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Dinosaur tracks at Cañadón de las Campanas and Villa El Chocón area (Late Cretaceous, Candeleros Formation), Patagonia, Argentina

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ABSTRACT

Several locations are known along the coast of the Ezequiel Ramos Mexía Dam, Neuquén province in Northwestern Argentinian Patagonia, comprising one of the richest dinosaur-tracking areas in South America. In this contribution we study a total of 166 dinosaur footprints and 31 dinosaur trackways recorded at the base of the Candeleros Formation (Cenomanian) from a new tracksite - Cañadón de las Campanas - and other localities nearby the Villa El Chocón area. The dinosaur footprints identified correspond to six morphotypes assigned to two ichnotaxa and three others are left with open nomenclature: *Bressanichnus patagonicus*, cf *Brontopodus* isp. (*Sauropodichnus giganteus*), large U-shaped tridactyl footprints (*Limayichnus major*), medium-siz ed tridactyl footprints and small-sized tridactyl footprints. The ichnotaxa *S. giganteus* and *L. major* are considered *nomen dubium*. Particularly, *B. patagonicus* presents two morphologies at the posterior margin of the footprint (rounded and narrow) most likely related to varying gaits and/or changing behavior. As a result, the herein presented ichnofauna is interpreted as produced by non-avian theropod of varied sizes (large sized = large U-shaped tridactyl footprints, medium to large size = B. *patagonicus*, medium size = medium-sized tridactyl footprints and small size = small-sized tridactyl footprint) and one large-sized sauropod dinosaur (cf. *Brontopodus* isp.).

Keywords: Vertebrate ichnology, Mesozoic, Neuquén Basin, sauropods, non-avian theropods.

RESUMEN

Huellas de dinosaurios del Cañadón de las Campanas y el área de la Villa El Chocón (Formación Candeleros, Cretácico Tardío) Patagonia, Argentina

Numerosos afloramientos a lo largo de la costa del Embalse Ezequiel Ramos Mexía, provincia de Neuquén en el noroeste de la Patagonia argentina, comprenden uno de los sitios icnológicos de dinosaurios más ricos de Sudamérica. En esta contribución estudiamos un total de 166 huellas y 31 rastrilladas de dinosaurios registradas en la base de la Formación Candeleros (Cenomaniano) de la nueva localidad Cañadón de las Campanas y en otras áreas en los alrededores de la Villa El Chocón. Las huellas de dinosaurios identificadas corresponden a seis morfotipos asignados a dos icnotaxa y tres morfotipos mantenidos en nomenclatura abierta: *Bressanichnus patagonicus*, cf. *Brontopodus* isp. (*Sauropodichnus giganteus*), huellas tridáctilas grandes en forma de U (*Limayichnus major*), huellas tridáctilas medianas y huellas tridáctilas pequeñas. Los icnotaxones *S. giganteus* y *L. major* son considerados *nomen dubium.* Particularmente, *B. patagonicus* presenta dos morfologías del margen posterior de las huellas (redondeado y angosto) posiblemente relacionados con variaciones en el tipo de marcha y/o cambios en el comportamiento. Como resultado se interpreta a la icnofauna aquí presentada como producida por dinosaurios terópodos no avianos de diferentes tamaños (grande = huellas tridáctilas grandes en forma de U, mediano a grande = *B. patagonicus*, mediano = huellas tridáctilas medianas y pequeño = huellas tridáctilas pequeñas) y un dinosaurio saurópodo de gran tamaño (cf. *Brontopodus* isp.).

Palabras Clave: Icnología de vertebrados, Mesozoico, Cuenca Neuquina, saurópodos, terópodos no avianos.

INTRODUCTION

The Candeleros Formation records one of the most significant dinosaur footprint assemblages of South America in terms of abundance, diversity, and excellent preservation of dinosaur tracks. The ichnoassemblages are recorded along the coast of the Ezequiel Ramos Mexía Dam and in the north of Neuquén province in Agua de Tuco area, Argentina. The pioneer ichnologic studies were carried out by Calvo (1989, 1991) at the South extreme of the Ezequiel Ramos Mexía Dam nearby Picún Leufú (Fig. 1). Later other studies were performed around the same area (Calvo 1999, Calvo and Mazzeta 2004) and at the northwest and central east margin of the Ezequiel Ramos Mexía Dam at the Villa El Chocón and la Buitrera areas respectively (Calvo and Moratalla 1998, Calvo and Lockley 2001, Candia Halupczok et al. 2018) and, more recently in a new locality between Chos Malal and Añelo cities in the central-north of Neuquén province (Heredia et al. 2019, 2020). So far, a total of ten ichnogenera of pterosaur, non-avian theropod, sauropod and ornithopod tracks were described. Eight were presented to describe the Picún Leufú material (Calvo 1991, 1999, Calvo and Moratalla 1998) and one was introduced to describe material of a norther area (Heredia et al. 2020). In addition, in the Candeleros Formation other three unnominated morphotypes (Krapovickas et al. 2007, Krapovickas 2010, Heredia et al. 2019) and multiple tracks in cross section (Candia Halupczok et al. 2018) are recorded.

Regarding the vertebrate body fossil record of the Candeleros Formation, it comprises a great diversity of forms, including dipnoan fishes, pipimorph amphibians, chelid turtles, uruguaysuchid crocodylomorphs, basal snakes, iguanian squamates, sphenodontians, pterodactyloid pterosaurs, sauropod and theropod dinosaurs, and mammals, recovered in the central-south of Neuquén and west of Río Negro provinces (Calvo and Salgado 1995, Coria and Salgado 1995, Calvo 1999, Ortega et al. 2000, Baez et al. 2000, Apesteguía and Novas 2003, Apesteguía et al. 2005, 2007, Apesteguía and Zaher 2006, de la Fuente et al. 2006, Otero et al. 2011, Rougier et al. 2011, Haluza and Canale 2013, Novas et al. 2013, Canale et al. 2016).

Herein we present a study of the dinosaur tracks preserved in the vicinity of the Villa El Chocón area (Villa El Chocón and, Balneario Villa El Chocón) and Cañadón de las Campanas at the NW margin of the Ezequiel Ramos Mexía Dam. The focus of this work is to evaluate the footprint record in terms of richness of morphotypes, ichnotaxonomy and possible producers.

GEOLOGIC SETTING

The Neuquén Group (Stipanicic et al. 1968) conform a succession of continental deposits of fluvial, aeolian and shallow lacustrine origin of approximately 1,200 m thick (Cazau and Uliana 1973). They were accumulated during Cenomanian-Early Campanian times in the Neuquén foreland basin system (Franzese et al. 2003).

The litostratigraphy framework of the group was proposed by Cazau and Uliana (1973) and latter modified by Ramos (1981) and Garrido (2010). The basal unit of the Neuquén Group is the Río Limay Subgroup that comprises the Candeleros and Huincul Formations. The Río Neuquén Subgroup comprise the Cerro Lisandro, Portezuelo, Los Bastos, Sierra Barrosa and Plottier Formations. Finally, the Río Colorado Subgroup integrated by the Bajo de la Carpa and Anacleto Formations.

