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TITANOSAUR TRACKWAYS FROM THE LATE CRETACEOUS EL MOLINO FORMATION OF BOLIVIA (CAL ORCK’O, SUCRE)

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Abstract: The Cal Orck’o tracksite is exposed in a quarry wall, approximately 4.4 km NW of Sucre (Department Chuquisaca, Bolivia) in the Altiplano/Cordillera Oriental, in the El Molino Formation (Middle Maastrichtian). Fossiliferous oolitic limestones, associated with large, freshwater stromatolites and nine levels of dinosaur tracks in the El Molino Formation document an open lacustrine environment.

The main track-bearing level is almost vertical with a surface area of ~ 65,000 m^2. The high-resolution mapping of the site from 1998 to 2015 revealed a total of 12,092 individual dinosaur tracks in 465 trackways. Nine different morphotypes of dinosaur tracks have been documented. Amongst them are several trackways of theropods, ornithopods, ankylosaurs and sauropods, with the latter group accounting for 26% of the trackways.

Two different types of sauropod trackways are present. One exhibits speech-bubble-shaped manus impressions that are rotated outwardly and located more outwards than pes prints, and oval to rounded pes imprints with few details, but with a characteristic oval track shape. The second morphotype has more rounded and axially compressed pes imprints and horseshoe-like manus impressions. The manus shows clear impressions of digits I and V.

The first morphotype with the more rounded manus can be attributed to a derived titanosaur. The second is assigned to the new ichnogenus *Calorckosauripus* and was probably made by a basal titanosaur. Both sauropod morphotypes exhibit a narrow-gauge and a wide-gauge stance along the same trackway, and therefore the authors suggest that trackway width may not be correlated, or may not be correlated completely with the osteological characters of the trackmaker’s skeleton.

Key words: Track morphotypes, sauropods, new ichnogenus, quadrupedal, trackway gauge variation.

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INTRODUCTION

Dinosaur tracks in South America are well-known since the seminal work of Leonardi (1989, 1994), although reports from Argentina were known earlier (e.g., Alonso, 1980). The first account of dinosaur tracks from Bolivia is that of Branisa (1968), who briefly mentioned surfaces from the El Molino Formation of Toro Toro. In 1994, Leonardi figured four different Cretaceous localities with dinosaur tracks, i.e., Toro Toro, Parotani (not verified), Arampampa (not verified) and Camargo (not verified). The footprints of ankylosaurs, theropods and sauropods from the Toro Toro site were figured by Leonardi (1994), but a detailed description of the site is missing. Furthermore, the presence of dromaeosaurid footprints at Toro Toro was mentioned by Apesteguía *et al.* (2007, 2011).

In 1994, Jose Hugo Heymann (geologist) and Klaus Schuett (at that time Director of Tourism in Sucre) discovered tracks in the Cal Orck’o Quarry and brought them to the attention of the first author. In 1998, the first field work was carried out (mapping, casting) and the tracks were subsequently studied during field seasons in 2002, 2003, 2006, 2009, 2015 and 2017, respectively. The first results and subsequent studies revealed 3,500 footprints of five different dinosaur morphotypes (Meyer *et al.*, 1999a, b; Meyer *et al.*, 2001; McCrea *et al.*, 2001; Meyer *et al.*, 2006; Apesteguía *et al.*, 2007). During these visits, other sites also have been brought to the attention of the authors. In 1998, a site in the Maragua syncline was mapped close to the village of Humaca, in the Chaunaca Formation (Lockley *et al.*, 2002a).

This surface contains the trackways of 11 sauropods walking in a herd and several theropod footprints. Another site, which is close to the village of Potolo in the underlying Ariofilla Formation, contains the underprints of sauropods and theropod footprints (Meyer *et al.*, 2016).

The Cal Orck'o site (derived from Quechua meaning "Cerro de Cal"; in Spanish, Hill of Limestone) is located in a quarry of the "Fábrica Nacional de Cemento", 4.4 km NW of downtown Sucre, and forms a ridge with a convergence to the NNW-SSE (Figs 1, 2). The highest point in Cal Orck'o has an altitude of 3,029 m. The southern corner of the site is at 19°00′28.16″S / 65°14′00.66″W and the northern corner is located at 18°59′.48.72″S / 65°14′22.38″W (Figs 1, 2). The area is in the Municipal Park FANCESA, which corresponds to the legally-protected Paleontological Reserve of Cal Orck'o. The wall of Cal Orck'o integrates the southwestern flank of a syncline in a North-South-East direction, composed of intercalated claystones and limestones of the El Molino Formation. The exposed wall is parallel to the axis of the syncline; the Parque Cretácico, a Museum, is located to the west (Fig. 2).

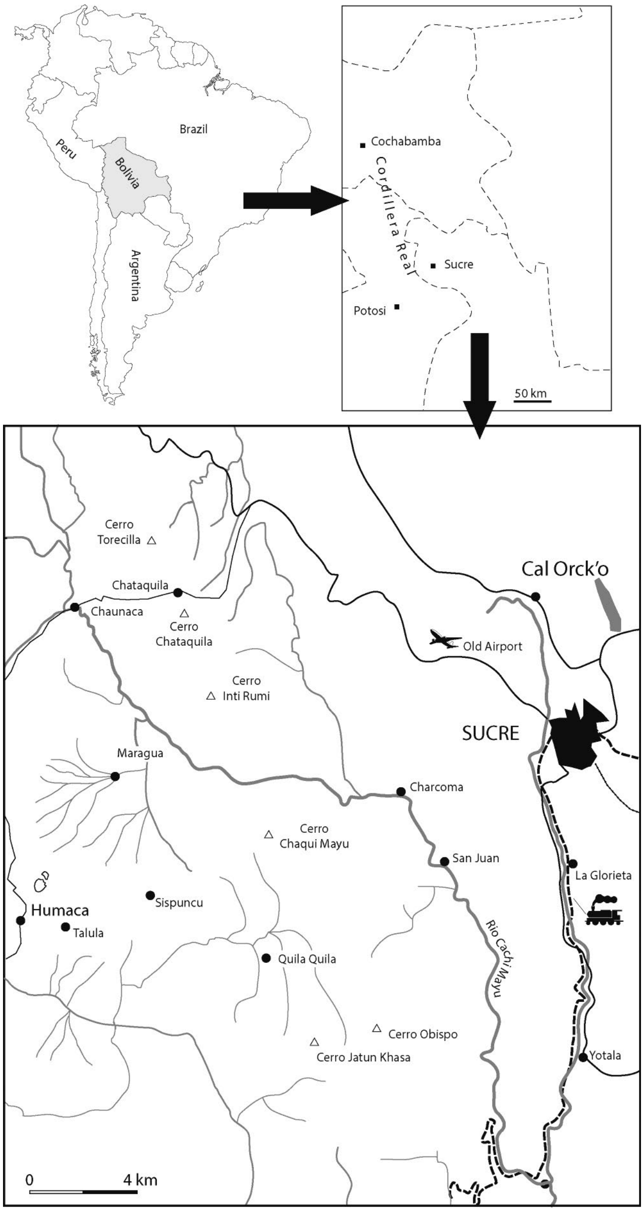

Fig. 1. Geographic position of the Cal Orck'o fossil locality in Bolivia and South America.

Since 1998, the perception of the palaeontological sites, both by government and general public, has changed considerably in Bolivia. Just after the first scientific mission in 1998, the Bolivian government declared the study area a National Monument (law of October 30, 1998), and passed many more important laws, concerning the formal and legal protection of Cal Orck'o and other palaeontological sites. The joint effort of the local and national authorities made significant advances in the conservation and sustainable development of this important palaeontological site as a tourist destination. With financial support from the Banco Interamericano de Desarollo (BID), these efforts also allowed the planning and inaugurating of a park and a museum (Parque Cretácico) in 2006.

In this paper, the authors analyse the sauropod tracks from the Cal Orck'o tracksite, identifying two distinct morphotypes (E and F). Morphotype F is recognized as belonging to a new ichnotaxon: *Calorckosauripus lazari* ichnogen. nov. and ichnosp. nov. The analyses of both morphotypes highlighted the frequent variability (from narrow to wide) in the trackway gauge along the same trackway. Consequently, the authors infer that the trackway gauge may not, or may not completely correlate with the osteological characters of the trackmaker's skeleton and should not be used as a key proxy in ichnotaxonomy.

GEOLOGICAL SETTING

The Cretaceous of the Cordillera Oriental is mainly represented by the Puca Group (Kimmeridgian to Paleocene) that uncomformably overlies Palaeozoic sedimentary rocks (Sempere *et al.*, 1997). Today Cretaceous rocks are found only as relicts in small overthrusted nappes or synclines. The best section through the Puca Group (Fig. 3) is in the Miraflores syncline, northwest of Potosi. The Puca Group can be correlated with the Yacoraite Formation and Pirgua Formation of northern Argentina as well as with the Vilquechico Group of southern Peru (Fig. 4; Jaillard *et al.*, 1993).

