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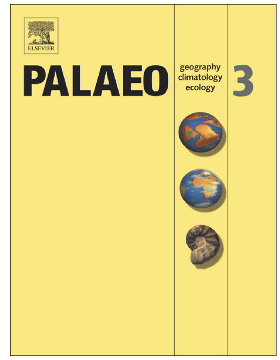

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Gregarious behaviour among non-avian theropods inferred from trackways: A case study from the Cretaceous (Cenomanian) Candeleros Formation of Patagonia, Argentina

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ABSTRACT

Gregarious behaviour among dinosaurs has been inferred from several lines of evidence (monospecific bonebeds, skeletal morphology, phylogenetic inferences, comparison with modern ecosystems and parallel trackways with particular characteristics), but is relatively poorly documented for non-avian theropods. Here, we report five parallel theropod trackways of large track size (average length of 28 cm) in the Cretaceous (Cenomanian) Candeleros Formation from northwestern Patagonia, Argentina. The tracks are provisionally assigned to aff. *Asianopodus pulvinicalx* and considering the autopod morphology of the theropod taxa documented in the Candeleros Formation, abelisaurid theropods are suggested as trackmakers. The trackways possess similar stride, speed estimation, direction and preservational features, and track show uniform depth and do not overlap. Physical barriers (i.e., large fluvial channels or perennial lake) that could influence the direction of the theropod trackmaker gaits were not recognised in the section. Taking into account these considerations, a gregarious behaviour for the abelisaurid theropod trackmakers is proposed. The tracks are preserved as shallow undertracks in a medium-grained sandstone bed deposited in a floodplain setting. The tracking surface is interpreted as the overlaying layer of muddy-siltstone. The occurrence of swelling clays and microbial

mats in the track-bearing level could have contributed to the substrate stabilisation and their role in the preservation is discussed.

Key words: Theropod footprint; gregariousness; dinosaur behavior; Abelisauridae; Upper Cretaceous; Neuquén Basin

1. Introduction

Since the beginning of dinosaur research, some relevant palaeoecological aspects, such as social strategies, have been matter of debate (e.g. Ostrom, 1972). For instance, gregariousness has been attributed to a number of purposes, such as protecting individuals from common aggressors, providing effective access to food sources, defending and raising youngs, or increasing the efficiency of breeding or success of migration (Currie and Eberth, 2010). Tracks and trackways, considered as the product of animal behaviour, are excellent indicators to evaluate the possible social relationships among different dinosaur groups. Currie and Eberth (2010) proposed that parallel trackways, as well as skeletal morphology, bonebed assemblages, phylogenetic inferences and comparison with modern ecosystems, are evidences of gregariousness. Thulborn and Wade (1984) suggested that the trackways should have similar preservation, uniform depth, lack of superposition, and indicate similar speeds to support the gregariousness hypothesis. However, some parallel trackways have been explained as solitary individuals who would pass at different times through the same place and direction due to a geographical barrier (Getty et al., 2015, 2017).

Dinosaur gregarious behaviour has been inferred from several worldwide tracksites focused mainly in sauropods and ornithopods (e.g., Ostrom, 1972; Thulborn and Wade, 1984; Farlow et al., 1989; Lockley et al., 1994a; Lockley and Hunt, 1995; Matsukawa et al., 2001; Lockley et al., 2002; Day et al., 2004; Myers and Fiorillo, 2009; Castanera et al., 2011, 2014; Lockley et al., 2012; Piñuela et al., 2016). Parallel theropod trackways as an evidence of gregariousness were addressed by some authors (e.g., Moreno et al., 2012; García-Ortiz and Pérez-Lorente, 2014; McCrea et al., 2014; Lockley et al., 2015). Nevertheless, the social nature of theropod dinosaurs is still discussed (e.g. Barco et al., 2006; Roach and Brinkman, 2007).

In Patagonia (Argentina, southern South America), a high diversity of saurischian and ornithischian dinosaurs was found in the Upper Cretaceous continental deposits of the Mesozoic–Cenozoic Neuquén Basin (Leanza et al., 2004). The Cenomanian Candeleros Formation, characterised mainly by fluvio-aeolian interaction deposits, constitutes the basal unit of the Neuquén Group deposited in the foreland basin of the Neuquén Basin (Garrido, 2010; Fennell et al., 2017). The Candeleros Formation presents one of the richest dinosaur fossil records from the basin and includes both, diplodocoid and titanosaurid sauropods (Otero and Salgado, 2015, and references therein), and a great diversity of theropods: abelisaurids, carcharodontosaurids, basal coelurosaurs, alvarezaurids and dromaeosaurids (Coria and Salgado, 1995; Calvo et al., 2004; Makovicky et al., 2005; Makovicky et al., 2012; Novas et al., 2012, 2013; Canale et al., 2016). Taking into account the published data, the Candeleros Formation presents the highest track ichnodiversity from the basin and includes: sauropod, theropod, iguanodontid and other ornithopod, and also pterosaur tracks and trackways (Calvo, 1991, 1999; Calvo and Lockley, 2001; Calvo and Mazzetta, 2004; Calvo and Rivera, 2018; Candia Halupczok et al., 2018; Heredia et al., 2019).

While theropod tracks are abundant for the Cretaceous (Cenomanian) worldwide (e.g. Mezga and Bajraktarević, 1999; Lockley et al., 2014 and references therein; Romilio and Salisbury, 2014; Calvo and Rivera, 2018), ichnological evidence for theropod gregariousness from this stage has been poorly documented. In this work, several parallel trackways of tridactyl tracks found in a new tracksite from the Cenomanian Candeleros Formation (Northern Patagonia) will be analysed. The aim of this paper is fourfold: i) to describe in detail the surface bearing the tracks focusing on several parallel tridactyl trackways as well as the accompanying sauropod tracks and the substrate properties; ii) to discuss the role played by the substrate in track morphology and preservation; iii) to provide an ichnotaxonomical analysis and compare this record with similar theropod trackways worldwide; and, iv) to discuss the possible trackmakers and their palaeobiological implications focusing on gregarious behaviour.

2. Geological setting

The Neuquén Basin is located in west-central Argentina and it extends from 32° to 40° S latitude along the Andean foothills (Fig. 1A). It covers an area of about 120,000 km² and includes a continuous Late Triassic–Palaeogene stratigraphic record of marine to continental facies, more than 7000 m thick (Legarreta and Gulisano, 1989; Yrigoyen, 1991; Vergani et al., 1995). In the Late Cretaceous–Palaeogene interval, the Neuquén basin represents a foreland basin mainly composed of continental deposits with minor marine intervals (Howell et al., 2005; Aguirre-Urreta et al., 2011). The Cenomanian–Campanian Neuquén Group lies above the Rayoso Formation (Bajada del Agrio Group) overlying an angular unconformity known as Patagonídica; it is 1 km thick and comprises fluvial, aeolian and lacustrine deposits (Stipanicic et al., 1968; Leanza, 2009; Garrido, 2010).

The Neuquén Group is divided into three units (Fig. 1B) known as Río Limay, Río Neuquén and Río Colorado subgroups (Cazau and Uliana, 1973; Ramos, 1981). However, the stratigraphy of the group is not uniform throughout the entire basin, and the tripartite division is only recognizable between 37º and 41º S (Fennell et al., 2017). There is no clear consensus about the internal lithostratigraphic scheme for the Neuquén Group (Garrido, 2010; Asurmendi et al., 2017). The Candeleros Formation, the focus of this study, is the basal unit of the Río Limay subgroup (Fig. 1B). This formation is known for its purple to red continental deposits and is overlain by the Huincul Formation, which is clearly differentiable by its yellow to white coloured sandstones (Sánchez et al., 2008; Garrido, 2010).

