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First Jurassic to earliest Cretaceous dinosaur footprints for Bolivia at the Castellón formation (Tacurú Group), Tarija

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ABSTRACT

Bolivia has an outstanding tetrapod ichnological record from the uppermost Cretaceous deposits plus a new Triassic locality recently reported. Here, we report a new ichnosite, the first for the Jurassic to earliest Cretaceous in the Castellón Formation (Tarija, Bolivia) bearing about 350 dinosaur tracks. With the exception of few tridactyl tracks, all exhibit sauropod characteristics. The exposed set consists of three mediumgauge, subparallel large quadrupedal trackways, with one trackway oriented in opposite direction to the other two. The best preserved trackway shows large pedes of about 95 cm and 75 cm in length and width, respectively. The trackmaker was about 3.80 m in height at the hip and walked at a speed under 5 km/h. Available evidence suggests that the producer of the more detailed trackway may be a member of non-Neosauropoda Eusauropoda, even if a titanosauriform producer cannot be discarded. Dozens of small-sized sauropod tracks, less than 15 cm in pes diameter, appear associated with two of the trackways. The distribution of these trackways provides elements to test gregariousness among trackmakers if a possible synchronism is accepted. Wanderings recognisable on the sediment surface suggest that they may collectively represent an ichnological example of herd behaviour.

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Sauropod tracks; ichnites; palaeoecology; dinosaur behaviour; Jurassic

Introduction

The tetrapod ichnological record from Bolivia is of great importance in the context of the worldwide Cretaceous dinosaur track record (Lucas 2007; Meyer et al. 2020). Different ichnosites in the Chuquisaca Department, namely Cal Orck'o (Sucre Area), Humaca and Niñu Mayu (Maragua Area), as well as the Toro Toro ichnosite in the Potosí Department, reveal a quite high abundance and diversity of theropod, sauropod, ankylosaur and ornithopod footprints (Leonardi 1994; McCrea et al. 2001; Lockley et al. 2002a; Apesteguía et al. 2011; Meyer et al. 2016, 2018, 2020; Riguetti et al. 2021) assigned to taxa typical of latest Cretaceous times (Hunt and Lucas 2006). This record mainly occurs in inland (Lockley et al. 2002a; Meyer et al. 2018) or coastal (Tomaselli et al. 2021) lacustrine environments, related to coastline variations of either the Pacific or the Atlantic (Marquillas et al. 2011). The latter possibility is supported by the Atlantic transgressive event vastly recognised in northwestern Argentina (e.g. CónsoleGonella et al. 2017). Two new sites in the Chuquisaca region, respectively named Tunasniyoj and Ruditayoj, extend the dinosaur ichnological record back to the Middle to Late Triassic (Apesteguía and Gallina 2011; Apesteguía et al. 2021).

Recently, during a geological survey in the Entre Ríos municipality (O'Connor Province, Department of Tarija, Bolivia) (Figure 1 AB), abundant dinosaur tracks were discovered on a large rock surface along the shore of the Santa Ana River. Dinosaur footprints are preserved on eight different stratigraphic levels within the Upper Jurassic to earliest Cretaceous Castellón Formation, part of the Tacurú Group, which in the area consists of more than 700 m of stratigraphic section, also exposing rocks of the underlying Ipaguazú Formation. The first five trackbearing levels occur in a 14 m thick succession of reddish brown, medium to coarsegrained sandstones with intercalated reddish pelite layers. The remaining three trackbearing levels occur several metres above in coarse-grained sandstones. Here, we report the study of the lowest track-bearing level, which is the best exposed along the local stratigraphic section, with several hundred dinosaur tracks made by different bipedal and quadrupedal trackmakers diachronously walking on a medium-grained sandy substrate, also preserving desiccation cracks. After describing track morphologies and trackway configurations, we discuss the potential ichnotaxonomic attribution of the best preserved tracks and the putative producer, also focusing on some ichnological features likely related to their behaviour.

Considering that the track-bearing surface is under intense erosion, the site will probably not remain in good preservative conditions for a long time. The finding of dinosaur tracks in the Castellón Formation significantly increases the tetrapod ichnological record from Bolivia and extends the Bolivian ichnological record to the three periods of the Mesozoic Era.

Geological setting

The Entre Ríos area is located in the transition between the Eastern Cordillera and the Chaco Sub-Andean Belt morphostructural provinces (Serraiotto 1977). The tectono-sedimentary evolution of the area encompasses different geodynamic cycles and is strictly related

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Figure 1. (a) Location map of Entre Ríos area (white star), O'Connor province, Autonomous Department of Tarija, southern Bolivia; (b) Close-up of Santa Ana river canyon, where the Castellón Formation is exposed. Yellow pins respectively indicate base and top of the studied stratigraphic section, and position of the trampled surface (TBL1); (c) Location of Entre Ríos Sheet 6729 according to the SGB Series 1 CGB; (d) Geological map of Entre Ríos and close-up (e) of the core area of Entre Ríos syncline where Jurassic succession crops out (black star indicates the studied area; Upper Palaeozoic to Jurassic lithostratigraphic units are reported in the synthetic log at the upper right corner – redrawn and slightly modified from Moretti et al. 2002); (f) General view of the outcrops along the Santa Ana river canyon.

during the Mesozoic to the Eastern Cordillera Rift System observed in several stratigraphic successions of present-day Peru and Bolivia (Sempere et al. 2002). The Eastern Cordillera Rift System affected the western Gondwana diachronously, starting from the Lopingian (Mégard 1978; Jacay et al. 1999) up to the Middle Jurassic (McBride et al. 1983; Sempere 1995). In its southern portion, the system splitted in two branches, one continuing the main rift axis (i.e. Tupiza branch), whereas the other, named 'Entre Ríos branch', was southeasterly directed, extending into the Chaco Subandean belt and tipping in the area of the current Bolivia-Argentina geographical border (Sempere et al. 2002). In Bolivia, where rifting is younger, crustal thinning occurred since the Triassic and tensional tectonics originated graben-type basins where continental sediments laid down associated to mafic and alkaline magmatism (Jacay et al. 1999; Sempere et al. 2002).

Syn-rift deposits in Bolivia are included into the Ipaguazú Formation (Padula and Reyes 1958), classically a part of the Cuevo Group of Schlatter and Nederloff (1966; see also Tomezzoli 1996) and the Tiquina Formation, included in the lower part of the Serere Group (Sempere et al. 1998, 2002). The Ipaguazú Formation consists of a basal sandy portion passing upward to the red shales and siltstones (locally intruded by mafic sills), capped with an evaporite of lacustrine origin. The Tiquina Formation consists of red sandstones intercalated with mudstones interpreted as alluvial in origin (Sempere et al. 2003).

Post-rift deposits in the Chaco Sub-Andean belt are represented by mainly fluvio-aeolian sediments, locally associated to the basaltic flows and sills, and conglomerates with basalt clasts (Sempere et al. 2002). Starck (1995) assigned these fluvio-aeolian sediments to the Tacurú Group, a lithostratigraphic name also used in geological maps (e.g. Rubiolo et al. 2003). We use the lithostratigraphic scheme established by Anderson and Bazley (1971 fide Rubiolo et al. 2003), who redescribed the succession giving it the rank of Group after the first description as Formation by Mather (1922). The Tacurú Group includes, in ascending stratigraphic order, fluvio-aeolian sandstones of the Tapecua Formation, fluvial sandstones and subordinate red and green mudstones of the Castellón Formation and, finally, aeolian sandstones of the Ichoa Formation (Rubiolo et al. 2003). Few data about the relative age of the stratigraphic succession are available, and some of these data are conflicting. Nevertheless, we briefly report all the available information. The Ichoa Formation is interpreted as deposits formed in desert environments during the Jurassic (Chandler et al. 1992; Tineo 2017), probably related to the contemporaneous large South American Botucatú Desert (Bertolini et al. 2020). A different nomenclatural scheme can be found in Sempere et al. (1998), who included the aforementioned succession in the Tacurú sub-Group as the upper portion of the Serere Group (see Sempere et al. 2002 and references therein for regional correlations). According to Sempere et al. (1988), the succession is limited at its top by an erosional unconformity that would be originated in the Kimmeridgian and upon which Cretaceous rocks of the Puca Group rest (Sempere 1995). Other indirect temporal constraints for the age of the Tacurú Group are suggested by the purported age of the Ipaguazú Formation, considered Lower Jurassic by Kusiak et al. (2014), even if part of this unit must be considered Upper Triassic on the basis of chirotheriid tracks recently discussed (Bertrand et al. 2014; Apesteguía et al. 2021).