The 1000-m-thick Puca Group (Fig. 3) can be subdivided into seven formations (La Puerta and equivalents, Tarapaya, Miraflores, Aroifilla, Chaunaca, El Molino, Santa Lucia Fm.). Dinosaur tracks occur in the Coniacian-Maastrichtian Ariofilla, Chaunaca and El Molino formations (Fig. 3; Leonardi, 1994; Meyer *et al.*, 2016). Sedimentation started with the medium- to coarse-grained sandstones of the La Puerta Formation. In the Sucre area, the equivalent of this is the Sucre Formation (reddish sandstones with conglomerates). The overlying Tarapaya Formation is composed of claystones, siltstones and marls, whereas the Miraflores Formation indicates shallow-water, marine conditions during the Cenomanian. After a major unconformity at the Turonian-Coniacian boundary, the continental sediments of the Ariofilla and Chaunaca formations were deposited. The latter is dominated by terrestrial redbeds and palaeosols with some carbonate intercalations; both formations contain dinosaur tracks (Leonardi, 1994; Meyer *et al.*,

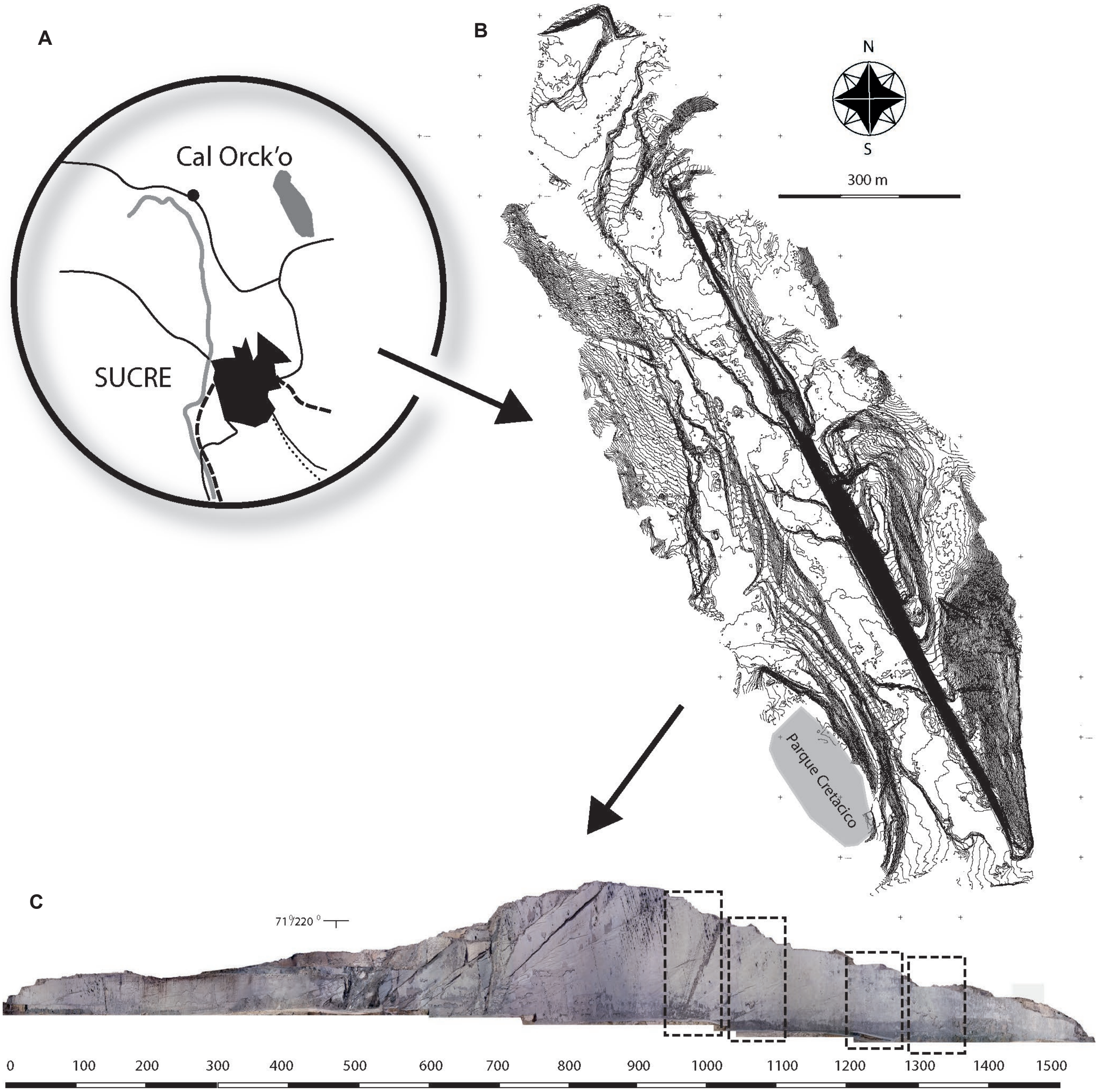

Fig. 2. Location maps. **A**. Location of the Cal Orck'o Quarry, near the city of Sucre. **B**. Detailed map of the Cal Orck'o Quarry (Digital Elevation Model). **C**. Overview of the quarry wall with the main track-bearing level. Trackway sectors are marked with dashed rectangles.

2016). The overlying El Molino Formation (middle Maastrichtian) is composed of sandy limestones and claystones.

MATERIAL AND METHODS

During the first scientific mission, the entire length of the wall was equipped with climbing bolts in order to reach any point on the surface with 200 m static ropes. The first map was created with a laser distometer by two people hanging from a rope and indicating each individual footprint on the surface. The georeferencing of the wall was carried out in 2007 by measuring common vertex coordinates. This was done by installing static GNSS equipment on two concrete posts, located on the slope of the wall and parallel to it, static GNSS equipment in the UTM coordinate of the previously mentioned points, with the function of control and link to the Municipal Geodetic Network. It was referenced to the Ellipsoid WGS84 and the UTMZ 20 South projection, using a Qstar 8 GIS data collector (Fig. 2). Orthophotographs with an accuracy of 1 cm were produced and a laser scan of the entire wall was used to deskew the individual photographs. On this basis, a vector map of the wall was created, using Adobe Illustrator with each individual trackway segment drawn and subsequently numbered, according to its metric position along the wall (e.g., S1150.01 denotes the first sauropod trackway in the

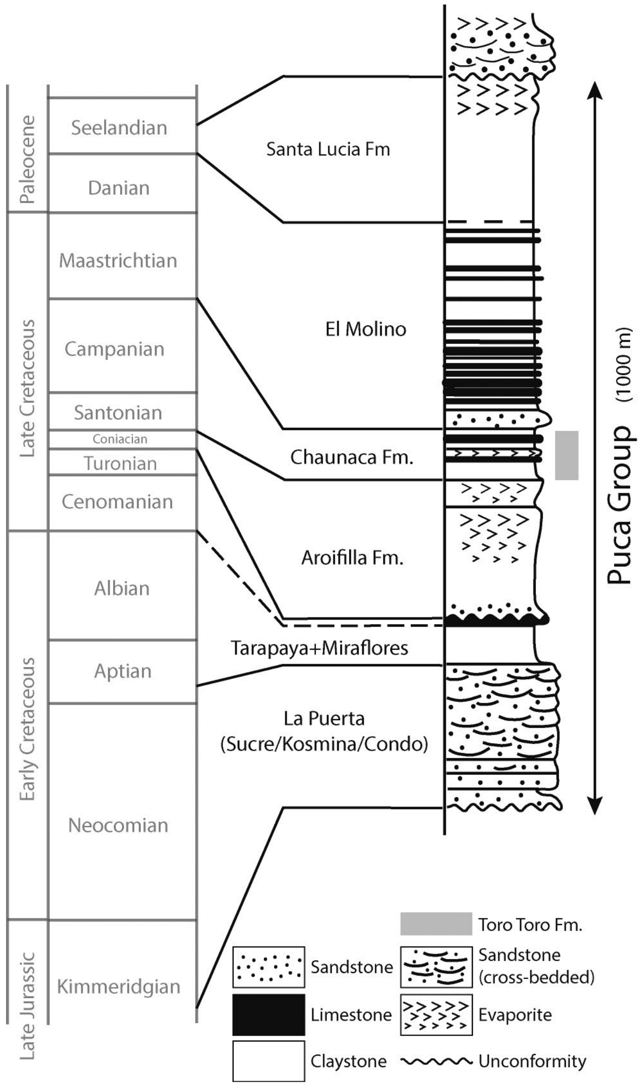

Fig. 3 Lithostratigraphy of the Upper Cretaceous of Bolivia (redrawn from Semperé *et al.,* 1998).

segment from 1150 to 1160 m). Outline drawings were made on monofilm.

Digital photogrammetric models were created with Agisoft Photoscan Pro (v. 1.3.2 and 1.4.1), starting from pictures taken with different cameras (a Canon EOS 70D for the model of Fig. 10, and a Canon EOS 5D Mark III for models of Figs 6, 8). The isolation of the tracks from the cast surface (Fig. 10A) and the refined orientation of all models were done in CloudCompare (v. 2.9.1). The models were then imported in DigTrace to produce the false-colour depth maps and the contour lines. Mediotypes (Belvedere *et al.*, 2018) for the manus and the pes of morphotype F were generated with DigTrace from the isolated tracks of the cast preserved at the Naturhistorisches Museum Basel (Fig. 10).

Furthermore, photographs and high-resolution videos of selected sectors were made with a Drone (DJI Phantom 4 Pro) in 2017. High dynamic Range (HDR) photographs were taken of individual morphotypes and trackways and subsequently enhanced with Aurora HDR Express (Vers. 1.1.2; Filter: Landscape realistic, contrast 45, aperture-0.28). All the tracks are still left *in situ*; the only cast that exists is a segment of the type trackway S 1080.01 that is housed in the Natural History Museum of Basel (Switzerland) under the number NMB SA.M.2. The original was destroyed during a large rock fall in 2013. The large cast was made with standard methods, including three layers of silicone rubber (Wacker RTV M 53) and a supporting layer with epoxy resin and, owing to the lack of fiberglass mats, with flour bags. The cleaning of the wall was done by personnel hanging from ropes, whereas the casting part was made with a steel platform, suspended from a large crane.