The Candeleros Formation is the basal litostratigraphic unit of the Neuquén Group (Upper Cretaceous) and its type locality is located at the Los Candeleros hill, southeast of the Cerro Lotena south of Neuquén Province (Wichmann 1927). The thickness of the sequence reaches up to 300 m of coarse- to medium-grained massive sandstones and conglomerates of reddish to violet color and it was interpreted as deposited in braided fluvial systems and by eolian processes. The unit is Cenomanian in age (Vergani et al. 1995, Leanza et al. 2004) and overlies discordantly the Lohan Cura Formation of early Cenomanian age. At Villa El Chocón the unit comprises an approximately 100 m thick alluvial sequence of composed by fine-grained red to violet sandstone, greywacke and siltstone with thin evaporitic intercalations and, thin tuff levels occasionally preserved (Fig. 2). The succession is attributed to playa lake deposits, ephemeral fluvial channels, and aeolian dunes in a distal terminal fan context (Garrido 2010, Sánchez and Asurmendi 2015, Candia Halupczok et al. 2018). The dinosaur footprints are preserved at the base of the Candeleros Formation on playa lake and wet interdune deposits (Fig.

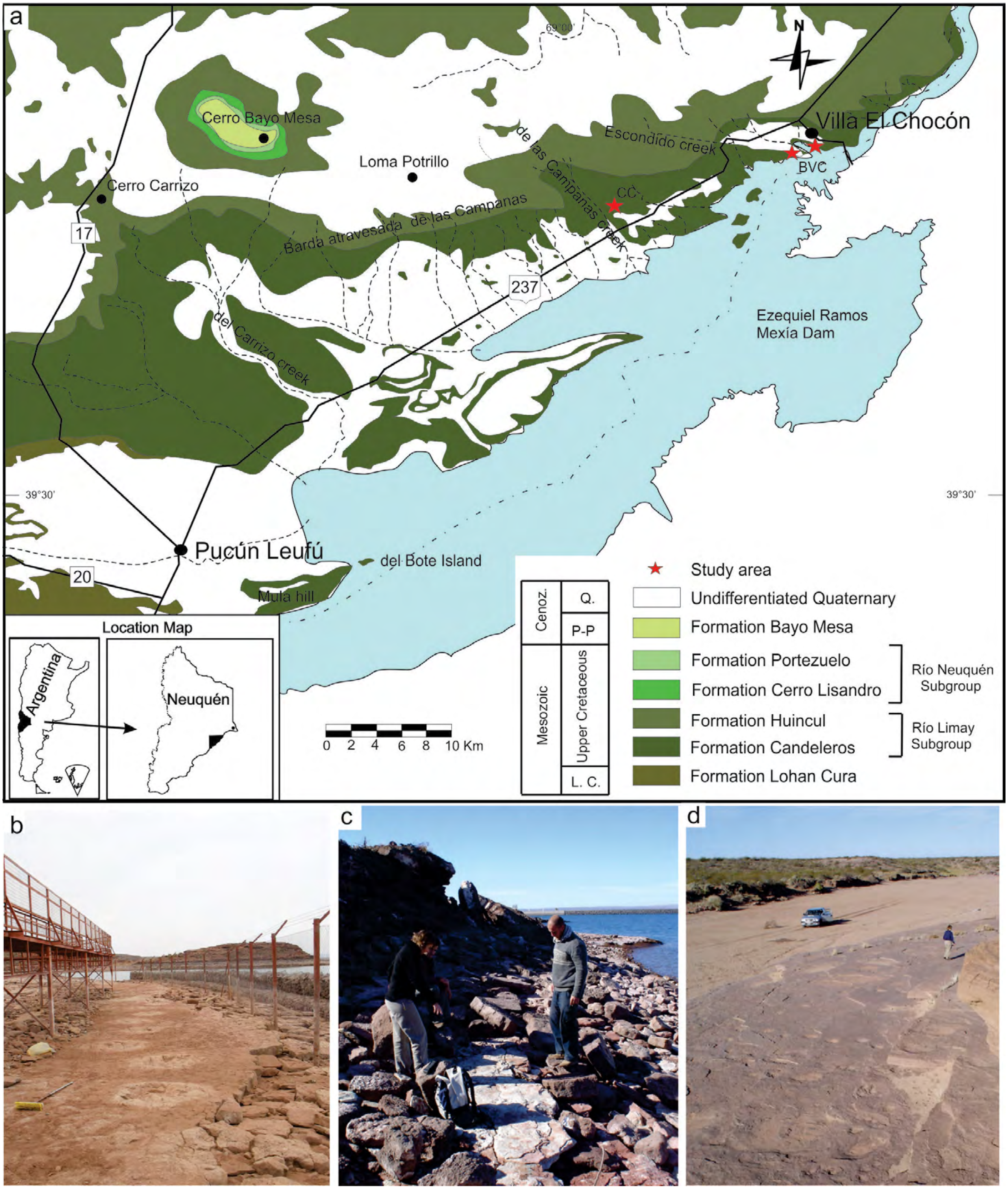

Figure 1. a) Geologic map of the Neuquén Group along the margins of the Ezequiel Ramos Mexía Dam, Neuquén Province. Modified from Garrido 2005 and Krapovickas 2010. Study area: b) Balneario Villa El Chocón (BVC); c) Villa El Chocón (VC); d) Cañadón de las Campanas (CC).

2) (see Krapovickas 2010). Wet interdunes are recorded by moderated sorted, medium- to fine-grained sandstone with a low percentage of mud matrix. Adhesion ripples, fluidization structures, and polygonal desiccation mud-cracks on mud-drapes are frequently preserved. Playa lakes are represented by intercalations of massive to laminated mudstones and massive, laminated to thin-bedded fine-grained sandstone. They are arranged in individual 5-15 cm thick tabular beds. Polygonal desiccation mud-cracks, deformational structures, and small gypsum fragments are frequently preserved. It is also observed local obliteration of sedimentary structures due to high bioturbation.

We studied three major areas (tracksites): 1) Villa El Chocón (39°15'56.2''S, 68°46'12.7''W), 2) Balneario Villa El Chocón with three tracking levels of lateral continuity (TI1 39°16'22.0'' S, 68°49'16,.''W; TI2 39°16'20.0'' S; 68°49'43.5'' W; TI3 39°16'19.5'' S; 68°49'28.8'' W) and 3) Cañadón de las Campanas preserved in five tracking levels of lateral continuity (TI1 39º20'05.6''S; 68º56'06.1''W; TI2 39º19'32.6''S; 68º56'43.1''W; TI3 39º19'04.3''S; 68º56'53.0''W; TI4 39º18'35.3''S; 68º57'08.6''W; TI5 39º18'27.4''S; 68º57'26.9''W) (Fig.1).

Particularly, at Cañadón de las Campanas the tetrapod footprints preserved corresponds to *B. patagonicus* and cf. *Brontopodus* recorded in playa lake and wet interdune deposits (Krapovickas 2010). At Villa El Chocón medium- and small-sized tridactyl footprints in playa-lake deposits (Krapovickas et al. 2007). At Balneario El Chocón, *B. patagonicus*, cf. *Brontopodus*, and large u-shape tridactyl footprints are recorded in playa-lake deposits (Krapovickas 2010).