Starck (1995) based on regional correlations and structural studies assigned the age of the Castellón Formation to the Early Jurassic. Additionally, Gayet et al. (2001) reported from this unit semionotiform fish remains referred to the Late Triassic-Early Jurassic interval. However, an (Upper?) Jurassic has been proposed by several authors based on ostracod taxa (Serraiotto 1977; Sempere et al. 2002; Figure 1C-E). However, Suárez Riglos and Carvalho (2018) published the finding of the conchostracan Cyzicus pricei in rocks of middle to upper section of the Castellón Formation. Although both conchostracans and ostracods in the top of this unit were already mentioned by Pinto and Sanguinetti (1987) and Suárez Riglos and Carvalho (2018) related this finding with similar associations in Brazil and Gabon, and that the age would be Lower Cretaceous, but its presence could also be considered in earlier Upper Jurassic strata. Actually, Gallego and Martins-Neto (2006) write that C. pricei (recorded in 11 Brazilian basins) is probably the most common species for the Brazilian Jurassic-Cretaceous successions. They include this form in their Assemblage III (AIII): from Late Jurassic to Early Cretaceous (Albian) comprised by *Pteriograpta* cf. *reali, Estheriina costai, Pseudestheria* (=*Cyzicus*) *pricei, Pseudograpta brauni* and *Pseudestheria abaetensis*.

The additional finding of the ostracod *Alicenula leguminella* (as *Darwinula leguminella*) actually does not provide precision since this species also shows a stratigraphic distribution considered with records from the Jurassic to the lower Aptian (Anderson 1985) (i.e. a span of more than 20 my), making its stratigraphic precision too poor to decide between an Upper Jurassic or a Lower Cretaceous age (Tomé et al. 2022). *Alicenula leguminella* has been recorded from Late Jurassic to Early Cretaceous rocks of England (Anderson and Bazley 1971; Anderson 1985), Germany (Martin 1940), Poland and other countries from distant places.

Based on the results of the 40Ar/39Ar Entre Ríos Basalt datation, the zircon fission track method on the aeolian Tapecua and Castellón Formation sands (Kusiak 2008), a stratigraphical analysis plus local and regional Kusiak (2008, 2014) supported the existence of three Mesozoic depocentres in the Subandean region of Bolivia. The older, being Jurassic in age, was developed in the southern Subandean belt, identified as the Villamontes basin, and filled as a synrift process with tholeitic basalts associated to the Camiri Basalt, Ipaguazu Formation, San Diego Formation, Entre Ríos Basalt and Tapecua Formation. Accordingly, the termal subsidence sequences (sag) are represented by the sedimentites of the Castellón and Ichoa formations. Conversely, in the central Subandean (Santa Cruz Basin), the synrift sequence corresponds to the Late Cretaceous units. New Toarcian ages were obtained from the Entre Ríos (181.5 ± 0,9 Ma) and Camiri Basalts, characterised by tholeitic and alcaline intraplate basalts formed during the Pangea fragmentation since Early Jurassic times (Marzoli et al. 1999), both in the Entre Ríos Basalt (185.5 ± 6.3 Ma), Tarabuco Basalt (201.2 ± 10.6 Ma) and Camiri Basalt (189.5 ± 1.4 Ma to 200.0 ± 2.7 Ma). In this general context, we prefer to rely the present study age mainly on the chronostratigraphic chart of Kusiak (2008),

The track-bearing layers in the Castellón Formation occur on the top of thick to very thick layers of medium- to coarse-grained sandstones, except TBL4, which occurs on the surface of a layer of pelites. Desiccation cracks are common in the sandy intervals associated with the tracks. The entire stratigraphic section containing the tracks consists of alternation of red to brown pelites and sandstones, with interspersed conglomerates and thin carbonates. This succession is interpreted as formed by episodic fluvial or braided river sediment discharges on a flood plain, and it has been described as such in other areas (Xu et al. 2017; Wilmsen et al., 2021). The absence of structures indicative of soil development (e.g. rhizoliths) suggests an arid or semi-arid environment with wetting-drying cycles. The occurrence of desiccation cracks associated with the tracks indicates an interval of time between the deposition of the track-bearing sandy layers and the deposition of the finer pelites that cover them. However, the preservation of tracks requires rapid cementation of the track-bearing layer and deposition of sediment on top in relatively low energy conditions. We suggest that dinosaurs walked on soft but firm sandy sediments which, after a short interval of desiccation and cementation, got covered with finer sediments. The deposition/track formation/ cementation cycles occurred many times, with short time between them, attested by the absence of soil structures.

The castellón formation in the canyon of the santa ana river

The exposed layer with tracks is N175° along strike and dips 45°. The local stratigraphic section starts with the bottom of the

Ipaguazú Formation (21°29'37.88" S; 64°13'44.79" W; 1403 m a.s.l.), whereas it ends with the top of the Ichoa Formation (21°30'19.14" S; 64°12'47.97" W; 1296 m a.s.l.) (Figure 1A-B). An almost continuous stratigraphic succession of 1077 m in total thickness, including the Castellón Formation, is exposed in the studied area, which is part of the western limb of the Entre Ríos syncline (Figure 1C-E). The Tacurú Group is represented by 726 m of continental deposits. The basal unit of the Group, the Tapecua Formation, has a total thickness of 85 m, while the topmost unit, the Ichoa Formation, is 205 m thick. The intermediate unit, the track-bearing Castellón Formation, has a total thickness of 436 m in the area.

In the canyon of the Santa Ana River area, the lower portion of the Castellón Formation starts with a basal graded lag, overlain by an interbedded light grey to whitish, locally light orange, finegrained sandstone beds, ranging between 4 and 10 m in thickness, and pelitic layers less than one metre in thickness. Desiccation cracks characterise the top surface of both sandy and pelite layers. Along the section, sandstones and pelites show constant texture and grain size, but progressively become thinner and thicker, respectively. Upward, the succession shows a sharp change in the style of sedimentation, evidenced by an increase in the grain size of the exposed rocks (Figure 2A-B, E-H). The stratigraphic section, where the tracks are preserved is, characterised by prevailing light grey to reddish brown, parallel- to cross-laminated, medium-grained sandstones locally displaying desiccation cracks (Figure 2C) at the topsurfaces, within which coarse-grained sandstones and lenses of conglomerate occur interspersed (Figure 2D). Sandstone beds often reach and exceed thickness of 15 m, interbedded with brown to reddish pelite beds.

Eight track-bearing levels (hereafter TBL), displaying footprints seemingly produced by bipedal and quadrupedal trackmakers, have been recognised in the upper portion of the succession, about 220 m in thickness (Figure 3). Five of the TBL are concentrated in less than 15 m of strata. The first TBL (TBL1) occurs at the top surface of a 25-m-thick interval of reddish brown, medium- to coarse-grained sandstone beds. This surface is overlayed by an interval consisting of less than a metre of reddish brown, faintly laminated pelites, filling the tracks, and about five metres of light grey to pinkish, medium-grained sandstones. The top surface of this interval is the second TBL (TBL2) displaying tracks with roughly similar morphology as the previous TBL. The third TBL (TBL3) occurs two metres above in a light grey sandstone with footprints filled with pelites. The top surfaces of TBL1, TBL2 and TBL3 show desiccation cracks. The overlying layer of pelites have a thickness of one metre and preserve dinosaur tracks at the top (TBL4). The fifth TBL (TBL5) is found at the top surface of a 5-m-thick layer formed by a light grey, coarse-grained sandstone. Similarly, pelites overlie the sandstones and fill the tracks. The stratigraphic section continues upward with a 20-m-thick interval of light grey, mediumto coarse-grained sandstones, with interspersed pelite layers each not exceeding 50 cm in thickness, with the sixth TBL (TBL6) on top. Light-grey, massive, well-sorted, and coarse-grained sandstones, organised in metric layers and intensely fractured perpendicularly to the main bedding, lie above and reach a thickness of 45 m, followed by two metres of reddish-brown pelites. The succession continues upward with 55 m of light-grey coarsegrained sandstones, each about five metres in thickness, overlain by two metres of reddish-brown pelites. The following sandy interval, 25 m in thickness, is coarse-grained and light-grey in colour, with thin interspersed conglomerate lenses. The seventh track-bearing level (TBL7) is preserved on the top surface of this interval, covered by three metres of reddish-brown pelites. The eighth track-bearing level (TBL8) occurs on top of a 12 m thick layer of light-grey, coarse-grained sandstone. The succession continues with 30 metres of light-grey, fine- to medium-grained, cross-stratified sandstones referred to as Ichoa Formation.

