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ABSTRACT. We describe sixteen theropod dinosaur trackways from site III (Lower Cretaceous?) of the Quebrada Chacarilla in the Chacarilla Formation (Jurassic-Lower Cretaceous), northern Chile. The trackbed belongs to a meandering river environment, with recurrent track assemblages. We find that the main direction of the ichnites from site III parallels that of water flow. Two theropod footprint morphotypes are recognized: **A)** digit II and IV occupying about 0.5 times the total footprint length, and **B)** digit II and IV occupying less than 0.35 times the total footprint length. We estimate similar speed (~7 km/h) for the two parallel theropod trackways of morphotype A, suggesting synchronized walking. We also describe some of the largest theropod footprints from South America (>60 cm), which are all of morphotype B.

Keywords: Large theropod, Behaviour, Synchronized walking, Footprints, Ichnites, Lower Cretaceous, Northern Chile.

RESUMEN. Pistas de dinosaurios terópodos del Cretácico Inferior de la Formación Chacarilla, Norte de Chile. Se describen dieciséis pistas de dinosaurios terópodos localizadas en el sitio III (Cretácico Inferior?) de la Formación Chacarilla (Jurásico-Cretácico Inferior) en Quebrada Chacarilla, norte de Chile. La unidad con huellas fue depositada en un ambiente de río meandriforme y presenta recurrentes niveles con asociaciones de trazas. Las icnitas tienen una dirección paralela a la dirección del flujo de agua. Dos morfotipos de huellas de terópodos fueron reconocidos: **A)** Con los dígitos II y IV, ocupando cerca de 0,5 veces el largo total de la huella y **B)** con los dígitos II y IV ocupando menos de 0,35 veces la longitud total de la huella. Estimaciones de similar velocidad (~7 km/h) de dos pistas paralelas pertenecientes al morfotipo A, sugieren caminata sincronizada. Además, describimos algunas de las huellas de terópodos más grandes de América del Sur (>60 cm), las que corresponden al morfotipo B.

Palabras claves: Terópodos grandes, Comportamiento, Caminata sincronizada, Huellas, Icnitas, Cretácico Inferior, Norte de Chile.

1. Introduction

The record of Mesozoic continental vertebrates in Chile consists mainly of dinosaur tracks (Theropoda-Sauropoda-Ornithopoda), remains of titanosaurid sauropods, and pterosaur bones (Casamiquela and Fasola, 1968; Casamiquela *et al.,* 1969; Casamiquela and Chong, 1980; Chong, 1985; Bell and Suárez, 1989; Salinas *et al.,* 1991a; Salinas *et al.,* 1991b; Moreno and Pino, 2002; Rubilar-Rogers, 2003; 2006; Moreno and Benton, 2005).

Galli and Dingman (1962) mentioned the presence of diverse dinosaur footprints in different outcrops of Quebrada Chacarilla, northern Chile (Fig. 1). This was the first description of dinosaur ichnites in this country. On that occasion Joseph T. Gregory (*in* Galli and Dingman, 1962) identified different morphologies from pictures, including theropods, sauropods, ornithopods, and perhaps stegosaurs. These footprints are distributed in two separated tracksites, although most of the description was focused in the first locality examined.

We re-study the different outcrops of this formation, and present here the first detailed information on the vertebrate ichnofauna of the tracksite mentioned by Galli and Dingman (1962) as 'second locality' with dinosaur footprints, named 'site III' in this paper (Fig. 2). The locality shows numerous eastern-western and northern-southern striking outcrops with a pronounced west-dip (44º) and dozens of dinosaur trackways exposed in a thick sequence of sandstones. Their preservation is generally good, depending on the weathering of the different levels. A detailed track mapping of the Chacarilla Formation is far from complete, thus only preliminary results will be presented here. The present study only describes theropod trackways of an outcrop in Quebrada Chacarilla. The cast of a footprint from this site is housed in the Paleontological Collection of the Servicio Nacional de Geología y Minería, Chile (SNGM-311).