The Candeleros Formation (Keidel, 1917; Di Paola, 1973) is considered Cenomanian in age (Leanza et al., 2004, and references therein) based on U–Pb dating of detrital zircons (Tunik et al., 2010; Di Giulio et al., 2012, 2015). This unit is composed of massive, coarse- to medium-grained sandstones and conglomerates, with intercalations of thin siltstone beds, with a total estimated thickness of 200–300 m (e.g. Garrido, 2010; Asurmendi et al., 2017). Modal petrographic studies, supported by U–Pb-dated detrital zircons, indicate that the main source area of sediment input was located to the west, associated with the Late Cretaceous thrust front with a subordinate input from eastern basement areas (Tunik et al., 2010). Several palaeoenvironmental settings were documented, which are related to their location within the palaeogeographical context of the basin. Accordingly, the Candeleros Formation was interpreted in the type locality Los Candeleros, about 200 km to the SSW of the area studied here, as a braided and meandering fluvial system associated with muddy floodplain deposits and palaeosoils (Garrido, 2010). Close to the Agrio River (Quili Malal locality), the unit exhibits meandering fluvial setting associated with alluvial plains and fluvio-aeolian deposits (Gazzera and Spalletti, 1990). The record of a fluvio-aeolian interaction was also reported by Candia Halupczok et al. (2018) towards the southeast area of the Huincul High and referred as the Kokorkom palaeodesert. Facies analysis in outcrops of the southeastern border of the basin, near the El Chocón locality, indicates aeolian and playa-lake deposits representing arid to semiarid conditions (Spalletti and Gazzera, 1994). Terminal fan deposits were analysed close to the eastern limit of the Agrio Fold and Thrust Belt around the Colorado River (Sánchez and Asurmendi, 2015). The location of all the aforementioned studies from the Candeleros Formation is shown in the map of the Neuquén Basin (Fig. 1A). In the study area (Aguada de Tuco), the basal part of the unit (the first 25 m) is represented by unconfined flow deposits possibly related to ephemeral fluvial systems and channelized to poorly channelized flows and floodplain deposits (Heredia et al., 2019).

3. Materials and methods

The study area included in this work is located in the westernmost outcrops of the Candeleros Formation, next to the Provincial Road 7, between Chos Malal and Añelo cities, Neuquén province (Fig. 1A). The new tracksite in the Aguada de Tuco area (GPS point for reference: 37° 26′ 40″ S, 69° 53′ 48″

W) is approximately 350 m in straight line from the sauropod trackway documented by Heredia et al. (2019). The logged section (1:100) comprises the basal part of the unit (the first 36 m) and follows Heredia et al. (2019). The new track-bearing level is found at the top of the logged section.

The general measurement procedures of the track and trackways follow the criteria of Thulborn (1990) and Marty (2008). Track length, track width and pace length were measured *in situ*. Other measurements were obtained from the orthomosaic generated by photogrammetric techniques. They were compared with some measurements made in the field to see their accuracy. Measurements on individual tracks (Fig. 2A, B) comprised: footprint length (FL), footprint width (FW), digit impression length (II, III and IV) and divarication angles of digit impression (II–III, III–IV, II–IV). To analyse the degree of mesaxony *sensu* Lockley (2009), the ratio between maximum height (ATl) and the perpendicular transverse base (ATw) of the anterior triangle (AT) was calculated (AT l/w). The anterior triangle was defined and measured from the tip of the distal pad of digits II, III and IV; it was not measured from the claw marks because they are not always preserved. Measurements on individual trackways (Fig. 2C) comprised: pace length (PL), distance between two consecutive tracks; pace angle (PA), angle formed by the two segments linking three consecutive tracks (oblique pace length *sensu* Leonardi, 1987); stride length (SL), distance between two consecutive tracks on the same side (either left or right) of the trackway; width of the angulation pattern (WAP), measured perpendicular to the stride length *sensu* Marty (2008). In the present work, trackway measurements were made from the most posterior end of the heel, because it is the only feature of the track that was preserved in all cases. Small, medium and large tridactyl tracks will be considered for those with less than 12 cm, between 12 and 25 cm, and those larger than 25 cm, respectively. To estimate the trackmaker speed, the formula of Alexander (1976) was followed. This speed equation was defined as $V = 0.25\ g^{0.5}\ SL^{1.67}\ H^{-1.17}$ where V is the speed, g is the acceleration of free fall, H is the hip height and SL is the stride length. The hip height was estimated following the consideration of the same author for bipedal dinosaurs: if the metatarsophalangeal joint rested on the ground but the tarsometatarsal joint did not (as in the present case) the length of the hind track is 0.25H. To calculate the speed for each SL, the average of H obtained from the corresponding trackway is implemented; this avoids the problem that one particular track could be incomplete making it impossible to measure their FL (from which H is estimated). For sauropod tracks, the heteropody (H) was calculated with the manus-pes ratio as the (manus imprint area/pes imprint area) × 100 (Lockley et al., 1994b). These areas were obtained using the public domain, java-based image processing program ImageJ.

The preservational terminology, such as true track, elite track, underprint, undertrack and natural cast, are based on the approach and definitions of Thulborn (1990), Lockley (1991), Lockley and Meyer (2000) and Marty et al. (2009).

Photogrammetric models were obtained using Agisoft Metashape 1.5.0 Professional Edition (Educational License, www.agisoft.com) following the procedures indicated by Falkingham, (2012), Mallison and Wings (2014) and Falkingham et al. (2018). The false-depth colour images and contour lines were produced with the free software Paraview (www.paraview.org). An orthomosaic was generated with the purpose of obtaining a detailed map of the track-bearing surface to show, with the highest degree of fidelity, the proportions in size and the relative positions between the ichnites (Díaz-Martínez et al., 2018). The orthomosaic is available as supplementary material.

This work includes optical petrography, electron microscope and X-ray diffraction (XRD) in order to determine the different detrital grains, particle size distribution and arrangement (sorting), as well as mineralogy and diagenetic components of the sandstone track -bearing substrate and muddy-siltstone beds above it. Two samples from the track-bearing surface and from the overlaying muddy-siltstone, respectively, were analysed. Scanning electron microscopy (SEM) images were taken with a JEOL-JCM 6000 coupled with a qualitative EDS (energy dispersive spectroscopy). Quantitative and qualitative XRD analysis of whole-rock powders and oriented preparations of the clay fraction were conducted using a Philips 3020 goniometer (Ni-filtered CuKa radiation, 40 kV, 20 mA, without secondary monochromator) and following the methodology described in Comerio et al. (2018 and references therein). The stratigraphic divisions used in the present work follow the ICS International Chronostratigraphic Chart 2018 (Cohen et al., 2013, updated).

4. Sedimentology

The sedimentological facies of the lowermost part of the Candeleros Formation in the Aguada de Tuco area were previously analysed by Heredia et al. (2019) and summarized in the Fig. 3. According to this work, a lower interval (12 m thick) and an upper interval (24 m thick) were distinguished (Fig. 3A). The lower one begins with fine-grained conglomerates characterised by poorly channelized geometries that suggest unconfined flow deposits. Conglomerates are capped by cm-thick muddy siltstones with symmetrical and few asymmetrical ripples. Upwards, tabular sandstone beds (0.3–0.5 m) and m-thick heterolithic deposits composed of fine-grained massive sandstones and parallel laminated siltstones occur. These deposits are interpreted as floodplain deposits containing temporary ponds due to the preservation of laminated muddy siltstones with small-scale symmetrical ripples. Nevertheless, muddy drapes with desiccation cracks indicate that these areas dried out between discharge events. The occurrence of halite molds probably replaced by hematite cubic crystals (Fig. 3B) suggest eogenetic alterations from saline-alkaline ground water (Hay, 1981) to intense weathering of the parental minerals associated with a well-drained alluvial plain (Retallack, 2001).

The upper interval is characterised by amalgamated sandstones with channelization features. These deposits are interbedded with heterolithic deposits (1.7–2.0 m thick) and occasionally with fine-grained conglomerates. Sandstones consist of tabular to lenticular beds, showing planar and tangential cross-stratification (0.3–0.8 m-thick sets), and limited by low-angle reactivation surfaces (Fig. 3D). This suggests the lateral migration of small-scale channels interpreted as more permanent fluvial conditions than those observed in the lower interval. Some sandstones beds exhibit mud intraclasts towards the base and are limited on top by muddy siltstones that exhibit desiccation cracks. The heterolithic floodplain deposits consist of ripple and parallel laminated cm-thick sandstones (Fig. 3E) that alternate with thin intercalations of laminated muddy siltstones and mottled mudstones. Additionally, trace fossils assignable to *Arenicolites* Salter, 1857 are found in these deposits (Fig. 3C). Some indurated massive beds with a high content of carbonate point out to periodic dewatering of the floodplains and the alternation between wet and dry periods. Muddy drapes on tops of sandstones with desiccation cracks and possible biostabilized substrates suggested by the presence of glossy surfaces associated with corrugations also occur.

The new track-bearing level is found in the uppermost deposits interbedded with sandstones showing cross-stratification and reactivation surfaces interpreted as small-scale channel bodies. As in the case of the sauropod trackway (Heredia et al., 2019), the tracks studied here are exposed on a flat surface of about 150 m^2 (Fig. 3F). The track-bearing level is a medium-grained sandstone bed that shows partially preserved symmetrical ripples capped by a discontinuous level of muddy siltstones with desiccation cracks and a maximum thickness of 2 cm. Ripple crests are oriented SW-NE and characterised by wavelengths of 6.0–8.0 cm and heights of 1.0–1.5 cm.