Materials and methods

The studied site crops out in the Canyon of the Santa Ana River, at about 6.5 km from Entre Ríos town, close to the main road between Entre Ríos and Tarija. TBL1 is at GPS position 21°29′59.01" S; 64° 13′12.71" W; 1330 m a.s.l. As mentioned above, TBL1 shows the effects of erosion due to periodical runoff waters in the rainy season, which also triggers landslides of the overlying Pleistocene deposits and deposit of eluvium-colluvium on the surface of the track-bearing layer. Thus, track morphology is prone to significant change with time due to weathering and runoff processes (see Marty et al. 2016). However, the studied tracks are well preserved and do not show deformation due to shearing. The sitemap produced in this study is based on the combination of several photographs.

Sauropod trackways were labelled as SrT_n , where n is a consecutive number identifying the trackway; individual tracks were identified and numbered with the letter p or m, for pes and manus track, followed by a number. Sauropod tracks of small and medium size were groupwise numbered as Ssg1 to 3. Tridactyl tracks were labelled as Tr, followed by a consecutive number identifying the track (Figure 4). Tracks were measured using a metric ruler and following guidelines by Leonardi (1987); interpretive drawings of some footprints were made on acetate film and later digitised in Adobe Illustrator 24.0.1. Photographs were taken with a digital camera Canon PowerShot SX60 HS.

Parameters measured were pes length (PFL), pes width (PFW), oblique pace length (OPL), stride length (SL), pace angulation and trackway ratio (PTR and MTR for pes and manus), and the ratio between the side width and the overall width of a trackway expressed as percentage (Romano et al. 2007) (Figure 5). Ratios between widths of pes and manus angulation patterns (WAP/WAM) and between width of pes angulation pattern and pes length (WAP/PFL) were also calculated (Marty 2008). Heteropody was calculated according to Lockley et al. (1994a) and heteropody index (HI) according to the relation of González Riga and Calvo (2009), who estimated the HI as manus length x manus width/pes length x pes width and expressed as percentage. Gleno-acetabular distance was estimated according to Leonardi (1987), assuming amble gait for the producer. Height at the hip (h) for the sauropod producer of SrT₃ trackway was estimated following the equation by Alexander Rmc (1976) and Lockley et al. (1986), but see Lockley et al. (1986), Thulborn (1990) and González Riga (2011) for different equations. Acetabular heigth for the producers of tridactyl tracks was estimated based on the equations by Thulborn (1990) for theropods and ornithopods. Moreover, we tentatively estimated the speed of the producer of SrT₃ trackway by using the relation of Alexander Rmc (1976), who found that Froude's number $v^2/(gh)$ and nondimensional speed (relative stride length) λ/h (Thulborn and Wade 1984) are related by the relation $\lambda/h^2 2.3[v^2/(gh)]^{0.3}$, where λ is the stride length, *h* is the height at the hip, *v* is the speed and g the acceleration of free fall. The absolute speed v is then calculated as a function of λ and h as follows: $v \simeq 0.25g^{\circ.5}\lambda$ -^{1.67}h^{-1.17} (Alexander 1976, but see Ruiz and Torices 2013 for a similar relation). The equation of Thulborn and Wade (1984) for running dinosaurs, originating from the relation found by Serraiotto (1977) for running ungulates, was not applied considering the result of non-dimensional speed, suggesting crossing in walking gait (see below)



Figure 2. Washed bulks and sedimentary features of Castellón Formation; (a, b) Fine-grained sand; (c) Polygonal cracks at the top-surface of a sandstone layer; (d) Conglomerate lens within a sandstone layer; (e-h) Coarse-grained sand. Scale bars (a-b, e-h) equal to 2 mm.

Results

Surface, tracks and trackway configuration

The surface of TBL1 shows abundant and uniformly distributed polygonal desiccation cracks, although better developed in the central area of the studied surface (Figure 6), and a high degree of dinoturbation (see Lockley and Conrad 1989). Forty-eight tracks of large dimension (PFL>60 cm; MFL>50) were found arranged in three trackways, hereafter SrT_1 , consisting of 17 tracks with 9 pedes and 8 manus; SrT_2 , consisting of 12 tracks with 7 pedes and 5 manus; and SrT_3 , consisting of 19 tracks with 9 pedes and 10 manus (Figure 4B). We found about 300 tracks of small and medium size, according to size classes of Marty 2008 (pes footprint length between 25 cm and 56 cm), some of which are arranged in



Figure 3. Stratigraphic section of the upper portion of Castellón Formation, where different track-bearing levels were recognised.

sets suggesting a quadrupedal trackmaker, possibly arranged in trackways, but whose identification is hindered by data presently available. Additionally, in the same level as sauropod trackways Srt2 and SrT3, we found few tridactyl theropod footprints and also two large ornithopod pes trackways.

The large sauropod trackways are aligned sub-parallel to each other, but SrT_2 exhibits an opposite direction of motion with respect to SrT_1 and SrT_3 . Most of the small tracks are oriented in roughly the

same direction of movement as SrT_1 and SrT_3 , although some exhibit a different transversal direction of motion as well as a different degree of morphological detail (Figures 4 and 6). On the east side of the surface, some smaller tracks, both shallow and deeper, occur inside the pes tracks of SrT_3 , suggesting that one or more dinosaur walked stepping on previously printed tracks of SrT_3 (Figure 4B – tracks m2, p4 and p5; see white rectangle in Figure 6A). No small footprints of similar orientation with that reconstructed for SrT_3 lie





Figure 4. (a) Panoramic photo of the track-bearing level 1 (TBL1) and schematic drawing (b) of dinosaur tracks. SrT1 to SrT3 refer to sauropod trackways; Tr1 to Tr5 refer to tridactyl tracks assigned to theropods. Or1 to Or3 refer to tridactyle tracks here assigned to ornithopodan producers. Ssg1 to 3 indicate the groups of small sauropod trackways. Arrows indicate direction of movement of the sauropod producers. Dinosaur tracks drawn in black are interpreted as small to medium sized sauropod footprints (see text).





Figure 5. (a-c) Field operations on TBL1 aimed to interpret some of the sauropod footprints impressed on the surface; (d) Main ichnological parameters measured in the field. Blue and green solid lines indicate two consecutive oblique pace lengths, for manus and pes print respectively.

within the area of SrT₃. A reason for this absence is the presence of an obstacle during the movement of the trackmaker, like a large bush or the large sauropod that produced SrT₃ trackway. Another possibility is that a firmer substrate prevented smaller trackmakers from forming footprints. In the former case, the absence of smaller footprints should be considered as an indirect evidence of synchronism of crossings; in the latter, absence would entail variable synchronous conditions of the substrate but not necessarily a synchrony of crossings between larger and smaller producers

Ichnological description

D

The trackway SrT₃ exhibits manus and pes prints in slightly better detail than the other trackways. For manus, mean footprint length



Figure 6. (a) Close-up of SrT3 trackway. Note the plethora of small-sized sauropod footprints evident on the left side of the trackway. Red arrows indicate digit I impression in pes footprints; (b-c) SrT1 (left) and SrT2 (right) trackways. Note polygonal cracks affecting the top-surface of the TBL1 and two tridactyl tracks on the right side of SrT2 trackway.

is 34.75 cm (38 cm, 22 cm, 35 cm, 44 cm), mean footprint width is 61.25 cm (67 cm, 54 cm, 54 cm, 70 cm), oblique pace length is 157 cm and stride length is 246 cm. Manus prints are semicircular to crescent-shaped in morphology, wider than long, sometimes with two or three short, well-separated digit impressions. In few cases, the impression of digit I seems preserved, roughly medially oriented and exhibiting slightly tapered ends and a suboval outline (red arrows in Figure 6A). Some manus tracks were marginally overprinted by pes prints, and that left the crescent shape of the former. Pes prints are longer than wide and up to about three times longer than manus prints, but comparatively as wide as the latter.