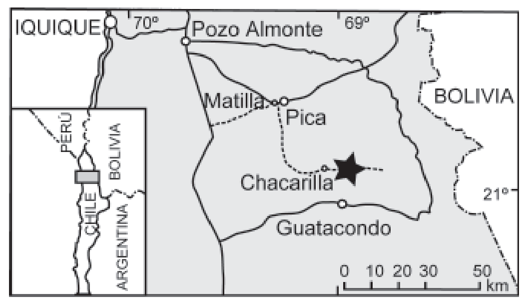

FIG. 1. Map of northern Chile showing the location of Quebrada Chacarilla (star).

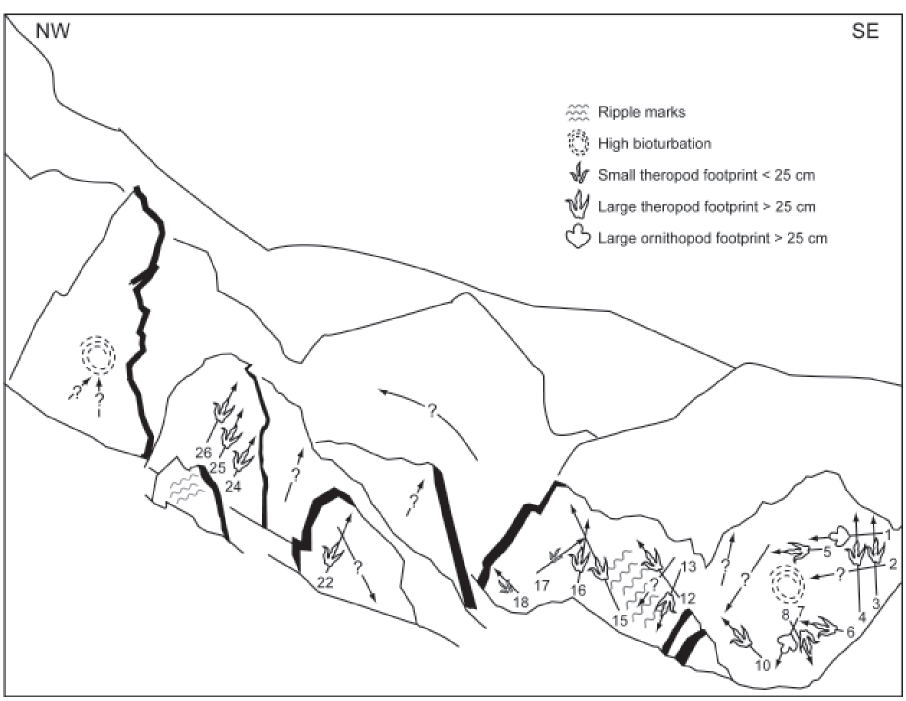

FIG. 2. Line drawing of site III of Chacarilla, showing the distribution of trackways (numbers). Question mark indicates unidentified footprints. NW-SE horizontal tracksite exposure is approximately 120 m.