For the description and measurements of the sauropod tracks, the authors follow Farlow *et al.* (1989) and Lockley *et al.* (1994). The relative width of the trackway or gauge (PTR) was measured according to the proposal of Romano *et al.* (2007). Estimation of hip height follows Thulborn (1990).

RESULTS

Sedimentology

The track-bearing layers described in this study are situated in the El Molino Formation (Puca Group), which is Late Cretaceous (middle Maastrichtian) on the basis of age-diagnostic microfossils (ostracods, see Hippler, 2000). Within the quarry, the Cretaceous to Palaeogene Sucre, Ariofillo, Chaunaca and El Molino formations are exposed in the core of the so-called Cal Orck'O syncline that is NW of Sucre (Figs 3, 4). Since 1954, ongoing quarry operations exposed a dinosaur-track-bearing wall that dips at 72° towards the W, is 1.5 km long and varies in height from 20 to 135 m.

Detailed sedimentological, palaeoecological and geochemical analyses (TOC) of the 170 m thick El Molino Formation (Maastrichtian to Early Palaeogene) in the Cal Orck'O-syncline (Hippler, 2000) indicate almost continuous continental deposition in this part of the central palaeo-Andean Basin (Fig. 5). The section can be divided into a lower fluvio-deltaic part (Chaunaca Formation) and a predominantly lacustrine upper part (El Molino Formation). During the basal fluvio-deltaic deposition (Sempere *et al.,* 1997),

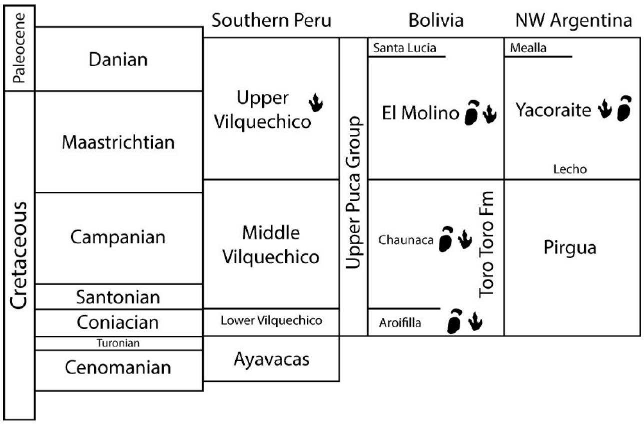

Fig. 4. Chronostratigraphic correlation chart of the El Molino Formation and coeval stratigraphic units in southern Peru and northwestern Argentina (redrawn from Jaillard *et al.,* 1999).

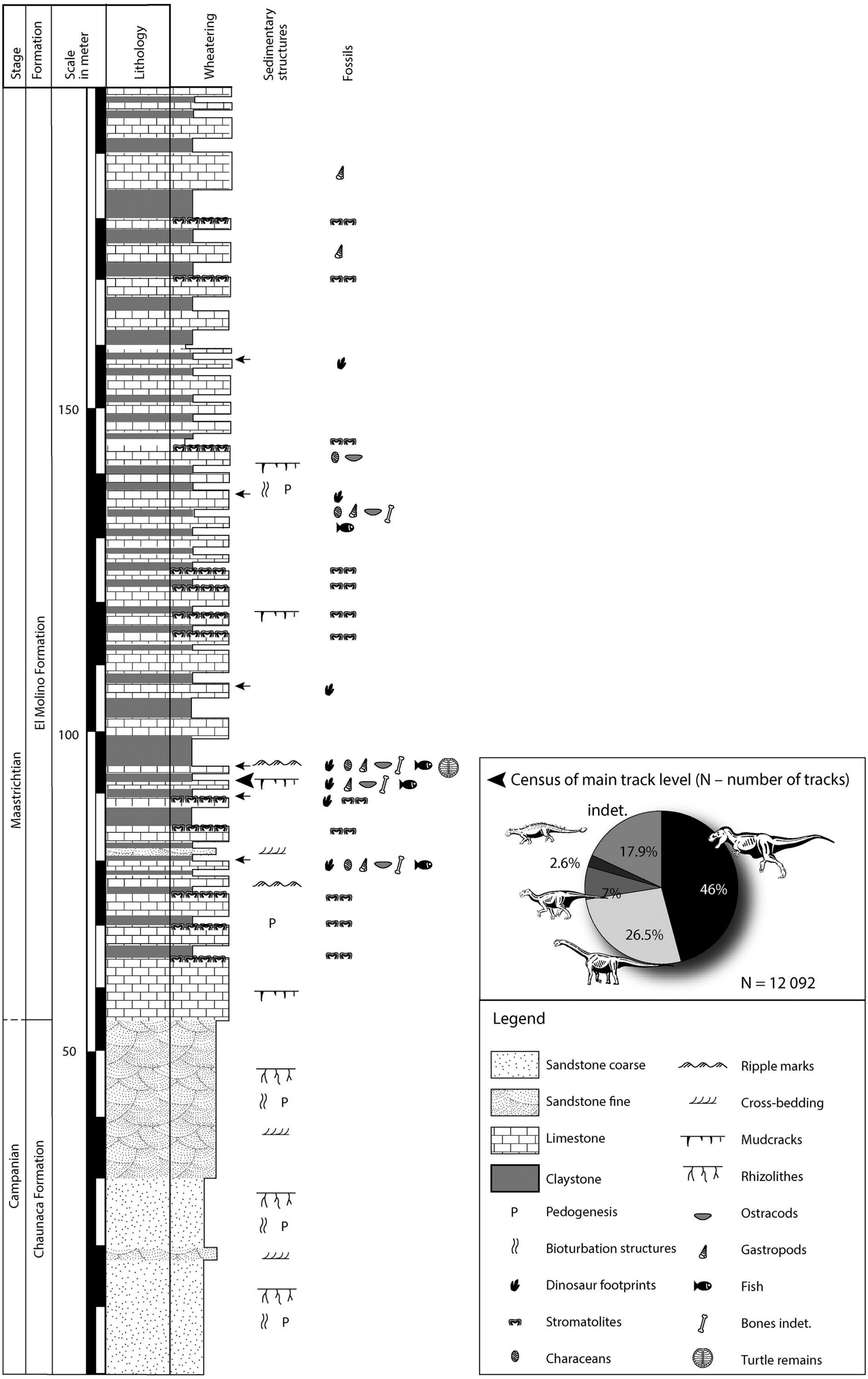

Fig. 5. Detailed stratigraphic section of the Chaunaca and El Molino formations at the Cal Orck'o Quarry (redrawn after Meyer *et al.*, 2001), showing the ichnodiversity of the main track-bearing level.

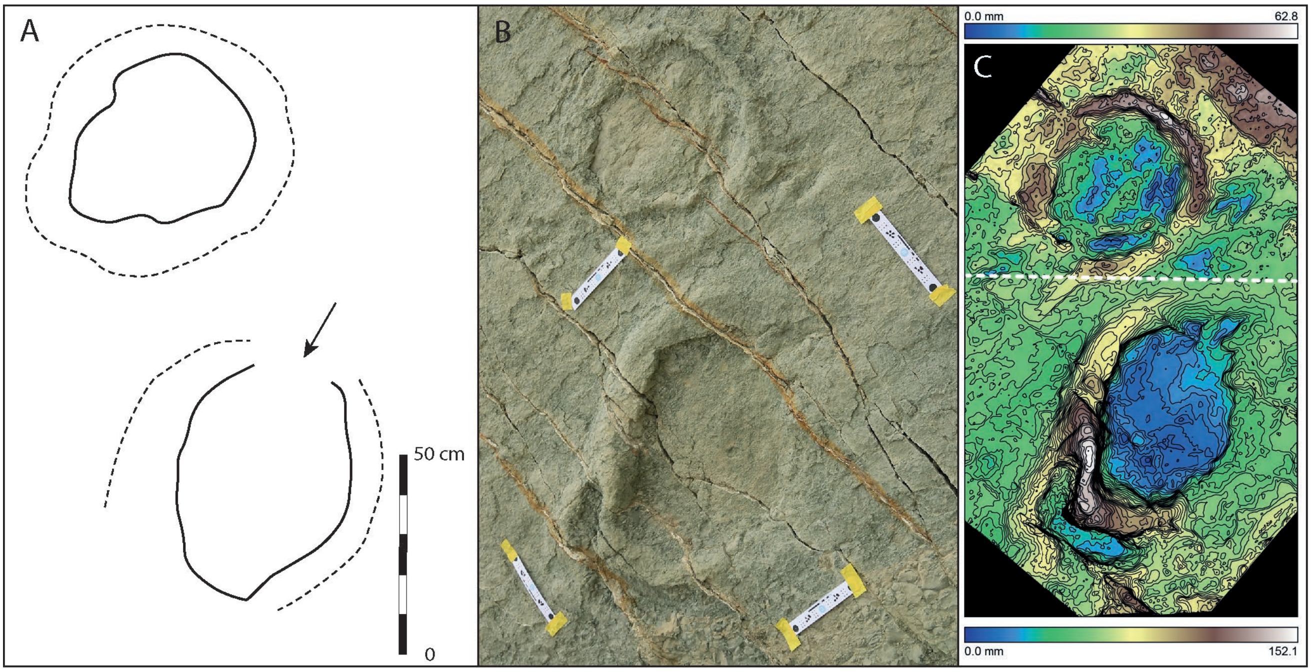

Fig. 6. Manus-pes set of morphotype E in Trackway S 1260.01. **A.** Outline drawing from monofilm **B**. Photograph. **C.** Digital elevation and false-colour model. Note that manus and pes have a different depth scale. For relative position within the trackway, see Figure 7.