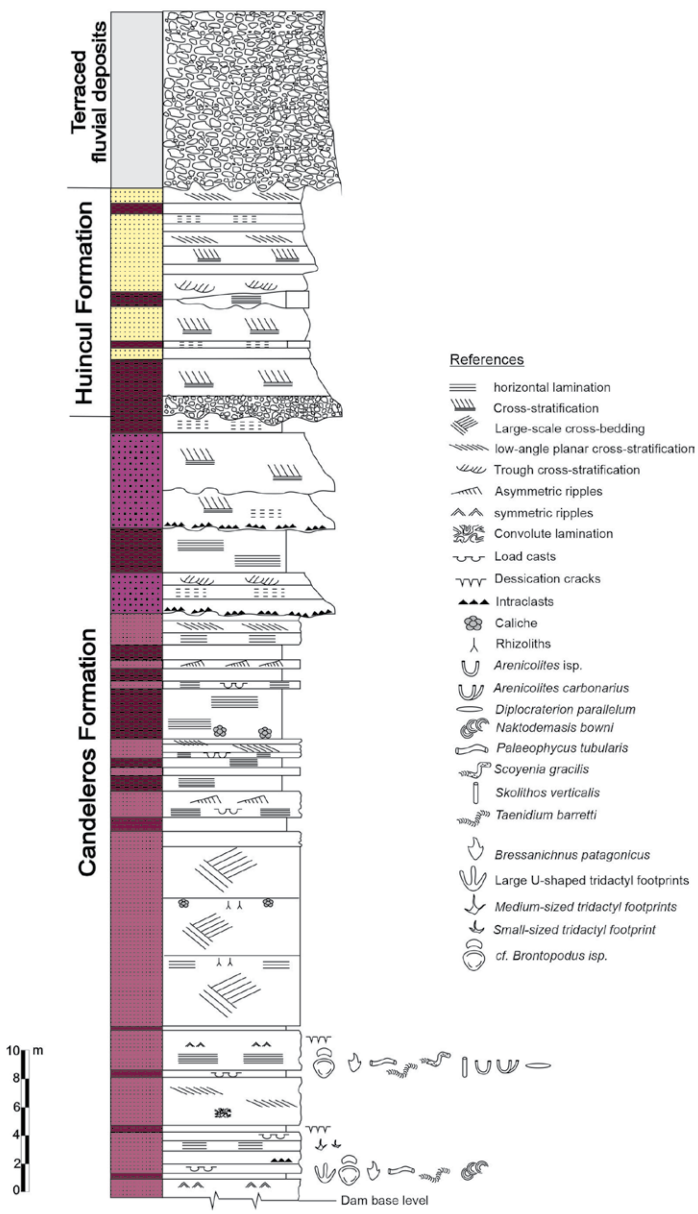

Figure 2. Schematic log of the Candeleros Formation at the Villa El Chocón area. Modified from Garrido 2005.

MATERIALS AND METHODS

A total of 166 individual footprints and 31 trackways are studied in this contribution. Most of the material is preserved *in situ*. Plaster casts of individual footprints and maps of the tracking surface are performed to preserve some of the most significant morphologies. Maps are made as 1m x1m grid and 1:1 scale map in transparent polyaniline. Two plaster casts are housed under MCF-PVPH-818, MCF-PVPH-819, and one map in transparent polyaniline under MCF-PVPH-817. Measurements are directly taken over the studied material. Institutional abbreviation: Museo Carmen Funes, Plaza Huincul, Neuquén Province, Argentina (MCF-PVPH).

Parameters to describe tracks and trackways are mostly used following Leonardi (1987) and Thulborn (1990). Track is employed as a synonym of footprint and defined as the impression on the substrate of the autopodium or part of the autopodium of a tetrapod. Parameters to describe footprints are: Track length (TL), measured parallel to the axis of the longest digit from the most anterior point to the most posterior point of the footprint. Trackwidth (TW), measured parallel to the transverse axis between the furthest medial and lateral points. Digit length (L), measured from the tips of the individual digits to the posterior outline of the footprint (Mccrea and Sarjeant 2001). Digit width (W) numbered in correspondence to each digit number as for digit length (e.g., LIV, WIV for the fourth digit). Interdigital angle (Div), measured from where the longitudinal axis of one digit intersects the posterior outline of the footprint and, to the longitudinal axis of another digit

(Currie 1981). Parameters to describe trackways are oblique pace (P), stride (S), pace angulation (P ang) (Leonardi 1987). In this work, trackway parameters were measured between pes. Extended tables of footprint and trackways morphometric data are available in (Krapovickas 2010). In sauropod tracks and trackways, heteropody [(*manus* area/*pes* area) x 100] is based on Lockley et al. (1994a), and the pes trackway ratio (PTR) to evaluate gauge patterns [(FW /TW) x 100], as proposed by Romano et al. (2007).

SYSTEMATIC ICHNOLOGY

Bressanichnus patagonicus **Calvo 1991**

Figs. 3-6. Tables 1-4.

Material: 108 footprints within 21 trackways preserved at Cañadón de las Campanas (CC) and Balneario Villa El Chocón (Table 1.1-1.6). MCF-PVPH-818 plaster cast of CC-TI4-R2-1, MCF-PVPH-819 - plaster cast of Nq-CC-TI2-R1-2, MCF-PVPH-817 map of the trackway CC-TI2-R4.

Description: Tridactyl footprints with well-defined claw

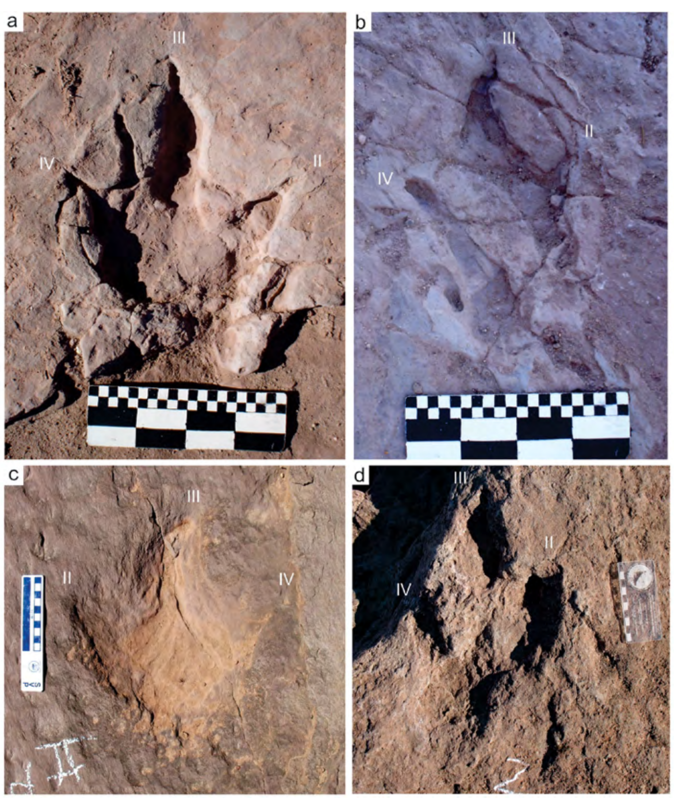

Figure 3. *Bressanichnus patagonicus* preserved at the Candeleros Formation: a) CC-TI4-R2-1, left impression. Note the rounded posterior margin of the footprint; b) CC-TI4-R1-3, left impression. Note the narrow posterior margin of the footprint; c) CC-TI2-R1 -2, right impression. Note the rounded posterior margin of the footprint; d) BC-TI2-R3-2, left impression. Note the rounded posterior margin of the footprint. Scale: white area = 1cm.

