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The Late Cretaceous dinosaur track record of Bolivia – Review and perspective

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ABSTRACT

We present an update and a review of the Late Cretaceous dinosaur tracksites of Bolivia. The Puca Group (Coniacian – Late Maastrichtian) records the tracks and trackways of two different titanosaurid sauropods, ankylosaurs, hadrosaurs and different theropod groups from the Central Andean lacustrine back arc basin. We review the sites from the Maragua syncline (Chuquisaca) and present new data on the famous Toro Toro site (Potosi).

Furthermore, the first complete map of the world's largest dinosaur tracksite, Cal Orck'o (El Molino Formation, Sucre) gives an insight into behavior and movement patterns. Parallel trackways of subadult ankylosaurs provide the first unequivocal evidence of social behavior amongst these dinosaurs worldwide. The El Molino Formation and the coeval deposits of Southern Peru and Northern Argentina form a megatracksite with a size of around 100,000 km^2. The paleogeographic position of the main sites within the basin suggests that they are part of a seasonal migration route along the shoreline and deltas of an ancient lake system.

1. Introduction

Cretaceous dinosaur tracks from South America have been well known since 1980 (Alonso 1980) and the seminal work of Leonardi (1984, 1994), although the first mention of dinosaur tracks goes back to Huene (1931). The first account of vertebrate tracks from Bolivia came from Lohmann and Branisa (1962), who mentioned footprints of iguanodontids in the El Molino Formation from the Miraflores syncline near Potosí; unfortunately, there are neither pictures nor locality information in the respective fieldnotes (H.H. Lohmann pers. comm. to the first author in 2019). In 1994 Leonardi figured four different Cretaceous localities with dinosaur tracks, i.e. Toro Toro, Parotani (17°26′10.24″S, 66°21′32.80″W; destroyed by a landslide), Arampampa (17°54′4.69″S, 66° 3′39.85″W; not verified) and Camargo (not verified). The footprints of ankylosaurs, theropods and sauropods from several surfaces in vicinity of the village Toro Toro in the middle to upper part of the El Molino Formation (Maastrichtian) were also figured. In an earlier work (1984), Leonardi named one trackway after the late Italian patron Giancarlo Ligabue, who financed one of his expeditions to the then remote locality. *Ligabueichnium bolivianum* was attributed to an ankylosaur or a ceratopsian dinosaur. After the initial discovery in 1994 of a large surface with dinosaur tracks in the quarry of FANCESA by the Bolivian geologist Hugo Heymann in the Cal Orck'o syncline near Sucre, the first field work was carried out in 1998 (mapping, casting). The tracks were subsequently studied by a team of the Natural History Museum of Basel in 2002, 2003, 2006, 2009, 2015, and in 2017 and 2019 by the senior author. The first results revealed 3500 footprints of five different dinosaur morphotypes (Supplement 7; Meyer et al., 1999a, b; Meyer et al., 2001; McRea et al., 2001; 2007). In 1998 a site in the Maragua syncline close to the village of Humaca in the Chaunaca Formation was mapped and revealed the first unequivocal evidence of gregariousness of titanosaurid sauropods in the Late Cretaceous (Lockley et al., 2002). Apesteguía et al. (2007a, b, 2011) signaled the presence of dromaeosaurid footprints from the Toro Toro Formation from a locality north of Leonardi's (1994) sites. Since Leonardi's initial work (1994) a series of dinosaur tracksites have been discovered, triggered by public awareness of the importance of Cal Orck'o. However, they have not been published until now. Just outside the Maragua syncline in the underlying Ariofilla Formation, close to the village of Potolo, a steeply inclined surface contains underprints of sauropods and theropod

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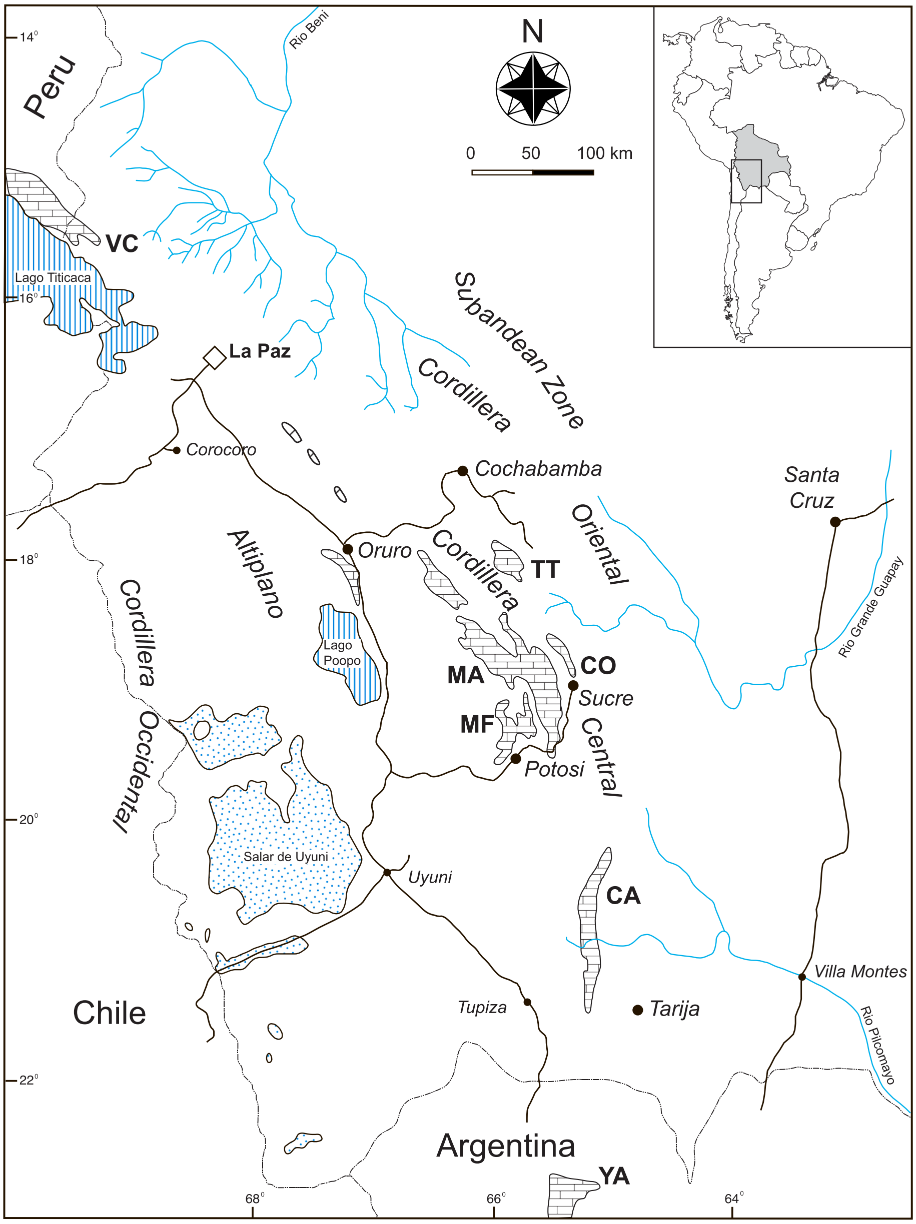

Fig. 1. Map of Southwestern Bolivia and adjacent countries with the main Cretaceous basins (hatched limestone pattern). VC: Vilquechico, TT: Toro Toro, CO: Cal Orck'o, MA: Maragua, MF: Miraflores, CA: Camargo, YA: Yacoraite.

footprints (Meyer et al., 2016). Apesteguía et al. (2016) reported the purported largest theropod footprint from the El Molino Formation of the Maragua syncline. Meyer et al., 2018, Meyer et al., 2018 published a detailed description of the sauropod footprint morphotypes from Cal Orck'o, erecting the new ichnotaxon *Calorckosauripus lazari* and attributing it to a basal titanosaurid sauropod.

The present paper provides an overview of the known Late Cretaceous dinosaur tracksites in Bolivia and discusses them in a larger context. As there are many sites that have been announced in local newspapers, we review these where relevant, and we present new data on the localities Lirio Mayo (Potolo), Cal Orck'o (Sucre) as well as Toro Toro (Potosi).

2. Material and methods

For each individual morphotype, the best-preserved footprints were chosen for photogrammetry. We produced photogrammetric 3D models for accurate documentation and precise measurements following the protocols of Mallison and Wings (2014), Matthew et al. (2016) and Falkingham et al. (2018). Digital photogrammetric models were created with Agisoft Photoscan Pro (v. 1.3.2 and 1.4.1) and Metashape Pro (v 1.6.2), starting from pictures taken with a Canon EOS 5D Mark III, with different lenses. The isolation of the tracks, the refined orientation, and the false-color depth maps of all models were produced in Cloud Compare (v. 2.9.1). Contour lines were generated in Digtrace and superimposed onto the depth maps in Adobe Illustrator. In addition, in 2017 and 2019 photographs and high-resolution videos of selected sectors were made with a drone (DJI Phantom 4 Pro). Post flight treatment of the pictures was done with Air Magic (1.0). 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). To further enhance the quality and contrast of the photographs, they were treated with Luminar (4.0). The map of the Cal Orck'o tracksite was initially made with measurements taken from a Laser distometer on the quarry floor and one person hanging on the rope in the wall, and then drawn on

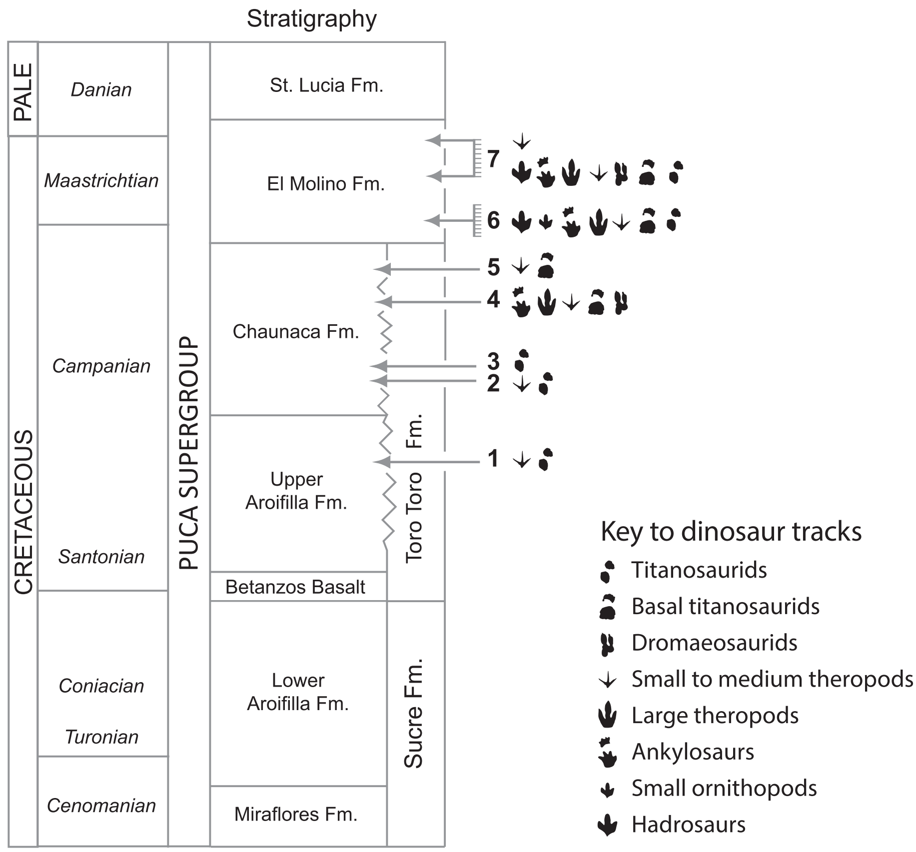

Fig. 2. Overview of litho- and chronostratigraphic context of the studied dinosaur tracksites (adapted from Deconinck et al., 2000).1: Lirio Mayo (Meyer et al., 2016), 2: Chaunaca 1 (Meyer, 1998), 3: Chaunaca 2 (Meyer et al., 2016), 4: Maragua (D. Keremba/O. Medina pers. comm.), 5: Humaca (Lockley et al., 2002), 6: Cal Orck'o (Meyer et al., 1998; Meyer et al., 2019), 7: Toro Toro (Branisa 1968, Leonardi, 1983; Meyer et al., 2019). PALE = Paleogene.

graph paper. These results were transferred to a digital map in 2003. In 2017 a completely new digital map of the site was made. The base of this map was formed from precise orthophotographs taken with a distortion-less Zeiss universal measuring camera UMK 13/18 cm with an opening of the lens of 10 and 20. The basic requirement was a laser scanner with a range of 1000 m and a precision of ± 1 cm that was positioned every 100 m within a distance of 100 m to the wall. This resulted in a point cloud with 100 million points. All tracks and trackways were remapped precisely on site and compared to older analog maps (individual tracks are depicted as symbols). Each trackway was given an individual number starting with a letter (i.e. A = Anklyosaur, S= Sauropod, T = Theropod, O= Ornithopod) followed by a number that indicates the starting sector of the trackway (Supplementary data 9). The size classes of dinosaur footprints follow those defined by Razzolini et al. (2017).