For pedes, mean footprint length is 94.25 cm (100 cm, 100 cm, 84 cm, 93 cm), mean footprint width is 75.6 cm (82 cm, 70 cm, 75 cm), oblique pace length is 155 cm and stride length is 245 cm. The outline is sub-ovoidal to roughly sub-rectangular in shape. Most pes tracks show three claw impressions with tapered ends; exceptionally, they may show four, but in this case, digit I is printed in a more proximal position compared to the others, and digit traces are straight or slightly laterally oriented (i.e. externally divergent). Claw impressions appear almost antero-laterally oriented and are sub-equal in dimension. Measured pace angulations are 96° for pedes and 87° for manus. Both manus and pedes footprints are slightly outwardly rotated with respect to footprint midline. Pes and manus trackway ratio (PTR and MTR) that characterise the trackway gauge have mean values 41% and 37%, respectively, placing trackway SrT₃ in the medium gauge category (Romano et al. 2007). WAP/WAM ratio is 0.6, meaning that manus tracks are positioned farther away from the trackway midline than pes tracks (Marty 2008). WAP/PFL ratio is 1.55, which would indicate widegauge category, even if the value is close to the arbitrary boundary between medium-gauge and wide-gauge trackways, fixed at 1.2, while very wide-gauge trackway are considered those with ratio equal or higher than 2.0 (Marty 2008). Heteropody is 1:3.3 and heteropody index is 30%. Mean gleno-acetabular distance is 3.60 m considering amble gait for the producer, 3.61 m considering pace gait condition and 2.87 m considering lateral sequence single-foot walk condition, both according to Lallensack and Falkingham (2022). Estimate of the height at the hip is 3.8 m. The ratio stride length/height at the hip (λ/h) for the footprints of SrT₃ trackway is 0.65 and suggests that the trackmaker walked the surface in walking gait (Thulborn and Wade 1984) at an estimated speed of 2.7 km/h.

The other two trackways composed of large-sized tracks (i.e. SrT_1 and SrT_2 in Figure 6B-C) show less morphological details than SrT_3 ; however, their general three-dimensional morphology is that of the typical sauropod tracks. Manus tracks in SrT_1 trackway have a crescent shape and lack clear digit impressions. Pes tracks are mainly sub-ovoidal, with some characterised by three claw impressions oriented anteriorly or slightly laterally, as seen in pes tracks of the SrT_3 trackway. Differently from the pes of SrT_3 trackway, some pes tracks of SrT_1 overlap manus tracks in the more proximal sets. SrT_2 trackway consists of manus-pes sets without anatomical details but showing a similar outline to the other two trackways and a greater manus-pes distance (no marginal overlapping was observed).

Tracks of overall smaller dimension, as above mentioned, are primarily differentiated on the basis of faintness of impression, which in cases could account for the timing of surface crossing. These tracks do not exhibit anatomical details (e.g. digit impressions) but a simple, sub-circular morphology, more precisely in pes tracks. Manus tracks appear as sub-circular or as crescent-shaped impression distally deeper (i.e. over the area supposedly of the acropodials), a feature common in tetrapod tracks, but related to kick-off phase and then not particularly diagnostic in terms of ichnotaxonomy or producer identification. General appearance of these footprints and their mutual arrangement as observed and interpreted in the field point to a producer similar to those that formed larger quadrupedal trackways, even if a different producer cannot be completely discarded.

Tridactyl tracks

The limited occurrence of theropod tracks and two ornithopod trackways in the studied exposure is enigmatic. Theropod tracks are variate in size in the different bearing levels of the area but homogeneous in the TBL1 described site, with 25 cm in length and with deep digit impressions and slightly diverging digits (Figure 8A, B). Estimate of height at the hip is about 1 metre. Other small 10-cm tracks assigned to theropods were recorded in the TBL2 (height at the hip about 40 centimetres), and the larger isolated 40-cm track in the TBL3 (Figure 8D), suggesting a height at the hip of about 1.60 metres. In TBL5 ,several monodactyl, didactyl and tridactyl traces are preserved and randomly oriented (Figure 8E). Most digit traces are very narrow and tapered in their proximal and distal tips, likely suggesting a waterlogged substrate. Putative producers of these traces could be small-sized non-avian theropods or, most probably, birds scratching a water body bottom. TBL10, at several hundred metres from TBL1, also includes diverging and diverse 5 to 20 cm theropod tracks (Figure 8F). The estimate of height at the hip for the producer of larger tracks is about 80 centimetres. The only available measure of stride length is 126 cm; SL/h (equal to 1.6) suggests a walking producer.

In TBL1, two independent trackways probably made by ornithopod dinosaurs (Figure 8G-I) are impressed were recorded. The two recognised trackways are distant about 10 metres from each other and in non-parallel directions. They both exhibit two or three large tracks each with rounded, petal-shaped digits and a large, wide pad trace characterising the proximal footprint portion. These ornithopod tracks are particularly large (45 cm in length, suggesting a height at the hip of about 1.80 metres) and show deep distal rounded digit impressions. The only available measure of stride length resulted in about 176 centimetres. SL/h is 0.97, suggesting a walking producer also in this case. The left trackway shows some degree of outward rotation of the tracks. Footprint morphology in this case could be considered slightly modified by current weathering, particularly affecting the heel and, in general, the proximal portion of the better preserved track, and no evidence of hoofs or ungual claws are visible, resembling somehow specimens of Iguanodontipus isp. (Pascual-Arribas et al. 2009) and Caririchnium (Leonardi 1984) but not entirely identifiable with none of them. The most similar track is that of Sinoichnites youngi Kuhn, 1958, from the Middle Jurassic of China. In this case, they can be considered as Iguanodontipodidae indet. Both types are well marked, and therefore, we expect that more of them should have been preserved. One possibility for the lack of more tridactyl tracks is that they were obliterated by the sauropods walking on the same area after the theropods and ornithopods or that the substrate was not homogeneously compliant. Still, there are several areas in the exposure where no sauropod tracks are preserved and tridactyl tracks could have been formed. Nevertheless, it is possible that both theropods and ornithopods walked on the same surface and the sauropods did later, which would explain the absence of the former. This enigmatic absence may be resolved when further rock surface becomes exposed due to erosion or excavation of the overburden.

Discussion

Tracks of SrT₁ and SrT₃ trackways appear as slightly deeply impressed than those of SrT₂, with some footprints to the right side of SrT₁ overlapping the area where polygonal cracks are pervasive (Figure 6). The three trackways show no important difference in size and can be included in the large size class of Marty (2008). The depth of impression of these tracks could indicate that the trackmaker walked on the surface during the process of desiccation but when the substrate still had a sufficient degree of moisture content to allow track impression, and we hypothesise that walking occurred before that of the trackmaker of SrT₂. Assuming that the surface was not re-inundated after desiccation, the similarity between SrT₃ and SrT₁trackways likely indicates a temporal proximity. Yet, the slightly different depth of impression and detail suggest that trackmakers deformed the substrate during different times. We infer from track distribution coupled with track morphology that the trackmaker of trackway SrT₂ walked synchronously or shortly after the desiccation event, as evidenced by polygonal cracks broken by the trackmaker feet and by the lack of displacement of track edges.