5. Description of tracks and trackways

In the studied surface, at least 55 tracks have been recognized. For the description the track-bearing surface was divided into two areas: A and B (Fig. 4). Area A has several parallel bipedal trackways of large and small tridactyl tracks (Figs. 5, 6). Area B has three extensive trackways with intermediate-sized tridactyl tracks (Fig. 7); these are associated with sauropod tracks most of which are isolated and three of which are interpreted as a trackway (Fig. 8). Measurements and parameters on the tridactyl track and trackways are presented here in Tables 1 and 2 (summary version showing averages) and the complete tables are provided as Supplementary Material.

The track-bearing area A, indicated in the general orthomosaic (Fig. 4B), includes 21 tridactyl footprints arranged in seven trackways, five with large footprints and two with small footprints. All the tracks from this area are preserved in medium-grained sandstones as concave epirelief. The large tridactyl tracks are relatively well preserved (grade 2 *sensu* Marchetti et al., 2019) while the small ones are poorly preserved (grade 0-1 *sensu* Marchetti et al., 2019). A thin muddy siltstone overlies this surface and is followed by a sandstone bed containing the natural cast in convex hiporelief of some tracks (e.g. track 4.3, Fig. 6A–C). Accordingly, the trackmaker must have stepped on the muddy siltstone layer (the tracking surface), and the concave epirelief tracks would actually consist of shallow undertracks.

The large tridactyl tracks usually preserve three digit impressions. The mean length and width track is 28 cm and 23 cm, respectively, and length/width ratio ranges between 1.16 and 1.39. No evidence of hallux imprint was observed. The mean pace length, pace angle, stride and WAP for the five trackways is 95 cm, 164º, 188 cm and 13 cm, respectively. The average speed calculated is 2 m/s, while the lowest speed is 1.78 m/s and the highest is 2.2 m/s. These five trackways trend in a southeasterly direction.

The large tracks show moderate to marked mesaxony: the mean anterior triangle length/width ratio is 0.55 and ranges between 0.48 and 0.61. The mean divarication of digits II-IV is 60.8º and ranges between 47.9º and 76.4º. Digit imprint III and IV are subequal while digit II is much shorter: the digit III is slightly longer (average length 19.3 cm) than the digit IV (average length 19 cm) and digit II is 13 cm long in average. The best preserved track, right track 1.2 (Fig. 6G–J), shows the typical phalangeal pad formula of x-2-3-4-x for theropod tridactyl footprints. The deepest pad imprints consist in the most proximal of digits III and IV. Tracks 1.2 and 4.2 show a sub-rounded proximal pad of digit IV situated posteriorly and aligned to the axis of digit III (Fig. 6G–M).

Trackways 2 and 3 present small tracks, mean length 11 cm and 10 cm, and mean width 6 cm and 7 cm, respectively. Both trackways are narrow and show similar pace of 47 cm and 50 cm and pace angle of 164º and 172º, respectively. The speed was only possible to estimate for trackway 2: 1.95 m/s. Also, both trackways show similar orientation and no digit imprints are clearly preserved, although it is possible to distinguish the central digits with a northwest direction. The orientation of the large footprints is almost the opposite of the small ones, and there is no overlap between any of the large and small footprints.

Area B comprises a group of three parallel, bipedal and narrow trackways of 16, 6 and 7 tracks each one (trackways numbered as 8.1–8.16, 9.1–9.6, 10.1–10.7, respectively). These tracks are medium-sized; mean track length is 14 cm for each of these trackways while the mean track width is 10 cm for trackways 8 and 9 and 11 cm for trackway 10. All the tridactyl footprints from this area are poorly preserved (grade 0-1 *sensu* Marchetti et al., 2019); the only track measurements that were obtained are length and width. Almost all the tracks are preserved as concave epirelief with the exception of two tracks preserved partially as convex epirelief. They show evidence of digits (tracks 8.10 and 8.12, Fig. 7, A–D) and was possible to estimate the anterior triangle length/width ratio and the digit divarication angle. Accordingly, tracks 8.10 and 8.12 present moderate to marked mesaxony, the AT l/w ratio resulted in 0.66 and 0.61 and the divarication of digits II-IV is 56.1º and 50.6º, respectively. The three trackways are narrow with a mean pace, pace angle and stride of 68 cm, 171º and 135 cm, respectively. Trackway 8 displays the same direction but opposite to trackways 9 and 10. The speed was calculated for trackways 8, 9 and 10 as 2.27 m/s, 2.64 m/s and 2.76 m/s, respectively.

The only case of overlapping tracks (as a result of different trackmakers) recorded in the present tracksite is the tridactyl track 10.4 that overlaps the crescent-shaped track 11 (Fig. 8A, C, D). Tracks 11, 12 and 15 are large and present a symmetrical to slightly asymmetrical crescent shape typical of a sauropod manus track (Fig. 8A–D). The longest axis of each track (62 cm, 60 cm and 57 cm, respectively) has the same orientation (N 140). The three tracks are almost equidistant, with about 290 cm between tracks 11 and 12, and 293 cm between tracks 12 and 15, measured from the midpoint of each track (Fig. 8A). Accordingly, it is probable that these tracks belong to the same trackway. Other isolated sauropod tracks were recorded, including the only manus-pes set recognized: tracks 14 and 13, respectively (Fig. 8A, B). Track 14 is symmetric crescent in shape and the pes track is subcircular and presents a well-marked rim in the right lateral side. The manus imprint is wider than long (47 and 44 cm, respectively) while the pes imprint is longer than wide (76 and 65 cm, respectively). The manus-pes imprint distance is about 10 cm. The area of track 12 (manus) and track 13 (pes) was calculated as 1128 cm^2 and 2654 cm^2, respectively, and this resulted in a medium heteropody (H = 43% ~ 1/2.3). An isolated subcircular pes imprint (track 16) longer than wide (68 and 51 cm, respectively) close to the pes track 13 was recognized (Fig. 8B), and it is unlikely to belong to the same trackway due to the different size and orientation of both tracks. Also, a possible sauropod track with a slightly crescent shape and about 63 cm in length (track 17) close to manus track 11 was documented. Finally, an isolated subcircular track about 30 cm in length and adjacent to tridactyl track 2.3 (Fig. 5) was probably produced by a small-sized sauropod.

6. Substrate characterisation

The substrate attributes were analysed from samples from area A, where the large tridactyl trackways were recognized (Figs. 4, 5). Thin-section petrography of the trackway-bearing level indicates a moderately to poorly sorted, medium grained (0.25–0.5 mm, x̄: 0.36 mm) sandstone, that according to the modal composition ($Q_{30}F_{32}L_{38}$) plots as feldspathic litharenite in the ternary diagram of Folk et al. (1970). Equivalent results are shown in Tunik et al. (2010, Fig. 8A) for samples from the base of the Candeleros Formation. The sandstone shows sub-round grains, including some round to sub-angular grains, displaying a massive fabric (Fig. 9A, B). Lithic fragments are dominated by volcanic clasts with pilotaxitic and felsitic textures (andesitic composition), subordinated pyroclastic grains and also include sedimentary-lithic and polycrystalline (metamorphic) quartz clasts. The feldspar fraction is dominated by plagioclase (andesine-oligoclase), which is consistent with XRD-results. Monocrystalline quartz grains are limpid with straight extinction and, in some cases, show embayments typical of volcanic origin (e.g. Lee and Lee, 2000). The argillaceous matrix is scarce (< 5 %) and distributed as a reddish thin grain coating around lithic and crystalline fragments (Fig. 9A, B). Grain contacts are point or edge types suggesting a subordinate contribution of mechanical compaction. Hematite cement also occurs as a fringe around grains, probably originated from the dissolution of volcaniclastic fragments and/or heavy minerals (Pons et al., 2015). Occasionally, quartz cement fills the intergranular primary porosity (Fig. 9B) and is observed as both syntaxial and epitaxial quartz overgrowths (e.g. Worden and Burley, 2003). Poikilotopic calcite constitutes late cement also filling the intergranular porosity, partially replacing the crystalline grains and corroding quartz cement overgrowths (Fig. 9A). In the overlying muddy siltstone, lithic and crystalline fragments are supported in the argillaceous matrix (Fig. 9C, D).