3. Geology and paleoenvironment of the Puca Group

The Cretaceous of the eastern Cordillera is represented by almost 1000 m thick sediments of the Puca Group, which unconformably overlie Paleozoic rocks. Sedimentation took place in the N-S stretching Andean back arc basin with swells and throughs. This explains rapid facies changes over short distances (Riccardi, 1988). Today Cretaceous sediments are found in small synclines and anticlines (Fig. 1; Supplementary Data 1). The Cretaceous Puca Group of the eastern Cordillera of Bolivia can be correlated with the Yacoraite Formation in Northern Argentina (Cónsole- Gonella et al., 2012) and the Vilquechico Formation of Southern Peru (Jaillard et al., 1993).

The Puca Group (Cretaceous-Paleogene) can be subdivided in seven different formations (Fig. 2: La Puerta and equivalents, Tarapaya, Miraflores, Aroifilla, Chaunaca, El Molino and Santa Lucia formations). The Puca Group has a mean thickness of about 1 km but can reach up to 5.6 km in the Potosi Basin, and consists of siliciclastic sediments with intercalated carbonates that are of marine and lacustrine origin (Sempere et al., 1997). Russo and Rodrigo (1965) were the first to study the stratigraphy and paleogeography of the Puca Group. Remains of characeans from the El Molino Formation of the Maragua syncline indicate a Late Cretaceous – Early Paleocene age (Branisa et al., 1969), and ostracods from samples at the Cal Orck'o locality corroborate a Maastrichtian age (Hippler, 2000). Above the Turonian/Coniacian unconformity the Aroifilla and Chaunaca Formations represent continental fluvial deposits (terrestrial red beds and evaporites) in an underfilled basin. The Chaunaca Formation contains carbonate sequences at the base and at the top and was deposited in a distal alluvial to salt-lacustrine playa environment. This is supported by the presence of organic matter of type III which indicates a continental setting (Blanc-Valleron et al., 1994). The presence of ostracods as well as characeans indicates the presence of freshwater bodies (Lohmann and Branisa, 1962). The overlying El Molino Formation is very variable. Fluvial sands at the base are overlain by an alternation of claystone and fossiliferous lacustrine carbonates associated with stromatolites (Blanc-Valleron et al., 1994).

The paleoenvironment of the El Molino Formation has long been the subject of controversy. Gayet et al. (1991, 1992, 2001) and Sempere (1994) favored fully marine conditions, based on the presence of selachians and (estuarine) actinopterygian fishes. However, stable isotope records and palynomorphs point to an almost continuous lacustrine system during the Late Cretaceous of the central paleo-Andean basin in Bolivia (Rouchy et al., 1993). During humid periods, lake level increase and salinity decrease led to freshwater stromatolitic build-ups and

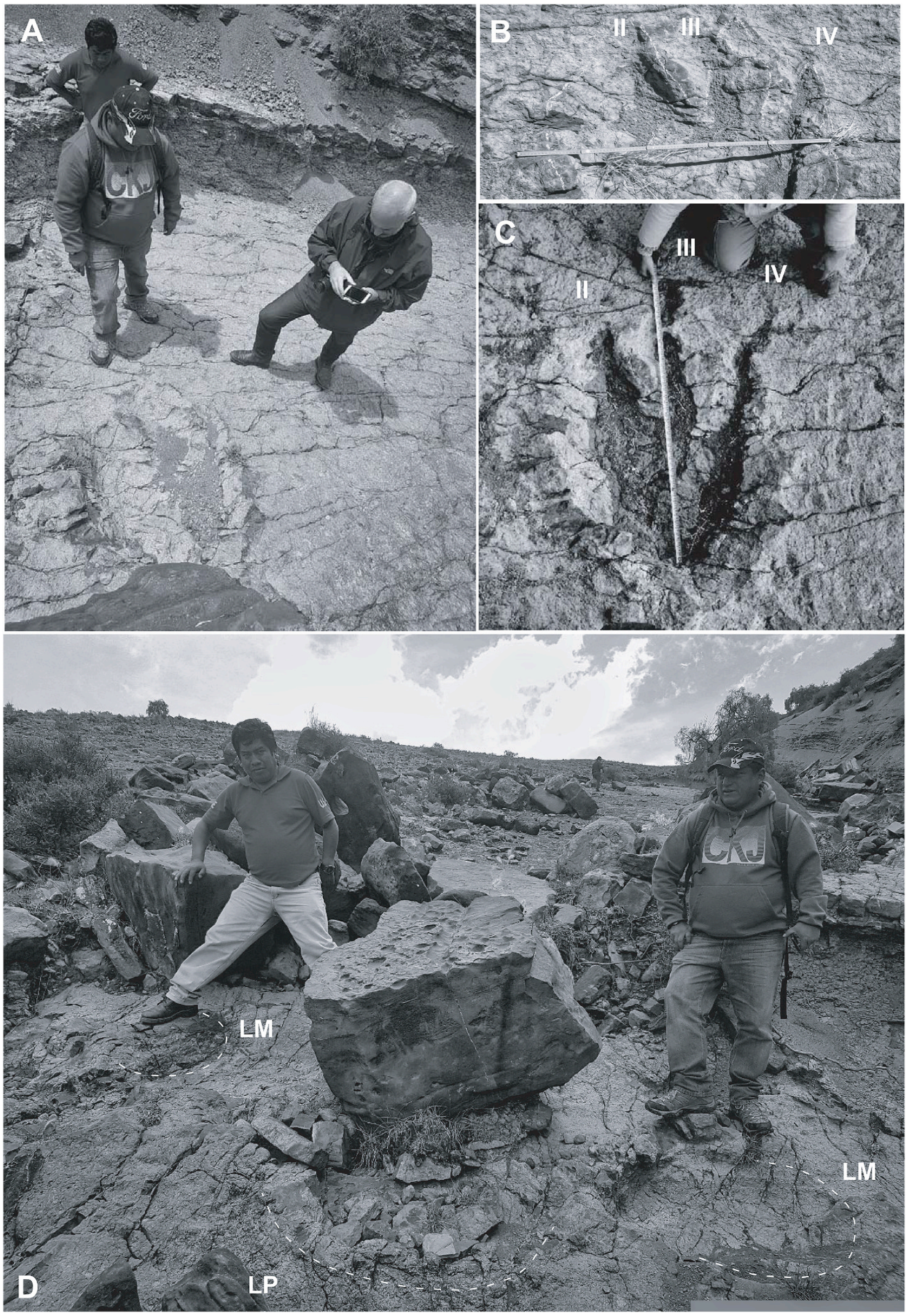

Fig. 3. Photographs of the purported largest theropod footprint from Niñu Mayu (see Apesteguía et al., 2016). A: Footprint before cleaning, B: Details of footprint showing the supposed digit imprints (ruler: 80 cm), In A and B, digit IV looks like an erosional artefact (separated from the track) that only looks like a digit when enhanced with water. C: Footprint contrast enhanced with water, D: Trackway of a sauropod (LM = left manus, LP = Left pes); imprint on the right side is the same as in A and B. (Photographs courtesy of Beimar Ramallo Sosa, Sucre).

oolitic bars. This scenario is corroborated by the study of the clay minerals (Camoin et al., 1997). The El Molino Formation contains lacustrine ostracods, characeans, freshwater gastropods, turtles and catfish. Furthermore, the presence of mud cracks, paleosols, root horizons and numerous different levels with dinosaur tracks indicate deposition in an ephemeral lacustrine basin (Meyer et al., 2001). Marramà and Carnavale (2016) presented a detailed study of the clupeomorph fish species *Gasteroclupea branisai* Signeux that occurs throughout in the El Molino Formation and coeval formations of Venezuela, Argentina and Bolivia. They concluded that the body plan is similar to that of the extant freshwater hatchet fishes. Furthermore, the negative $\delta^{18}O$ isotope values measured in the El Molino Formation of Toro Toro by Vignol-Le Large et al. (2018) do not indicate any marine influence at all.

In the south, the coeval Yacoraite Formation of Argentina represents a fluvio-lacustrine system with fluctuating groundwater table and a progradational-aggradational shoreline architecture (Cónsole-Gonella et al. 2012, 2017). For the Métan and Alemanía subbasins, respectively, Marquillas et al. (2005) suggested restricted marine conditions for the Yacoraite Formation, although the presence of several characean taxa indicates a lacustrine environment. In the north, the upper part of the coeval Vilquechico Group of southern Peru contains dinosaur tracks, characeans and ostracods and is thought to have been deposited in a lacustrine system (Jaillard et al., 1993).

4. Results

4.1. Departamiento Chuquisaca

4.1.1. Maragua syncline

The Maragua syncline lies approximately 30 km east of Sucre and has a large potential for research in dinosaur ichnology. The first discoveries were made by the local fossil association *SOCIUPA* (Sociedad

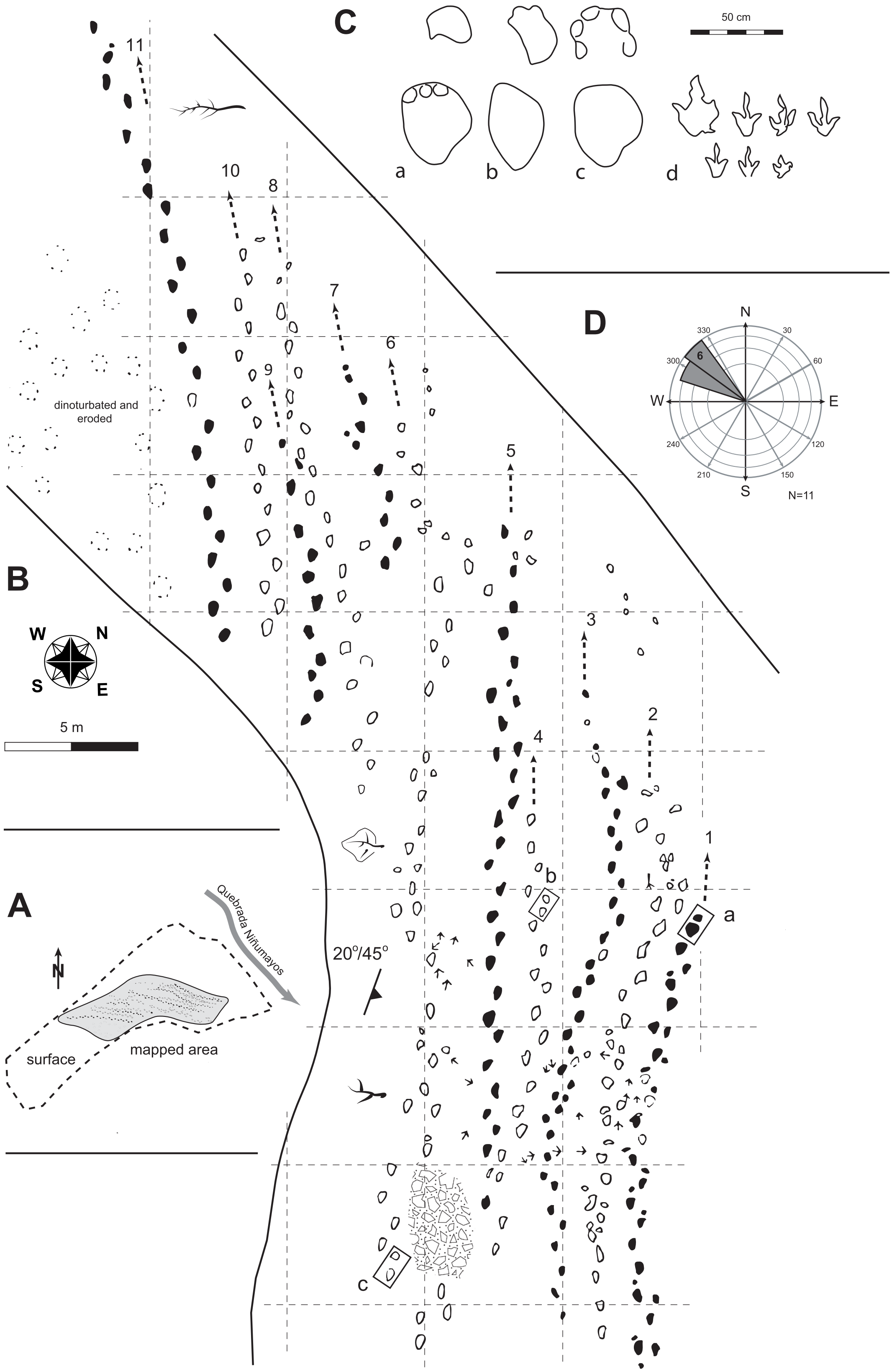

Fig. 4. Map of Humaca tracksite (adapted from Lockley et al., 2002). A: Outcrop overview of the track-bearing surface, B: Map of the surface that was mapped in detail, C: Outline drawings of selected footprints: a, b, c = individual manus–pes sets from titanosaur trackways 1, 4, 6 (location see B) respectively, d = selected theropod footprints (note curved digit III) (Location not shown in B), D: Rose diagram showing the orientation of the 11 titanosaur trackways.