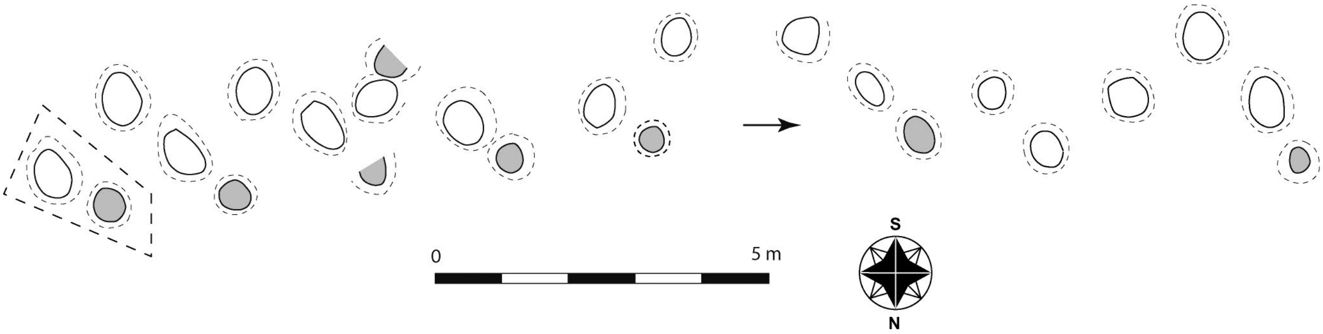

Fig. 7. Outline drawing of trackway S 1260.01 (morphotype E). Stippled outline indicates position of Figure 6.

floodplain sediments were overprinted by pedogenesis, root marks and bioturbation and locally eroded by distributary channels, which are represented by sandstones. The subsequent lacustrine deposition took place in an extensive, perennial lake system with low-gradient ramp-type margins and was episodically interrupted by fluvial sedimentation. Three different facies belts can be recognized in this upper, lacustrine part of the section, namely inner and outer marginal and open facies.

The inner marginal lacustrine facies includes sandy limestones, oncolite-bearing pack- or grainstones and stromatolites/microbialites, showing episodic desiccation features and calcretes that formed under semiarid climatic conditions. This facies type contains most of the dinosaur tracks that are considered in this study. High-energy environments are characterized by oolitic grainstones. The outer marginal lacustrine facies consists predominantly of ostracod-packstones and spherical or wavy- to pillow-shaped stromatolites (*Pucalithus* Fritzsche, 1924). The diverse fossil content (ostracods, gastropods, fish, characeans, see below) indicates the presence of freshwater during most of the lacustrine depositional phase.

The bones, plastra and carapaces of turtles are common, but the fragmentary preservation of these remains prevents taxonomic assignment. Other vertebrate remains include the teeth of crocodiles, the vertebrae of freshwater mosasaurs as well as fragments of pterosaurs. The isolated remains of freshwater fishes are the most common faunal element in the Cal Orck'O fossil assemblage. Two taxa are very common: the freshwater stingray *Pucapristis* Schaeffer, 1963, and *Gastroclupea* Signeux, 1964, which is a relative of the modern hatchet fish. The teeth and scales of pycnodontiform fish (*Coelodus toncoensis* Gayet, Marshall and Sempere, 1991) as well as the skull fragments of catfish (Siluriformes) occur throughout the succession, but are concentrated at the main track-bearing level.

The open lacustrine facies consists of greenish claystones, wackestones and coquinas. Feldspar-dominated, altered

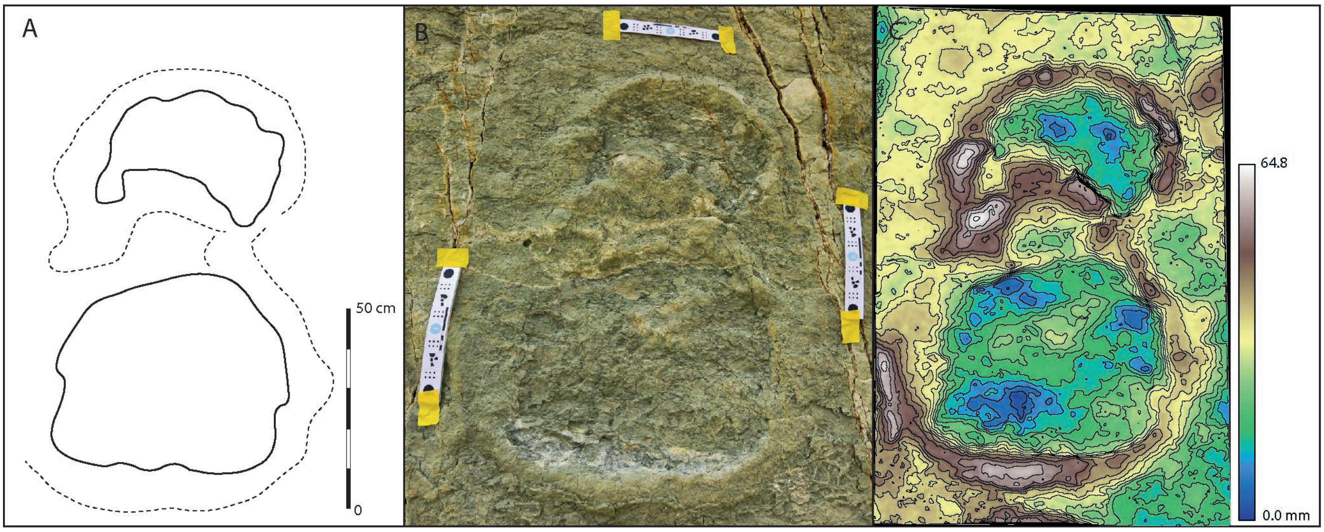

Fig. 8. Manus-pes set of *Calorckosauripus lazari* from Trackway S 1150.01. **A.** Outline drawing from monofilm. **B.** Photograph. **C.** Digital elevation and false-colour model.

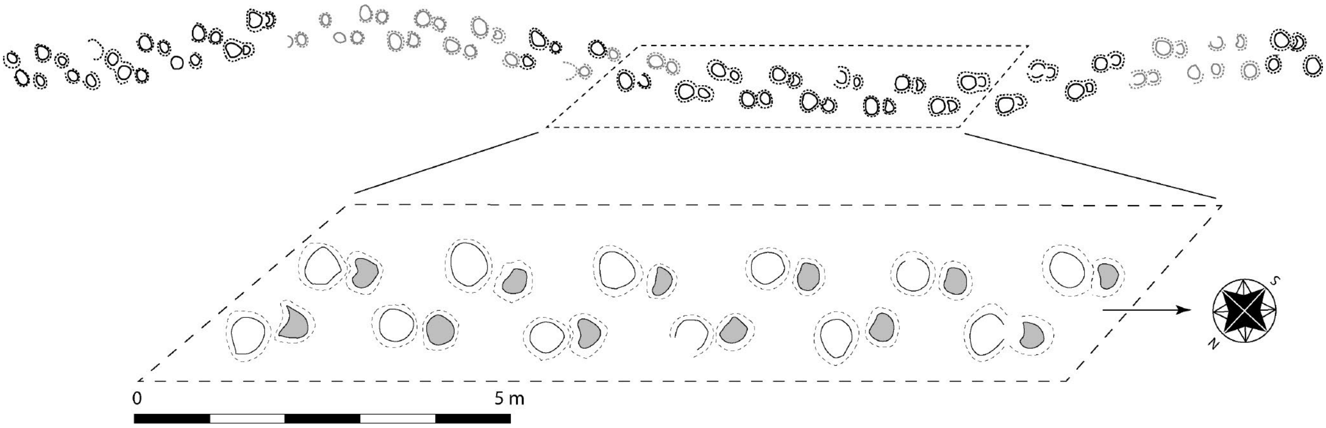

Fig. 9. Outline drawing of trackway S 1150.01, *Calorckosauripus lazari*. **A.** Longer segment, showing difference in substrate consistency (dark outline denotes tracks made in soft substrate, light outlines denote shallow tracks in drier sediment). **B.** Detail of trackway from a better-preserved segment. Grey – manus prints; white – pes prints; stippled lines – outer limit of mud rim.

volcaniclastic rocks indicate episodic deposition of volcanic ash in a shallow, alkaline lake during periods with high evaporation rates. The unusual shape of the ostracod shells indicates deposition in an ephemeral, high-stress environment. Palaeocurrent measurements using gastropods and the strike of ripple-crest lines show a preferred E-W-trending current pattern. These and the orientation of dinosaur trackways indicate a NNW-SSE-running palaeo-shoreline. Sedimentation in this continental environment was mainly controlled by climatic variations, hydrology and carbonate productivity (Hippler, 2000). Small-scale lake-level fluctuations were most probably caused by climatic changes, due to changes in the precipitation and evaporation rates. The observed shallowing-upward successions indicate a progradation of the shoreline. Large-scale hydrological changes were probably related to tectonic movements in the Andean orogenic belt.

Whether the El Molino Formation was a marine or lacustrine environment has been debated by different authors, mainly because of the fish fauna (Gayet *et al.*, 1991, 2001) in these units. However, the preservation frequency of the tropical freshwater fish *Gastroclupea branisai* in this succession demonstrates that the environment was most probably lacustrine (Marramà and Carnevale, 2016). This is corroborated by the studies of similar sedimentary environments of the Yacoraite Formation in Northern Argentina (Jujui) by Cónsolle Gonella *et al.* (2012). Fossiliferous oolitic limestones, associated with large freshwater stromatolites, seven levels of dinosaur tracks, gastropods, characeans as well as lacustrine ostracods further support the interpretation of an open lacustrine environment (Camoin *et al.*, 1997; Hippler, 2000; Meyer *et al.*, 2001).