2. General Geologic Context

Mesozoic tectonic evolution in northern Chile was dominated by subduction along the western margin of Gondwana (Coira *et al.,* 1982; Jordan *et al.,* 1983; Mpodozis and Ramos, 1989; Ramos and Kay, 1991; Mpodozis and Allmendinger, 1992). During the Jurassic and Lower Cretaceous, a magmatic arc was formed along the present-day Cordillera de la Costa. East of the arc, in the Central Depression and Precordillera in Chile, there was a contemporaneous ensialic back-arc basin, the Tarapacá Basin, which comprises thicknesses of thousands of meters of marine and continental sediments (Coira *et al.,* 1982; Groschke *et al.,* 1988; Mpodozis and Ramos, 1989). During Lower and Middle Jurassic, deposition of marine sequences was controlled by post-rift thermal subsidence and global sea-level fluctuations (Groschke *et al.,* 1988; Ardill *et al.,* 1998), whereas later on, in Middle Jurassic to Cretaceous times, the basin was controlled by tectonic movements related to the break-up of Pangea and fragmentation of Gondwana (Ardill *et al.,* 1998). The latter resulted in a widespread marine regression causing deposition of continental red-beds during Upper Jurassic and Lower Cretaceous in the backarc basin (Rutland, 1971; Chong, 1977; Bogdanic, 1990). Sedimentation stages in Lower Cretaceous times corresponds to the track-bearing deposits of various carnivorous and herbivorous dinosaurs tracks (Blanco *et al.,* 2000; Moreno *et al.,* 2000; Rubilar *et al.,* 2000a and b; Moreno, 2001).

3. Locality and Geologic Setting

The tracksite is located in Quebrada Chacarilla (coordinates 20°38'12.4"S, 69°4'25"W), Region I, northern Chile (Fig. 2).

The Chacarilla Formation is mainly a clastic succession with an exposed thickness of 1100 m. The lower part is of marine origin (Oxfordian), whereas the upper part was deposited in a continental setting (Galli and Dingman, 1962). The marine section at the Quebrada Chacarilla crops out in a box-fold anticline centre (Galli and Dingman, 1962), and the continental deposits form an open syncline. The top of the formation is marked by an angular unconformity, overlaid by volcanic and clastic rocks of the Cerro Empexa Formation (Upper Cretaceous-Lower Paleocene, Tomlinson *et al.,* 2001).

A certain discrepancy in age determination has been noted for lithostratigraphically equivalent continental red-bed successions exposed along the Precordillera in Chile's Regions I and II. This variability is due to the scarcity of biostratigraphically significant fossils in the continental facies rocks. As a result, previous workers have reported ages varying from Oxfordian (Galli and Dingman, 1962) or Kimmeridgian (Vergara, 1978) to entirely Lower Cretaceous (Ardill *et al.,* 1998). In addition, 60 km north of the study area, Herbst and Troncoso (1996) placed a part of this formation in the Middle Jurassic, based on a taphoflora association. However, the discovery of large ornithopod ichnites in the Chacarilla Formation indicates a Cretaceous age at least for the upper part of this formation (Blanco *et al.,* 2000; Rubilar *et al.,* 2000a). These tracks are correlated to the *Caririchnium* ichnofacies described by Lockley *et al.* (1994) for the Cretaceous of Laurasia, which are dominated by large ornithopod tracks preserved in silicoclastic rocks from coastal plain environments, in medium to high latitudes (Lockley *et al.,* 1994). The studied strata are located in the uppermost part of the Chacarilla Formation, hence it is likely to be of a Lower Cretaceous age.

The measured section (Fig. 3) contains 140 m of rhythmically alternating shales and red sandstones, and is structured in multiple, superposed fining- and thinning-upward sequences of decametric to metric scale. Within this section we observed two facies associations, which represent point bars and floodplains of a meandering river environment.

The point bar facies association consists of several superposed fining- and thinning-upward cycles, with each cycle being 30-50 cm thick and reaching an overall thickness of 4-10 m. Each cycle is composed of medium-grained quartzose sandstone with trough cross-bedding stratification, which passes gradually into sandstone with parallel plane lamination. The highest part of the cycle shows reddish mudstone with current ripple marks. Sedimentary structures such as trough cross-bedding and parting lineation indicate paleocurrents toward the NW, WNW and W (150 measurements). In sections perpendicular to the paleoflow, the sandstone shows a sigmoidal geometry that forms a large-scale cross-stratification of the epsilon type (Allen, 1963).