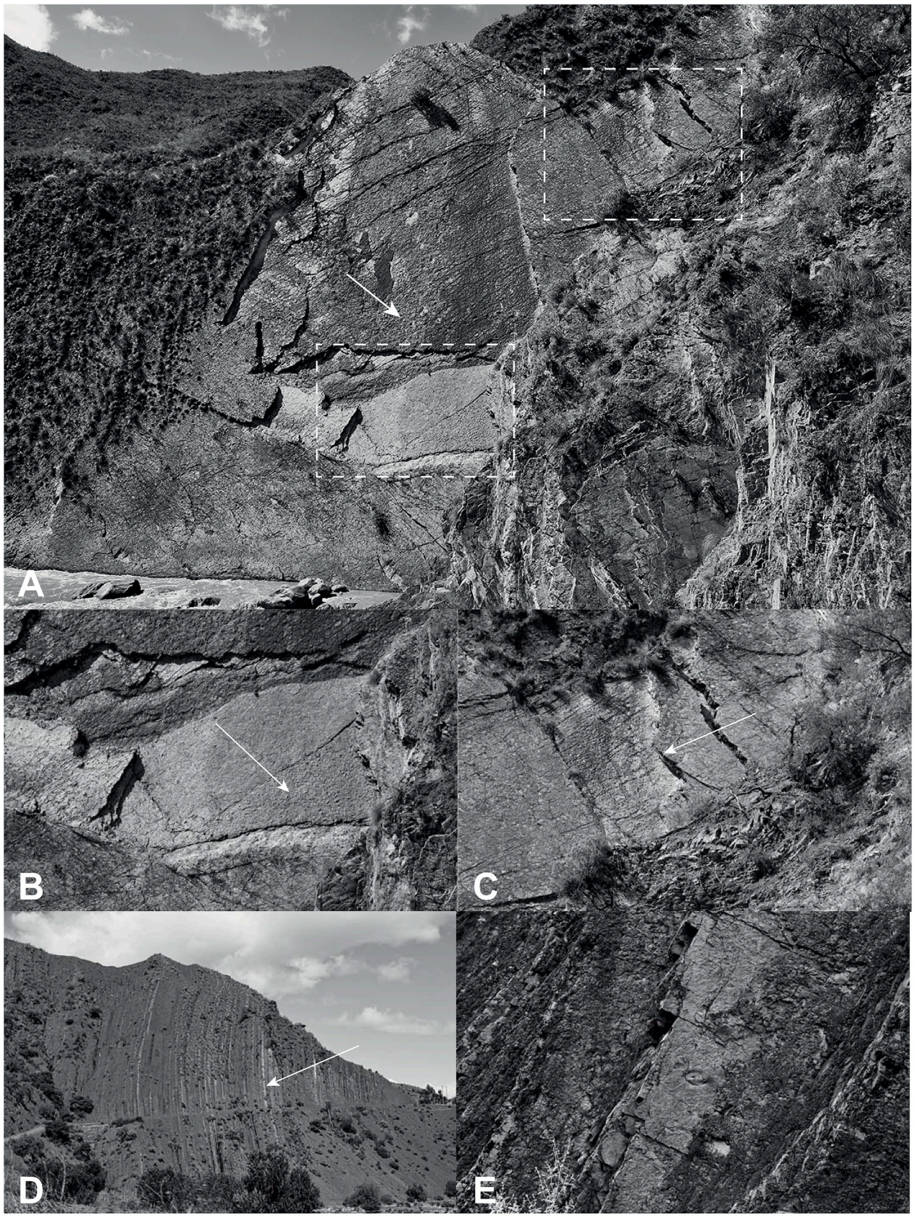

Fig. 5. Tracksites at the type locality of the Chaunaca Formation at Chaunaca (see also Fig. 4). A: Overview of site 1 northeast of the bridge (arrow points to sauropod trackway). B: Track level with theropod tracks, C: Theropod tracks on the lower level. D: Overview of site 2 (arrow points at lower track level. E: Close-up of a sauropod pes imprint on a sandstone surface (arrow in D). Dashed rectangles in A indicate position of photographs in C and D.

Universitario de Paleontologia) as early as 1995, the same year of discovery of dinosaur tracks in the quarry of Cal Orck'o (Sucre). However, further exploration of the sites was prohibited because the local ethnic group of the *Ayllus of Qhara Qhara* was in a fight with the *Sindicato de Maragua*. Subsequently, many sites have been documented with pictures, mainly by David Keremba Mamani and the group *PALEOFORMA,* under the guidance of Omar Medina (Sucre). Most of the localities on the map of Maragua are derived from documents made by David Keremba Mamani and Omar Medina (Supplementary Data 2). There are numerous sites within the Maragua syncline, as depicted on our map compilation. Only a very few of these have been verified by professional paleontologists, although many pictures have been published in local newspapers as well as on the internet. Judging from the photographs, footprints of titanosaurid sauropods, medium-sized to small theropods, and ankylosaurs have been observed. In this chapter, we only review and describe the sites we have visited and those for which enough information for a first assignment is available.

4.1.1.1. Niñu Mayu. In 2016 Grover Marquina, a local tour guide, reported a possible dinosaur footprint to a visiting scientist. The locality lies close to the hamlet Niñu Mayu (19°4′0.07″S; 65°28′39.85″W) and was the focus of worldwide social media hype. CNN quoted the very same scientist as saying "that the 114 cm long tridactyl imprint from an abelisaurid (theropod) was the largest footprint of its kind in the world" (Fig. 3). Apesteguía et al. (2016) described the imprints as showing an asymmetrical shape, with digit IV being longer than digit II (Fig. 3 A. – C). Because the metatarsal II impression was interpreted as shorter and behind the mark of digit IV, they assumed an abelisaurid or spinosaurid affinity. Upon a closer inspection of pictures taken by the Director of Tourism in Sucre and a "modelled" cast deposited in the Parque Cretácico (Sucre), the senior author could identify the print in question as a poorly-preserved pes print of a sauropod (Fig. 3 D); the apparent tridactyl shape is the result of erosion and cracks on the surface (Fig. 3 C). This alone would not be worth mentioning, except that press coverage reignited the old conflict among local authorities, because both

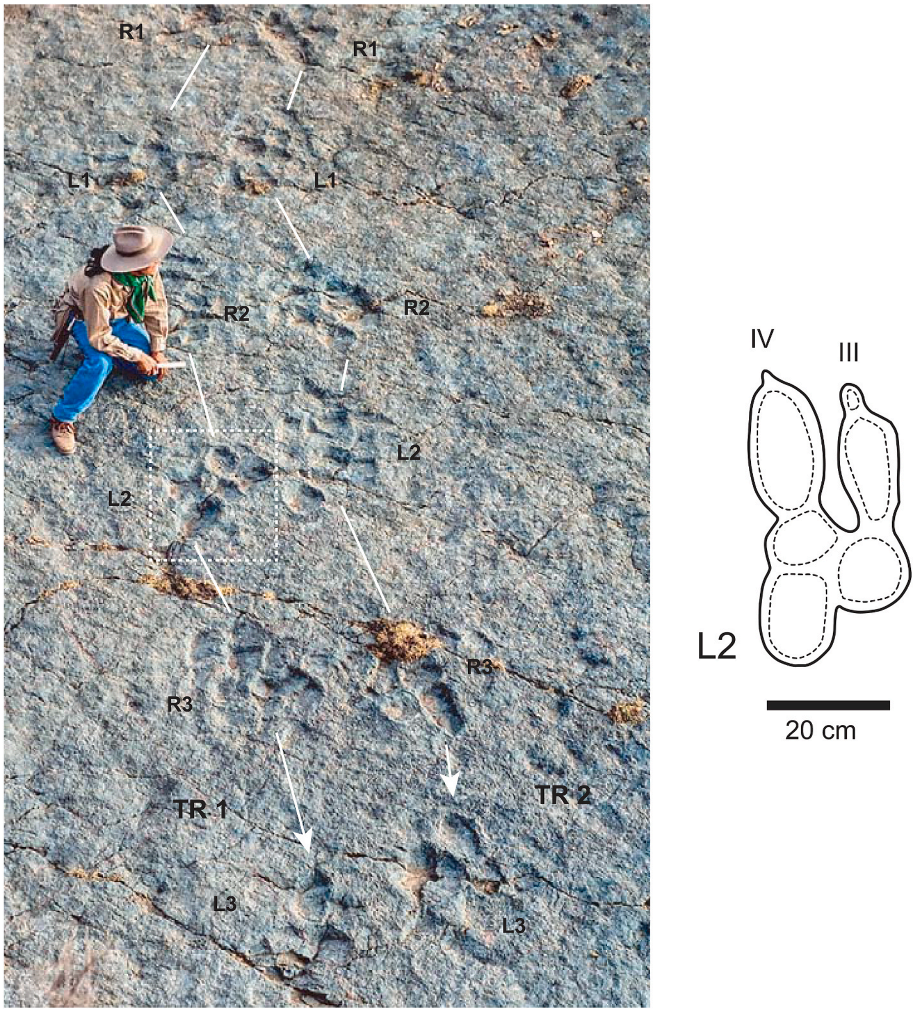

Fig. 6. A: Overview of the Pujacata tracksite (two dromaeosaurid theropod trackways TR1 and TR2 are marked). B: Outline drawing of a left, didactyl dromaeosaurid pes track. (Photo A courtesy of David Keremba Mamani).

of the rival ethnic groups wanted to profit from this discovery by claiming entrance fees for visits (Cuentas Cedro, 2018). This led to a ban for all paleontologist doing research on fossil footprints; access was denied to our working group in 2015, 2017 and 2019. Close to the disputed footprint is a surface with parallel sauropod trackways that can be attributed to the ichnotaxon *Calorckosauripus lazari*, which are very similar to those in Humaca. Additionally, trackways of medium-sized theropods and ankylosaurs can be observed.

4.1.1.2. Humaca (Ore-Pájla). This site was discovered in 1995 by a group of amateurs including David Keremba Mamani and Vicente Manuel Rial Cez, who were looking for fossil gastropods based on information from Walter Otondo (pers. comm. D. Keremba Mamani). In May 1998 the senior author visited the site and confirmed the presence of sauropod and theropod footprints; later that year the site was mapped and published by Lockley et al. (2002).

The site lies close to the eastern margin of the Maragua syncline. The entire surface covers approximately 1400 m^2 (Fig. 4 A; Supplementray Data 2), and dips gently toward the east. The lower part immediately adjacent to the Quebrada Niñumayos is strongly eroded. The track-bearing layer is a fine grained, brownish sandstone of fluvial origin and is situated in the uppermost part of the Chaunaca Formation (19°4′40.59″S; 65°28′0.45″W). The track-bearing part that has been mapped has a surface of about 750 m^2 and yields a total of 327 individual footprints (Fig. 4 B), 21 attributed to theropods and the rest to sauropods. Eleven trackways can be seen on the surface, and are attributed to sauropods. Given the pronounced horse-shoe shaped manus, the well-developed imprints of digits I and V and the rounded outline of the pes, we attribute these trackways to the ichnotaxon *Calorckosauripus lazari* (Fig. 4 A- C). We have redrawn the original map (Lockley et al., 2002: Fig. 4) and added directional data. The sauropods were small individuals (FL manus 22 cm; FW manus 25.3 cm; Pes length 44.6 cm, FW pes 33.2 cm) and formed a group moving simultaneously in the same direction; this can nicely be seen in trackways 1 to 3, which turn in the same direction (Lockley et al., 2002).