Ichnology

The present contribution focuses on the description of the tracks and trackways of sauropod dinosaurs that occur on the main track-bearing level, forming the steep wall.

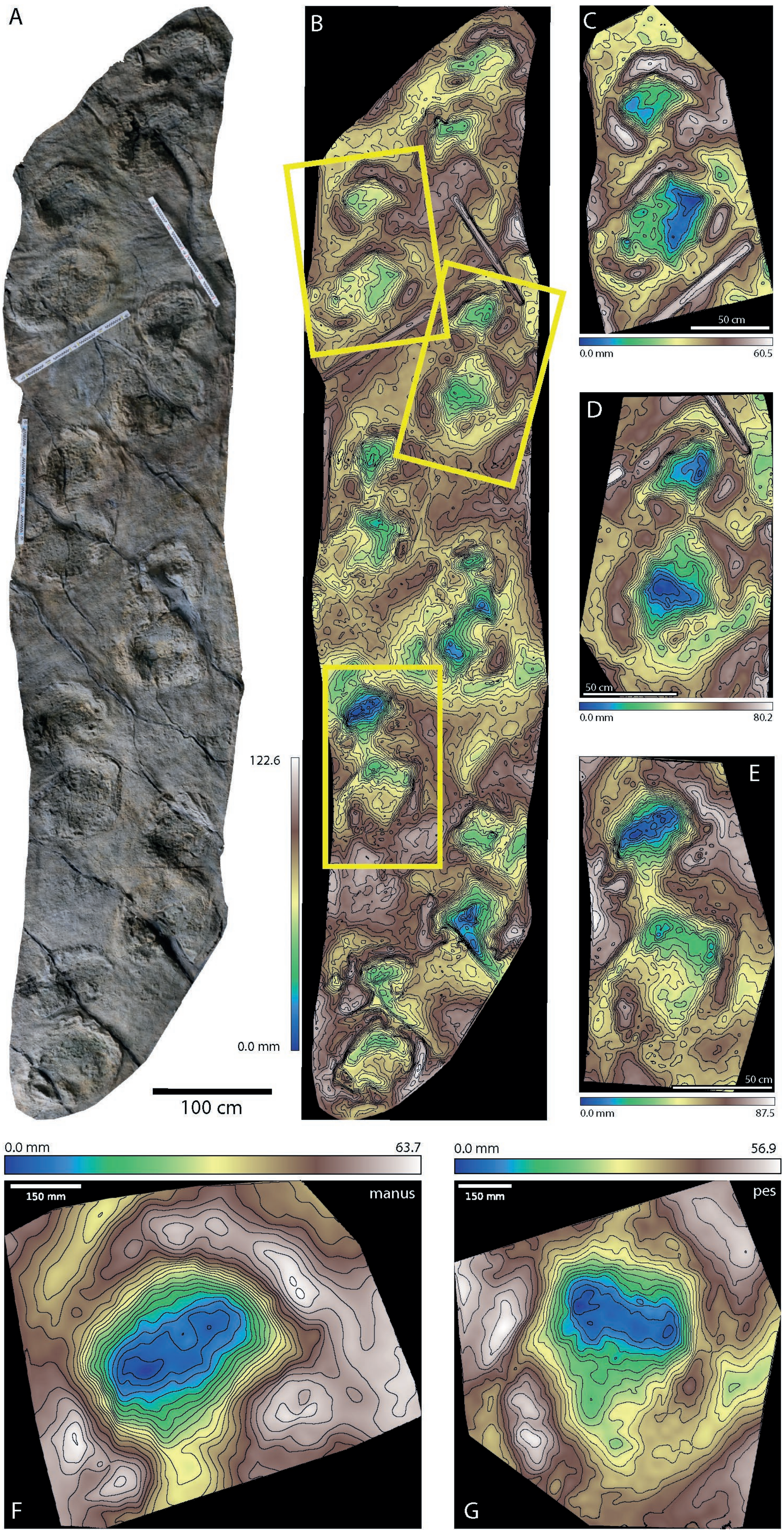

Fig. 10. Cast of S 1080.01 (NMB SA.M.2), *Calorckosauripus lazari*. **A.** Orthofotograph of the cast. **B.** Digital elevation and false-colour model. **C–E.** Digital elevation and false-colour model of individual manus-pes sets (for location, see frames in B). **F**. Manus mediotype generated from LM17 (holotype) and LM19 (paratype). **G.** Pes mediotype generated from LP17 (holotype) and RP18 (paratype). Both tracks figured as left. Contour-line interval: 3 mm.

Level CO 80 (Hippler, 2000) is a sandy limestone, containing up to 30% of quartz grains and marks a lake lowstand. All the tracks occur as negative epichnia, sometimes still filled with clay. The main track-bearing level (bold arrow in Fig. 5) contains remains of catfish, turtles, gastropods, ostracods and characeans and displays in some parts mud cracks. A total of nine different morphotypes of dinosaur tracks have been documented. Amongst those are large, intermediate and small theropods, ornithopods of different sizes, ankylosaurs and sauropods (e.g., McCrea *et al.*, 2001). First-hand observation allows the authors to separate two different trackway types of sauropod dinosaurs, both showing the basic morphology of a smaller rounded or kidney-shape manus and a larger elongated or oval-shaped pes.

Morphotype E

This morphotype is rare with only 10 of the 120 sauropod trackways on the wall attributable with certainty to this type so far. Of the 10 trackways, 5 are pes-only trackways with low preservation grade (maximum of 1.5 on Belvedere and Farlow, 2016 scale). Furthermore, pes-dominated trackways can result from either a manus failing to deform the substrate or from a pes overstepping and obliterating the preceding manus print (Falkingham *et al.,* 2012). Therefore, the authors have chosen to leave the ichnotaxonomic assignment of these tracks open, despite their distinctiveness from all other known Late Cretaceous footprints and trackways.

Material: *In situ* trackways S 1260.01; S 1430.01; S 1480.02; S 1520.01; S 1560.01. Figs 6, 7, 13, Appendix.

Description: Pes impressions are generally elliptical, mostly longer than wide (average PL: 62.5 cm, and PW: 47.5 cm; PL/PW: 1.3). Neither clear digit impression nor claw marks are present, and the depth of the tracks is quite uniform (Fig. 6). Pes tracks show a positive rotation of 45°.

Manus tracks are elliptical (Figs 6, 7), always wider than long (average ML: 41.5 cm, and MW: 37.8 cm; ML/MW: 1.1). No claw marks or digit impressions are present. The manus impressions are strongly outward oriented. The depth of the track is semi-homogeneous, with the external side slightly deeper than the internal side.

Trackway heteropody is quite low, with the manus almost the size of the pes, and varies between 1: 1.85 and 1: 2.2. The gauge is narrow to intermediate, with a PTR of 25–36% (Fig. 13, Appendix). Manus pes configuration is fairly constant all along the trackways, with the manus generally located in front of the pes, although some degree of variability is possible.

Interpretation: The rounded pes morphology with no claw marks or digit impressions points to a columnar manus that is present in more derived titanosaurs. These characters correspond well with the known skeletal record of advanced titanosaurs in the Late Cretaceous of South America (Carballido *et al.,* 2017) and points to a derived titanosaur as the trackmaker. Glenoacetabular distance is difficult to measure exactly because not many trackways preserve enough manus-pes sets, but is estimated to be ~ 3 m. Hip height in S 1260.01 reaches 2.97 cm (Thulborn, 1990) and stride averages at 2.40 m.

SYSTEMATIC ICHNOLOGY

The second morphotype, initially identified as morphotype F (Meyer *et al.*, 2018), is unique and shows some morphological features, so far unknown in the Late Cretaceous sauropod track record. As it differs quite remarkably from all known sauropod trackways in the Late Cretaceous of South America and elsewhere and is fairly well-preserved morphologically (up to grade 2.5, following Belvedere and Farlow, 2016), the authors have decided to erect a new ichnotaxon and a new ichnospecies.

Ichnogenus *Calorckosauripus* ichnogen. nov.

Etymology: Ichnotaxon named after the type locality Cal Orck'o, Sucre (Dep. Chuquisaca), Bolivia.

Calorckosauripus lazari ichnosp. nov.

Etymology: *lazari* (from Hebrew = God has helped; Lazarus was the patron saint of gravediggers) because primitive titanosaurs were thought to be extinct in the Late Cretaceous.

Type material: Holotype – trackway S 1080.01 (trackway segment: cast and holotype NMB SA.M.2). Paratypes – pes track RP 18 and manus track LM 19 (Fig. 10).

Repository: Natural History Museum of Basel (Switzerland) NMB SA.M.2

Additional material: *In situ* trackways S 1080.02; S 1150.01; S 1430.03; S1470.01 S 1480.01; S 1480.04; S 1490.03; S 1490.04. Figs 8, 9, 10, 13.

Type horizon and locality: El Molino Formation (middle Maastrichtian), Quarry of FANCESA, Cal Orck'o (Sucre, Dep. Chuquisaca; Bolivia) Level 80 (Fig. 2).

Stratigraphic distribution: middle Maastrichtian (Late Cretaceous)

Diagnosis: Pes tracks are entaxonic and always longer than wide (average PL: 49 cm, and PW: 42; PL/PW: 1.6), but with a shape that is variable from slightly elliptical to bell-shaped, with a narrow "heel" and a wider anterior area. The phalangeal region is generally the deepest part of the track (e.g., Figs 8–10), although with a certain degree of variability, due to locomotion- or sediment-related preservation issues. Pes impressions are slightly rotated outward, with the left pedes sometimes rotated to a higher angle (S1150.01: 17.5°) than the right (S1150.01: 7.5°). Digit impressions are not present and only one of the tracks analysed (Fig. 8) shows a deeper area that might correspond to digit I impression. Pes impressions are slightly rotated outward, with the left pedes sometimes rotated by a higher angle (S1150.01: 17.5°) than the right (S1150.01: 7.5°).