Figure 4. *Bressanichnus patagonicus* tracks and trackways recorded at TI2 Cañadón de las Campanas.

marks of a parasagittal biped animal of medium to small size. The impression of the central digit (III) is medially curved and longer that the lateral digits, that sometimes are not well defined (Fig. 3b-c). The impression of digit III shows at least two well defined digital pads. Digits II-III hypex is positioned more backward than that of digits III-IV. The posterior margin of the footprint is sub-rounded (Fig. 3a, c) to elongate (Fig. 3b, d) and varies within the same trackway. Digital impressions are relatively narrow. The average total length of the footprints is

Table 1. Footprint morphometrics of *B. patagonicus*. Cases with a rounded posterior margin of the footprint. 95 footprints measured. Measures in cm.

	FL	FW	DIV	ANG II-III	ANG III-IV	L II	L III	L IV	W II	W III	W IV
MAX	44.00	33.00	82.00	45.00	42.00	36.00	44.00	32.00	8.00	8.00	5.00
MIN	19.50	12.00	36.00	20.00	15.00	3.00	8.50	2.60	2.30	3.50	2.50
AVG	28.70	20.80	59.00	32.00	29.00	18.21	23.04	14.83	3.76	5.18	3.54
SD	4.55	3.74	10.00	6.00	7.00	10.71	10.13	8.54	1.52	1.12	0.99

Table 2. Trackway morphometrics of *B. patagonicus.* Cases with a rounded posterior margin of the footprint. 19 trackways measured. Measures in cm.

	PACE	STRIDE	P ANG
MAX	160.00	310.00	180.00
MIN	70.00	135.00	125.00
AVG	94.44	179.38	156.00
SD	16.02	27.18	14.00

Table 4. Trackway morphometrics of *B. patagonicus*. Cases with a narrow posterior margin of the footprint. 1 trackway measured. Measures in cm.

	PACE	STRIDE	P ANG
MAX	94.00	151.00	180.00
MIN	59.00	121.00	150.00
AVG	68.80	130.25	168.00
SD	14.34	14.08	13.00

Table 3. Footprint morphometrics of *B. patagonicus*. Cases with a narrow posterior margin of the footprint. 6 footprints measured. Measures in cm.

	FL	FW	DIV	ANG II-III	ANG III-IV	L II	L III	L IV	W II	W III	W IV
MAX	28.00	19.00	57.00	35.00	30.00	6.50	16.00	8.00	3.30	5.00	3.50
MIN	26.00	15.50	50.00	21.00	20.00	2.50	11.00	3.00	2.00	4.30	2.00
AVG	27.58	17.42	52.00	28.00	24.00	4.67	12.92	4.88	2.72	4.80	2.73
SD	0.80	1.24	3.00	5.00	4.00	1.60	1.69	1.70	0.47	0.32	0.54

281 mm (maximum length 400 mm, minimum length 200 mm). The average total width is 191 mm (maximum width 330 mm, minimum width 120 mm). The average inter-digital span between digits II-IV is 55º although it varies between 82º-36º.

The footprints with a rounded posterior margin have a long pace (average pace length 944 mm, stride length 1793 mm, and pace angle 156º) while those of an elongate posterior margin of the footprint have a shorter pace (average pace length 688 mm, stride length1302 mm, and pace angle 168º). The footprints are assigned to the category 1-3 of the preservation scale proposed by Marchetti et al. (2019).

Comments: The material herein described was previously assigned to *Irenesauripus* isp. by Krapovickas (2010) due to the footprints adjust to general description and dimensions of *Irenesauripus* Sternberg 1932. However, the larger and curved impression of digit III results characteristic of *B. patagonicus.* Recently, Calvo and Rivera (2018) mentioned the material of Cañadón de las Campanas as *Bressanichnus patagonicus* and herein we agree. However, the material of Balneario Villa El Chocón and Cañadón de las Campanas are bigger than the holotype described for Picun Leufú. *B. patagonicus* presents a rounded posterior margin of the footprint as well as most of the material included herein, although some footprints have an elongate posterior margin. *Deferrariischnium mapuchensis* Calvo, 1991 from the Ezequiel Ramos Mexía Dam results also comparable with some of the footprints in the elongate posterior margin. However, *D. mapuchensis* records a longer digit III impression compared to the lateral digit (II, IV) impressions and is markedly smaller (approximately 10 x 17 cm in width and length, respectively).

The material of the Candeleros Formation is also comparable to *Anchisauripus* Lull, 1904 on its general morphology and configuration of digital impressions. Although it differs on its size range (20-40 cm in length for *B. patagonicus* and 15-25 cm in length for *Anchisauripus*). The footprints are comparable in size to *Eubrontes* Hitchcock, 1845 although it differs on the sorter relative length of digit III, respect to the lateral digits and on the wider impression of the digits.

cf. *Brontopodus* isp.

Figs. 6 and 7. Table 5.

Material: Numerous footprints preserved in situ at Balneario Villa El Chocón and Cañadón de las Campanas.

Description: Footprints of a quadruped animal with impressions of the forefoot of sub-circular to kidney shape and hindfoot impressions sub-circular to triangular shape. In both