XRD results for the sandstone and the muddy siltstone of show that quartz (30–40 wt%), plagioclase (40–17 wt%) and calcite (10–20 wt%) represent the main mineral phases (Fig. 10A). Hematite attains values of 5–7 wt% while analcime content is about 4 wt% and is only recorded in the sandstone samples. The clay fraction is 5 and 15 wt% in the sandstone and muddy siltstone, respectively, suggesting that clay minerals/phyllosilicates are subordinate components. In both rock types the clay fraction (Fig. 10B) consists of chlorite-smectite (C/S) interstratified minerals, and minor illite/mica and illite-smectite interstratified minerals with less than 15% of expandable layers or of R3 order (e.g. Moore and Reynolds, 1997).

Furthermore, SEM images of the trackway-bearing sandstone and the overlying muddy siltstone (Fig. 11A) reveal clay particles oriented parallel to the surface of the grains, mainly in the fine-grained fraction (Fig. 11B). In addition, authigenic crystals of chlorite-smectite rosettes composed of pseudohexagonal flakes are conspicuous in the matrix of muddy siltstones (Fig. 11C, D). EDS analyses show Ca, Na, K, Al in conjunction with high Fe and Mg suggesting that chlorite was probably derived from the transformation of smectite minerals as was previously documented by Pons et al. (2015). This observation agrees with a C/S composition observed in the X-ray diffraction of the clay fraction (Fig. 10B). Organic structures are recognized at the sandstone-mudstone boundary, as a µm-thick layer composed of densely oriented tubes (Fig. 11A, E), that partially surround clay particles (Fig. 11F, G). According to the EDS analyses, these structures are characterised by the presence of Ca, Na, K and a high content of C. The role of clay minerals and the possibly occurrence of microbial mats related to the stabilization of sand-sized grains will be discussed in section number 7.

7. Substrate properties controlling footprint morphology and preservation

The morphology of tracks and differences in preservation are linked to physical parameters like grain size, humidity, substrate consistency, as well as response to the limb dynamics and foot anatomy of the trackmaker (Marty et al., 2009). As it was previously mentioned, the bipedal trackmakers of all the tridactyl tracks from this tracksite are interpreted to have stepped on a thin muddy siltstone layer (the tracking surface), and consequently the tracks preserved in medium-grained sandstones as concave epirelief would be shallow undertracks. The five large-sized tridactyl trackways produced by theropods (area A) exhibit similar preservation in both anatomical and extra-anatomical features: they have the same depth and morphology, their digit pads are preserved and they do not present rims. Accordingly, it is possible to assume a similar substrate consistency for all these trackways and for the entire area A. As a result of the thinness of the muddy-siltstone layer, there are no discernible morphological differences between their undertracks and its natural casts counterpart (e.g. Fig. 6A–F). Furthermore, it is possible to interpret that the muddy tracking layer behaved as a plastic surface adapting the true track to the same morphology of the undertrack. It is important to point out that the percentage of clays in the tracking level is small (< 20%). However, considering the original occurrence of swelling clays, C/S in the clay fraction (Fig. 10B) likely derived from the transformation of smectite precursors (Pons et al., 2015) and contributed to increase the plastic properties of sand-sized sediment (e.g. Murray, 1991). In other words, swelling clays enhanced cohesiveness favouring the preservation of the footprints. Additionally, SEM images from area A evidence the existence of organic structures that might represent microbial mats (Fig. 11). These biogenic components could have also played a key role by binding and stabilizing the sand-sized sediment in which the tracks were preserved (e.g. Noffke et al., 2001; Marty et al., 2009; Fernández and Pazos, 2013). In spite of the absence of microbially induced sedimentary structures (MISS) such as wrinkle structures (e.g. Schieber, 2004; Noffke, 2009; Davies et al., 2016), the analysed interval records deformed ripple crests associated with desiccation cracks and glossy surfaces that suggest the overgrowth of microbial mats. Shallow-water bodies within the floodplain subjected to flooding and drying periods (Heredia et al., 2019) might have represented ideal scenarios for the occurrence of mats. The preservation potential of footprints increases directly with the consolidation and partial lithification of microbial mat-bearing sediments (Marty et al., 2009). For instance, dinosaur tracks recorded in fluvial deposits of the Sousa Formation, Lower Cretaceous (Sousa Basin, Brazil) are associated with biofilms that promoted the consolidation and early lithification of the beds preventing the erosion of footprints (de Souza Carvalho et al., 2013). In the study case, swelling clays and the co-occurrence of microbial mats might have played an important role in the stabilization of the substrate and preservation of the tracks. Small-sized tridactyl tracks are deeper (relative to their size) than the large ones and also are poorly preserved (they do not preserve digit imprints). Accordingly it is possible to interpret a substrate with a lower degree of consistency for the small tracks than for the large tridactyl tracks.

Area B contains a set of three long tridactyl trackways (numbered as 8, 9 and 10). They are deeply impressed relatively to the other tracks, without variation in the morphology along each trackway. This observation suggests that no changes in substrate properties (e.g. consistency, moisture content) occurred between them. However, some discontinuous and shallow sauropod tracks were produced before the tridactyl trackways as they are overlapped (Fig. 8 A, C, D). As were aforementioned, small ripples are covering some of the sauropod tracks (Fig. 8E) but no tridactyl tracks. Therefore it is possible to suppose that the substrate was firm when the sauropods walked through this palaeosurface and soft when the biped dinosaurs produced the medium-sized tracks.

The large tridactyl tracks of area A are shallower than the medium-sized tridactyl tracks of area B (compare colour depth in Figs. 8, 9 and 11). Given this difference in depth and the fact that the trackmaker of the large tracks must have been heavier, it is possible to assume that the substrate was firmer in the first case. Accordingly, the general track morphologies in the study surface are predominantly conditioned by changes in the substrate consistency over time. In the context of fluvial system characterised by moderate to high-sinuosity fluvial channels (Spalletti and Gazzera, 1994), periods of flood discharges as well as fluctuations of the phreatic level likely represent the main variables affecting the local consistency of the substrate.

Arid to semiarid conditions during the deposition of the Candeleros Formation were inferred from facies associations which suggest a temperate palaeoclimate with alternating dry and rainy periods (Calvo and Gazzera, 1989; Spalletti and Gazzera, 1994; Candia Halupczok et al., 2018). Under a relatively arid climate with alternating dry and humid periods clay minerals assemblages are dominated by smectites (e.g. Worden and Morad, 2003), as also recorded in the present study.

Therefore, it is possible that the alternation of volcaniclastic components contributes not only in the formation of smectite→ chlorite-smectite but also in the occurrence of zeolites (analcime-heulandite) and hematite, typical authigenic components of the Candeleros Formation (Marchese, 1971; Di Paola, 1973).

8. Ichnotaxonomy

As mentioned before, there are preservational differences among the tridactyl tracks of the study site. The small and intermediate-sized tracks are poorly preserved and are considered as undetermined tridactyl tracks. On the other hand, the large tridactyl tracks, although not elite tracks, are preserved well enough to discuss their ichnotaxonomy.

The ichnological record of the Candeleros Formation in the Neuquén Province is well constrained to the border of the basin (easternmost outcrops), where several dinosaur track ichnotaxa are known from the west coast area of the Ezequiel Ramos Mexía dam, close to the El Chocón locality (Calvo and Rivera, 2018, and references therein). The theropod ichnospecies known from the Candeleros Formation include *Abelichnus astigarrae* Calvo, 1991, *Bressanichnus patagonicus* Calvo, 1991, *Deferrariischnium mapuchensis* Calvo, 1991, *Picunichnus benedettoi* Calvo, 1991, and *Candeleroichnus canalei* Calvo and Rivera, 2018. To compare the degree of mesaxony using the same criteria *sensu* Lockley (2009), the AT l/w ratio was calculated for the five theropod ichnotaxa known from the Candeleros Formation, and the corresponding length and width AT values were obtained by measuring from the figures from Calvo and Rivera (2018; Figs. 3, 4, 7, 10 and 11).