Manus tracks are always wider than long (average ML: 34 cm, and MW: 29 cm; ML/MW: 1.17). When not (partially) overprinted and deformed by the pes impression, the manus is horseshoe-shaped, with two clear lobes corresponding to digits I and V. In Fig. 8, the lobes are fainter, with only the one corresponding to digit I discernible. No claw marks are present. Generally, manus tracks are outward rotated (20–60°), with the deepest part of the track constantly on the external side.

Trackway heteropody is marked, but not extreme (e.g., 1: 1.85), with the manus being roughly half of the size of

Fig. 11. Photograph of sectors 1470–1500, showing different crossing trackways of the morphotypes E (S 1560.01) and *Calorckosauripus lazari.*

the pes. The gauge is wide/intermediate, with a PTR that varies from 22–34%. Despite being highly variable, trackways S1080.01 and S1080.02 show a trend, whereby most of the manus tracks on the left side of the trackway are impressed more internally than on the right side, where the tracks are impressed more externally. The latter could be the results of walking on a palaeoslope along the shoreline.

Glenoacetabular distance is fairly constant and estimated around 2.8 m. Hip height in S 1120.01 (type trackway) reaches 2.24 cm and stride averages at 2.29 m.

Remarks: *Titanopodus mendozensis* González-Riga and Calvo, 2009, has wide-gauge trackway, a high heteropody (1:3), asymmetrical U-shaped manus tracks, subtriangular to subcircular pes tracks with no digit impression. This ichnotaxon differs from *C. lazari* for the trackway gauge, heteropody and general shape of manus and pes.

Sauropodichnus giganteus Calvo, 1991, has high heteropody (1:2.9) shows rounded pes impressions with no details, U-shaped manus tracks with a concave posterior border and no digit impressions. This ichnotaxon differs from *C. lazari*, heteropody and general shape of manus and pes.

DISCUSSION

Late Cretaceous dinosaur track localities are known form different parts of the world, notably from Spain (Schulp and Bronx, 1999; Vila *et al.*, 2008), Croatia (Dalla Vecchia *et al.*, 2001), Argentina (e.g., Díaz-Martínez *et al.,* 2017) and Bolivia. Tracks and trackways of sauropods and titanosaurs, respectively, have been described in some detail mainly from Argentina and to a lesser extent from Bolivia (Novas, 2009).

The tracks and trackways from the Maastrichtian Tremp Formation at Fumanya in the Spanish Pyrenees have been studied in detail by Vila *et al.* (2005, 2013) and Oms *et al.* (2016). The overall preservation is poor and details are rarely seen (pers. obs.). Pes tracks have four laterally oriented claw marks and no lateral notch. The symmetrical manus is U-shaped and subrectangular. Their heteropody ratio is 1:3 (Fig. 13A). Neither the morphology nor the overall aspect is similar to those of the sauropod tracks from Cal Orck'o.

Lockley *et al.* (2012) described partial sauropod trackways from the Campanian-Maastrichtian Chudo shales of Sado island (South Korea). The manus is U-shaped positioned anterolaterally with no digit impressions, and the pes prints show three laterally oriented claw marks. According to the authors, the stance is slightly wide-gauge; however, the trackway segment is too short to ascertain this (pers. obs. C.M., 2007).

Titanopodus mendozensis (Fig. 12B) from the Agua del Choique locality (Loncoche Formation, late Campanian – early Maastrichtian) exhibits a wide-gauge trackway and high heteropody (1:3). The U-shaped manus is asymmetrical and has an acuminate external border. Pes tracks are subtrinagular to subcircular in shape, digit impressions are absent. The lack of manual phalangeal impressions led González-Riga and Calvo (2009) to the conclusion that the trackmaker was a medium-sized saltasaurine or aeolosaurine titanosaur (14–16 m long). Morphology, heteropody ratio (1:2) size and trackway pattern do not match with the trackways presented here.

Sauropod tracks from the Candeleros Formation (Albian–Aptian) on the shore of Lago Ezequiel Ramos Mexià (Neuquén, Argentina) also were reported by Calvo (1991, 1999), Calvo and Salgado (1995) and Calvo and Mazetta (2004). The trackway of *Sauropodichnus giganteus* (Fig. 12C) was defined on the basis of several outline drawings, and unfor-

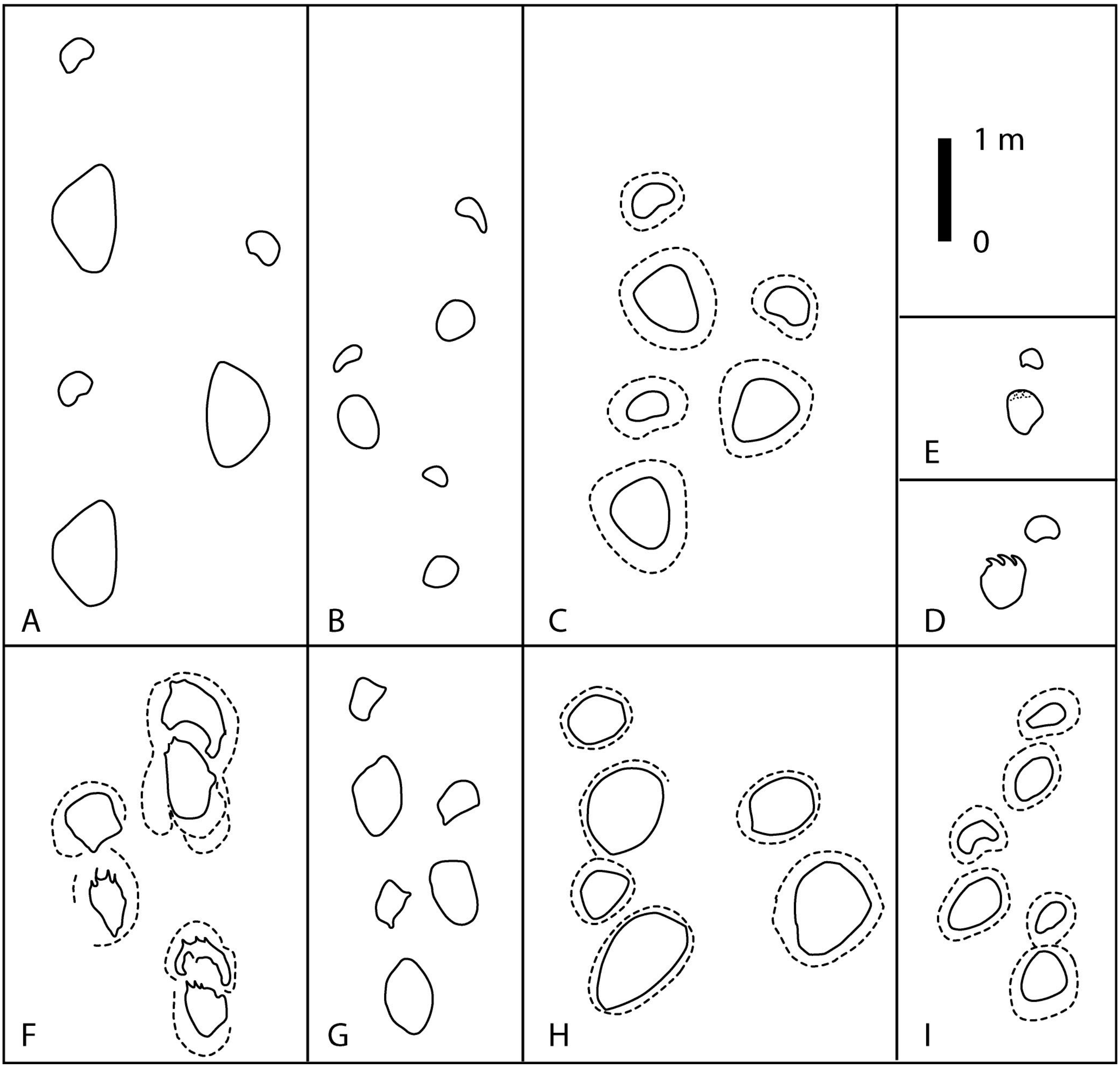

Fig. 12. Late Cretaceous Sauropod trackways. **A.** cf. *Brontopodus*, Tremp Formation (late Campanian – early Maastrichtian), Fumanya, Spain (redrawn from Vila *et al.*, 2013). **B**. *Titanopodus mendozensis*, Loncoche Formation (late Campanian – early Maastrichtian) Agua del Choique, Mendoza, Argentina (redrawn from González-Riga *et al.*, 2009). **C.** *Sauropodichnus giganteus*, Rio Limay Formation (Albian–Cenomanian), Picún Leufú, Neuquén, Argentina (redrawn from Calvo, 1999). **D.** Anacleto Formation, Agua del Choique (early Campanian), Neuquén, Argentina (redrawn from González-Riga *et al.,* 2015). **E.** Chaunaca Formation (Campanian), Humaca, Bolvia (redrawn from Lockley *et al.*, 2002a). **F**. Toro Toro Formation (Campanian), Toro Toro, Bolivia (redrawn from Leonardi, 1994). **G**. Yacoraite Formation (Maastrichtian), Valle del Tonco, Salta, Argentina (redrawn from Díaz Martínez *et al.*, 2017). **H.** El Molino Formation (Maastrichtian), Cal Orck'o, Bolivia, morphotype E, this paper. **I**. El Molino Formation (Maastrichtian), Cal Orck'o, Bolivia, *Calorckosauripus lazari* (S 1080.1), this paper.