The theropod footprints are mostly preserved as iron-stained crusts on the surface and not as negative epichnia like the sauropods, and therefore formed on a higher level which is no longer present and are thus preserved as undertracks. Their overall morphology can be compared to those from the localities of Lirio Mayo, Cal Orck'o and Toro Toro. Despite the substrate differences (sandstone, limestone) they share a very distinctive feature. In most of the medium-sized theropod imprints the distal part of digit III curves strongly inward.

4.1.1.3. Chaunaca. During a field trip in May 1998 the senior author discovered several dinosaur trackways on a large, west-dipping limestone surface in the lower part of the Chaunaca Formation at the type locality just northeast of the bridge (18°58′50.19″S; 65°26′27.74″W, Fig. 5). Here, three sectors yield dinosaur tracks. On the northern part of the wall a single trackway of a sauropod is present (Fig. 4 A); just a few

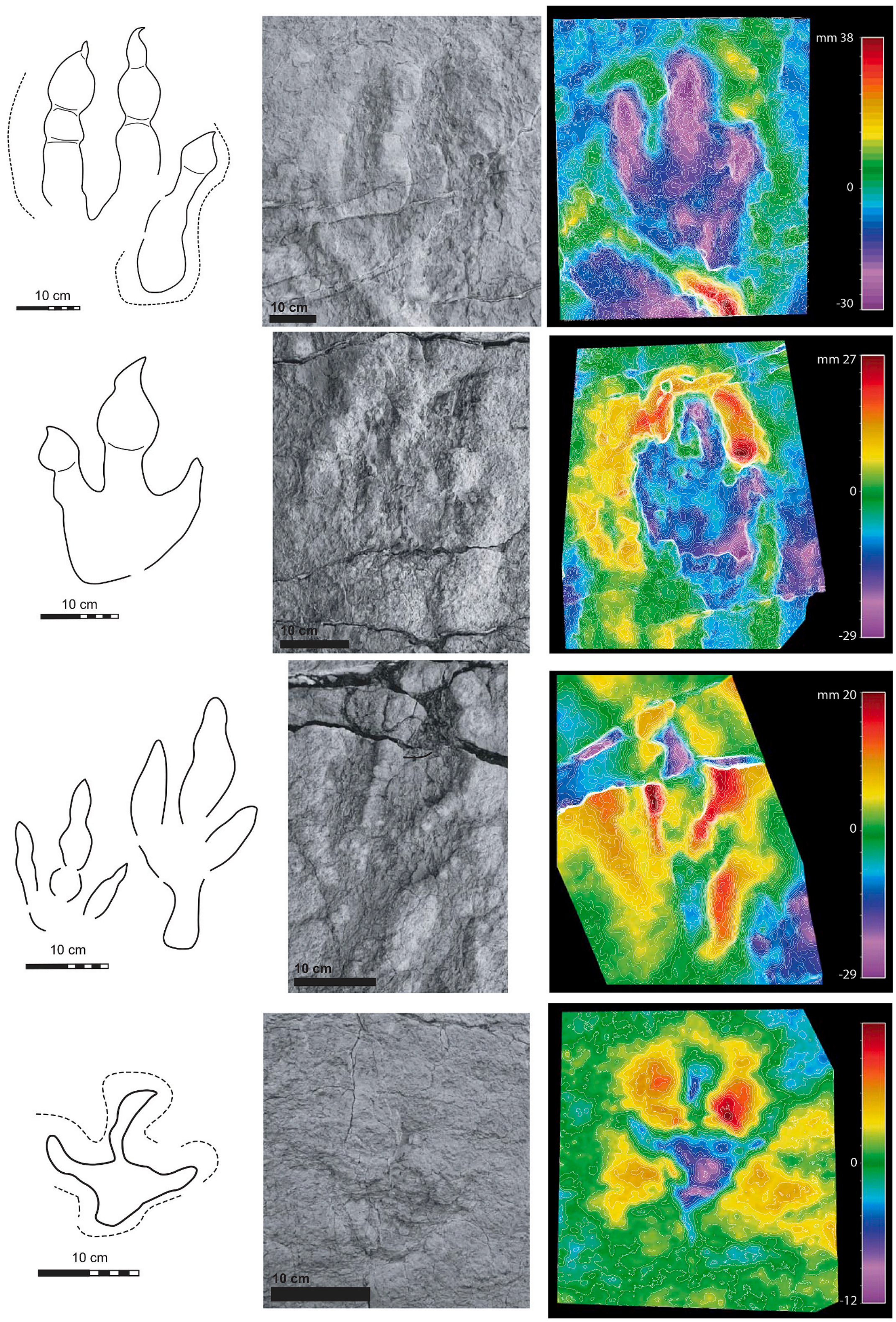

Fig. 7. Cal Orck'o locality: Outline drawings, photographs and false-color depth maps and contour-lines (1 mm spacing) four tridactyl theropod track morphotypes. First row: Morphotype A, large theropod. Second row: Morphotype B, medium-sized theropod. Third row: Morphotype C small theropod, fourth row Morphotype D: small avian theropod. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

meters below (Fig. 4 B) some theropod tracks can be seen. Further west on a higher level, a surface with more than 50 theropod tracks is recorded (Fig. 5 D). In 2015 isolated sauropod footprints were observed on a sandstone bed higher up in the section (Fig. 4 D, E; 18°59′16.42″S, 65°26′22.96″W). However, they occur on steeply inclined and strongly weathered surfaces and are not very well preserved. A more accurate documentation could not be made because secure belaying for rappelling was not possible in such an unstable terrain.

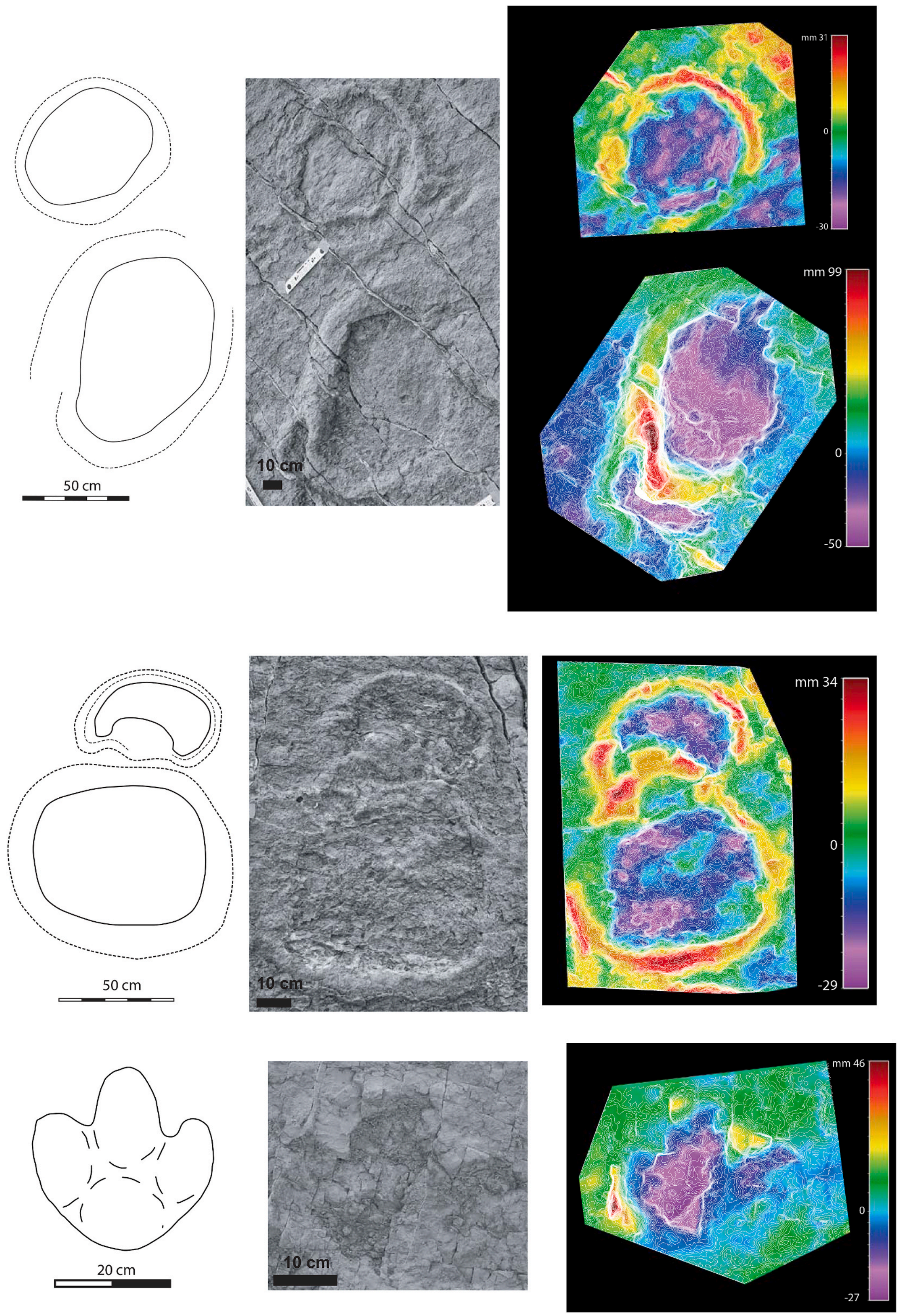

Fig. 8. Cal Orck'o locality: Outline drawings, photographs and false-color depth maps and contour-lines (1 mm spacing) of track morphotypes. First row: Morphotype E, titanosaurid sauropod. Second row: Morphotype F = *Calorckosauripus lazari*, non-derived titanosaur. Third row: Morphotype G, large hadrosaur. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

4.1.1.4. Ch'ullcumayu and Pucajata (Majara). Two localities are worth mentioning in the Maragua syncline apart from those depicted in the map (Fig. 4). Ch'ullcumayu and Pucajata both show tracks and trackways of a very large and unusual dinosaur (Fig. 6 A). In Pucajata a well-exposed surface shows two intersecting trackways and an isolated trackway outside of the picture.