Among the theropod ichnospecies documented by Calvo (1991) and Calvo and Rivera (2018) in the present unit, *A. astigarrae* displays the largest track size, with a mean length and width of 48.5 and 43.5 cm, respectively (FL/FW ratio = 1.11). Also, it was defined as a tridactyl track with wide and very prominent digit imprints, AT l/w ratio of 0.21 and mean stride, pace and pace angle of 255 cm, 130 cm and 146º–150º, respectively. The theropod tracks studied here are smaller in size and exhibit a higher FL/FW ratio (mean about 1.26), slender digit imprints, lower mean stride and pace (about 189 cm and

95 cm, respectively) and both higher pace angle (164º, which means it's a narrower trackway than *A. astigarrae*) and degree of mesaxony (mean about 0.55). The ichnotaxon *B. patagonicus* comprises medium-sized tridactyl footprints, mean length between 20 and 25 cm and FL/FW ratio of 1.5. The AT l/w ratio was calculated in 0.39, the impression of digit III is internally curved and the mean divarication of digits II–IV is 40º. In reference to the characteristics of trackway, the mean stride, pace and pace angle is 161 cm, 80 cm and 172º, respectively. Among the theropod ichnotaxa documented from the Candeleros Formation, *B. patagonicus* presents the most similar size to the studied tracks but the former is slightly smaller and shows a higher FL/FW ratio. Also, the studied theropod tracks display a higher degree of mesaxony and divarication of digits II–IV, and do not present the digit III internally curved as *B. patagonicus*. Moreover, the studied theropod trackways present a higher stride and pace and a lower pace angle than this ichnotaxon. The ichnogenus *Picunichnus,* whose diagnosis was amended by Melchor et al. (2019), includes the aforementioned *P. benedettoi* from the Candeleros Formation and the type ichnospecies *Picunichnus quijadaensis* Melchor, 2019, from the Albian Lagarcito Formation (San Luis, Argentina). The icnotaxon *Picunichnus* presents marked elongation (FL/FW ratio ranges between 1.5 and 2.15) and moderate to marked mesaxony (AT l/w ratio ranges between 0.6 and 0.9). The studied trackway shows clear differences from *Picunichnus* in both footprint parameters and additionally in the divarication of digits II–IV: the former is in the range of 48º–76º while *Picunichnus* is usually in the range of 23º–42º. The remaining theropod ichnogenera known from the Candeleros Formation consist in tridactyl footprints of small size, less than 17 cm long. *D. mapuchensis* shows a FL/FW ratio of 1.7 and a high degree of mesaxony as indicated by an AT l/w ratio of 0.98. The impression of a long digit III almost represents half the length of the footprint and the divarication of digits II–IV is 35º. The trackway mean stride, pace and pace angle are 138 cm, 68 cm and 178º, respectively. The studied theropod tracks are bigger in size and exhibit a significantly lower FL/FW ratio and degree of mesaxony than *D. mapuchensis*. Furthermore, the former present lower degrees of divarication of digits II–IV. The studied theropod trackways display a higher stride and pace but a lower pace angle than *D. mapuchensis*. *C. canalei* includes small-sized tridactyl footprints of 11 cm in length

and 6 cm in width with a FL/FW ratio of 1.8. This ichnotaxon shows an intermediate to high degree of mesaxony pointed out by an AT l/w ratio of 0.57–0.75. The finger III imprint is longer and more robust than the lateral ones and the divarication of digits II–IV is in the range of 13º and 31º (measured from Figs. 10 and 11, Calvo and Rivera, 2018). The trackways are very narrow and straight, the pace angle ranges between 175–180° while the stride and pace is in the range of 91–101cm (mean 94 cm) and 41–53 cm (mean 47 cm), respectively. The theropod tracks studied here are significantly bigger in size, exhibit a considerably lower FL/FW ratio and higher divarication of digits II–IV than *C. canalei*, and the degree of mesaxony is similar (the range of AT l/w ratio slightly intersects, 0.48–0.61 vs. 0.57–0.75, respectively). Moreover, the studied theropod trackways show a lower pace angle and higher stride and pace than *C. canalei*.

Other theropod tracks known from the Neuquén Basin, beyond those already mentioned from the Candeleros Formation, include those documented in the Valanginian–Hauterivian/Barremian Agrio Formation from the Mendoza Group (Pazos et al., 2012) and the Campanian–Maastrichtian Loncoche Formation from the Malargüe Group (González Riga et al., 2015). The theropod tracks from the Agrio Formation assigned to cf. *Therangospodus* include large tracks characterised by a mean length and width of 34.5 cm and 23.8 cm, respectively (average FL/FW ratio = 1.45). They lack digital pads and show an intermediate to high degree of mesaxony (mean AT l/w ratio of 0.45). The divarication of digits II–IV is in the range of 69º and 83º (both measured and estimated from Fig. 5b, Pazos et al., 2012). The trackways present a pace that ranges between 100 cm and 130 cm and a pace angle of 160º–180º (all the data are means). The studied theropod tracks are smaller in size than the Agrio Formation ones, and display lower FL/FW ratio (1.26 vs. 1.45, respectively) and higher degree of mesaxony. Moreover, the studied theropod tracks exhibit similar divarication of digits II–IV (48º–76º vs. 69º–83º, respectively) and similar pace angles (157º–169º vs. 160º–180º, respectively), but display a lower mean pace than the cf. *Therangospodus* tracks and preserve digital pads. The theropod tracks documented in the Loncoche Formation include three morphotypes numbered as 3, 4 and 5 (each one represents an isolated track) and characterised by a FL/FW ratio of 1.17, 1.68 and 1.28, respectively (González Riga et al., 2015). These tracks do not preserve digital pads. The AT l/w ratio and the divarication of digits II–IV for morphotype tracks 3, 4 and 5 were measured and calculated from Fig. 5 of González Riga et al. (2015), resulting in the values: 0.32, 0.46 and 0.24 and 56º, 32º and 39º, respectively. The studied theropod tracks are bigger in size and display only a similar FL/FW ratio with morphotype 5. Moreover, they exhibit slender digit imprints and higher degree of mesaxony than the Loncoche Formation theropod tracks. Also, they display higher values of divarication of digits II–IV than morphotype 4 and 5, while morphotype 3 is included among the range values of the present theropod tracks. As a result of these comparisons, it is possible to conclude that the present theropod footprints are different from all those previously documented in the Neuquén Basin.

In order to assign an ichnotaxonomical status to the studied theropod tracks, they are compared with the ichnotaxa that are generally considered as valid (see Razzolini et al., 2017; Marty et al., 2018; Melchor et al., 2019).

The ichnofamily Grallatoridae Lull, 1904, includes ichnogenera such as *Grallator* Hitchcock, 1858; *Anchisauripus* Lull, 1904, *Prototrisauropus* Ellenberger, 1970, and *Picunichnus* Calvo, 1991, and comprises typically tridactyl (occasionally tetradactyl) footprints displaying moderate to marked elongation (FL/FW ratio > 1.50) and moderate to marked mesaxony (AT l/w ratio > 0.6) *sensu* the emended diagnosis by Melchor et al. (2019). In reference to these two parameters, the present theropod footprints exhibit a FL/FW ratio lower than 1.4 and a mean AT l/w ratio lower than 0.6.

Within the ichnofamily Eubrontidae Lull, 1904, *Eubrontes* Hitchcock, 1845 from the Late Triassic and Early Jurassic of New England (USA) is among the best known theropod tracks and has a wide distribution (Lucas et al., 2006). The ichnotaxon *Eubrontes giganteus* Hitchcock, 1858 is a large tridactyl track showing a FL/FW ratio of 1.4 to 1.5, digits imprints II–IV subequal in length and divarication of these outer digits in the range of 30º–40º. The AT l/w ratio was measured and calculated from the type specimen (Fig. 5A of Olsen et al., 1998) resulting in 0.5. The studied theropod tracks show a similar AT l/w ratio than *E. giganteus*, but display a lower FL/FW ratio, the digit imprints II–IV are not subequal and the divarication of these outer digits presents a higher range. *Jurabrontes* *curtedulensis* Marty et al., 2018 from the Late Jurassic of Switzerland is a giant tridactyl track (also assigned to the ichnofamily Eubrontidae) characterised by subequal track length and width, a small anterior triangle and weak mesaxony, broad and blunt digit imprints, asymmetrical heel and well-preserved phalangeal pad impressions. The present theropod tracks show a similar FL/FW ratio and also preserve pad imprints but display slender digit imprints, a higher degree of mesaxony and a heel more symmetrical than *J. curtedulensis*.

The ichnotaxon *Iberosauripus grandis* Cobos et al., 2014 from the Jurassic–Cretaceous transition of the Iberian Range (Spain), presents a FL/FW ratio of 1.2, broad digit imprints, a general symmetric morphology with a low degree of mesaxony and lateral digit impressions (II and IV) subequal in length. The present theropod tracks show a similar FL/FW ratio but are characterised by slender digit imprints, a higher degree of mesaxony than *I. grandis*, and also the digit imprints II and IV are different in length and preserve pad imprints. *Irenesauripus acutus* Sternberg, 1932 from the Aptian–Albian of Canada differs from large tridactyl tracks of this work because of the very narrow and slender digits and the lack of pad imprints. Some giant theropod ichnotaxa, more than 70 cm in length, such as *Tyrannosauripus pillmorei* Lockley and Hunt, 1994 from the Late Cretaceous of New Mexico and *Bellatoripes fredlundi* McCrea et al., 2014 from the Late Cretaceous of Canada that present broader and more robust digit impressions, which are significantly different than the present theropod tracks.