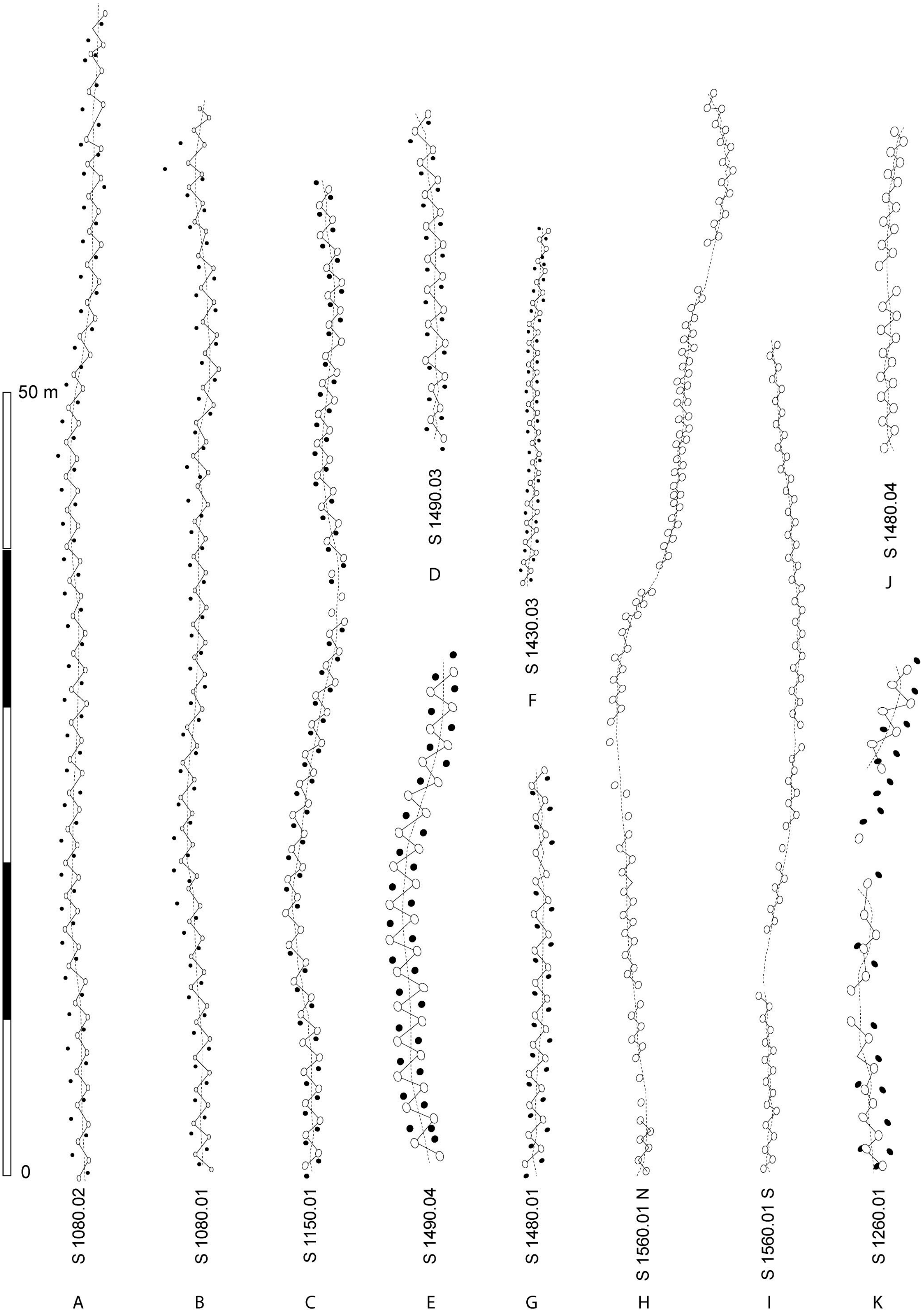

Fig. 13. Trackway patterns of sauropods from Cal Orck'o. **A–G**: *Calorckosauripus lazari*. **H–L**: morphotype E. Solid dots – manus prints; open circles – pes prints. Walking direction toward bottom of page.

tunately without photographic documentation. The original description (Calvo, 1991) shows the rounded outlines of pedes with no details. Calvo and Mazetta (2004) illustrated another trackway and compared it to the holotype, which shows that the footprints are not well preserved. The largest pes is triangular to rounded and the manus is U-shaped (concave posterior border) without digit impressions. These tracks compare in size to morphotype E from Cal Orck'o, but differ substantially in the outline of the manus and regarding heteropody (1:2.9).

González-Riga *et al.* (2015) reported dinosaur tracks from the upper part of the Anacleto Formation (early Campanian) from Agua del Choique (Malargüe, Mendoza, Argentina). In level An-1, one sauropod trackway shows a symmetrical, crescent-shaped manus impression with "posterior concave contours", which the authors interpret as impressions of digits I and V. The subcircular pes is longer than wide and exhibits claw impressions of digits I to III, which are rotated inwards (Fig. 13D). Size, morphology of the pes and the extreme outward rotation of the manus of these tracks clearly differ from both morphotypes in the present study.

The sauropod tracks from the Campanian Chanauca Formation at Humaca (Bolivia) (Fig. 12E) were left by juvenile individuals (Lockley *et al.,* 2002a). They show sometimes faint, digital claw marks in the pes and rarely in the manus. The heteropody index is very high (1:1.2). However, they differ in the pes outline (triangular) and the presence of a lateral notch and the inward rotation of the manus.

The Campanian Toro Toro tracksite (Toro Toro Formation) in Bolivia contains two sauropod trackways (Fig. 12F). The tracks display thick mud rims, which indicate strong deformation. Therefore the claw marks both in pes and manus seem to be extramorphological features (Leonardi, 1989). Some of the pes tracks seem to have anteriorly-directed claw impressions, and the manus impressions are U-shaped, with possible traces of digits I and V. They display a high heteropody (1:1.6) and look similar to *Calorckosauripus*. The Toro Toro tracks are much smaller in size and the outline of the pes differs strongly in having an almost trapezoidal outline. The lack of a detailed ichnological description of the Toro Toro site renders any additional comparison difficult.

Díaz-Martínez *et al.* (2017) described trackways from the Yacoraite Formation (Maastrichtian–Danian) of Valle del Tonco tracksite (Salta, north-western Argentina). The trackway-bearing surface is found in the Amblayo Member, the lower unit of the Yacoraite Formation in this area, and is most probably a time equivalent of the surfaces in Cal Orck'o (pers. obs.). The sauropod trackway is moderately well-preserved. The manus imprints are subrounded to rectangular and show two short, posteriorly-oriented digit imprints. The rhomboidal pes tracks are longer than wide, with a subtriangular posterior edge and laterally located digit-claw traces (Fig. 12G). These tracks share a similar manus morphology with *Calorckosauripus* in having distinct digital marks, but the outward rotation of the manus is much higher. However, their size as well as the outline of the pes prints, including digit impressions, differs substantially from both morphotypes at Cal Orck'o.

Several poorly-preserved tracks and trackways have been reported from the Yacoraite Formation of Jujuy (Maimara, Argentina) by Cónsole-Gonella *et al.* (2017). These occur on a trampled and weathered surface. The authors describe manus imprints with a semi-circular outline and indicate a heteropody ratio of 1:2. However, the state of preservation and the lack of details in the morphology of the footprints prevent a meaningful comparison with the ichnofauna at Cal Orck'o.

An expanding global database and current understanding of sauropod tracks challenges an earlier concept of a temporal distribution of narrow- and wide-gauge sauropod tracks (see Lockley *et al.,* 1994). Furthermore, authors have focused on other aspects, such as substrate properties, ontogeny or behaviour, to explain differences in trackway gauge (e.g., Marty, 2008; Marty *et al.*, 2010a; Falkingham *et al.,* 2012). The examples from Cal Orck'o further challenge the concept of Lockley *et al.* (1994), in that both sauropod morphotypes exhibit narrow-gauge and wide-gauge stance along the same trackway (Fig. 13). On the one hand, some of the trackways clearly show that substrate properties changed from wet to dry along a single trail without any changes in trackway width, and thus implying that substrate properties had no influence – or at least, not always – on the basic pattern (Fig. 9). On the other hand, Falkingham *et al.* (2012) concluded that the formation of manus-dominated tracks requires a specific substrate and wide-gauge trackways can be formed in any track-bearing substrate.

One particular trackway of *Calorckosauripus* (S 1560.01; Fig. 13) can be followed for more than 380 m and therefore is the longest sauropod trackway ever recorded (*contra* Mazin *et al.*, 2017). It exhibits an extremely narrow, if not negative gauge, with almost no spacing between consecutive pes tracks in some sections along the trackway; other sections show a wide-gauge pattern along curves with more interspace between pes tracks. The observations of the present authors of the long trackways that are preserved in Cal Orck'o indicate that trackway gauge is most probably subjected to speed and individual behaviour or locomotion issues, such as turning or changes in direction, since long and straight trackways exhibit a constant trackway gauge. Similar observations in terms of trackway width have been made in the Late Jurassic of Northern Switzerland, where sauropod trackways display narrow- and wide-gauge patterns within the same morphotype and along the same trackway (Marty *et al.*, 2010b; Paratte *et al.*, 2017). Moreover, Castanera *et al.* (2012) presented a similar example from the Cretaceous of Spain and suggested that substrate variations and the resulting change in walking resulted in changing trackway width (gauge) along the same trackway.