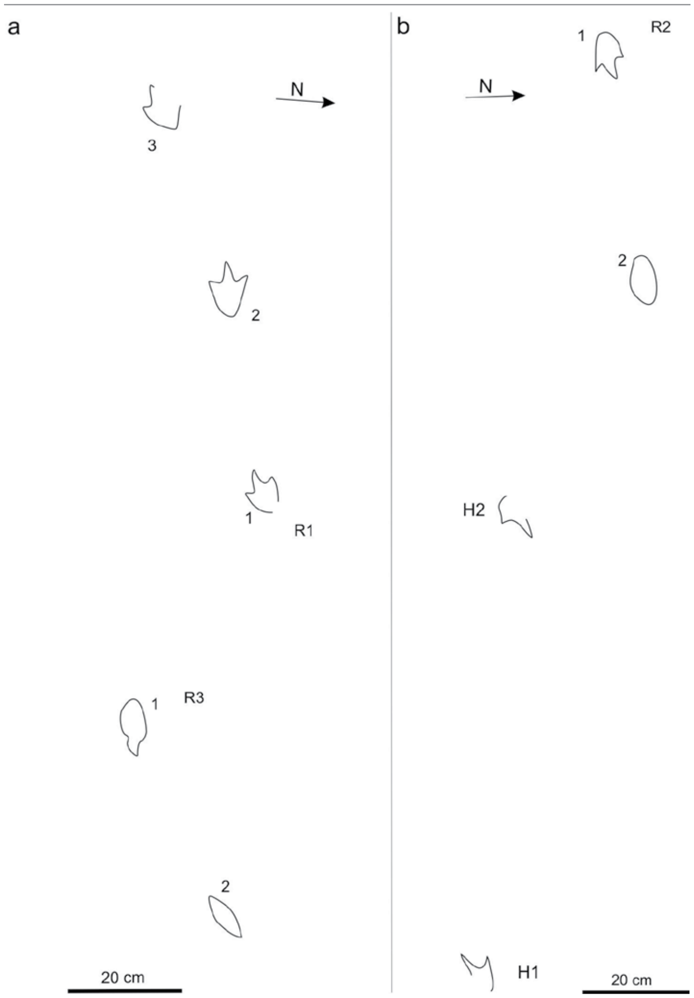

Figure 5. *Bressanichnus patagonicus* tracks and trackways recorded at TI1 Cañadón de las Campanas.

manus and *pes* digital impressions are not observed. *Manus* impressions are wider than long (average length 381 mm, average width 735 mm), are placed in front of the hindfoot impression, and are smaller than the pes impressions. The hind foot impressions are slightly longer than wide (average length 817 mm, average width 960 mm). A few examples show the posterior margin of the foot narrower than the anterior margin. Both *manus* and pes dimensions vary depending on the preservational context. The pes footprints produced in a soft and plastic substrate are preserved as sub-circular impressions of 120 to 140 cm in diameter and 25 cm in depth. The heteropody in trackways is marked (36.3 - 42.7 %), being manus less than half the area of the pes. Due to the fragmentary exposure of the outcrops, complete and large trackways are not observed. Numerous *manus-pes* sets are isolated in the same surface and, in most cases, they correspond to trackways that only preserved one side of the body. However, *manus-pes* set of both (left and right) sides of the body are observable in two short trackways (Fig. 6b) suggesting a wide-gauge type of trackway with a PTR of 22.8 - 24.7 %. The footprints are assigned to the categories 1-2 of the preservation scale proposed by Marchetti et al. (2019).

Comments: Several authors suggested that sauropod trackways can be placed in two general categories: narrow-gauge and wide-gauge (e.g., Farlow et al. 1989, Farlow 1992, Lockley et al. 1994b, Wilson and Carrano 1999) which mostly determine two ichnogenera *Parabrontopodus* (Lockley et al. 1994a) and *Brontopodus* (Farlow et al. 1989), respectively. On *Parabrontopodus* trackways the manus and pes imprints are placed nearby or at the midline of the trackways and the *manus* preserve the pollex impression. On the contrary, on *Brontopodus* the impressions of the sets *manus-pes* are well separated from the midline and they lack pollex imprint. The material preserved at Cañadón las Campanas and Villa El Chocón lacks morphological details such as digital impressions. However, a wide-gauge pattern is identified on trackway fragments. The morphology of the individual footprints, the manus-pes relationship and the putative pace and trackway fragments relate the footprint with the *Brontopodus* pattern as in Krapovickas (2010). The ichnotaxa *Sauropodichnus giganteus* proposed by Calvo (1991) and emended in (1999) is considered *nomen dubium* by Lockley et al. (1994a). As mentioned by Calvo (1999) both ichnotaxa (*Brontopodus* and *Sauropodichnus*) are strongly comparable. The other sauropods ichnotaxon erected for the Late Cretaceous of Argentina is *Titanopodus mendozensis* (González Riga and Calvo 2009). However, *T. mendozensis* differs from cf. S. giganteus on the manus impression of crescent shape with strongly asymmetrical contour and acuminate and thinner external border. In addition, cf. *Brontopodus* differs from *Calorckosauripus lazari* from the Late Cretaceous (Maastrichtian) of Cal Orck'o, Sucre Bolivia in the lower heteropody, the outward rotation of the *manus*, and the quadrangular shape of the *pes* in C. *lazari* (Meyer et al. 2018).

Table 5. Footprint morphometrics of cf. *Brontopodus* isp. 9 set m-p measured. Measures in cm.

	LT		AT	
	m	p	m	p
MAX	440.0	860.00	830.0	1050.0
MIN	290.0	750.00	610.0	830.0
AVG	381.1	817.5	735.6	960.0
SD	59.5	35.8	78.9	80.2

Large U-shaped tridactyl footprints

Figs. 6 and 8. Tables 6 and 7.

Material: 37 footprints in 5 trackways preserved at Bal-

Figure 6. Tetrapod footprints preserved at Balneario Villa El Chocón: a) cf. *Brontopodus* isp. preserved at TI3; b) cf. *Brontopodus* isp. and *B. patagonicus* preserved at TI2; c) *B. patagonicus* and large U-shape tridactyl footprints preserved at TI1.

Table 6. Footprint morphometrics of large U-shaped tridactyl footprints. Cases with a narrow posterior margin of the footprint. 37 footprints measured. Measures in cm.

	FL	FW	DIV	ANG II-III	ANG III-IV	L II	L III	L IV	W II	W III	W IV
MAX	90.00	74.00	72.00	40.00	35.00	66.00	90.00	78.00	54.00	28.00	21.00
MIN	54.00	51.00	45.00	20.00	20.00	46.00	48.00	28.00	14.00	15.00	8.00
AVG	72.68	63.30	56.00	28.00	28.00	58.44	72.54	60.79	29.95	21.43	17.14
SD	10.37	5.13	7.00	6.00	4.00	5.29	13.72	7.91	16.57	3.16	4.05

Table 7. Trackway morphometrics of large U-shaped tridactyl footprints. 5 trackways measured. Measures in cm.

	PACE	STRIDE	P ANG
MAX	200,00	382,00	172,00
MIN	160,00	327,00	150,00
AVG	183,00	358,78	160,89
SD	7,47	12,71	5,60

neario Villa El Chocón.

Description: Tridactyl footprints of a biped animal of large size. The impression of the digit III is longer than the lateral ones. The impression of the claws is present although is not well defined and in some poorly preserved examples it is blunt. In most of the footprints, digits II and IV are connected, so the posterior margin of the footprint is U-shaped.

The average total length of the footprints is 726 mm (maximum length 900 mm, minimum length 540 mm). The average total width is 633 mm (maximum width 740 mm, minimum width 510 mm). The average inter-digital span between digits II-IV is 56º although it varies between 72º-45º. The average pace length is 1830 mm, the average stride length is 3587 mm, and the pace angulation is in average 161º. The footprints are assigned to the category 1 of the preservation scale proposed by Marchetti et al. (2019).