The pes length varies between 30 and 65 cm and the width between 20 and 45 cm, and the footprints have a somewhat trapezoidal outline. They exhibit well-defined, rounded digital and phalangeal pads, and they are didactyl and asymmetrical. They show two well-pronounced

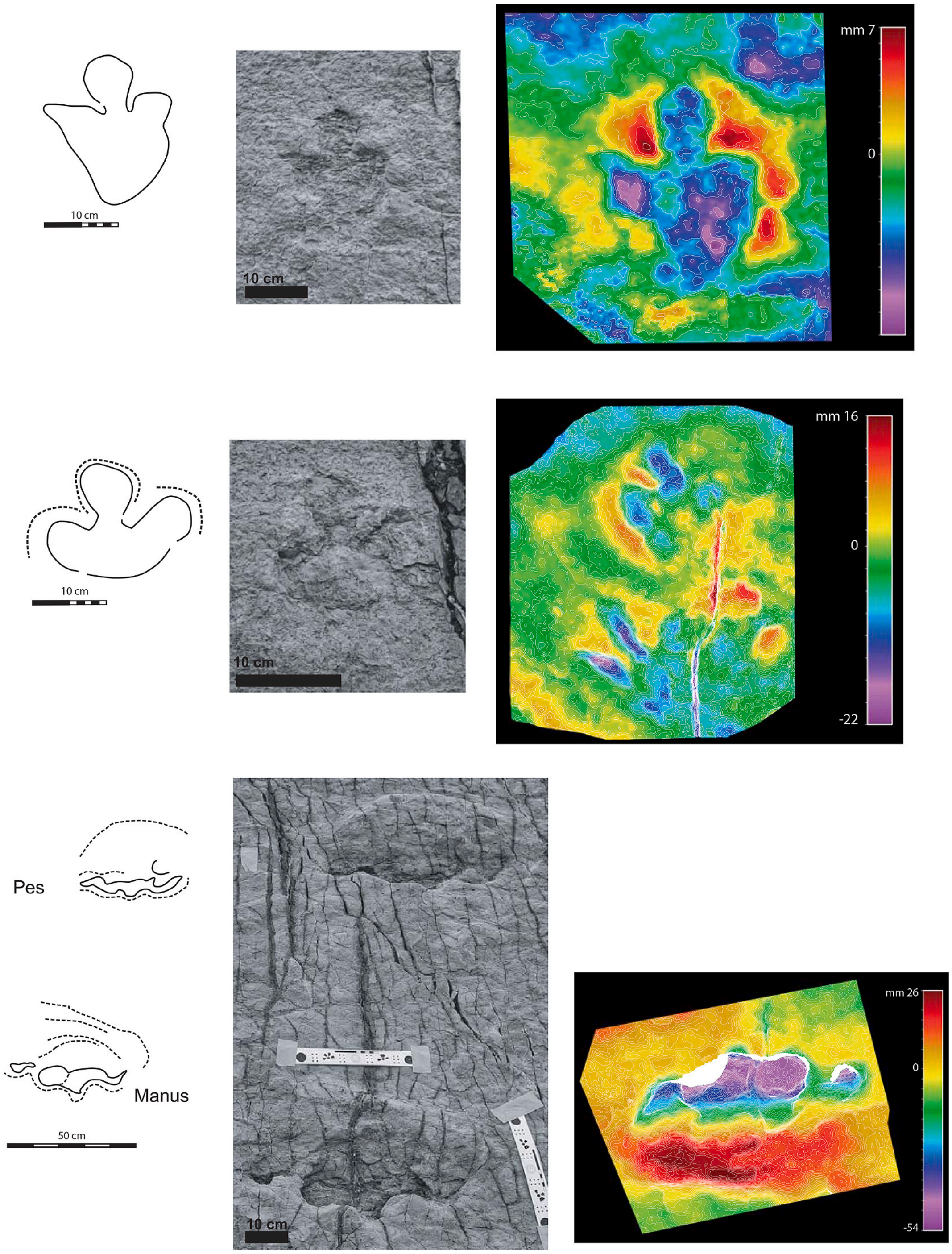

Fig. 9. Cal Orck'o locality: Outline drawings, photographs and false-color depth maps and contour-lines (1 mm spacing) track morphotypes. First row: Morphotype H, derived iguanodontid. Second row: Morphotype I derived iguanodontid. Third row: Morphotype K Ankylosaur. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

digits which we interpret as traces of digit III and digit IV, which are of subequal length and nearly parallel with no visible imprint of digit II (Fig. 6 B). These features are consistent with articulated fossil feet of deinonychosaurs. Deinonychosaurian ichnotaxa comprise four ichnogenera that represent a considerable size range (*Velociraptorichnus*, *Dromaeosauripus*, *Menglonipus* and *Dromaeopodus*). Our tracks and trackways closely resemble the ichnotaxon *Dromaeopodus shangdongensis* known from the Tianjialou Formation (Barremian–Aptian) from the Shandong Province in China (Li et al., 2008). The footprint length of the Bolivian tracks is almost twice that of their Asian counterparts. Large dromaeosaurids body fossils with a length over 3 m have been described from the Early Cretaceous of North America (Kirkland et al., 1993) and Mongolia (Perle et al., 1999). Recent studies show the presence of small and larger members of the group in South America, such as *Unenlagia* and *Neuquenraptor* (Gianechini and Apesteguía, 2011); the only larger member of the group that could have left such footprints is the unenlagiin taxon *Austroraptor cabazai* (Novas et al., 2008) from the Late Campanian/Maastrichtian Allen Formation of Argentina. This corroborates a continental wide distribution of the deinonychosaurian group that has previously been discussed (i.e. Novas, 2009; Gianechini and Apesteguía, 2011). Despite the close resemblance of the tracks and trackways from the Pucajata locality to the ichnotaxon *Dromaeopodus*

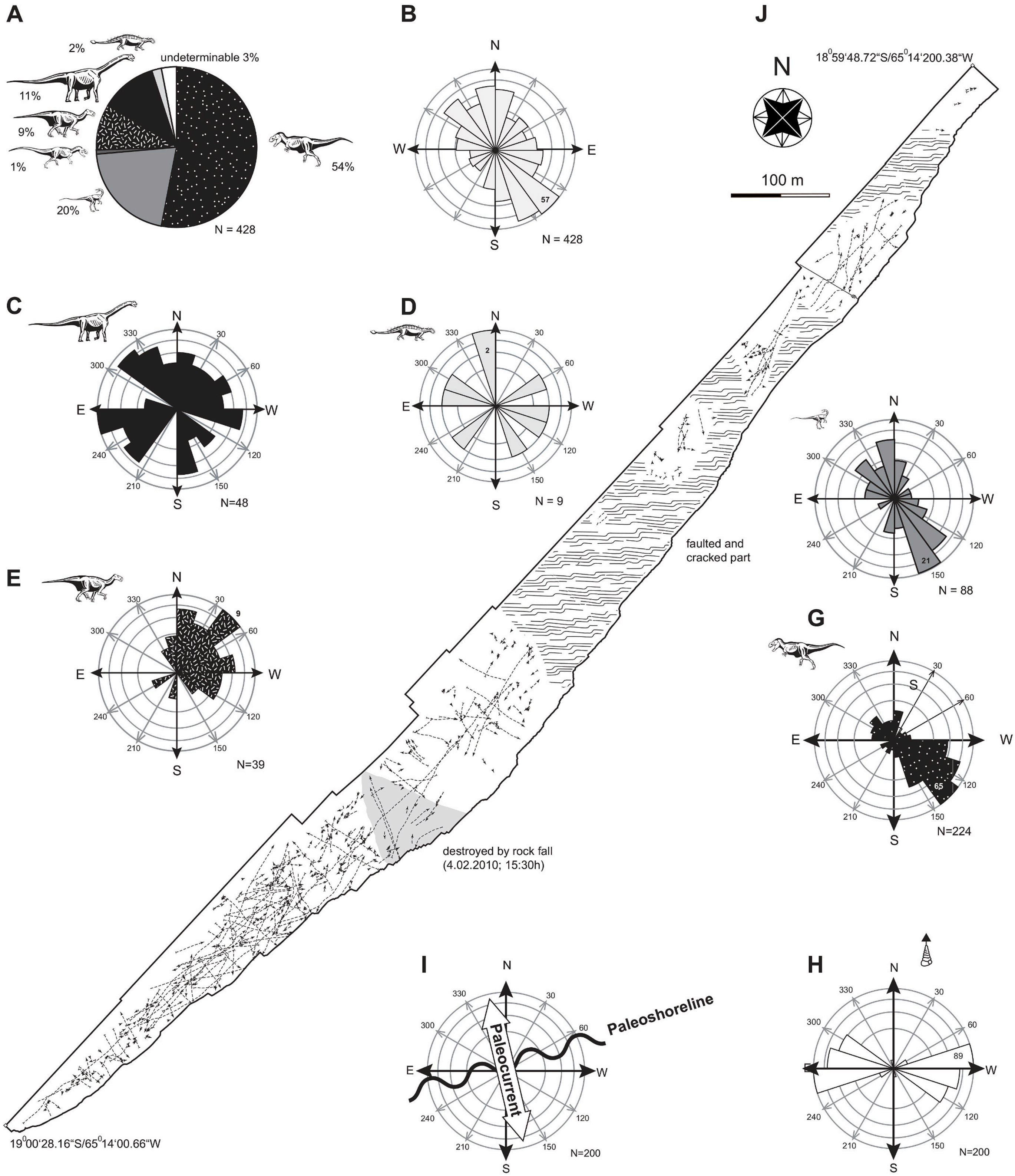

Fig. 10. Cal Orck'o locality: Overall trackway orientation of the main surface. A: Pie chart of all trackways by dinosaur groups, B: Overall direction of all trackways, C: Walking directions of sauropods, D: Walking directions of ankylosaurs, E: Walking direction of ornithopods, F: Walking direction of small theropods, G: Walking direction of medium and large theropods, H: directions of gastropods (Melania sp.), I: Paleoshoreline and paleocurrents derived from directions of gastropods and ripple marks, J: Complete surface of Cal Orck'o with walking directions of dinosaurs (see also Supplementary Data 9).

from Asia, size and individual morphology point to a different ichnotaxon. However, we refrain from erecting a new taxon until we have more thorough documentation at hand.

4.1.2. Cal Orck'o syncline

The Cal Orck'o site is situated in the active quarry of FANCESA (*Fabrica nacional de Cementos*) and has been mapped on several occasions (Meyer et al., 1999a, b; Meyer et al., 2001; McCrea et al., 2001; Meyer et al., 2006). Altogether nine levels with dinosaur tracks have been recorded, and all are situated in the middle part of the El Molino Formation. Details on the sedimentology and stratigraphy of the site can be found in Meyer et al. (2002) and Meyer et al., 2018, Meyer et al., 2018.

Here, we present three different maps of the Cal Orck'o site that demonstrate the advance of research. The first map dates back from 1998 and was created using photographs only (Supplementary data 7). In this assessment, some of the large theropod trackways were mistakenly interpreted as those of hadrosaurids. The second map sums up the state of knowledge gained after three successive field trips in 1998, 2002 and 2003 (Supplementary data 8). The third and most recent map, from 2017, is the most detailed and largest map of any dinosaur tracksite in the world, documenting not only the longest dinosaur trackways recorded anywhere in the world, but also behaviour (turning around, stopping, etc.) not having been observed before (Supplementary data 9).

All in all, 12.093 single imprints have been documented, but we estimate the total number of tracks to be much higher (around 14.000). Theropod and sauropod dinosaurs left most of them. Forty trackways can be followed over more than 100 m; among them is one segment of a small theropod trackway that can be followed for more than 620 m, making it the longest recorded in the world. Theropods (75%), titanosaurid sauropods (11%) and ornithopods (9%) were the dominant taxa in the dinosaur paleocommunity.

Nine different morphotypes have been documented (Figs. 7–9). Among those are large tridactyl footprints (Pes length 40–50 cm; Morphotype A, Fig. 7 first row) with elongated digits and fleshy pads. One medium-sized form that ranges from 30 to 40 cm in length and can easily be mistaken as hadrosaurid imprints has clearly inwardly curved and pronounced digit III impressions (Morphotype B, Fig. 7 second row). A smaller morphotype (Pes length 15 cm) shows fleshy but straight digits (Morphotype C, Fig. 7 third row). The smallest theropod morphotype (Pes length <10 cm) is almost triangular in its outline, with curved, slender digits and a pronounced heel, and might be attributed to an avian theropod (Morphotype D, Fig. 7 fourth row).

Morphotype E is characterized by coupled oval-shaped manus and large pes imprints (Pes length: 70 cm, Fig. 8) with few anatomical details, which include a characteristic overall slender track shape, an outward position of the manus and a narrow-gauge trackway configuration. Morphotype E shows circular, rather blunt manus impressions and oval pes prints and is somewhat larger than morphotype F (estimated glenoacetabular length 5 m). The second sauropod morphotype (Morphotype F, Fig. 8 first row) has more rounded and axially compressed pes imprints (Pes length 50 cm), but more horse-shoe-like manus impressions. The manus shows clear impressions of digits I and V, and the trackways have a wider gauge. This rather indistinct morphotype is assigned to an advanced titanosaur. Morphotype E has been interpreted as belonging to a basal titanosaurid sauropod because of the presence of impressions of digit I and V in the manus, and classified as a distinct ichnotaxon, *Calorckosauripus lazari* (Meyer et al., 2018, Fig. 8 second row). These tracks have an anterior-posterior lengthening with a broad anterior part and a manus whose digits I and V can clearly be distinguished (estimated glenoacetabular distance 2.8–3.2 m).

Blunt-toed tridactyl footprints of larger ornithopods (Morphotype G, length 30 cm, Fig. 8 third row) are rare and are attributed to hadrosaurs. Similar but smaller morphotypes (Pes length 12–15 cm) can also be observed. Those with a more triangular heel impression can be attributed to non-hadrosaurid iguanodontians (Morphotype H, Fig. 9 first row), whereas the more cloverleaf-shaped prints most probably belong to small hadrosaurs (Morphotype I, Fig. 9 second row). Ellipsoidal rake-like manus and pes prints of medium to intermediate size have been attributed to ankylosaurs (Pes width 50–60 cm; Morphotype K, Fig. 9 third row). They are tetradactyl, wider than long, with well-developed toes (digits II and III) and are the first reported from the South American continent (McCrea et al., 2000).