Ullmann *et al.* (2017) explained the differences in the abduction/adduction of the hind limb between titanosauriforms and other sauropods with a different stance, wherein greater hind limb abductive and adductive capability may have been necessary to maintain stability during wide-gauge locomotion over an uneven terrain. Mannion and Upchurch (2010) found supporting evidence in the common occurrence of wide-gauge trackways and titanosaur body fossils in fluvio-lacustrine deposits and suggested that sauropods may have preferred inland environments that can present a wider range of topographic variability than most coastal carbonate platforms. However, the tracks of titanosaurs have been found in many different environments and time intervals, ranging from deltaic to fluvial and lacustrine settings as well as in carbonate tidal flats. Therefore, the present authors strongly doubt that there is a correlation between palaeoenvironment, stability of locomotion and trackway gauge.

CONCLUSIONS

Trackway gauge has often been used as an indicator of presence/absence of basal or more derived sauropods. Ullmann *et al.* (2017) stated that the broadening of sacral width and the varying shape of the femoral condyles have an effect on the body gauge in sauropods, resulting in wider-gauge trackways. This is also supported by the earlier work of Wilson and Carrano (1999), who indicated that titanosaurs, especially saltasaurids display a wide-gauge stance. These authors also noted a complete absence of narrow-gauge sauropod trackways in the Late Cretaceous. In this context, it is remarkable that Salgado and Bonaparte (2007) noted a complete absence of basal titanosaurians in the Campanian–Maastrichtian interval, at least in Patagonia.

Since titanosaurids are the only sauropods present during the Campanian–Maastrichtian, the observations of the authors indicate that trackway width may not – or may not completely – correlate with the osteological characters of the trackmaker's skeleton (Meyer *et al.*, 2018). Sauropod trackways from Cal Orck'o demonstrate that narrow-, intermediate- and wide-gauge stances are present in both morphotypes and along single trackways. Furthermore, the presence of two morphotypes, morphotype E and *Calorckosauripus*, indicates the coeval presence of a more basal and a more derived titanosaur in the Late Cretaceous. This is corroborated by the presence of tracks in the coeval Yacoraite Formation in the Valle del Tonco (Salta, Argentina) that exhibit clear digit impressions in the manus imprints, which are reminiscent of those of basal titanosaurine sauropods (Díaz-Martínez *et al.*, 2017). Furthermore, the presence of manus prints with digital impressions from the Toro Toro Formation (Campanian) indicates that basal titanosaurs were present during most of the Cretaceous in South America.

The gauge variability shown by both morphotype analysed here, combined with similar observation from the Swiss Late Jurassic tracksites (Marty *et al.*, 2010b; Paratte *et al.*, 2017), casts doubt on the use of this parameter for trackmaker identification or as an ichnotaxonomical proxy, as suggested by Lockley *et al.* (1994). The ichnotaxonomic assignment of wide-gauge trackways to the ichnotaxon *Brontopodus* and narrow-gauge ones to *Parabrontopodus* is, in the view of the present authors, no longer valid.

Neoichnological and ichnological studies by Marty *et al.* (2009) and observations by the present authors on-site indicate that the main track-bearing level was formed within one hydrological cycle. Careful analysis of level 80 (the main track-bearing level) reveals different generations of mudcracks that seem to have formed after the tracks were left. The different preservation of individual tracks along certain trackway segments indicates differences in moisture content along the shoreline during track formation (Fig. 9). Furthermore, all true tracks were left during the end phase of the wet season, before the shoreline dried up completely. Taphonomic observations on the vertebrate remains on the surface show that turtle and fish remains occur dispersed and are always completely disarticulated (single bones, bony plates, scales, vertebrae). Collectively, these observations indicate that the main track-bearing level displays a body and ichnofossil assemblage with a unique view into a Late Cretaceous lacustrine ecosystem.

Cal Orck'o provides a rare window into the diversity of dinosaurs in South America and documents individual behaviour, as well as different types of locomotion (e.g., limping, stopping, spinning) and wide variations in locomotion speed. Cal Orck'o is clearly an outstanding example, not only in terms of outcrop size, number of footprints and trackways, but also for preserving one of the most diverse assemblage of Mesozoic dinosaur tracks in the world and documenting the diversity of Gondwana dinosaurs in the Late Cretaceous.

Supplementary data archiving

Supplementary 3D data for the holotype of *C. lazari* are available on Figshare: https://doi.org/10.6084/m9.figshare.7172225.

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Appendix

Selected Late Cretaceous trackways showing their gauge (PTR) and heteropody index.

Ichnotaxon	Locality	Country	Age	OW	SW	TRW	Heteropody	References	Trackway nr
	Sado	South Korea	Campanian–Maastrichtian	241	50	20.7	1 : 1.86	Lockley *et al.* (2012)	
	Cal Orck'o Mo E	Bolivia	Maastrichtian	185	42	22.7		this paper	S1150.02
?Breviparopus	El Mers	Morocco	Bathonian–Callovian	130	30	23.1		Meyer and Thüring, 2005	
Brontopodus	Chabut	China	Barremian–Aptian	133	32	24.1	1 : 2.2	Lockley *et al.*, 2002b, fig. 6b	
	Cal Orck'o Mo E	Bolivia	Maastrichtian	260	65	25.0	1 : 1.4	this paper	S1430.01
	Toro Toro	Bolivia	Campanian	153	40	26.1	1 : 1.6	Lockley *et al.* (2002a)	
Calorckosauripus lazari	Cal Orck'o	Bolivia	Maastrichtian	158	43	27.0		Holotype cast	S1150.01
cf. Brontopodus	Fumanya	Spain	Maastrichtian	200	54	27.0	1 : 3	Vila *et al.*, 2013	Tr 50
cf. Brontopodus	Fumanya	Spain	Maastrichtian			28.0		Vila *et al.*, 2013, table 2	
	Cal Orck'o Morphotype E	Bolivia	Maastrichtian	91	26	28.6	pes only	this paper	S880.2
Calorckosauripus lazari	Cal Orck'o	Bolivia	Maastrichtian	180	52	28.9		this paper	S1440.1
Rotundichnus	Barkhausen	Germany	Kimmeridgian	112	33	29.5	1 : 3.6	Lockley *et al.*, 2004, fig. 5A	
Calorckosauripus lazari	Cal Orck'o	Bolivia	Maastrichtian	190	56	29.5		this paper	S1480.04
	Toro Toro	Bolivia	Campanian	140	42	30.0		Leonardi, 1994, plate 8/1a	
Rotundichnus	Münchehagen	Germany	Berriasian	208	63	30.0	1 : 3.4	Lockley *et al.*, 2004, fig. 5B	
Brontopodus	Chabut	China	Barremian–Aptian	266	87	32.7	1 :2.4	Lockley *et al.*, 2002b, fig. 6c	
	Carigador	Croatia	Late Cenomanian	100	33	33.0		Dalla Vecchia *et al.*, 2001	
Calorckosauripus lazari	Cal Orck'o	Bolivia	Maastrichtian	207	70	33.8	1 : 1.85	this paper	S1260.1
Calorckosauripus lazari	Cal Orck'o	Bolivia	Maastrichtian	150	51	34.0		this paper	S1480.02

Ichnotaxon	Locality	Country	Age	OW	SW	TRW	Heteropody	References	Trackway nr
Titanopodus mendozensis	Mendoza	Argentina	Campanian	200	70	35.0		González-Riga and Calvo, 2009	
	Cal Orck'o Morphotype E	Bolivia	Maastrichtian	100	35	35.0	pes only	this paper	S1560.1
	Valle del Tonco	Argentina	Maastrichtian	125	45	36.0	1 : 3.5	Diaz-Martinez *et al.*, 2017	
Brontopodus birdii	Paluxy River	USA	Albian			35.04		Farlow *et al.*, 1989	
	Cal Orck'o Morphotype E	Bolivia	Maastrichtian	140	51	36.4		this paper	S1520.1
Sauropodichnus giganteus	Picun Leufu	Argentina	Aptian	227	90	39.6	1 : 2.9	Calvo, 1999, fig. 19	
	Rochefort	Switzerland	Kimmeridgian			41.9		Marty *et al.*, 2013	
	Briar Site	USA	Albian			44.37		Pittman and Gilette, 1989, p. 328	
Breviparopus taghbaloutiensis	Iouaridène	Morocco	Oxfordian–Kimmeridgian			44.7		Belvedere, 2008	Lava A
	Humaca	Bolivia	Campanian			45.3	1 : 1.2	Lockley *et al.*, 2002a	
	Courtedoux Tchâfoué	Switzerland	Kimmeridgian			49.2		Marty *et al.* (2013)	
Breviparopus taghbaloutiensis	Iouaridène	Morocco	Oxfordian–Kimmeridgian			49.4		Belvedere, 2008	Detk IX
Breviparopus taghbaloutiensis	Iouaridène	Morocco	Oxfordian–Kimmeridgian			49.4		Belvedere, 2008	Detk MXLI
Breviparopus taghbaloutiensis	Iouaridène	Morocco	Oxfordian–Kimmeridgian			50.2		Belvedere, 2008	Deio CI
Breviparopus taghbaloutiensis	Iouaridène	Morocco	Oxfordian–Kimmeridgian			50.2		Belvedere, 2008	Deio D
Breviparopus taghbaloutiensis	Iouaridène	Morocco	Oxfordian–Kimmeridgian			50.9		Belvedere, 2008=	Detk MXLII
Parabrontopodus	Courtedoux	Switzerland	Kimmeridgian			52.9		Marty *et al.*, 2003, fig.10	S 4
Parabrontopodus	Courtedoux	Switzerland	Kimmeridgian			56.0		Marty *et al.*, 2003, fig. 5	S 10
	Maimara	Argentina	Maastrichtian				1 : 2	Consolé-Ganella *et al.*, 2017	