:NSFSSC>2.0.CO;2)
- Curry-Rogers K, Erickson GM (2005) Sauropod histology: Microscopic views on the lives of giants. In: Curry Rogers K, Wilson JA (Eds) *The sauropods - Evolution and paleobiology*. University of California Press, 303–326. <https://doi.org/10.1525/california/9780520246232.003.0012>
- Dhiman H, Verma V, Singh LR, Miglani V, Jha DK, Sanyal P, Tandon SK, Prasad GV (2023) New Late Cretaceous titanosaur sauropod dinosaur egg clutches from lower Narmada valley, India: Palaeobiology and taphonomy. *PLoS ONE* 18(1): e0278242. <https://doi.org/10.1371/journal.pone.0278242>
- Esperante R, Rocha-Rodríguez G, McLarty JA, Biaggi RE, Nick KE, Baltazar HD, Varquera AC (2024) Diversity of dinosaur tracks and swim traces in a new site in the Upper Cretaceous El Molino Formation, Torotoro National Park, Bolivia. *Journal of South American Earth Sciences* 128(2023): 104480. <https://doi.org/10.1016/j.jsames.2023.104480>
- Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, Castanera D, Citton P, Díaz-Martínez I, Farlow JO, Fiorillo AR, Gatesy SM, Getty P, Hatala KG, Hornung JJ, Hyatt JA, Klein H, Lallensack JN, Martin AJ, Marty D, Matthews NA, Meyer CA, Milán J, Minter NJ, Razzolini NL, Romilio A, Salisbury SW, Sciscio L, Tanaka I, Wiseman ALA, Xing LD, Belvedere M (2018) A standard protocol for documenting modern and fossil ichnological data. *Palaeontology* 61(4): 469–480. <https://doi.org/10.1111/pala.12373>
- Fondevilla V, Vila B, Oms O, Galobart A (2017) Skin impressions of the last European dinosaurs. *Geological Magazine* 154(2): 393–398. <https://doi.org/10.1017/S0016756816000868>
- Gayet M, Marshall LG, Sempere T (1991) The Mesozoic and Paleocene vertebrates of Bolivia and their stratigraphic context: A review. In: Suarez-Soruco R (Ed.) *Fosiles y Facies de Bolivia: Vertebrados*, Vol. I. *Revista Tecnica de YPF* 12, Santa Cruz, 393–433. [In Spanish]
- Gayet M, Marshall LG, Sempere T, Meunier FJ, Cappetta H, Rage JC (2001) Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles) from Pajcha Pata (Bolivia). *Biostratigraphic, palaeoecologic and palaeobiogeographic implications*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 169: 39–68. [https://doi.org/10.1016/S0031-0182\(01\)00214-0](https://doi.org/10.1016/S0031-0182(01)00214-0)
- Grellet-Tinner G, Chiappe L, Bottjer D (2006) Dinosaur eggs and nesting behaviors: A paleobiological investigation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232: 294–321. <https://doi.org/10.1016/j.palaeo.2005.10.029>
- Jarman PJ (1972) The use of drinking sites, wallows and salt licks by herbivores in the flooded Middle Zambezi Valley. *East African Wildlife Journal* 10: 193–209. <https://doi.org/10.1111/j.1365-2028.1972.tb00727.x>
- Jouve S, de Muizon C, Céspedes-Paz R, Sossa-Soruco V, Knoll S (2021) The longirostre crocodyliforms from Bolivia and their evolution through the Cretaceous–Palaeogene boundary. *Zoological Journal of the Linnean Society* 192(2): 475–509. <https://doi.org/10.1093/zoolinnean/zlaa081>
- Lacovara KJ, Lamaan MC, Ibiricu LM, Poole JC, Schroeter ER, Ullmann PV, Voegelé KK, Boles ZM, Carter AM, Fowler EK, Egerton VM, Moyer AE, Coughenour L, Schein JP, Harris JD, Martínez RD, Novas FE (2014) A gigantic, exceptionally complete Titanosaurian sauropod from Southern Patagonia, Argentina. *Scientific Reports* 4: 6196. <https://doi.org/10.1038/srep06196>
- Leonardi G (1984) Le impronte fossili di dinosauri. In: Bonaparte JF, Colbert EH, Currie PC (Eds) *Sulle orme dei Dinosauri*. Erizzo, Venezia, 163–186.
- Llempen Salinas NA (2024) Caracterización icnológica, estratigráfica y sedimentológica del yacimiento de huellas de aves “Camino El Vergel”, Formación El Molino (Maastrichtiano), Parque Nacional Torotoro, Bolivia (unpublished Tesis de grado). Universidad de Concepción.
- Lockley MG, Meyer CA (2022) The megatracksite phenomenon: implications for tetrapod palaeobiology across terrestrial-shallow-marine transitional zones. In: Console-Gonella C, de Valais S, Díaz-Martínez I, Citton P, Verde M, McLroy D (Eds) *Ichnology in Shallow-marine and Transitional Environments*. Geological Society, London, Special Publications, 522 pp. <https://doi.org/10.1144/SP522-2021-164>
- Lockley MG, Schulp AS, Meyer CA, Leonardi G, Mamani D (2002) Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23: 383–400. <https://doi.org/10.1006/cres.2002.1006>