Using standard ichnological procedures (Thulborn, 1990) we deduce that titanosauriform sauropods were represented by two different species with an estimated total length between 9 and 15 m; younger individuals with a total length of about 7–10 m were also present but are extremely rare. Theropod dinosaurs vary from small individuals with a maximum body length of 1 m, through an intermediate size class with a body length of 2–3 m, to larger animals with an estimated total body length of 3–6 m. Ornithopods range from small individuals (1–2 m) up to larger forms with 4–6 m total body length. Ankylosaurs had an estimated body length of 5–6 m (estimated glenoacetabular length 3 m); rare larger footprints indicate animals with a body length of up to 8–10 m.

Careful analysis of the main track level reveals different generations of mud cracks on its surface, all of which formed after the tracks were left. The variable preservation of individual footprints along certain trackway segments points to a different moisture content of the substrate during the track formation. Furthermore, all true tracks (not the undertracks) were left during the end phase of the wet season, before the shoreline dried up completely. Neoichnological and ichnological studies (Marty et al., 2009; Falkingham et al., 2017) and our observations on site suggest that the main level was formed within one hydrological cycle. This is corroborated by taphonomic observations of the vertebrate remains on the main surface, which shows that turtle and fish remains (pycnodontids, catfish) are dispersed and always completely disarticulated (single bones, bony plates, scales, vertebrae, teeth). Taking these observations together, we can conclude that the main track level displays a census assemblage with a unique view into a Late Cretaceous lacustrine ecosystem.

The pie chart of all encountered trackways shows that almost 75% were left by theropod dinosaurs (Fig. 10 A). This has also been observed in other tracksites (i.e. Rio do Peixe basin, Brazil: Leonardi, 1994) and was taken as providing a valid basis for determining the relative abundance of individuals. Although we think that most of these track sites are census assemblages, the composition of the ichnofauna with more or less 75% of carnivorous dinosaurs does - in our view - not reflect a regular trophic pyramid.

We can assume that the activity level of theropods was much higher than in herbivorous dinosaurs, leading us to conclude that they also had a larger daily range than their herbivorous counterparts, thus leaving more tracks (see also Farlow, 2001). This would explain the high proportions of theropods and result in comparatively much more trackways on any given surface. A similar ichnoassemblage composition has been reported from many tracksites in the Americas, (Leonardi, 1994; Lockley and Hunt, 1999), Africa (Belvedere et al., 2010) as well as from Europe (Switzerland; Marty, 2008).

Rose diagrams of the trackway directions show a differential behaviour among the dinosaur taxa (Fig. 10 B). Most of the carnivorous theropods preferred a N-S travelling direction, parallel to the ancient lakeshore (Meyer et al., 1999a,b; Fig. 10 F, G). Paleocurrent measurements using gastropods and the strike of ripple-crest lines show a preferred E-W trending current pattern (Fig. 10 H, J). This indicates an NNW-SSE-running paleo-shoreline. The trackways of sauropods, ankylosaurs and ornithopods however, moved preferentially East-West, almost perpendicular to the direction of the theropods (Fig. 10 C – E). We interpret this pattern as an indication of a different hunting or feeding strategy.

Although the surface of Cal Orck'o is extremely large, we could neither observe any trackways that suggest chasing of prey (i.e. Paluxy River, Thomas and Farlow 1997) nor any others that indicate social

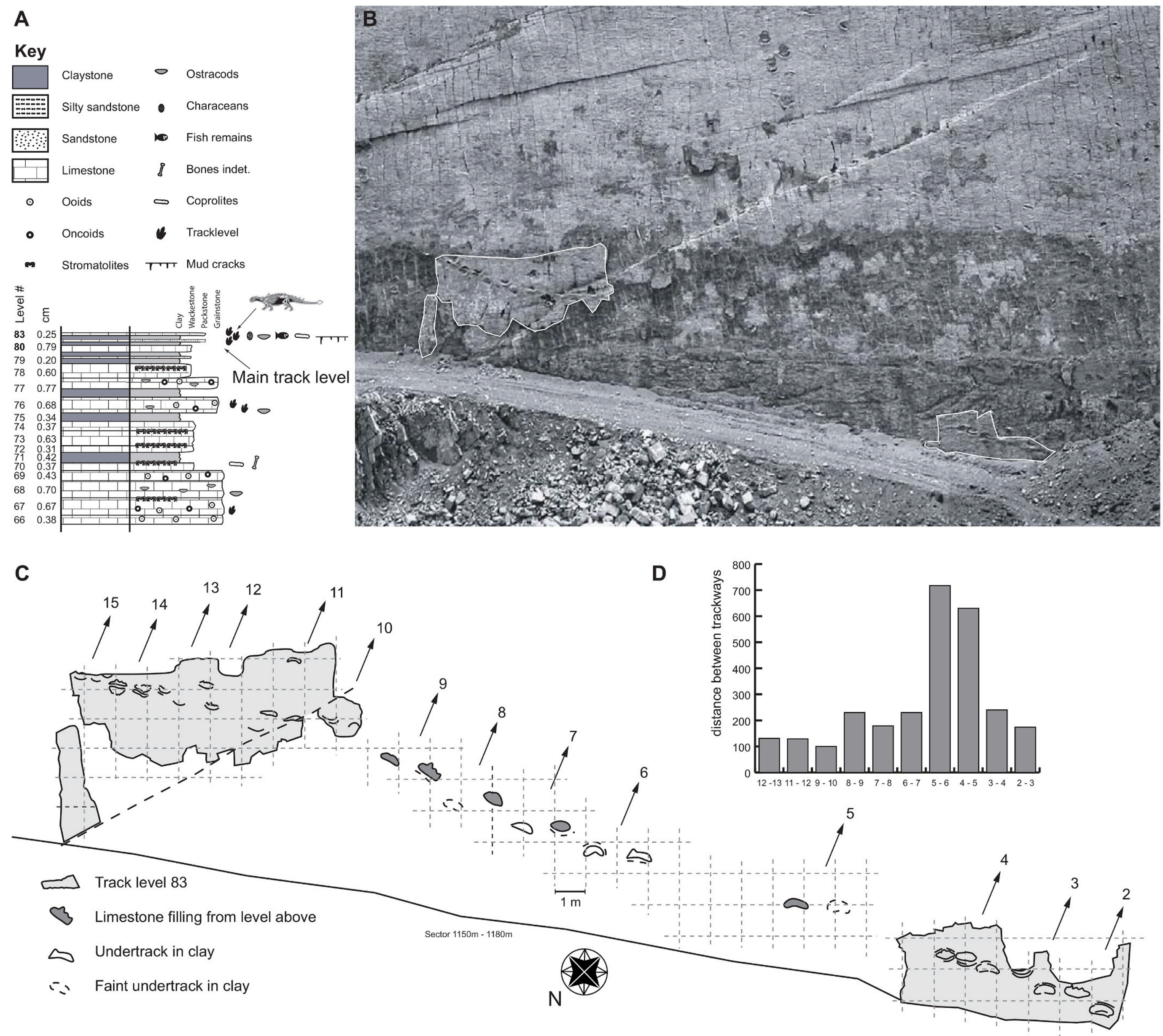

Fig. 11. Cal Orck'o locality: Parallel ankylosaur tracks from level 83. Arrows indicate the direction of travel of the individuals, each animal is represented by a single or only a few footprints A: Detailed section of the tracklevels (main track level is CO 80; see also Meyer et al., 2018, Meyer et al., 2018) B: Photograph of the surface C: Analog map of the parallel trackways D: Intertrackway spacing (distance between trackways).

behaviour. However, we noted other peculiarities. There are two trackways of running ankylosaurs, one that was documented at the northern edge margin of the site but subsequently destroyed by quarry activities (T2/3/11 in McCrea et al., 2003: Fig. 20.27). A second one can be followed over 64 m and is around sector 1200 m (A 1200.01, Supplementary data 9). A rather unusual pattern can be seen in a theropod trackway, where the animal stopped and used its left foot to start walking again. (T1190.01, Supplementary data 9). Furthermore, one very long trackway of a small theropod was documented that makes a wide curve after walking 130 m in a straight line (T1400.05, Supplementary data 9), then returning to the point of origin; the reason for this behavior remains unclear.

Two interesting, almost parallel trackways attributed to non-derived titanosaurs (*Calorckosauripus lazari*, Holotype of S-1080.1 and S 1080.2. Supplementary data 9) were regrettably destroyed by a rockfall in 2008. At the very beginning one of the trackmakers seems to have been closely following the other over a distance of 17 m, resulting in a peculiar trackway pattern. Thereafter the two trackways stay very close for another 30 m before separating and becoming parallel for the remainder of the occurrence (36 m). Their footprint size is very similar, indicating individuals of the same age group, as does their moderate speed. As there are no big size differences between male and female sauropods (Ikeiri, 2004) they could represent trackways of a couple, but just as readily two females or two males. The local press has repeatedly suggested that these two trackways are those of coupling sauropods. However, the possible virtual mating poses of sauropods (Vidal, 2018) the 'backwards mating pose' would result in a completely different trackway pattern. We interpret the trackway pattern as being the result of two sauropods that just followed each other; any other explanation seems to be in the realm of geopoetry.

In 2006 we mapped, a few centimeters above the main level (Fig. 11, CO 83), a total of 15 partial trackways of ankylosaurs; the surface was subsequently destroyed by quarry activities (Fig. 10). The pes tracks are about the same size (FL: 32 cm; FW 57 cm), indicating smaller

Fig. 12. Lirio Mayo tracksite: Photograph of the track-bearing surface. Length of the scale bars is 50 cm.

individuals, possibly subadults, as compared to other tracks in the quarry (i.e. McCrea et al., 2003). Apart from a gap in the preserved surface, the intertrackway spacing is extremely regular. Although we cannot follow the trackways for more than a few meters, we suggest that these animals were moving in a herd. Records of herding in thyreophorans is unknown so far. Apart from multiple trackways from the Gates Formation of Alberta (McCrea and Currie, 1998), there is only one site, from the Early Cretaceous Dakota Sandstone of Colorado, that is dominated by tracks of small ankylosaurs (Lockley et al., 2006). Despite the presence of multiple trackways, none of these examples mentioned above provide direct evidence of herding. However, our observation in Cal Orck'o is the first unequivocal evidence of social behavior among ankylosaurs worldwide.

4.1.3. Lirio Mayo (Potolo)

This is a small tracksite from the Aroifilla Formation (Coniacian), close to Potolo in the Central Andes (19°2′0.36″S, 65°33′4.15″W). The surface was accidentally uncovered by local construction workers while blasting rocks for the construction of a dam (Fig. 12; Supplementary data 3). Because the site would be covered by an irrigation dam in the future, in 2015 the local authorities invited our team to document the surface before its final destruction (Meyer et al., 2016).

The sedimentary succession consists of medium - to fine-grained reddish sandstones with trough cross bedding (Supplementary data 3 B). Sandstones are thin-bedded (cm-to dm-scale), coarse to fine-grained, and contain abundant current and wave ripple marks, small-scale cross stratification, mud cracks, and mudstone rip-up clasts. These features point to deposition in an alluvial plain of a shallow braided river system. Mud cracks, caliche and rip-up clasts indicate paleosol development in an arid climate.