Moreover, tracks did not induce cracking in the sediment and did not favour enucleation of polygonal cracks from their margins, thus giving a further indirect indication that during trampling, the substrate was not characterised by high water content (Carvalho and Leonardi 2020). The high density of smaller tracks prevents trackway identification for their respective trackmakers, but based on the different degrees of morphological details, it is possible to differentiate between those shallow and deep tracks.

A common feature associated with almost all the tracks on TBL1 is the morphology and extent of expulsion rims, which are low and narrow, most likely indicating a compact and quite firm substrate characterised by high cohesiveness and low water content (de Souza Carvalho and Leonardi 2020). Of the three trackways, SrT_2 exhibits the least developed expulsion rims to occur, among other, in fluvial-lacustrine environments (de Souza Carvalho and Leonardi 2020).

Ichnotaxonomy of SrT3 trackway

The ichnotaxonomy of sauropod footprints is controversial (Lockley et al. 1994a; Castanera et al. 2011), and a thorough discussion of the plethora of ichnotaxa erected to this date is beyond the aim of this article. Nonetheless, footprints from the TBL1 exhibit anatomical features that can be compared with some of ichnotaxa that are related to sauropod producers (Figure 7). Few trackway parameters are commonly considered in the ichnotaxonomic discussion of sauropod tracks, and following Wright (2005), we primarily consider manus and pes morphological features and gauge to compare our material with other sauropod tracks.

A commonly used classification of sauropod tracks has been based on trackway gauge, with the distinction of narrow-gauge and wide-gauge categories based on the inner width of the trackway (Farlow 1992). Using this criterion, two ichnogenera *Parabrontopodus* and *Brontopodus*, respectively, have been established and later adopted in a revised sauropod ichnotaxonomy (Lockley et al. 1994a). Paradigmatic representatives of wide-gauge conditions are *Brontopodus birdi* Farlow, Pittman and Hawthorne 1989 (Figure 7A) and *Rotundichnus muenchehagensis* Hendricks 1981 (Figure 7B) from the Lower Cretaceous of Texas and Germany, respectively. Representatives of narrow-gauge conditions are the ichnotaxa *Breviparopus taghbaloutensis* Dutuit and Ouazzou, 1980 (Figure 7C) and *Parabrontopodus mcintoshi* Lockley et al. 1994a (Figure 7D) from the Upper Jurassic of Morocco and Colorado, respectively. As a result of this ichnotaxonomic framework, sauropod footprints were referred to as *Parabrontopodus* or *Brontopodus* according to the trackway gauge (Lockley et al. 1994a), and many other sauropod tracks and trackways were later classified accordingly (e.g. Gierlinski et al. 2004; Moreno; Benton 2005; Lockley et al. 2002a; Vila et al. 2008). On the other hand, gauge configurations and shift between different gauge conditions have been largely discussed and turned out to be possibly related to different biological taxa, different ontogeny (e.g. Xing et al. 2015; Meyer et al. 2018) and different gait and behaviour (e.g. Lockley 2001; Castanera et al. 2012) with obvious repercussion on the ichnotaxonomic framework, depending on the adopted philosophy in classification.

Moreover, the morphology of other wide-gauge sauropod ichnotaxa presents some challenges about the direct relationship between wide-gauge condition and the ichnogenus *Brontopodus* (e.g. Dalla Vecchia and Tarlao 2000; Calvo and Mazzetta 2004; González Riga and Calvo 2009) because it is not possible to identify *Brontopodus* based solely on trackway gauge, and to this date, several descriptions based on manus and pes morphology have been adopted and preferred to distinguish sauropod tracks (e.g. Díaz-Martínez et al. 2018; Tomaselli et al. 2021; Torcida Fernández-Baldor et al. 2021).

The ichnogenus *Breviparopus* Dutuit and Ouazzou 1980 is generally considered a valid ichnotaxon for narrow-gauge trackway configurations (Farlow 1992), even if the ichnotaxon is not formally erected (Marty et al. 2010). The ichnogenus include specimens exhibiting narrow-gauge trackways with pes tracks exceeding the trackway midline, marked heteropody, manus tracks with semicircular or crescent shape lacking digit impressions, placed in front of and/or possibly slightly overprinted by pes tracks but away from the midline with respect to the pes tracks. The latter exhibit an oval shape with at least four digit impressions, displacement rims and claw marks (Dutuit and Ouazzou 1980; Ishigaki 1989; Marty et al. 2010).

The ichnogenus *Parabrontopodus* Lockley et al. 1994a was erected on a trackway from the Upper Jurassic Morrison Formation and later suggested to be a junior synonym of *Breviparopus* (Wright 2005 but see Marty et al. 2010). The ichnogenus include narrow-gauge sauropod trackways with medium to large size footprints (over 50 cm in overall footprint length), high degree of heteropody of about 1:4 or 1:5 (Lockley et al. 1994a), similar to *Breviparopus* (Marty et al. 2010), with pes tracks longer than wide and outwardly rotated, equipped with outwardly rotated claw impressions on digits I, II and III, and semicircular manus tracks (Lockley et al. 1994a; Marty et al. 2010; Schumacher and Lockley 2022).

The ichnotaxon *Brontopodus birdi* Farlow, Pittman and Hawthorne 1989 is based on a trackway from the Aptian-Albian of Texas. The ichnogenus include medium- to wide-gauge trackways, with pes and manus tracks distanced from the midline, small to large size footprints (from 50 cm to over 100 cm in overall footprint length), manus tracks as long as wide, medial to the midline with respect to pes tracks and possibly outwardly rotated, crescent-shaped, clawless, with digit impressions I and V separated by digits II and III; pes tracks longer than wide, equipped with laterally directed claw marks associated to digit impressions I–III and showing a small claw, and pad marks or callosities on digit impressions IV and V (Farlow et al. 1989; Lockley et al. 1994a; Romano et al. 2007; Dos Santos Vf et al. 2009).

With *Brontopodus*, our material has in common the large size of tracks, longer than wide pes tracks, number of claw impressions and, to a lesser degree, the trackway gauge and heteropody. The studied material, however, differs from *Brontopodus* in the orientation of claw marks in pes tracks, the relative dimensions of manus

tracks and, mainly, the completely different manus track morphology with respect to the U-shaped morphology typical of *Brontopodus* tracks and the presence of claw marks in manus tracks. Similarly, we exclude the ichnotaxon *Rotundichnus münchehagensis* (Hendricks 1981; Lockley et al. 2004) (Figure 7B) for its wider gauge, higher heteropody and manus morphology, and *Gigantosauropus asturiensis* Mensink and Mertmann 1984 for its lower heteropody (Lockley et al. 2007).

Considering the whole set of features used to differentiate the aforementioned ichnotaxa and those that we observed in the footprints of SrT_3 trackway, we exclude the ichnogenera *Breviparopus* (see Figure 7C) and *Parabrontopodus* (see Figure 7D-E) primarily based on the trackway gauge, heteropody and position of pes prints with respect to the trackway midline. At the same time, the studied material shares with the ichnogenus *Parabrontopodus* the large size of tracks and number of claw impressions. However, we do not consider these features sufficiently characteristic as to allocate our material in this ichnotaxon. We exclude the ichnospecies *Parabrontopodus barkhausensis* (formerly *Elephantopoides barkhausensis* Kaever and Lapparent 1974; see Meyer et al. 2021) (Figure 7E) because the narrower trackway gauge and the higher heteropody.

We exclude *Sauropodichnus giganteus* Calvo 1991, considered a *nomen dubium* by Lockley et al. (1994a), on the basis of the trackway gauge and the manus morphology exhibited in Argentina by additional material from the Cenomanian Candeleros Formation (Calvo and Mazzetta 2004) (Figure 7F).