Megalosauripus Lessertisseur, 1955 is mainly known from Upper Jurassic–Lower Cretaceous deposits of Europe, America, and Asia (Razzolini et al., 2017 and references therein). Lockley et al. (2000) amended this ichnogenus as a medium to large, elongate tridactyl track and elongate heel, the trackway is very variable ranging from narrow to moderately wide, with pace angulation close to 120º. The type ichnospecies, *M. uzbekistanicus* Gabuniya and Kurbatov, 1982, is a large theropod track (length>40 cm) that has been amended by Fanti et al. (2013). This ichnotaxon is characterised by elongated (average FL/FW ratio of 1.2) and asymmetric tridactyl tracks, shows clear phalangeal pad imprints with the sigmoidal shape of digit III, and an average divarication angle between digit II–III and III–IV of 40º and 30º, respectively. The present theropod tracks are smaller in size but display a similar

FL/FW ratio than *Megalosauripus* (1.26 vs. 1.2). Both tracks exhibit pad imprints but the studied tracks lack the sigmoidal impression of digit III and present the impression of the proximal pad of digit IV situated posteriorly more aligned to the axis of digit III than *Megalosauripus*.

The ichnotaxon *Asianopodus pulvinicalx* Matsukawa et al., 2005 from the Valanginian–Barremian Kuwajima Formation of Japan is a small to medium-sized (27.0–30.0 cm in length) tridactyl, mesaxonic and subsymmetric track that shows a well-developed and sub-rounded heel pad situated posteriorly and aligned to the axis of digit III. Xing et al. (2014) also reported tracks assigned to the ichnogenus *Asianopodus* from the Lower Cretaceous of the Lanzhou-Minhe Basin, China. Although the present theropod tracks from the Candeleros Formation are slightly more asymmetrical (due to the unequal lenght external digit imprints) than *A. pulvinicalx* and present different FL/FW ratio (range 1.16–1.39 vs. 1.38–1.62 in *A. pulvinicalx*), they show strong similarities including: size (mean length 28.2 cm vs. 28.6 cm in *A. pulvinicalx*), AT l/w ratio (0.48–0.61 vs 0.40–0.46 in *A. pulvinicalx*, measured from tracks 2 and 4 of Fig. 8A, Matsukawa et al., 2005), divarication of digits II–IV (48º–76º vs. 42º–59º in *A. pulvinicalx*) and pace length (89–99 cm vs. 91–136 cm in *A. pulvinicalx*). Also, the distinct circular heel impression situated posteriorly and aligned to the axis of digit III is an identical feature shared between *Asianopodus* and the theropod tracks studied in this work. This feature, although present in some tracks from the Jurassic, is most common in theropod tracks from the Early Cretaceous (Xing et al., 2014), and there is also documented from the earliest Late Cretaceous.

Based on the similarities and especially the differences between the tridactyl tracks studied in this work and *A. pulvinicalx*, and taking into account the preservation of the studied tracks (not optimal), we consider that there are insufficient diagnostic features to erect a new ichnotaxon. Therefore, the studied tracks are here referred to aff. *Asianopodus pulvinicalx*.

9. Trackmaker

The Candeleros Formation presents one of the most diverse theropod faunas from any Cretaceous formational unit in South America (Canale et al., 2016; Novas et al., 2012, 2013). This theropod diversity includes: the huge carcharodontosaurid *Giganotosaurus carolinii* Coria and Salgado, 1995 of approximately 13 m in length; abelisaurids such as *Ekrixinatosaurus novasi* Calvo et al., 2004, estimated in almost 8 m in length; a basal coelurosaur *Bicentenaria argentina* Novas et al., 2012 of about 3 m in length; and small theropods, less than one metre long, such as the alvarezsaurid *Alnashetri cerropoliciensis* Makovicky et al., 2012 and the dromaeosaurid *Buitreraptor gonzalezorum* Makovicky et al., 2005.

Taking into account the theropod track record documented from the Cenomanian Candeleros Formation, Calvo (1991, 1999) and Calvo and Rivera (2018) suggested trackmakers for the registered ichnotaxa: *A. astigarrae* could have been produced by carcharodontosaurids; *B. patagonicus* and *D. mapuchensis*, by a medium-sized theropod (probably a coelurosaurid); and both *P. benedettoi* and *C. canalei* could have been produced by undetermined theropods. Also, Krapovickas (2010) proposed that the ichnospecies *Limayichnus major* Calvo, 1991 previously attributed by Calvo (1991, 1999) to ornithopods, is actually a theropod track: the blunt digit imprints would be due to extra anatomical issues influenced by the consistency of the soft substrate. Therefore, due to the extremely large size (about 60 cm in length), *L. major* was probably produced by carcharodontosaurid theropods. No abelisaurid trackmaker has been proposed for any track in this Cenomanian unit.

The footprint length (FL) of the foot of a bipedal dinosaur comprises the total sum of lengths of phalanges in digit III (ΣP) together with claw sheath, joint capsules, base of the metatarsus and possibly a fleshy heel (Kim and Hug, 2010). ΣP and the metatarsals length of *Bicentenaria* were measured from Fig. 5 of Ezcurra and Novas (2016), resulting both in about 18 cm in length. This is consistent with the observations for bipedal dinosaurs of Thulborn and Wade (1984) that the length of metatarsus is often about the same as ΣP. Considering the measurement of ΣP for *Bicentenaria* and that this represents about 80% of the total length of the theropod foot (Kim and Hug, 2010, Fig. 4), it is possible to estimate a footprint size of about 20 cm long. Accordingly, between the theropods documented so far in the Candeleros Formation, only the abelisaurids and carcharodontosaurids had such a large posterior autopod that they could have left footprints of the dimensions recorded in the present work (28 cm in length).

Carcharondontosaurids and abelisaurids present clear differences in their posterior autopods, especially in the metatarsals. For instance, the carcharodontosaurids have the typical theropod pes with robust metatarsians II, III and IV, and the distal end of metatarsian IV laterally projected. Abelisaurids, however, have a robust metatarsian III and poorly developed metatarsians II and IV (the "antarctometatarsalian" condition; see Carrano and Sampson, 2008), and metatarsals are straight distally. The "antarctometatarsalian" pes structure is comparable, as a whole, with the arctometatarsalian pes present in tyrannosaurids, ornithomimids and troodontids among others (Holtz, 1994), and the tarsometatarsus pedes typical of birds (Milàn, 2006). While the majority of theropod pedes are clearly asymmetric (Wright, 2004), the last two type of pes would impress more symmetrical footprints (Wright, 2004). It is possible that antarctometatarsalian pes, and hence the abelisaurids, could also leave symmetrical tracks. Therefore, abelisaurids are suggested as the possible trackmakers of the large theropod tracks from the present new tracksite.

The tridactyl tracks of medium and small size are poorly preserved. As a result there is no evidence to determine whether these tracks were produced by a theropod or an ornithopod trackmaker, and they remain attributed to an undetermined bipedal dinosaur.

10. Palaeobiological discussion: gregarious behaviour

The gregariousness among non-avian theropods from monoespecific bonebed assemblages was proposed by several authors and is presented in at least seven clades: coelophysoids, ceratosaurians, carcharodontosaurids, coelurosaurs, tyrannosauroids, ornithomimosaurids, troodontids, dromaeosaurids and oviraptorids (Colbert, 1990; Varricchio, 1995; Horner, 1997; Currie, 2000; Eberth and McCrea, 2001; Kobayashi and Lü, 2003; Coria and Currie, 2006; Martínez and Novas, 2006; Roach and Brinkman, 2007; Funston et al., 2016). Taking into account this kind of evidence it was proposed that the gregarious behaviour represents an ancestral ethological condition for the clade Theropoda, and perhaps even for Dinosauria (Novas et al., 2012).