The track-bearing surface is steeply inclined, approximately 30 m^2 are accessible without danger. Sixty tridactyl footprints and 8 oval shaped footprints have been observed (Fig. 12; Supplementary data 3 B and 4). The tridactyl tracks occur as negative epichnia and show a strongly inward-curved middle digit (Fig. 13, Supplementary Data 6; mean FL 25.4 cm; mean FW 17 cm), and so resemble the tracks reported from the Humaca site (see above). They have slender toes, well-developed digital pads, and pointed claw marks. Moreover, in R1 of T4 an antero-medially directed scimitar-like impression of a hallux can be seen (Fig. 13 A: arrow). The axis of the hallux impression is 90^0 to the impression of digit II; the angle between the hallux midline and the axis of digit III is 60°. Digit III is the longest, followed by digits II and IV. The

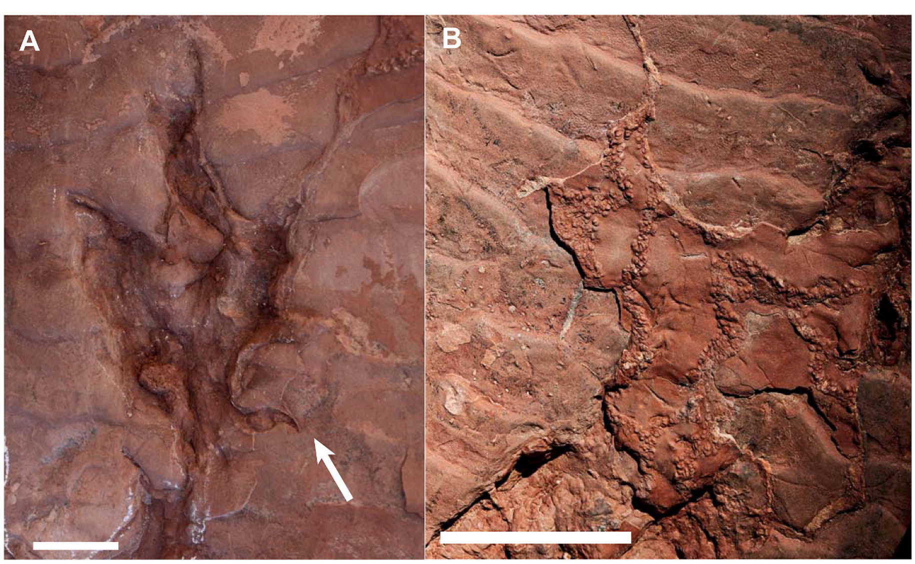

Fig. 13. Lirio Mayo surface: A: Photograph of right theropod footprint R1 of trackway 4, arrow points to hallux impression. B: *Steinichnus* sp. invertebrate traces. Scale bar in A and B is 5 cm.

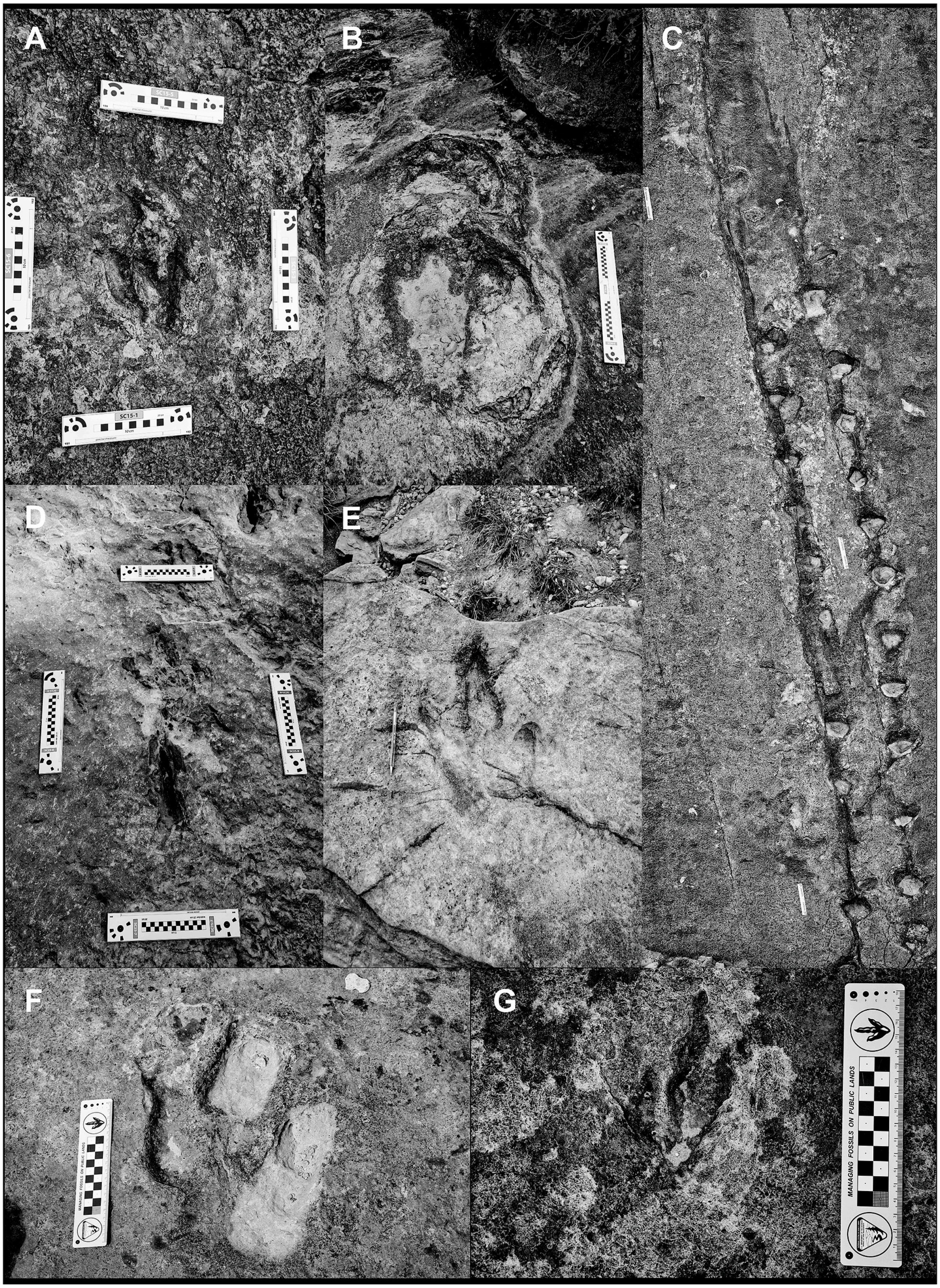

Fig. 14. Toro Toro syncline A: Medium-sized theropod track from the main tracksite (right pes; scale10 cm). B: Right manus and pes titanosaur track assigned to *Calorckosauripus lazari* from the main tracksite (scale bar is 1 m), see also Leonardi (1994, Plate VIII; 1a). C: Aerial view of an ankylosaur trackway of *Ligabuechnium bolivianum* from the Bridge site (scale bar is 1 m, travel direction from bottom to top), see also Leonardi (1994, Plate VII; 1a). D: Left pes track of a small theropod with maniraptoran affinity, Rìo T'ira Tani locality (scale bar is 15 cm). E: Large theropod track (pen is 15 cm) from the Kuchu Rodeo locality (outside of the map shown in Supplementary data 6; photograph courtesy of Alfonso Alem). F: Large theropod track from the Cerro Huayllas site (H5; scale bar is 18 cm). G: Small theropod track from the Cerro Huayllas site (H5; scale bar is 18 cm).

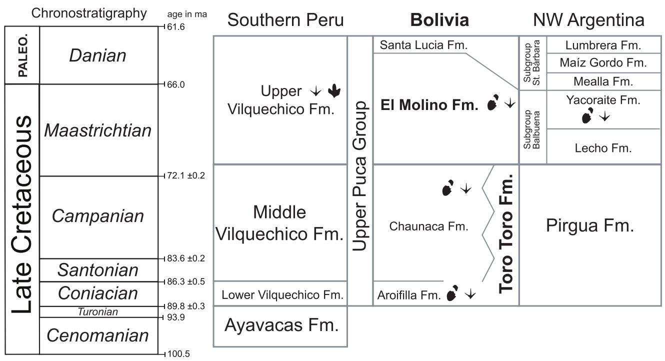

Fig. 15. Correlation of lithostratigraphic units between Northwestern Argentina, Bolivia and Southern Peru (adapted from Sempere et al., 1993). For key see Fig. 3.

right pes length varies between 24 and 28 cm whereas its width ranges from 16 to 19 cm. The length of digit II is between 14 and 16 cm and in digit IV between 13 and 16 cm. In T1 the pace is 56 cm and stride measures 134 cm respectively.

All the theropod tracks closely resemble those of Cal Orck'o (Morphotype C; Fig. 7 C) and from Humaca (Fig. 4 C) and Toro Toro (compare Fig. 15 G). This specific track type shows one main character, the strongly bent or inwardly curved digit III, that can be seen in all the sites despite the different track preservation in sandstone and limestone beds.

The oval-shaped footprints were left by sauropods, but due to their preservation as underprints, no details can be seen. They formed before the imprints of the theropods were left. The preferred walking orientation of the theropods was to the SE, perpendicular to the main current (as inferred from the ripple marks).

The surface contains invertebrate burrows that can be observed following the mud cracks or as fillings in the individual footprints. These burrows are 0.5–1 cm in diameter and occur as transverse crescentic ridge or as mensicate back fills and are occasionally branched (Fig. 13 B). Because of their architecture and morphology, we assign these endichnia to the ichnotaxon *Steinichnus* (Hasiotis, 2004). They are thought to be constructed by orthopterans such as heterocerid mud-loving beetles or mole crickets (Gryllotalpidae) in the uppermost part of the substrate (Clark and Ratcliffe 1989). According to Hasiotis (2004) *Steinichnus* isp. is constructed in water-saturated sediments at the sediment–water–air surface and is often associated with bedding surfaces that exhibit ripple marks and desiccation cracks.

That leads to the assumption that the burrows were constructed during brief periods of subaerial exposure, but after the trackways were left and mud cracks had been formed.

4.2. Departamento Potosi

4.2.1. Toro Toro

The El Molino Formation in the Toro Toro syncline (Department of Potosi, Bolivia) has long been known for its Cretaceous dinosaur tracks. They were briefly mentioned by Branisa (1968). Giuseppe Leonardi led the first expedition in 1983 and mapped several surfaces. In 1984 he published the description of a trackway, *Ligabueichnium bolivianum,* attributed to either to a ceratopsian or to an ankylosaur. The preservation of the type trackway is nowadays such that no details can be seen (see Fig. 14 C). Clearly visible are still manus and pes impressions and the morphology and trackway pattern are similar to that of other known ankylosaur trackways. Although we agree with Leonardi (1984, 1995: Plate VII) and McCrea et al. (2001) that it was produced by an ankylosaur, we need to find better-preserved tracks in order to validate the above-mentioned ichnotaxon. In his atlas, Leonardi (1994) figured five larger surfaces with tracks and trackways of theropods and sauropods; they are all situated close to the village (Supplementary data 6, Main site, Bridge, Rio Mission Cruz 2). We have visited these sites and attribute most of the sauropod trackways to the ichnotaxon *Calorckosauripus lazari* (Meyer et al., 2018, Fig. 14 B; see Leonardi 1994, Plate VIII). Apesteguía et al. (2011) described purported dromaeosaurid tracks which they placed stratigraphically into the Toro Toro Formation. However, the locality (Supplementary data 6, Rio Mission Cruz 1) and whole area form part of a syncline-anticline system and is situated in the upper member of the El Molino Formation; the closest outcrops of the Toro Toro Formation are more than 5 km to the west in the Toro Toro canyon. The “dromaeosaurid tracks” are isolated footprints that occur on a surface of a fine-grained sandstone layer that also yields tracks of sauropods. These isolated manus/pes sets show a strong extramorphological overprint, i.e. highly deformed bulges and no morphological details. Furthermore, the surface itself is the sole of a creek and is strongly eroded. The preservation of the “dromaeosaurid” tracks is rather poor; they are very shallow and do not appear to be true tracks; Apesteguía et al. (2011) also stated, “that they are probably undertracks”. This is somewhat intriguing, even more because they were assigned to the ichnogenus ?*Dromaeopodus*. Our observation in situ did not reveal a didactyl morphology; therefore, we regard these tracks as belonging to medium-sized theropods that cannot be assigned to any specific family. There have been several attempts to document the sites around Toro Toro (Esperante et al., 2018) but they remain rather sketchy (i.e. Rios Cordero, 2005).

In 2019 the senior (CM) author visited several new sites situated on the Cerro de Huayllas, in the Rio T'iratani and around the Quebrada Chiflon. They are situated at the base and the top of the middle member of the El Molino Formation (Maastrichtian: see Vignol et al., 2018), and thus far as many as 15 different track levels have been recorded. The tracks are mainly preserved as negative epichnia on fine-grained sandstones, occasionally also on limestones. In some sites, such as Las Golondrinas, positive hypichnia of theropods are present and sauropod footprints can also be seen in cross sections. Since then many more sites have been reported and have yet to be studied (Supplementary data 6).