We also exclude Titanopodus mendozensis González Riga and Calvo 2009 for having lower MTR and PTR (wider gauge), a different orientation of claw marks in pes tracks, the manus morphology and the absence of claw impressions (Figure 7H). Nevertheless, our material exhibits a similar heteropody with tracks included in this ichnotaxon. Moreover, footprints and trackways from the Maastrichtian-Danian Yacoraite Formation (Maimará and Valle del Tonco localities, Argentina) are here considered different from the studied material because of the general outline of manus tracks and heteropody (Cónsole-Gonella et al. 2017; Díaz-Martínez et al. 2018). Our material only shares a similar PTR with the footprints from Valle del Tonco (Díaz-Martínez et al. 2018), which nevertheless display a different manus morphology. A slightly higher value of PTR and MTR characterises Teratopodus malarguensis Tomaselli et al. 2022 (medium-gauge category). Tracks from Santa Ana river differ in manus morphology, which is symmetrical and kidney-shaped in this ichnotaxon. Studied material also differs from tracks included in the ichnotaxon Oobardjidama foulkesi Salisbury et al. 2016; Castanera et al. 2016 from the Lower Cretaceous Broome Sandstone (western Australia) mainly due to pes track morphology, that is piriform and asymmetrical.

The studied material from the Santa Ana River also differs from sauropod tracks reported from the Upper Cretaceous of Bolivia (Leonardi 1994; Meyer et al. 2001; Lockley et al. 2002a; Apesteguía et al. 2007). Sauropod footprints from the Campanian Chaunaca Formation (Humaca) described by Lockley et al. (2002a) display high heteropody, wide gauge and inward rotation of the manus. The Santa Ana River tracks, on the contrary, have a low heteropody, a narrow gauge. Additionally, they have a different pes and manus outline morphology from the sauropod tracks described by Leonardi (1989, 1994) in the Campanian Toro Toro Formation. The only similarity is the presence of at least three claw impressions anteriorly directed, as already noted by Meyer et al. (2018). The ichnotaxon *Calorckosauripus lazari* Meyer et al. 2018 from the middle Maastrichtian El Molino Formation include wide/intermediate gauge trackways (Figure 71) with a lower PTR and



Figure 7. Schematic drawings of sauropod and ornithopod ichnotaxa selected for comparison (a) *Brontopodus birdi* (redrawn from Farlow et al. 1989); (b) *Rotundichnus muenchehagensis* (redrawn from Lockley et al. 2004); (c) *Breviparopus taghbaloutensis* (redrawn from Ishigaki and Matsumoto 2009); (d) *Parabrontopodus mcintoshi* (redrawn from Lockley et al. 1994b); (e) *Parabrontopodus (Elephantopoides) barkhausensis* (redrawn from Diedrich 2010); (f) *Sauropodichnus giganteus* (redrawn from Calvo and Mazzetta 2004); (g) *Polyonyx gomesi* (redrawn from Dos Santos Vf et al. 2009); (h) *Titanopodus mendozensis* (redrawn from González Riga and Calvo 2009); (i) *Calorckosauripus lazari* (redrawn from Meyer et al. 2018); (j) *Iniestapodus burgensis* (redrawn from Torcida Fernández-Baldor et al. 2021); (k) ornithopod track Or2; (l) *Sinoichnites youngi* (redrawn from Ferrusquía-Villafranca et al. 2007) Scale bar: 1 m (a-j); 20 cm (k-l).

a higher heteropody than footprints from Tarija. Manus tracks included in *Calorckosauripus* display a different morphology from our material, likely mirroring a columnar structure of the fore autopods of the trackmaker. Therefore, for this difference in manus morphology, we exclude *Calorckosauripus* as possible attribution.

Vila et al. (2005; 2008, 2013) reported many sauropod trackways from the Maastrichtian Tremp Formation of Spain. Pes tracks show four claw impressions laterally oriented and symmetrical, subrectangular to U-shaped manus tracks without claw impressions. Moreover, those trackways show a wider gauge with respect to the SrT_3 trackway. Heteropody is similar to our material, but not enough to compare the two records.

The following two ichnotaxa are the ones that share more features with the material under study. The first is *Polyonyx gomesi* dos Santos et al. 2009 from the Middle Jurassic of Portugal (Dos Santos Vf et al. 2009) (Figure 7G). This ichnotaxon includes trackways displaying a wider gauge and higher heteropody than our material. The number and orientation of claw impressions, as well as the general outline of pes tracks, are similar to our material, but definitely the large size of digit I impression of manus tracks in *P. gomesi* allows a distinction



Figure 8. Tridactyl tracks and trackways. (a) Close-up of a peculiar couple of tracks, produced by a pes and manus small sauropod pair (left), and a 25 cm theropod pes (right), both in the TBL1. Scale bar: 10 cm; (b) detail of the mentioned theropod track. Scale bar: 10 cm; (c) trackway of small, 10 cm tracks assigned to theropods in TBL2; (d) Close-up of a large, isolated 40 cm track in the TBL3. Scale bar: 20 cm; (e) sector of small probably swimming theropod/avian tracks in the TBL5. Scale bar: 5 cm; (f) View of several trackways from 5 to 20 cm in the TBL10. Scale bar: 30 cm; (g) panoramic view of several tridactyl tracks on TBL1, with the already mentioned theropod trackway in the middle (t) and two purported ornithopod trackways (O) to the sides, both with tracks of 45 cm in length. Scale bar: 1 m; (h,i) oblique (actual) and orthogonal (digital) views of one of the ornithopod tracks on the right side of SrT2 trackway and close-up. Scale bar: 20 cm.

with the studied material. Finally, the ichnotaxon *Iniestapodus burgensis* Torcida Fernández-Baldor, Fidel, Díaz-Martínez, Huerta, Montero Huerta, Castanera 2021, from the Tithonian-Berriasian Rupelo Formation (Burgos Province, Spain) has been based on tetradactyl, rectangular pes tracks with evidence of four sharp claw impressions, the most medial ones (digits I and II) anteriorly oriented and the other two (digits III–IV) laterally oriented, with digit I impression backwardly oriented and smaller

than digit II and III impressions (Torcida Fernández-Baldor et al. 2021; see also, 2015 for a preliminary discussion of these footprints) (Figure 7J). *Iniestapodus burgensis* trackway is mediumgauge and the heteropody similar to our material. However, the different pes track morphology, the configuration of digit I in manus tracks, and to a lesser extent the shorter manus-pes distance in SrT_3 trackway (a feature probably depending on gait, thus maybe of scarce significance in ichnotaxonomic terms), prevent the allocation of SrT_3 trackway in this ichnotaxon with confidence. Thus, we prefer not to designate our material with any of the described ichnotaxa, postponing ichnotaxonomic allocation to further analyses, which must include the other large and small footprints on the TBL 1 surface and a comprehensive revision of sauropod ichnotaxa.

Trackmaker identification of SrT₃ trackway

Sauropods, firstly appeared in the Late Triassic (Sereno 1999; Yates and Kitching 2003; McPhee et al. 2014), were a Mesozoic radiation of herbivorous dinosaurs including gigantic forms among the largest known terrestrial animals (Wilson 2002; Upchurch et al. 2004; Sander and Clauss 2008; Sander et al. 2010; Rauhut et al. 2011; González Riga et al. 2016; Carballido et al. 2017), achieving an almost global distribution by Middle Jurassic time (Weishampel et al. 2004). The clade experienced a major extinction event at the Jurassic-Cretaceous boundary (Barrett et al. 2009), with a further loss of diversity among remaining lineages during the Early Cretaceous, with the exception of rebbachisaurids and titanosaurs (Mannion and Upchurch 2010), these latter highly diversified during the Cretaceous (Salgado et al. 1997; Salgado 2001; Curry Rogers 2005).

The identification of sauropod trackmakers is difficult mainly because the track morphology may not match the anatomical details of pedes and manus, as evidenced by studies focused on osteology (e.g. Tschopp et al. 2015) or because pes morphology as the only proxy is insufficient (e.g. Torcida Fernández-Baldor et al. 2021). Trackways from the Santa Ana River study area exhibit typical sauropod features, i.e. quadrupedal gait and huge dimension of manus and pes tracks (Carrano and Wilson 2001; Wilson 2005). If gauge condition of SrT₃ trackway is considered, then according to Day et al. (2004) the producer should be within brachiosaurids and basal titanosaurs, even if it must be considered that data about manus claw impressions are missing. However, as mentioned above, trackway gauge in general does not seem to be a particularly reliable and enough feature for producer identification. A good example is provided by wide-gauge trackways that were originally related to brachiosaurid producers (Lockley et al. 1994b) and later referred to titanosauriformes on the basis of osteological features of the femoral shaft (Wilson and Carrano 1999). Subsequently, this type of gauge configuration has been deemed not exclusive of titanosauriformes sauropods on a purely ichnological basis (Dos Santos Vf et al. 2009). Moreover, Henderson (2006) suggested that this condition could reflect a more anteriorly directed position of the centre of mass, thus weakening the reliability of the wide-gauge condition as an indicator of a Titanosauriformes producer.