The floodplain facies association consists of finely laminated mudstone (generally shale). Plant remains, carbonaceous levels, and root marks are present, as well as some fossil trunks in life position. Furthermore, arboreal root casts and dinosaur footprints can be found. Intercalated in the mudstones are laterally extensive, but thin (0.1-0.3 m), tabular bodies of fine-grained lenticular sandstones, with a planar to slightly concave base, ripple marks, and parallel plane-lamination. These sandstones probably correspond to the distal deposits of crevasse splays covering floodplain areas (Miall, 1996). Asymmetric ripples in this association indicate a paleoflow toward WSW (50 measurements). The orientations of ornithopod and theropod dinosaur trackways are toward WSW and SW, approximately parallel to the water flow direction.

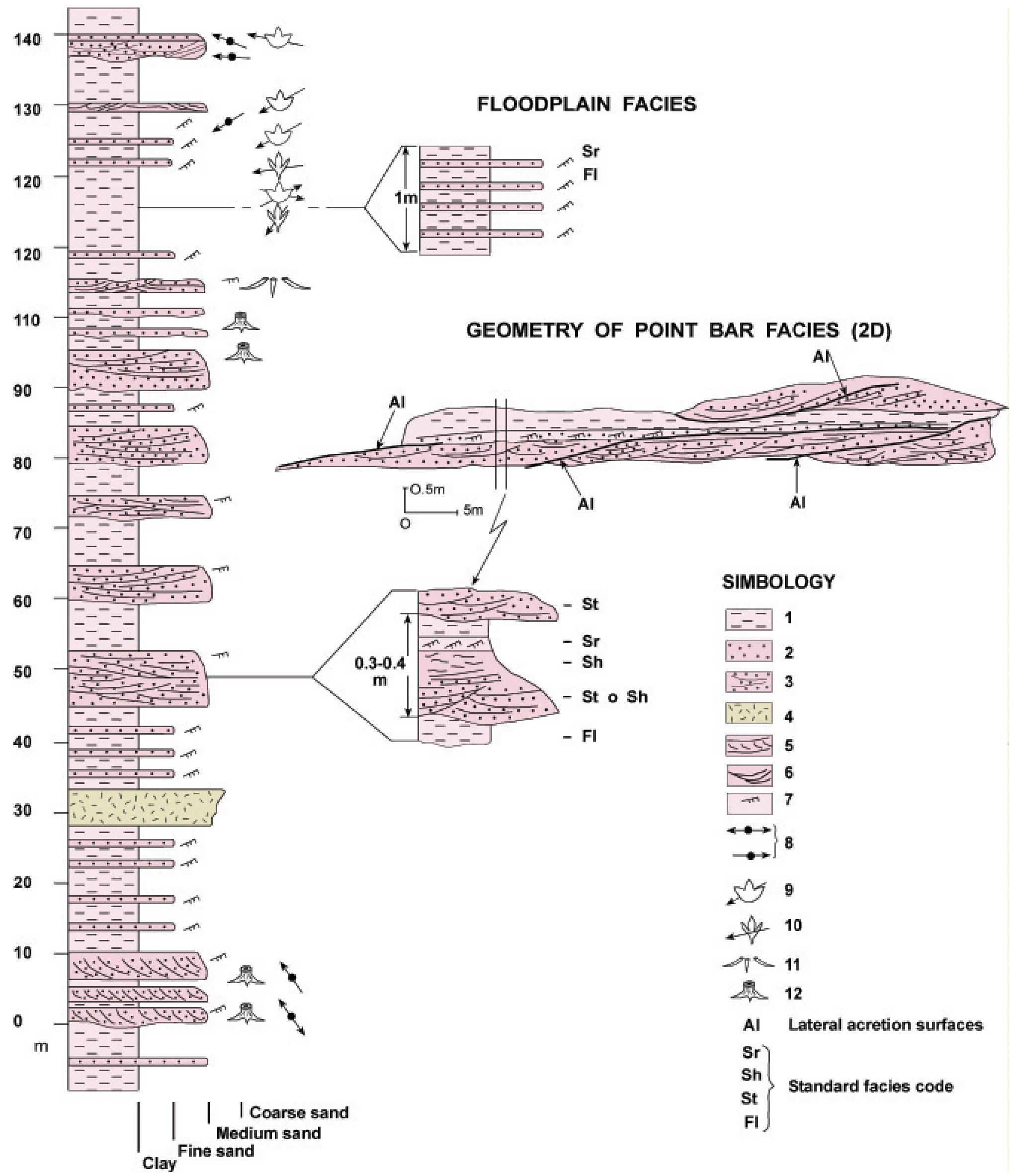

FIG. 3. Stratigraphic column and facies structure of tracksite III in Quebrada Chacarilla (based on Blanco *et al.,* 2000). **1.** mudstone; **2.** sandstone; **3.** laminated sandstone; **4.** andesitic sill; **5.** tabular cross-bedding; **6.** trough cross-bedding; **7.** ripple marks; **8.** direction of the paleoflow (uni-, bi- directional); **9.** ornithopod trackway direction; **10.** theropod trackway direction; **11.** arboreal root casts; **12.** trunks in life position.

4. Description of the dinosaur ichnites