The surfaces at the Cerro de Huayllas (H1-H5, Supplementary data 6) show tracks and trackways of minute, slender (FL 13 cm) and large blunt-toed theropods (FL 35 cm; Fig. 14 F, G). Medium-sized theropods are also present at the main site (Fig. 14 A). On most of the Cerro Huayllas surfaces, trackways of *Calorckosauripus lazari* can be observed. Some of the layers near the top are completely dinoturbated, but other surfaces show parallel trackways of titanosaurids. There are at least five different track-bearing levels; they consist of dolomitic limestones, calcarenites and fine-grained sandstones, the latter sometimes covered with insect traces. Large theropod tracks with slender digits are present on limestone surfaces at the Kuchu Rodeo locality (Fig. 14 E). The Quebrada Chiflon comprises two disjunct surfaces of 1600 and 1800 m^2 respectively, with a density of 1–2 footprints per m^2 of small-to medium-sized theropods (Supplementary data 6). This surface is overlain by a low angled cross bedded, well sorted sandstone with desert roses (gypsum pseudomorphs), which we interpret as an aeolian deposit; this is possibly the last layer before the K/Pg-boundary. The Río T'iratani site shows a limestone surface with 30 theropod footprints organized in four trackways and is situated in the lower part of the El Molino sequence. One of the trackways consists of three consecutive imprints of a crouching theropod that may be attributed to maniraptoriformes (Fig. 14 D; Meyer et al., 2019). Similar but much larger tracks have been documented from the Tigre Mayu site, which seems to be in the same stratigraphic position.

Today more than 28 sites have been discovered (Supplementary data 6) inside the proposed Geoparque and adjacent to it. So far at least 15 levels with dinosaur tracks are known that record the presence of titanosaurid sauropods, different types of theropods and ankylosaurs. In our view, the area around Toro Toro is of key interest because it records dinosaur track levels that are closely situated to the K/Pg-boundary.

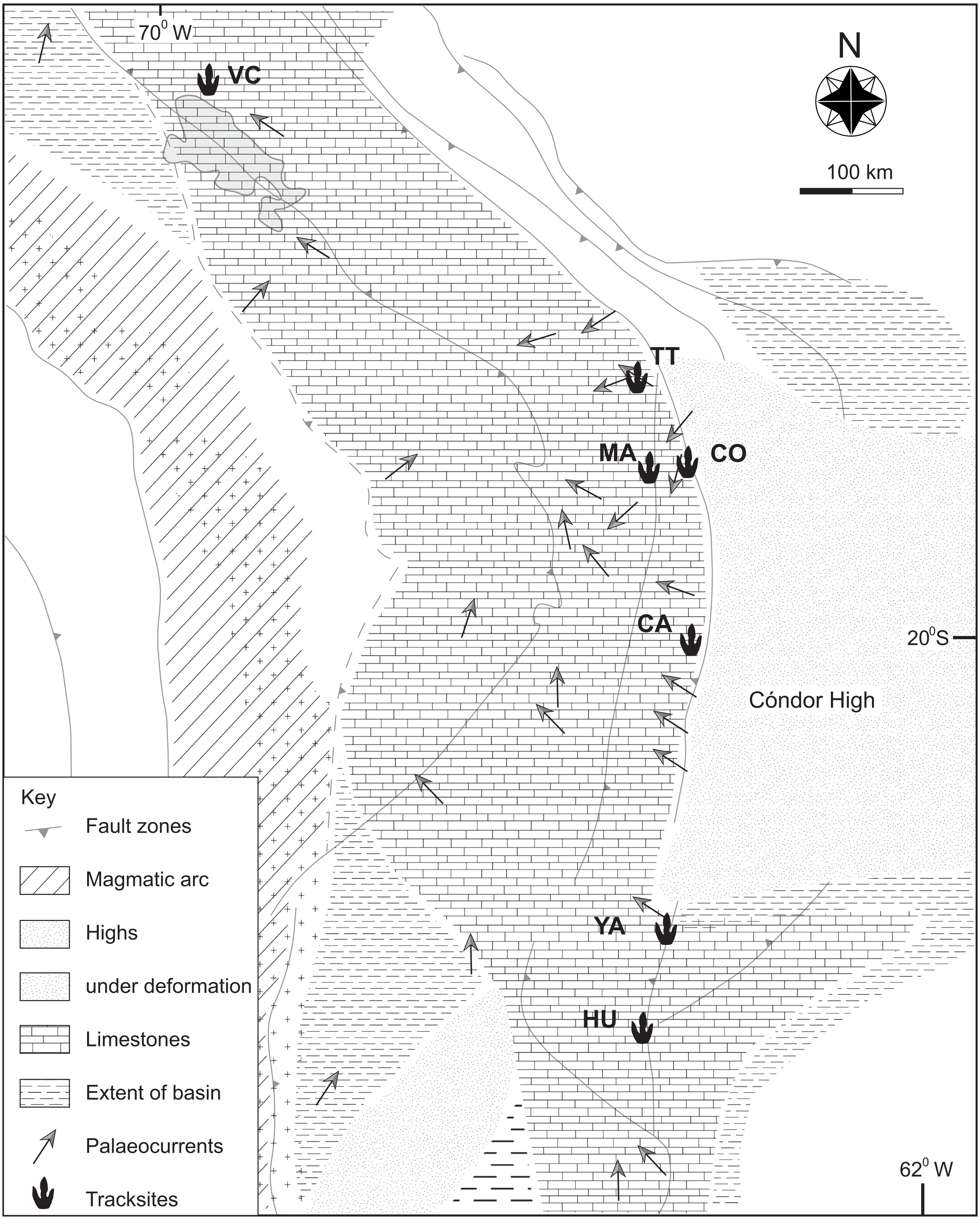

Fig. 16. Paleogeography and paleocurrents of the Late Cretaceous basins in Bolivia and adjacent areas with the main track localities (Map after Riccardi 1988). VC: Vilquechico, TT: Toro Toro, CO: Cal Orck'o, MA: Maragua, CA: Camargo, YA: Yacoraite, HU Humahuamaca.

4.3. Departamento Camargo

4.3.1. Camargo

At the carretera El Puente (21°14′54.84″S, 65°12′38.85″W) dinosaur tracks have been observed, but no documentation exists (pers. comm. K. Fiedler, 2019). The middle part of the El Molino Formation at Camblaya contains a single theropod imprint with a pes length of 30 cm (Fiedler 2002).

Puente Viña Vieja is another site northeast of Camargo that shows sauropod footprints that require further study (Suarez-Riglos et al., 2018).

La Quemada is a locality mentioned by Suarez-Riglos et al. (2018) that lies 15 km southeast of Camargo. We have no information considering the age of this surface that, according to the above authors, is trampled by dinosaurs. This interpretation is very doubtful, and we consider the irregular circular structures as negative epireliefs of ball and pillow structures.

5. Conclusions

The Ariofilla and Chaunaca Formations of the Puca Group contain a diversified dinosaur ichnofauna consisting of different theropods, sauropods and ankylosaurs in an alluvial system of an underfilled basin, one that has a large potential for future ichnological studies.

The overlying El Molino Formation is coeval with the Vilquechico Formation of Southern Peru and the Yacoraite Formation of Northern Argentina, and both sequences have a record of dinosaur tracks (Figs. 15 and 16). Their sedimentary sequences, as well as their vertebrate fauna indicate deposition in an extensive balanced-fill lake basin (*sensu* Bohacs et al., 2000). We therefore regard the Late Cretaceous formations of these countries that contain recurring levels with dinosaur tracks as a megatracksite (*sensu* Lockley and Meyer 2000) or "dinosaur freeway," and coin it the BAP (Bolivia/Argentina/Peru) megatracksite. The BAP has an extent from North to South of more than a thousand kilometers and we estimate its minimal size at around 100.000 km^2. This is almost equal in size to the megatracksite from the Early Cretaceous Glen Rose Formation in Texas that formed in a tidal flat setting. Megatracksites in a fluvial setting like the Dakota Group in Western Colorado have a similar extent, whereas the megatracksite of the Morrison Formation (lacustrine basin setting) is much smaller than the BAP megatracksite (Lockley 1991). All the known sites of the BAP megatracksite seem to be positioned along the shoreline and deltas of the ancient lake system, and so they might have been part of a seasonal migration route. Because the climate in most of the part of the BAP megatracksite was arid(De Souza Carvalho et al., 2010), possibly migration towards the north into more tropical zones during the dry season was an option.

The large single surface of Cal Orck'o shows no sign of herding in sauropods at all. Leonardi (1994) mentions a surface from Toro Toro with eight parallel trackways of sauropods among them two juveniles; unfortunately, no map of this site has been published.

However, in both sites, only tracks of adult sauropods have been documented so far. This seems to corroborate the idea that sauropods moved in age classes and that adults tended to move separately, as in the case of the sauropods from the Late Jurassic of North America and Portugal (Lockley et al., 1986, 1994).

Tracks and trackways of juvenile and adult non-derived titanosaurids are present from the Santonian up to the Maastrichtian in several localities in the large back arc lacustrine basin of the Central Andes (see also Meyer et al., 2018). The occurrence of the basal titanosaur *Kaijutitan maui* Filippi et al. (2019) together with eutitanosaurids (Filippi et al., 2019) in the Late Coniacian of Patagonia, and possible trackways form the Yacoraite Formation in Argentina (Díaz-Martinez et al., 2017), corroborate the track record from Bolivia. Merging these facts, we can now positively conclude the long-term presence of these sauropod families from the Coniacian until the Late Maastrichtian.

Despite of their very poor skeletal record in South America (Novas 2009), tracks and trackways of subadult and adult ankylosaurs are common from the Coniacian until the Late Maastrichtian. Moreover, Cónsole-Gonella et al. (2017) suggested the presence of ornithischian tracks in the Maimará locality from the Yacoraite Formation. We have documented the first global record of herding behavior for this dinosaur group. Ornithopods (i.e. hadrosaurs and iguanodontians) are a rare component of the megatracksite and are so far only known from the Cal Orck'o site. The presence of iguanodontid footprints is corroborated by the record of the basal iguanodontid *Talenkauen santacrucensis* from the Maastrichtian Pari Aike Formation of Argentina (Novas et al., 2004), whereas hadrosaurid footprints are known from the Yacoraite Formation of the Maimará locality of Argentina (Díaz-Martinez et al., 2017).

Looking at the different morphotypes and sizes of theropod tracks, they reflect the known and diverse skeletal records from the continent. Small-, medium-sized theropods and large apex predator theropods have been documented. The presence of dromaeosaurids in different localities and areas underlines the diversity of the group.

All in all, the sequence of the Late Cretaceous back arc basin of the Central Andes, and particularly in Bolivia, yields a continuous record of dinosaur footprints from the Coniacian to the Late Maastrichtian. It constitutes the most important continuous continental record in the Cretaceous of Gondwana and further demonstrates the high diversity of non-avian dinosaurs until their final demise.

6. Perspectives

There still remains much to be done in vertebrate ichnology in Bolivia, and many important sites are understudied for various reasons. Large and sometimes remote areas of the Cretaceous synclines need to prospect, such as those of Camargo, Potosi and El Molino as well as the area adjacent to the Geoparque Andino de Toro Toro. We think that the Toro Toro syncline is the most promising spot for future research because the levels can be easily studied over a vast area, whereas in Cal Orck'o, despite the main level, all others remain covered or are destroyed by quarry operations. Furthermore, the Toro Toro area yields a continuous record until the K/Pg-boundary. Moreover, the Maragua syncline contains more than 15 known tracksites that need to be documented in terms of stratigraphy, sedimentology and ichnology. We still hope that the ban for entering and doing research will be lifted before the sites will be lost to science.

However, it would be of utmost importance to train professional Bolivian paleontologists that could start to document their own rich geological heritage.

Author contributions

CAM did field work in all campaigns, collected the data, provided the description, discussion and figures, drafted the manuscript and was responsible for the funding of the expeditions. DM and ST did field work in Cal Orck'o and Liro Mayo in 2015, collected the data and drew the map of 2015, BT did field work in Cal Orck'o in 2003, 2007, 2012 and Liro Mayo in 2015, collected the data and drew the map of 2015. MB contributed to the Ms and did the photogrammetric work and some figures. MB, ST, BT, DM and CAM discussed all parts of the manuscript and contributed to the draft as well as to the revision. All authors read, contributed and approved the final manuscript.

Declaration of competing interest

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

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Appendix A. Supplementary data

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