Comments: These material, recorded at Balneario Villa El Chocón, is ascribed to *Limayichnus major* by Calvo and Rivera (2018). Detailed taphonomic analysis of the footprints show that they were produced in a highly-bioturbated soft substrate that prevented the preservation of morphological details allowing the precise characterization of the producer's autopodial morphology (Krapovickas 2010). Díaz-Martínez et al. (2015) consider *L. major* as *nomen dubium* due to the absence of diagnostic features and consider the footprints can-

Figure 7. Bearing levels of cf. *Brontopodus* isp. at Cañadón de las Campanas: a) Tl2; b) Tl5; c) cf. *Brontopodus* isp. preserved in mudstones of Tl2. Note the sub-circular *manus* impressions (m) and oval pes impressions (p). scale 30 cm; d) cf. *Brontopodus* isp. preserved in fine sandstones of Tl2. Note the kidney-like *manus* impressions (m) and the subtriangular *pes* impressions (p) with a narrow posterior margin of the foot. scale 10 cm.

not be assigned neither to theropod or ornithopod ichnotaxa. Moreover, they consider it to display a similar morphology to the ornithopod ichnogenus *Caririchnium* Leonardi, 1984. In South America, other Cretaceous large-sized tridactyl footprints are recorded in Querulpa Chico (Peru) and Chacarilla (Chile); both tracksites of Early Cretaceous age (Moreno et al. 2012). The large tridactyl footprints of Querulpa Chico and Chacarilla display a considerable smaller size than Balneario Villa El Chocón large tridactyl footprints (TL 59 ± 5 cm vs. 72.68 ±10.37 cm; 47 ±13 cm vs 72.68 ±10.37 cm, respectively). In addition, digits are slenderer and lack the typical U-shaped outline of the footprints.

They are also comparable on its general morphology and size to large tridactyl footprints produced by tyrannosaurids from the Upper Cretaceous of the USA (Manning et al. 2008). Some examples are similar to *Tyrannosauripus* from the Upper Cretaceous of the USA, although it presents the impression of digit I, absent in large U-shaped footprints (Lockley and Hunt 1995).

Medium-sized tridactyl footprints

Fig. 9a, c. Table 8.

Material: 11 footprints preserved *in situ* at Villa El Chocón

Description. Tridactyl footprints functionally mesaxonic with narrow digital impressions when the digit width represents a 10% of the total width of the footprint. The footprints are slightly longer than wide (maximum length 147 mm, minimum length 124 mm). Total digit divarication varies between 73º and 102º. They present claw marks and lacks hallux impression. A rhomboidal impression is placed on the posterior

Table 8. Footprint and trackway morphometrics of Medium size footprints. 11 footprints measured within 1 trackway. Measures in cm

	FL	FW	DIV	L II	L III	L IV	W II	W III	W IV	PACE	STRIDE	P ANG
MAX	16.7	13.9	102	10.4	16.7	10.61	1.3	2.3	1.5	70.0		
MIM	10.5	10.08	73	5.4	10.5	5.5	0.5	0.3	0.1	64.5		
AVG	14.7	12.4	87	8.4	14.7	8.8	0.7	1.2	0.7	67.25	133	170
SD	2.19	1.19	1.17	1.74	2.15	1.65	0.29	0.57	0.41	3.88		

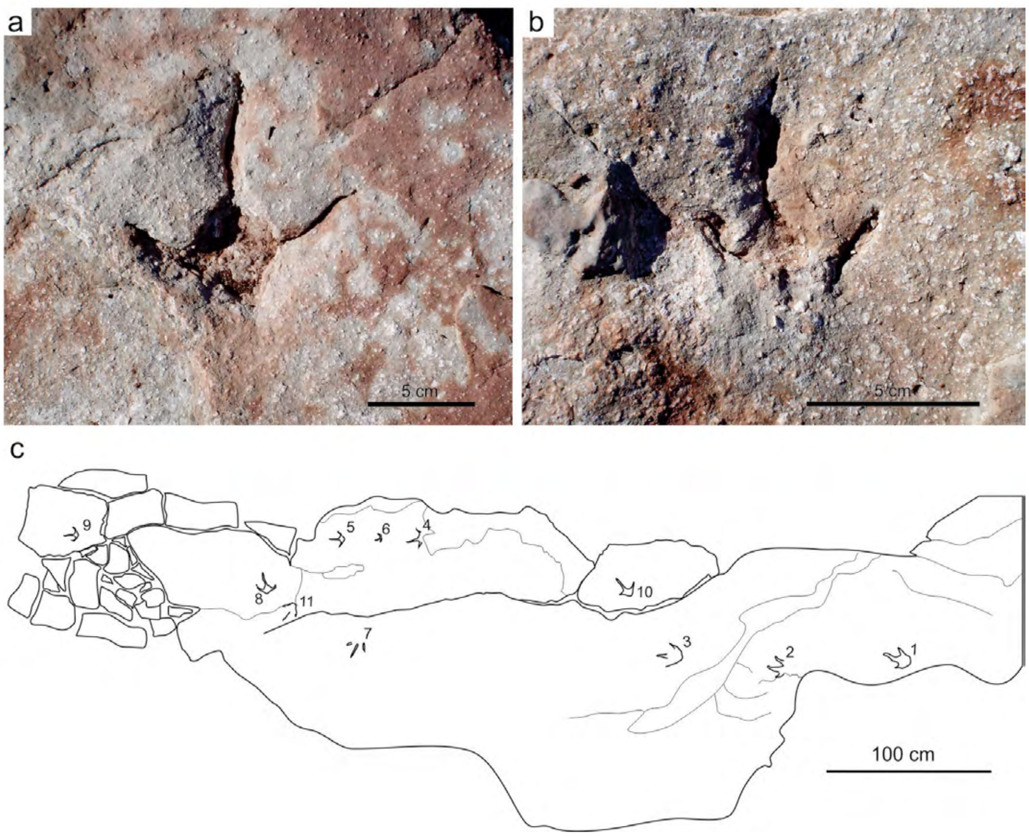

Figure 9. Small- and medium-sized tridactyl footprints preserved at Villa El Chocón: a) Medium-sized tridactyl footprints; b) Small-sized tridactyl footprint; c) map of tracks and trackways of small and medium-sized tridactyl footprints.

margin of the footprint where digits converge. Digit III is longer than the lateral ones (II and IV) which are sub equal in length. The average pace is 670 mm and the average stride is 1330 mm. The footprints are assigned to the category 1 of the preservation scale proposed by Marchetti et al. (2019).

Comments: The footprints differ from *Aquatilavipes* Currie, 1981 *Barrosopus* Coria et al., 2002 and *Yacoraitichnus* Alonso and Marquillas, 1986 in the smaller divarication angle. *Saurexallopus* Harris, 1998 are bigger footprints and have a well-preserved hallux impression. *Irenichnites* Sternberg, 1932 and *Magnoavipes* Lee, 1997 are bigger footprints and have a major length-wide ratio. *Columbosauripus* Sternberg, 1932 has a similar size and length-wide ratio but smaller divergence angle.

Small-sized tridactyl footprint

Fig. 9b-c.

Material: One footprint preserved in situ at Villa El Chocón.