- Lockley MG, McCrea RT, Buckley LG, Deock LJ, Matthews NA, Breithaupt BH, Houck KJ, Gierliński GD, Surmik D, Kim KS, Xing L, Kong DY, Cart K, Martin J, Hadden G (2016) Theropod courtship: Large scale physical evidence of display arenas and avian-like scrape ceremony behaviour by Cretaceous dinosaurs. *Scientific Reports* 6: 18952. <https://doi.org/10.1038/srep18952>
- Mallison H, Wings O (2014) Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques* 12: 1–31.
- Meyer CA, Hippler D, Lockley MG (2001) The Late Cretaceous vertebrate ichnofacies of Bolivia – facts and implications. In: VII International Symposium on Mesozoic Terrestrial Ecosystems. *Asociacion Palaeontologica Argentina Special Publication* 7: 133–138.
- Meyer CA, Belvedere M, Marty D (2018) Titanosaurid trackways from the El Molino Formation (Maastrichtian) of Bolivia (Cal Orck'o, Sucre, Dep. Chuquisaca). In: Bordy EM, Meyer CA, Belvedere M (Eds) *Proceedings of the 2nd International Conference on Continental Ichnology*. *Annales Societatis Geologorum Poloniae* 88: 223–241. <https://doi.org/10.14241/asgp.2018.018>
- Meyer CA, Marty D, Thüring B, Thüring S, Belvedere M (2019) The Late Cretaceous dinosaur track record of Bolivia – Review and perspective. *Journal of South American Earth Sciences*, 106 pp. <https://doi.org/10.1016/j.jsames.2020.102992>
- Meyer CA, Heymann JH, Alem Rojo A, Cespedes Paz R, Hippler D (2025a) Multiple observations on the preservation of dinosaur tracks in a lacustrine to fluvial setting (Late Cretaceous, El Molino Formation; Parque Nacional de Toro Toro, Bolivia). *Italian Journal of Geosciences* 144(3): 405–421. <https://doi.org/10.3301/IJG.2025.19>
- Meyer CA, Heymann JH, Alem Rojo A, Hippler D, Souza de Carvalho I, Sciscio L (2025b) Las huellas de dinosaurios del Cretacico superior en Bolivia: Nuevos hallazgos y revision de huellas conocidas. *Memorias III Congreso de Palaeontologia de Bolivia*, 68–73.
- Miall AD (2006) *The Geology of Fluvial Deposits: Sedimentary Facies, Basin Analysis, and Petroleum Geology*. 4th corrected printing. Springer-Verlag, Berlin and Heidelberg, 582 pp.
- Milán J, Christiansen P, Mateus O (2005) A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: Implications for sauropod manus shape and locomotor mechanics. *Kaupia Darmstädter Beiträge zur Naturgeschichte* 14: 47–52.
- Modha ML (1967) The ecology of the Nile Crocodile (*Crocodylus niloticus laurenti*) on central island, Lake Rudolf. *African Journal of Ecology* 5(1): 74–95. <https://doi.org/10.1111/j.1365-2028.1967.tb00763.x>
- Oliveira CEM, Santucci RM, Andrade MB, Fulfaro VJ, Basilo JAF, Benton MJ (2011) Crocodylomorph eggs and eggshells from the Adamantina Formation (Bauru Group), Upper Cretaceous of Brazil. *Palaeontology* 54(2): 309–321. <https://doi.org/10.1111/j.1475-4983.2010.01028.x>
- Paik IS, Kim HJ, Lee H, Kim S (2017) A large and distinct skin impression on the cast of a sauropod dinosaur footprint from Early Cretaceous floodplain deposits, Korea. *Scientific Reports* 7(1): 16339. <https://doi.org/10.1038/s41598-017-16576-y>
- Paixão GMX, Martinelli AG, Marsola JCA Hechenleitner EM, Nava WR, Chiappe LM, Jussiani EI, Rozadilla S, Kaluza J, Pinheiro FL (2026) Fossil evidence of exceptionally large egg-clutches sheds light on reproductive diversity in Late Cretaceous crocodyliforms from Brazil. *Journal of Vertebrate Paleontology* 45(4). <https://doi.org/10.1080/02724634.2025.2596997>