Here we describe sixteen trackways (3-6, 8, 10, 12-13, 15-18, 22, 24-26) from Quebrada Chacarilla site III (Fig. 2), which correspond to the theropod morphology. Measurements were taken *in situ* (Fig. 4, Table 1). Footprint dimensions clearly shows a tendency toward a longer than wide footprint shape (Fig. 5). This characteristic, together with the anatomical features described below support the assignation of these ichnites to the Theropoda Suborder. Most of these footprints exhibit a tridactyl morphology, with impressions of digits II, III and IV. However, trackway 26 also displays the impression of digit I (tetradactyl morphology), which corresponds to a deeper impression of the autopod into the substrate and subsequent collapse of the sedimentary structure (Fig. 6). Despite of this, two main pedal morphotypes are recognized, A and B, based on digital proportions:

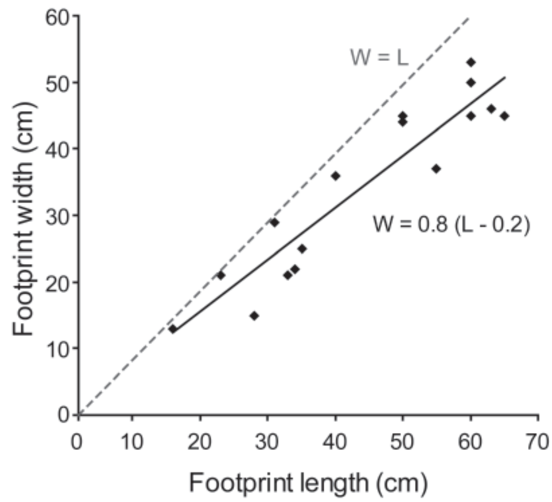

FIG. 5. Graph of the linear relationship between length and width for the theropod footprints (solid line) showing clear deviation from W=L (dashed line). This is one of the characteristics in support of their theropod origin.

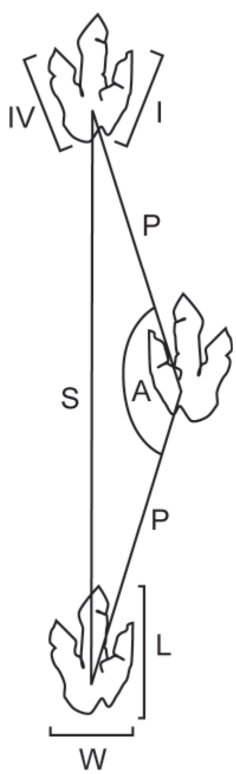

FIG. 4. Diagram showing the footprint and trackway measurements that were taken. **I:** length of digit I; **IV:** length of digit IV; **L:** footprint length; **W:** footprint width; **P:** pace length; **S:** stride length; **A:** pace angle.