Description: One isolated footprint preserved at the same level than the medium-sized tridactyl footprint. The footprint is slightly longer than wide, 75 mm long and 64 mm wide. It has delicate digital impressions, claw marks, II-IV interdigital angle of 100º, and lack of hallux impression. Lateral digits are shorter than the central one. The footprints are assigned to the category 1 of the preservation scale proposed by Marchetti et al. (2019)

Comments: The footprints are comparable to *Yacoraitichnus* and *Aquatilavipes* in its delicate digital impressions, an interdigital angle greater than 95º and, in lacking the hallux impression (Currie 1981, Alonso and Marquillas 1986, Lockley et al. 1992, Mccrea and Sarjeant 2001).

DISCUSSION

The tetrapod footprints preserved in the Candeleros Formation at Cañadón de las Campanas, Balneario El Chocón and Villa El Chocón are mostly attributed to non-avian theropods of varied sizes. *Bressanichnus patagonicus* record morphological traits and general dimensions that point toward a medium- to large-sized non-avian theropod dinosaur. These are tridactyl pedal prints of a bipedal animal with impression of digit III longer than II and IV and the presence of a pronounced ungual claw mark (Thulborn 1990, Carrano and Wilson 2001). In addition, in well-defined footprints produced on firm substrates of the Candeleros Formation and with almost non-existent post formational modifications (i.e., wind or water erosion, cracking, etc.) it is preserved a complete impression of digit IV, while the metatarsophalangeal joint of digits II and III is placed above the ground in a digitigrade position (Krapovickas 2010) (Fig. 3b). This generates an asymmetric posterior margin of the footprint classically produced by non-avian theropods and basal ornithischians (Farlow et al. 2000).

The material herein ascribed to *B. patagonicus* presents within the same trackways varying morphologies of the posterior margin of the footprint, reason why it is not considered a stable and diagnostic feature. This variability could represent distinctive locomotor postures of the same producer at varying gaits and changing behavior. Most of the footprints have a wide and rounded posterior margin and those of elongate margins are less frequently recorded (Tables 1, 3). The footprints with elongate posterior margin probably represent a more complete impression of the foot, with a total impression of digit IV. A preliminary study evaluated the morphological variation within *B. patagonicus* and its link to gait speed (as pace length), substrate consistency at the time of footprint implantation and post exhumation weathering of the footprints (Farina et al. 2019). The study did not show a clear association with any of these putative causes, suggesting it is more likely linked to varying postural gaits and changing behavior.

The Candeleros Formation has an extensive record of ichnotaxa attributed to non-avian theropods. Most of the footprints were documented along the coast of the Ezequiel Ramos Mexía Dam and corresponds to *Abelichnus astigarrae* Calvo, 1991, *Bressanichnus patagonicus, Deferrariischnium mapuchensis, Picunichnus benedettoi* Calvo, 1991, and *Candeleroichnus canalei* Calvo and Rivera, 2018. Recently, five new non-avian theropod trackways were documented at Agua de Tuco area, Neuquén province (Heredia et al., 2020). They were provisionally assigned to aff. *Asianopodus pulvinicalx* and assigned to abelisaurid theropods based on symmetric impression of the footprint most likely involving a robust metatarsian III and poorly developed metatarsians II and IV.

The large U-shaped tridactyl footprints from Villa El Chocón area and Cañadón de las Campanas are highly compatible with *Limayichnus major* from the nearby Picun Leufú locality. *L. major* was originally interpreted by Calvo (1991) as produced by large ornithopod dinosaurs mostly based on the absence of claw marks and the blunt anterior margin of the footprints. The taphonomic study of the footprints by Krapovickas (2010) revealed the footprints were produced in a strongly bioturbated soft substrate, both subaqueous and exposed to air. As a result, the morphological detail expressed in the footprints shows a low fidelity to the trackmaker pedal anatomy that neither allows a certain trackmaker identification nor sustains strongly supported ichnotaxa. Isolated footprints recorded at Balneario Villa El Chocón show claw marks and asymmetric posterior margin of the footprints with a notch behind digits II-III, pointing towards a large theropod dinosaur as putative producer. In addition, several authors (Meyer 2000, Krapovickas 2010, Apesteguía and Gallina 2011, Díaz-Martínez et al. 2015) suggested a theropod affiliation of the footprints and, moreover, Apesteguía and Gallina (2011) suggested carcharodontosaurid dinosaurs as possible trackmaker. It is not uncommon that large theropod footprints with low fidelity of the trackmaker autopodium are misinterpreted as ornithopod dinosaur footprints or even more distant taxonomic groups. So far, large U-shaped tridactyl footprints are herein interpreted as most likely produced by large theropod dinosaurs. The synapomorphies of the autopodium expressed on the footprints do not allow a farther certain interpretation. However, the size of the footprints, still enlarged by the preservation style, results coincident with those of carcharodontosaurid dinosaurs recorded at the Candeleros Formation. Another large-sized dinosaur footprint recorded in the unit corresponds to *A. astigarrae*, with an average footprint length and width of 48.5 cm and 43.5 cm, respectively (Calvo 1991, Calvo and Rivera 2018). They were also tentatively assigned to carcharodontosaurid dinosaurs (Calvo and Rivera 2018). Due to the comparable size and morphology of the footprints it is not discarded that large U-shaped tridactyl footprints (previously *L. major*) represent a preservational variant of *A. astigarrae.* However, that hypothesis needs yet to be tested.

Most of the medium-sized tridactyl footprints are preserved as true tracks and record collapse structures as they were produced in soft to soap grounds (Krapovickas 2010) (Fig. 9). A few footprints seem to be undertracks evidenced by its major dimensions and lower depths. Even though their morphology does not completely evidence the autopodium anatomy of the trackmaker, certain traits are evident. They present numerous traits that relate them with avian theropods as defined by Currie (1981), Lockley et al. (1992), Doyle et al. (2000), and Mccrea and Sarjeant (2001). They have a) narrow digit impressions, b) wide II-IV interdigital angle, c) a metatarsal pad impression where digits converge, and d) claw marks (Krapovickas et al. 2007). However, the thin digit impressions are most likely an artifact due to the collapse of sediments within the footprints and at least claw marks are not an exclusive avian trait. Moreover, there are other traits typical of Mesozoic avian footprints as pointed by the previously mentioned authors that are not present in the medium-sized footprints of the Candeleros Formation. They have a) interdigital divergence angle II-IV of 100º-120º or more, b) small size, c) length/width ratio of less than 1. Nevertheless, all these footprint morphological traits point specifically toward shorebirds rather than bird footprints in general. For example, certain cursorial birds (i.e., Rheiformes and Casuariiformes) lack delicate digits and the total divergence angle between digits II-IV is clearly less than 90º (Farlow et al., 2000); while some footprints attributed to non-avian theropods as *Magnoavipes* and *Saurexallopus* have interdigital angles as wide as any Mesozoic bird footprint (Harris, 1998). Martin et al. (2014) addressed a similar problem by distinguishing between similarly sized non-avian and avian dinosaur tracks in Early Cretaceous (Albian) of Victoria, Australia. All this suggests that there is a wide morphological superposition between avian and non-avian theropod footprints that needs to be treated more carefully. Thus, herein we interpret the medium-sized tridactyl footprints as produced by a medium to small non-avian theropod, even though birds cannot be completely discarded as producers.