In South America, body fossil evidence for gregarious behaviour in non-avian theropods is restricted to the early Late Cretaceous of Argentina: the large carcharodontosauridae *Mapusaurus roseae* from the late Cenomanian–early Turonian Huincul Formation (Coria and Currie, 2006; Coria, 2007) and small coelurosaurians including *Bicentenaria argentina* from the Cenomanian Candeleros Formation (Novas et al., 2012) and *Aniksosaurus darwini* from the Cenomanian–Turonian Bajo Barreal Formation (Ibiricu et al., 2013).

Parallel trackways with the same direction are key to propose gregarious behaviour in dinosaurs, but they must also satisfy certain additional conditions: the trackways should have similar preservation and uniform depth, lack of superposition, and indicate similar speed (Thulborn and Wade, 1984). Additionally, the existence of physical barriers could condition the passage of solitary individuals in the same place, with gaits of similar direction at different times (Getty et al., 2017).

The only footprint record of non-avian theropods from South America that has been suggested to indicate gregariousness corresponds to tracks from the Early Cretaceous of Chile: two parallel trackways showing similar pace lengths and footprint morphologies were attributed to spinosaurids and carcharodontosaurids (Moreno et al., 2012). In Argentina, another track record from the Cenomanian Candeleros Formation (Isla del Cerrito tracksite) comprises five theropod trackways attributable to *Candeleroichnus canalei* (Calvo and Mazzetta, 2004; Calvo and Rivera, 2018). Three of these trackways are parallel (see Fig. 12 from Calvo and Rivera, 2018) and present the same direction of travel, pace and stride and the apparent same preservation, suggesting theropod gregarious behaviour. For the Early Cretaceous of Argentina, four parallel theropod trackways orientated in the same direction were documented in mixed marginal marine siliciclastic-carbonate deposits from the Agrio Formation (Neuquén Basin; Pazos et al. 2012). These tridactyl tracks are preserved as true tracks and the parallel trackways present similar pace and pace angle and also the same track size. Some of these tracks appear superimposed by small wave ripples indicating that they were covered by water after their formation. Nevertheless, one of the trackways shows their footprints deeply impressed in the substrate and disturbing the ripples. It was concluded that this trackway was imprinted after withdrawal of the water, when the surface was subaerially exposed again, as a result showing the presence of more than one trampling episode on the same palaeosurface and fluctuations in the coast line (Pazos et al., 2012). For the other three parallel trackways, a gregarious behaviour is not disregarded.

The group of large-sized tridactyl trackways recorded in the present work (area A) show unvarying depth indicative of similar substrate consistency along each trackway. This suggests that the trackmakers walked at the same time, or the temporal window between them was short enough for the conditions of substrate consistency not to change. In addition, in area A no evidence of more than one trampling stage on the same palaeosurface was found. Following Alexander (1976) it was possible to estimate that all of the large-sized tridactyl trackways indicate normal walking progression at speeds between 1.78 and 2.20 m/s and a mean speed of 2 m/s. Both trackways 5 and 6 have exactly the same speed: 2.01 m/s.

Despite the fact that both theropod and undetermined tridactyl trackways are found in the same palaeosurface with sauropod trackways, no configuration that suggests hunters following prey *sensu* Lockley and Hunt (1995) has been recognized. In comparison with other tracksites (e.g. García-Ortiz and Pérez-Lorente, 2014) the present tracking surface is poorly dinoturbated; in an area of 150 m² there is no overlap between any of the parallel trackways (Fig. 4). In addition, in each of the groups of parallel trackways, no significant differences in track size and morphology were found. Thus, each group of trackways was made by individuals of the same size, disregarding the possibility of different ontogenetic stages (e.g. juveniles and adults). Even when the passage of two animals may be fortuitous as suggested by Ostrom (1972), the group of five parallel trackways with similar features analysed here greatly reduces this possibility. Furthermore, this author mentioned that the presence of parallel trackways in opposite directions is a starting point for suspecting the existence of some kind of physical barrier that affected the passage of individuals. Something similar was proposed by Getty et al.

(2017) for a tracksite from the Lower Jurassic of the Hartford Basin (USA) where parallelism is only outstanding in permanent lacustrine palaeoenvironments. These authors concluded that trackways show a bimodal orientation distribution that approximates the palaeoshoreline, and also that the differences in track morphology suggest that they were made at different times. Trackways with perpendicular orientations can be produced in environments with physical barriers as was observed in actual ecosystems such as lakesides; where some animals have left trackways perpendicular to the lakeshore, moving to watering, while others have produced trackways parallel to the shoreline (García-Ortiz and Pérez-Lorente, 2014). Nevertheless, in the last case, all the tracks were left by the same type of trackmaker involving both directions. In this way, the existence of other deviating trackways could indicate that the trackmakers were probably not confined in their passage by physical barriers (Ostrom, 1972). In the case of the present tracksite, the groups of parallel trackways have different orientations and consist in different track morphologies, each of which suggests different trackmakers who only moved in one direction. On the other hand, sedimentological evidence did not reveal the existence of any large scale fluvial channel, neither lake facies that can act as a physical constraint conditioning the direction of the theropod trackmakers gait.

Finally, although the small and medium-sized tridactyl tracks from the present tracksite could not be determined as theropod in origin, both groups of tracks are arranged in a pattern of parallel trackways. In the case of the small footprints consisting of two trackways (area A) with the same orientation (Figs. 4B; 5C) their tracks display similar morphology, depth imprint and length pace. On the other hand, medium-sized footprints consisting of three parallel trackways (area B) include two trackways (Figs. 4B; 7J) with equal orientation and similar track morphology, depth imprint, type of preservation, stride and speed estimation. Taking into account these observations and that the gregarious behaviour was common among small bipedal dinosaurs (e.g. Lockley and Matsukawa, 1999), it can be interpreted for each trackway set that they were probably made by bipedal dinosaurs walking together at the same time.

Conclusions

Several parallel theropod trackways have been recorded in the Cenomanian Candeleros Formation (Neuquén Basin) from northwestern Patagonia, Argentina. This evidence consists mainly of five non-overlapping tridactyl trackways of large track size (average length of 28 cm), which possess similar stride, speed estimation, preservational features, uniform depth and the same direction. They are preserved as shallow undertracks in a medium-grained sandstone bed interpreted as floodplain deposits, whereas the overlaying thin layer of muddy-siltstone is suggested as the tracking surface. Additionally, it is proposed that the presence of swelling clays (smectite) and the co-occurrence of microbial mats in the track-bearing level might have played an important role in the substrate stabilization and track preservation. The present theropod tracks are clearly different from the other theropod ichnotaxa known from the Candeleros Formation and other theropod track records documented in the Neuquén Basin. After the comparison with similar well-known theropod ichnotaxa worldwide, the studied theropod tracks show differences with all of these. However, considering the preservation of the studied tracks there are not enough diagnostic features to erect a new ichnotaxon. Therefore, it is proposed for the time being to assign the studied tracks to the most similar ichnospecies: aff. *Asianopodus pulvinicalx.* From the theropod taxa known from the Candeleros Formation only the abelisaurids and carcharodontosaurids had such a large posterior autopod able to produce tracks of the dimensions recorded in the present work. Taking into account the differences between the autopod and their metatarsal configuration from these two clades and comparing their morphology with the studied track, abelisaurid theropods are suggested as possible trackmakers. Furthermore, in the same stratigraphic surface other undetermined tridactyl parallel trackways, smaller in size and with different orientations than the aforementioned group of parallel theropod trackways, were recognized. A temporal sequence between sauropod tracks and the medium-sized tridactyl tracks, evidenced by overlapping and different preservations conditioned by changes in substrate consistency, was documented. Physical barriers (i.e., large fluvial channels or perennial lake) that could condition the direction of the theropod trackmaker gaits were not recognized in the track-bearing level nor were in the analysed interval. Therefore, taking into account that the five parallel trackways of large track size possess similar features (stride, speed, preservation, depth, and direction) and that there are no evidences of physical constraints, a gregarious behaviour for their theropod trackmakers is proposed.

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Fig. 1. A) Satellite image of the Neuquén Basin (Northern Patagonia) showing basin boundary and major structural features (modified from Naipauer et al., 2015). The Aguada de Tuco study area, that includes the tracksite documented by Heredia et al. (2019) and the new tracksite, is shown by a red star. Other localities of the Candeleros Formation cited in the text are displayed with green squares: the type localitiy and a work of Garrido (2010) in (1), Gazzera and Spalletti (1990) in (2), Spalletti and Gazzera (1994) in (3), Sánchez and Asurmendi (2015) in (4) and Candia Halupczok et al. (2018) in (5); B) Upper Jurassic–Palaeogene stratigraphic chart for the Neuquén Basin (modified from Howell et al., 2005 and Garrido, 2010). The Candeleros Formation is shown by a red arrow.