- Ramey EM, Ramey RR, Brown LM, Kelley ST (2013) Desert-dwelling African elephants (*Loxodonta africana*) in Namibia dig wells to purify drinking water. *Pachyderm* 53: 66–72. <https://doi.org/10.69649/pachyderm.v53i.325>
- Riguetti F, Citton P, Apesteguia S, Zacarias GG, Pereda-Superbiola X (2021) New ankylosaurian trackways (cf. *Tetrapodosaurus*) from an uppermost Cretaceous level of the El Molino Formation of Bolivia. *Cretaceous Research* 124: 1–16. <https://doi.org/10.1016/j.cretres.2021.104810>
- Rouchy JM, Camoin G, Casanova J, Deconinck JF (1993) The central palaeo-Andean basin of Bolivia (Potosi area) during the Late Cretaceous and early Tertiary: reconstruction of ancient saline lakes using sedimentological, palaeoecological and stable isotope records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105: 179–198. [https://doi.org/10.1016/0031-0182\(93\)90083-U](https://doi.org/10.1016/0031-0182(93)90083-U)
- Sempere T, Butler RF, Richards DR, Marshall LG, Swisher CC (1997) Stratigraphy and chronology of Upper Cretaceous–Lower Paleogene strata in Bolivia and northwest Argentina. *Geological Society of America Bulletin* 109: 709–727. [https://doi.org/10.1130/0016-7606\(1997\)109%3C0709:SACOU%3E2.3.CO;2](https://doi.org/10.1130/0016-7606(1997)109%3C0709:SACOU%3E2.3.CO;2)
- Tasistro-Hart A, Maloof A, Schoene B, Eddy ME (2019) Astronomically forced hydrology of the Late Cretaceous sub-tropical Potosí Basin, Bolivia. *Geological Society of America Bulletin* 132: 9–10. <https://doi.org/10.1130/B35189.1>
- Timms BV (2021) Pan gnammas (weathering pits) across Australia: Morphology in response to formative processes. *International Journal of Geosciences* 12: 984–993. <https://doi.org/10.4236/ijg.2021.1210051>
- Udomsak S, Choowong N, Chutakositkanon V (2021) Thousands of potholes in the Mekong River and giant pedestal rock from north-eastern Thailand: Introduction to a future geological heritage site. *Geoheritage* 13. <https://doi.org/10.1007/s12371-020-00524-w>
- Varicchio DJ, Jackson F, Borkowski JJ, Horner JR (1997) Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian traits. *Nature* 385: 247–250. <https://doi.org/10.1038/385247a0>
- Vila B, Galobart A, Oms O, Poza B, Bravo AA (2009) Assessing the nesting strategies of Late Cretaceous titanosaurs: 3-D clutch geometry from a new megaloolithid egg site. *Lethaia* 43: 197–208. <https://doi.org/10.1111/j.1502-3931.2009.00183.x>
- Vila B, Jackson FD, Fortuny J, Sellés AG, Galobart A (2010) 3-D modelling of megaloolithid clutches: Insights about nest construction and dinosaur behaviour. *PLoS ONE* 5(5): e10362. <https://doi.org/10.1371/journal.pone.0010362>

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

No AI tools were used in the preparation of this manuscript.

Funding

No funding was reported.

Author contributions

CAM: Research design, field work, data acquisition, writing of the manuscript, editing manuscript. HH: field work, data acquisition, writing of the manuscript, editing manuscript. LS: Research design, 3D modelling, writing of the manuscript, editing manuscript

Author ORCIDs

C.A. Meyer  <https://orcid.org/0000-0002-5069-8924>

L. Sciscio  <https://orcid.org/0000-0003-4178-2881>

Data availability

The data generated and analysed during this study, including 3D models and measurement datasets, are available as supplementary materials and can be accessed via FigShare: <https://doi.org/10.6084/m9.figshare.32987330>.