As in the previously mentioned case, the small tridactyl footprints have some morphological traits typically attributed to avian theropods as delicate digit impressions, wide interdigital II-IV angle and, small size even though they are not exclusive of birds.

The footprints assigned to cf. *Brontopodus* are with certainty assigned to sauropod dinosaurs and tentatively to titanosaurs. The incomplete exposure of the tracking levels avoids a profound evaluation of the trackway patterns. However, the record of isolated manus-pes sets well apart from the midline on trackway fragments and PTR of 22.8 – 24.7 %, (Fig. 6b), points towards a wide-gauge sauropod trackmaker. Wilson and Carrano (1999) stated that titanosaurs (specially saltasaurines) are wide-gauge sauropods due to synapomorphies as an outwardly angled femoral posture, beveled knee condyles, and asymmetrical femoral midshaft causing wide foot stances in this large graviportal animal. The hypothesis that “titanosauriforms were capable of a greater degree of hind limb abduction and adduction” was corroborated quantitatively by Ullmann et al. (2017). The wet interdune and playa-lake deposits of the Candeleros Formation results a propitious environment for the formation and preservation of footprints, but unfortunately they are not adequate for footprint morphological details (Mancuso et al. 2007). As mention above cf. *Brontopodus* from Picún Leufú was previously interpreted as a wide-gauge trackway (*S. giganteus* in Calvo, 1999) and compared to *Brontopodus* which lacks a pollex imprint and the impression of the sets *manus-pes* are well separated from the midline. Heredia et al. (2019) interpreted cf. *Brontopodus* (*S. giganteus*) as a medium-gauge trackway proposed through the indirect calculation of the *pes*-trackway ratio (PTR), as proposed by Romano et al. (2007). However, the authors mentioned that the ratio found is very close to that of wide gauge trackways. Several authors pointed out that some sauropod trackways exhibit both narrow-gauge and wide-gauge stances, suggesting that the stance is not exclusively linked to the producer’s identity but also to changes in substrate consistency, speed, and particular behaviors or change in direction (Romano et al. 2007, Meyer et al. 2018). According to Ullmann et al. (2017), the wide-gauge posture afforded titanosauriforms greater static and dynamic stability by providing wider stability triangles while moving. The ability of these giant graviportal animals of narrowing gauge if necessary (e.g., turning, increasing speed) has not been proved to be anatomically prevented. The opposite (i.e., narrow-gauge sauropods producing wide-gauge trackways) seems more unlikely, in despite both premises have still to be tested. Another sauropod trackway has been recorded at the Candeleros Formation at the Agua de Tuco locality, between Chos Malal and Añelo cities, Neuquén province, Argentina (Heredia et al. 2019). The material corresponds to one trackway not assigned to any ichnotaxon due to the absence of clear anatomical details. However, it was possible to determine a narrow-gauge type of trackway and it was suggested as produced by a large-sized rebbachisaurid diplodocoid (Heredia et al. 2019). This is based on the idea that narrow-gauged trackways have been typically attributed to diplodocoids in the fossil record and in the record of the diplodocoids in the same stratigraphic unit (see Heredia et al. 2019).

The bone dinosaur record of the Candeleros Formation is probably one of the most diverse in any stratigraphic unit of South America (Canale et al. 2016). It comprises the titanosaur *Andesaurus delgadoi* (Calvo and Bonaparte 1991), the rebbachisarids *Limaysarus tessonei, Rayososaurus agrioensis*, and *Nopcsaspondylus alarconensis* (Calvo and Salgado 1995, Carballido et al. 2010), and a large diversity of theropods.. The meat-eating dinosaur record of Candeleros includes the large abelisaurid *Ekrixinatosaurus novasi* (Calvo et al. 2004), the giant carcharodontosaurid *Giganotosaurus carolinii* (Coria and Salgado, 1995), the basal coelurosaur *Bicentenaria argentina* (Novas et al. 2012), the alvarezsaur *Alnashetri cerropoliciencis* (Makovicky et al. 2012), and the unenlagiid *Buitreraptor gonzalezorum* (Makovicky et al. 2005). Despite this extensive and diverse dinosaur record, the remains recovered stratigraphically near the track-bearing levels only includes the titanosaur sauropod *Andesaurus delgadoi* near the Balneario of Villa El Chocón.

As a total, the ichnologic record of dinosaurs of the Candeleros Formation comprises large-sized footprints (≈ 35-65 cm in length), attributed to non-avian theropods as A. *astigarrae* and large U-shaped tridactyl footprints (*L. major*) (Calvo 1991, Krapovickas 2010), medium- to large-sized footprints (≈ 22-42 cm in length) attributed to non-avian theropods corresponding to *B. patagonicus* and Aff. *Asianopodus pulvinicalx* (Krapovickas 2010, Calvo and Rivera 2018, Heredia et al. 2020), medium-sized tridactyl footprints, *D. mapuchensis*, and *P. benedettoi* as footprints of medium size (≈ 13-22 cm in length) attributed to non-avian theropods (Calvo 1991, Calvo and Rivera 2018). Finally, small tridactyl footprints and *C. canalei* corresponding to footprints of small size (≈ 7-13 cm in length) attributed to non-avian theropods (Calvo and Rivera 2018). There are sauropod trackways preserved pointing towards two gait styles: the wide-gauge cf. *Brontopodus* (*S. giganteu*s) and the Aguada de Tuco narrow-gauge trackway, both with large-sized footprints (80-100cm in length). *Sousaichnium monetae* Calvo 1991 has been attributed to iguanodontid ornithopods (Calvo and Bonaparte 1991, Calvo 1999), however other authors do not agree and regard it as a theropod track and a junior synonym of *Limayichnus* (Meyer 2000, Díaz-Martínez et al. 2015). Finally, pterosaur tracks were recorded at the Candeleros Formation and ascribed to *Pteraichnus* isp. (Calvo and Moratalla 1998).

CONCLUSION

The tetrapod ichnologic assemblage of the Candeleros Formation at the Villa El Chocón area and the Cañadón de las Campanas shows a high abundance of footprints but still a low diversity of morphologies (i.e., ichnotaxa). The footprint record suggests the presence of two large-sized dinosaurs: a sauropod that produced cf. *Brontopodus* (*S. giganteus*) and a non-avian theropod producing large U-shaped tridactyl footprints (*L. major*). The record of short trackways that reveal a wide-gauge foot stance point toward titanosaur sauropods as the most likely producers of cf. *Brontopodus*. Coincidental interpretations, that is comparable sized animals pointed out by the bone record of the same stratigraphic unit, could suggest that large U-shaped tridactyl footprints were produced by carcharodontosaurid dinosaurs. Within smaller footprint morphologies, the most abundantly represented is the medium- to large-sized non-avian theropod footprint (*Bressanichnus patagonicus*). This material includes varying morphologies of the posterior margin of the footprints, most likely involving varying postural gaits and changing behavior. Finally, the VLC record includes two less represented medium- and small-sized non-avian theropod footprints without taxonomic assignment.

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