Fig. 2. Measurements of tridactyl track: A) *FL* track length and *FW* track width, *DL* digit length for digits II-III-IV; B) interdigital angles II^III, III^IV and II^IV, anterior triangle (*AT* in grey colour), *ATw* is the width and *ATl* the length (measured perpendicular to the width) of the anterior triangle. Tridactyl trackway measurements and parameters in C): *L1* and *R1* represent the first left and right footprints, respectively, *lPL* and r*PL* are left and right pace length, respectively, *SL* stride length, α pace angulation, *WAP* width of the pes angulation pattern or trackway width. Scales are approximate.

Fig. 3. A) Schematic log for the lowermost part of the Candeleros Formation (Cenomanian) in the Aguada de Tuco area showing the lower and upper interval. Modified from Heredia et al. (2019). The sauropod tracks showing by an asterisk represent the finding documented by Heredia et al. (2019),

while the other dinosaur tracks belong to the present work; B) halite molds probably replaced by hematite cubic crystal. Scale bar = 1 cm; C) U-shaped burrows assigned to *Arenicolites* isp., the lower curved portion of the tube is indicated by a white arrow. Scale bar = 2 cm; D) sandstone beds with planar cross-stratification limited by low-angle reactivation surfaces (white arrow). Note the opposite palaeoflow direction (grey arrows). Rock pick = 33 cm; E) wave ripples. Rock pick = 33 cm; F) the track-bearing level analysed in this work.

Fig. 4. A) Photogrammetric orthomosaic of the track bearing surface. It is available in highest resolution in the supplementary material. B) Schematic map of the tracks. The footprints in area A outside the line were uncovered after the photographs to generate this orthomosaic. Black arrows indicate the direction of parallel tridactyl trackways. Scale bar = 3 m; C) Rose diagram with directions of the ten trackways recognized.

Fig. 5. Detail of the trackways shown in area A of Fig. 4. Large and small tracks can be observed in trackways 1 and 4–7 and 2–3, respectively. Besides the difference in size, these two sets of trackways have almost opposite gait directions. A) false-colour depth image in plane view; B) contour lines with 3 mm of equidistance; C) interpretative scheme. Scale bar = 1m. The 3-d model of this area is available as supplementary material.

Fig. 6. Track details from some theropod parallel trackways. The two upper row figures show the right track 4.3 preserved in medium-grained sandstones as natural cast in convex hyporelief (A–C) and their corresponding undertrack in concave epirelief (D–F): A) photograph in perspective; B) false-colour depth images in plane view; C) contour lines with 0.5 mm of equidistance; D) photograph in perspective; E) false-colour depth image in plane view; contour lines with 0.5 mm of equidistance. The

best preserved theropod track, right track 1.2 (G–J): G) photograph in plane view, H) interpretative scheme, I) false-colour depth images, J) contour lines with 0.5 mm of equidistance. Theropod tracks 5.1 and 4.2, right and left respectively, from different trackways and displaying the same direction: K) photograph in perspective, L) false-colour depth images in plane view; M) interpretative scheme of track 4.2.

Fig. 7. Parallel trackways with medium-sized tridactyl tracks. A–D, the only two tracks that show evidence of partially preserved digits as natural casts (gray colour): A) photograph of track 8.12, B) interpretative scheme of track 8.12, C) photograph of track 8.10, D) interpretative scheme of track 8.10; E) picture of trackway 8. Rock pick = 33 cm indicated by a circle. The tracks are preserved as negative epirelief as shown in track 8.2 (F–H): F) contour lines with 0.8 mm of equidistance, G) false-colour depth image, H) interpretative scheme. Scale bar = 10 cm; I) photograph of partial trackways 8 and 9. The three parallel trackways: J) interpretative scheme, the increasing numbering indicates the direction of movement. Scale bar = 1 m; K) false-colour depth image; L) contour lines with 3.4 mm of equidistance. The sauropod tracks associated are shown in Fig. 8.

Fig. 8. Parallel tridactyl trackways associated with sauropod tracks. A) Orthomosaic involving the tridactyl trackways 9 and 10, the only sauropod track with notorious rim (track 13) and three crescent-shaped manus sauropod tracks (11, 12 and 15) with similar orientation; B) false-colour depth image in plane view showing trackway 9; notice the rim from the subcircular track 13 represented by the strongest red colour. The only case of overlapping tracks (as a result of different trackmakers) recorded in the present tracksite: tridactyl track 10.4 overlaps the crescent-shaped track 11: C) interpretative scheme, D) false-colour depth image; E) photograph in perspective of what is shown in B). For both tridactyl trackways, their increasing numbering represents the direction of the trackmaker gait. A) and B) Scale bar = 60 cm, C) and D) Scale bar = 30 cm and E) Scale bar = 20cm.

Fig. 9. Petrographic characterisation of the track-bearing sandstone and the overlying muddy siltstone (tracking surface) under crossed (A, B, D) and parallel (C) nicols, respectively. A) and B) Representative examples of the sandstone with major framework grains: monocrystalline quartz (Qz), plagioclase (Pl) and volcanic lithic (Lv). Note a thin coating of clays around grains (red arrows) and cements of calcite (Calc) and quartz (Qzc). C) and D) Representative examples of the muddy siltstone with a clay and fine-grained silt sized matrix supporting sand-sized grains of quartz (Qz), plagioclase (Pl) and sedimentary lithic (Ls) of carbonate origin. Thin coating of clays also occurs around grains (red arrows).

Fig. 10. Mineralogical composition derived from XRD data. A) Bulk-rock powders from the track-bearing sandstone and the muddy siltstone. B) Oriented samples of the clay fraction. N: natural and G: glycol-24hs preparations. The sandstone (lower difractograms) and muddy siltstone (upper difractograms) in the oriented samples show the same mineral phases. Values are expressed in Å.

Fig. 11. SEM images. A) Boundary between the track-bearing sandstone and the overlying muddy siltstone. B–D) Different details showing very fine-grained detrital quartz (Qz) surrounded by clay particles. The delicate arrangement of chlorite/smectite (C/S) interstratified minerals indicates an authigenic origin. E–F) Organic structures at the top of the sandstone represented mainly by tubes. The detail in (G) shows filament-like structures that partially surround clay particles (arrows).

Declaration of interests

☒ 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Table 1. Average measurements and parameters of tridactyl trackways.

Trackways	Track Length (cm)	Track Width (cm)	FL/FW	Pace (cm)	Pace angle (degrees)	Stride (cm)	Hip height (cm)	Speed (m/s)
1. Large (3)	28	22	1.20	99	164	196	113	2.20
2. Small (4)	11	06	1.68	47	164	94	42	1.95
3. Small (2)	10	07	1.36	50	172	-	38	-
4. Large (3)	27	20	1.39	89	157	174	109	1.78
5. Large (3)	29	25	1.16	98	161	195	116	2.01
6. Large (3)	29	22	1.30	95	169	193	114	2.01
7. Large (3)	28	23	1.23	95	169	186	110	1.97
8. Medium (16)	14	11	1.23	66	168	131	59	2.27
9. Medium (6)	14	11	1.32	67	173	135	54	2.64
10. Medium (7)	14	10	1.30	70	171	139	54	2.76

Bold numbers indicate the trackways reference while those in brackets are the number of tracks per each trackway; Large, Medium and Small indicate the size category; *FL* track length and *FW* track width. The complete table is provided as supplementary materials.

Table 2. Average measurements of large-size tridactyl tracks for each trackway.

Trackways	Divarication of digits (degrees)			Total digit length (cm)			Anterior triangle (AT)		
	II-III	III-IV	II-IV	II	III	IV	ATl (cm)	ATw (cm)	AT l/w
1	31.4	29.4	60.9	14	19	23	10	20	0.50
4	22.5	29.2	51.7	11	18	18	11	18	0.61
5	40.9	34.5	76.4	12	20	19	11	23	0.48
6	27.8	20.7	47.9	-	-	-	11	20	0.57
7	26.9	40.3	67.2	14	19	18	12	21	0.57

ATl anterior triangle length and *ATw* anterior triangle width, *AT l/w* anterior triangle ratio. The complete table is provided as supplementary materials.

Highlights

- Parallel theropod trackways from the Cretaceous (Cenomanian) of Patagonia are described.
- Abelisaurid theropods are suggested as trackmakers and gregarious behaviour is inferred.
- Tracks are preserved as shallow undertracks in floodplain deposits.
- Swelling clays and microbial mats may have played a role in track preservation.