The number and dimension of ungual phalanges in pes tracks can be used to discriminate between sauropod producers. If claw impressions of Tarija tracks are considered, we can exclude basal sauropods for their relative dimension of ungual phalanges, decreasing in length from digit I to IV, and for a more anterior position of digit I (e.g. Nair and Salisbury 2012). In general, basal eusauropods and Eusauropoda have three large and broad ungual phalanges, anterolaterally oriented, decreasing in size from digit I to III. According to Wright (2005), the impression of digit IV claw in Eusauropoda, if formed, should be small, as for instance observed in the non-neosauropod eusauropod Janenschia from the Late Jurassic Tendaguru Formation of Tanzania (Mannion et al. 2019). Also, the number of ungual phalanges in some Late Jurassic-Early Cretaceous non-titanosaurian Titanosauriformes varies, with some having three (e.g. Gobititan; You et al. 2003) and others four (e.g. Cedarosaurus; D'Emic 2013), and nevertheless, their hind feet display claws without large differences in overall size. Titanosauriformes also exhibit a reduced manus ungual phalanx I (Salgado et al. 1997; Wilson and Sereno 1998; Carrano and Wilson 2001), a feature possible, yet not confirmed, in our material.

Diplodocidae are excluded for having a small manus/pes size ratio (Apesteguía 2005) and two claws on digit I and II (Remes 2009), while tracks of SrT₃ display at least three claw impressions. Moreover, Diplodocidae would produce narrow gauge trackways. At the same time, some diplodocids show ungual phalanges on digits I-III (Apatosaurus Marsh 1877), but they can be excluded because ungual phalanges of more proximal elements (i.e. digit I and II) are larger than that of digit III (Remes 2009), a condition not clearly observed in the studied material. Similarly, Dicraeosauridae can be excluded because, even if they display four claws in the foot (a condition possible in the studied material), digit size decreases from digit I to digit IV, and digit I is equipped with a robust claw. Camarasaurus Cope 1887, as representative of Macronaria, can be discarded as a possible producer of SrT₃ trackway for having well-developed claws on digits I-III, but decreasing in size and the claw of digit III very short.

Titanosauria is discarded due to the derived anatomy of both fore and hind autopod. The clade experimented a loss of ungual phalanges in the hind autopod, retaining two claws of comparable dimensions related to digit I and II and a digit III claw smaller, or roughly similar in size, while digit IV lacks ungual phalanges (Bonnan 2005; Wright 2005), and generally also a loss of ungual phalanges in the fore autopod (Salgado et al. 1997; Day et al. 2002; Mannion and Otero 2012). The clade is also discarded based on the configuration of the manus track morphology in SrT_3 trackway, because digit impressions seem quite separated from each other and likely mirror a non-columnar arrangement of metacarpals.

We tentatively suggest that the SrT_3 trackway was made by a member of non-Neosauropoda Eusauropoda (e.g. *Patagosaurus fariasi* Bonaparte 1979), most likely a somphospondyl producer (see Salgado et al. 1997), although we cannot discard a member within Titanosauriformes. Further studies are needed to better associate the Santa Ana River tracks to a possible sauropod trackmaker.

Sauropod tracks as palaeoecological proxy

It is commonly deemed that tracks and traces may provide abundant information about the behaviour of their producers (Sarjeant 1975; Thulborn 1990; Lockley 1991). The ichnological record preserves several, well-constrained cases of ecological interactions between the same type of producers (e.g. Lockley et al. 2016) and among different species, the latter including, for instance, ichnological evidence on body-fossils, as attack marks (e.g. de Valais et al. 2020). Possibly the most impressive case is gregarious behaviour, or group activity (Ostrom 1972), one of the infraspecific relationships within the broad category of social behaviour (see Díaz-Martínez et al. 2020 and references therein). Gregarious behaviour among dinosaurs has been inferred from parallel trackways in various groups (e.g. Ostrom 1972; Currie and Sarjeant 1979; Currie 1983; Carpenter 1992; Barnes and Lockley 1994; Cotton et al. 1998; Heredia et al. 2020). Based on the body-fossil evidence, gregarious behaviour has been assumed in several studies of ornithopods (e.g. Rogers 1990), ceratopsids (e.g. Qi et al. 2007), theropods (e.g. Coria and Currie 2006) and sauropods (e.g. Coria 1994) and has been proposed as an ethological trait for the clade Dinosauria (Novas et al. 2012).

The distribution of sauropod tracks and trackways on the TBL1 surface offers the opportunity to assess the potential relation between trackway pattern and trackmaker behaviour. Ichnosites displaying sauropod tracks and trackways are reported (Lockley et al. 1994b) from numerous sites around the world, including Argentina (e.g. Calvo 1991; Calvo and Mazzetta 2004; Díaz-Martínez et al. 2018; Tomaselli et al. 2021), Bolivia (Leonardi 1989, 1994; Lockley et al. 2002a), Brazil (Leonardi 1989, 1994), China (e.g. Lockley et al. 2002b; Xing et al. 2015), Italy (Leonardi and Mietto 2000; Avanzini et al. 2003; Nicosia et al. 2007; Petti et al. 2008), Madagascar (Wagensommer et al. 2010, 2012); Morocco (Ishigaki 1989), Portugal (Lockley and Dos Santos 1993; Dos Santos Vf et al. 1994, 2009), South Korea (Lim et al. 1989, 1994), Spain (Castanera et al. 2014, 2016; Torcida Fernández-Baldor et al. 2021), Switzerland (Meyer 1990, 1993; Marty 2008; Sciscio et al. 2022), United Kingdom (Day et al. 2004), United States (Bird 1944; Lockley et al. 1986; Farlow 1987; Lockley and Rice 1990) and Uruguay (Mesa 2012). In some cases, sauropod trackways are discussed as reliable evidence for gregarious behaviour (Pittman and Gillette 1989; Barnes and Lockley 1994; Lockley et al. 1994c, 2002a, b; Day et al. 2004; Castanera et al. 2011; 2014; García-Ortiz and Pérez-Lorente 2014) and, in general, the global sauropod track record likely suggesting gregarious behaviour is found in tracksites bearing either small-sized footprints or small- and large-sized footprints (Myers and Fiorillo 2009), as in the case of TBL1.

In general, there is a high degree of uncertainty in the interpretation of gregarious behaviour mainly because a reliable trackmaker attribution, as discussed above, and ontogenetic age estimation are very often difficult to achieve from tracks (Myers and Fiorillo 2009). Additionally, traits of the trackways including aspects related to the formation and preservation of tracks and post-formational variation (see Gatesy and Falkingham 2017), bear important information on how behaviour is reflected on the ichnites preserved on the same surface.

Some authors claim that the occurrence of tracks in high density showing the same morphology can be considered as a valid feature attesting herd behaviour (García-Ortiz and Pérez-Lorente 2014; Díaz-Martínez et al. 2020; but see Ostrom 1972).

Typical ichnological clues thought to suggest gregarious behaviour, especially when occurring collectively, are 1) similarity between tracks belonging to different trackways, 2) subparallel orientation of trackways, 3) regular spacing between trackways (it also should be consistent with estimate of producers' overall dimension), 4) similar speed values, 5) pace cadence, 6) stride, 7) lack of superposition or little overlap and 8) uniform depth (Thulborn and Wade 1984; Lockley et al. 1986; Castanera et al. 2011, 2014; Heredia et al. 2020).

The inference of behaviour is further supported by the cooccurrence of several of the above conditions, yet the complexity of the process of track formation, including mechanisms of locomotion and track preservational features, complicates the interpretation of behaviour based on the observable track morphology. Morphological similarity between tracks of different trackways, assuming different trackmakers of the same type, is an important condition. To be precise, the term 'type' should be replaced with 'species' (of course the biological, not palaeontological species), in the discussion about gregarism as social behaviour within the limits of its definition (see Immelmann and Beer 1989; Gould and McKay 1990; Pond et al. 2011). Obviously, this does not imply that gregarious behaviour cannot be inferred from fossil footprints; it is exactly the opposite, but we must be aware of the limitations in interpretation based on observable morphological traits.

Morphological similarity as a proxy for group behaviour should be evaluated considering that 1) substrate properties can be synchronically different on the same trampled surface, promoting formation of synchronous but morphologically different trackways and 2) substrate properties can re-occur diachronically over a relatively short interval of time, promoting formation of diachronous but morphologically similar trackways. Thus, morphologic similarity by itself is not sufficient for inferring herd behaviour, and synchronous formation of trackways related to group behaviour must take into account external (both ichnological and nonichnological) data. Among possible data external to morphology are those related to the timing of wandering, for instance, the identification of multiple (two are sufficient) overlaps performed by two different trackmakers, whose tracks are distinguishable, and in which the printing of tracks reversed in subsequent overlaps (e.g. trackmaker A treads upon footprint of trackmaker B, then trackmaker B treads upon footprint of trackmaker A; e.g. Romano et al. 2019). This possible situation would most likely ensure synchrony of wanderings, and curiously it cannot be satisfied when one looks only at parallel trackways.

The parallel or subparallel orientation of trackways may also be explained with the existence of physical barriers (i.e. a shoreline) that, obviously, can influence direction of roaming of solitary individuals, determining a configuration of tracks and trackways that suggest group or coordinate movement, as stressed by Ostrom (1972) and Getty et al. (2017). According to the former author, divergent trackways occurring on the same trampled surface bearing also parallel trackways undermine this explanation and makes the interpretation of gregarious behaviour more parsimonious (Ostrom 1972). However, divergent and perpendicular trackways are observed in present time ecosystems with topographic constraints, for instance, in lakeshore environments (García-Ortiz and Pérez-Lorente 2014), thus significantly weakening the putative parsimony.

The occurrence of regular spacing between trackways and lack of superposition or little overlap between tracks curiously suggests a 'need for order' or 'troop deployment', thus inferring gregarious behaviour in the producers. This clue probably works when one hypothesises gregarious behaviour only within a homogeneous herd in terms of producers' overall dimensions. We consider that the same applies to uniform depth as further clue for inferring gregarious behaviour.

Finally, the other evidence invoked for gregarious behaviour are similar speed values, pace cadence and stride between trackways. Pace cadence and stride, similarly to the latter conditions, can work within homogeneous herd in terms of trackmaker's overall dimensions but oblige to reject *tout court* such an interpretation if the trampled surface bear tracks of 'the same type of producer' but of different size classes, inferable from different track sizes.

Tracks of similar dimensions on the TBL1 surface share similar outlines but some appear faintly impressed. Close proximity and/or overlap with similar but more deeply impressed footprints most likely indicate that several episodes of dinosaurs walking on the surface occurred, preferentially on two areas of the surface that are highly dinoturbated. For these trackmakers, the scenario may have been a more or less elongated pond, suggested by the physical characteristics of the exposed site, which obviously is a minimal percentage of the overall landscape at the time of impression. This pond, after the passage of SrT_1 , SrT_3 and smaller tracks, would have undergone desiccation, after which the SrT_2 trackmaker walked on the surface, overriding polygonal cracks.

Excluding SrT_2 for its own direction of travel, SrT_1 and SrT_3 occur in subparallel alignment; yet, in our opinion, possible gregariousness may not be definitely inferred for these two trackmakers. The configurations that seem to us most interesting to explore and test concerns that of 1) SrT1 and SrT3 respectively associated to most of those smaller footprints made by the autopodia of both the right and left side and 2) small footprints considered as a different evidence not in temporal association with the larger one. For these

smaller footprints, an analysis of patterns of orientation is still lacking but, at first glance and considering single tracks, they should follow a comparable orientation. A thorough analysis of track overriding and depth of impression, by means of digital techniques, will probably help in disentangling this issue.

We propose that the quadruped configuration of the small tracks (rounded manus and pes prints) corresponds to sauropods. Although we cannot provide anatomical details, the only other possible candidate could be ankylosaurian thyreophores, but the configuration of their tracks, which is very well known in South America (e.g. Leonardi 1989; McCrea et al. 2001), is completely different from the tracks presented here.

The record from the Santa Ana River suggests gregarious behaviour for only the trackmakers of smaller footprints; in this case, insufficient evidence for recognition of age classes and possible relationship between large and small footprints prevents determining whether the record is an example of segregation in sauropod herds according to age (Myers and Fiorillo 2009); 2) The possible gregarious behaviour among producers of small and large overall size may indicate parental care among sauropods. Interestingly, complex social behaviour in Dinosauria, including social cohesion and age-segregation within herd structures, have been recently suggested to have originated in sauropodomorphs during the Triassic (Pol et al. 2021) and could support the latter hypothesis.

The presence of large tridactyl tracks here assumed as made by ornithopodan trackmakers could be also problematic, since some large ornithopod tracks have been assumed as indicative for the Cretaceous, especially for North America (Díaz-Martínez et al. 2015, Fig.2) but not necessarily for Gondwanan regions (e.g. Fernandes and Carvalho 2007; Díaz-Martínez et al. 2015, Figure 2). Although the record of Jurassic specimens of Iguanodonichnus and Camptosaurichnus was discussed by Díaz-Martínez et al. (2015), it has also been supported for the Late Jurassic-Early Cretaceous Botucatú Formation (e.g. Fernandes and Carvalho 2007), for the Upper Jurassic of Portugal (Mateus and Milán 2008), and the Late Jurassic of Yemen (Schulp et al. 2008). Similar both in shape and size massive ornithopod tracks were recorded in rocks of the Chacarilla Formation of northern Chile (Rubilar Rogers et al. 2008). Actually, the most similar track results that of Sinoichnites youngi Kuhn, 1958 from the Middle Jurassic of China. More information is still necessary to understand the distribution of large ornithopodans in both supercontinents.

Conclusions

The first Jurassic or earliest Cretaceous dinosaur ichnosite from Bolivia is here reported consisting of abundant dinosaur footprints in eight different stratigraphic levels within the Castellón Fm in the Entre Ríos area (O'Connor Province, Autonomous Department of Tarija). The ichnosite from Tarija extends the record of ichnological localities in Bolivia throughout the three periods of the Mesozoic Era. The best exposed track-bearing surface preserves more than 300 sauropod tracks, both adult and juveniles, herein presented, plus one theropod trackway and two ornithopod trackways. The absence of additional tridactyl tracks is enigmatic, probably due to obliteration by sauropods walking on the track-bearing surface at an early stage. Some large footprints are arranged in three medium-gauge trackways, and numerous tracks of smaller size concentrated in different, highly dinoturbated portions of the surface, most of these seemingly associated to at least two sub-parallel trackways.

The best detailed trackway displays large pedes, sub-ovoidal to roughly sub-rectangular in outline, with three or four claw impressions, and sub-circular manus tracks with two or three digit impressions. Trackway parameters indicate a producer about 3.80 m tall at the hip, moving on the surface in walking gait. Although SrT3 trackway bear similarities with other known sauropod ichnotaxa, this trackway as well as the rest of the Santa Ana River tracks are unique and no identification of the possible trackmaker has been achieved. Pes and manus morphology, as well as the purported Upper Jurassic age, points to a non-neosauropod eusauropod trackmaker, yet a titanosauriform producer may not be discarded.

The peculiar distribution of some large and small tracks on the studied surfaced BTL1 provides some clues for inferring gregarious behaviour, stressing the importance of walk synchronism among producers, a condition that appears not directly satisfied by those ichnological clues that are accepted and currently used.

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No potential conflict of interest was reported by the author(s).

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