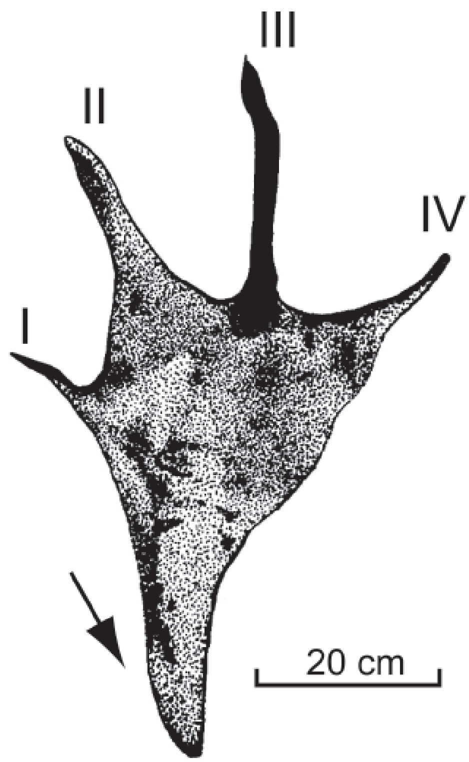

FIG. 6. Schematic drawing of the second footprint of trackway 26 showing metatarsal (arrow) and digit I-IV impressions.

In morphotype A, the length of digits II and IV is about half the total footprint length. This morphology is observed in trackways 3, 4 and 18 (plastotype SNGM-311, Servicio Nacional de Geología y Minería). Trackways 3 and 4 show surprising similarities. Footprints have comparable shape and size. Also, these two trackways are parallel (separated by about 80 cm), and have approximately the same length (6 m) and same number of footprints (8 each). Later on, trackways 1, 2 and 5 crossed trackways 3 and 4 (Fig. 7). In morphotype B (trackways 5, 6, 8, 10, 12, 13, 15, 16, 22, 24, 25 and 26), the length of digits II and IV are proportionally smaller than in morphotype A, and are about a third of the total footprint length. Morphotype B displays a wide variety of footprint dimensions, from 28 cm long and 15 cm wide to 65 cm long and 53 cm wide (Figs. 7-11), including some of the largest in South America (see discussion). Also, the tetradactyl footprints (trackway 26) mentioned above are included in this morphotype. These footprints show deep impressions of digits I to IV plus a metatarsal impression. The impression of digit I is directed anteromedially (Fig. 6). The total anteroposterior length (1 m) of this footprint was taken without accounting for the metatarsal impression, which is approximately one third of the total length (Table 1).

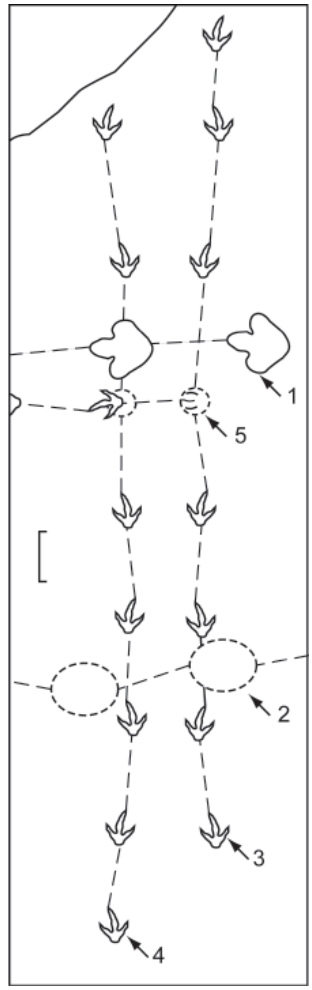

FIG. 7. Schematic drawing of trackways 3 and 4 crossed by trackways 1, 2 and 5. Scale bar 50 cm.

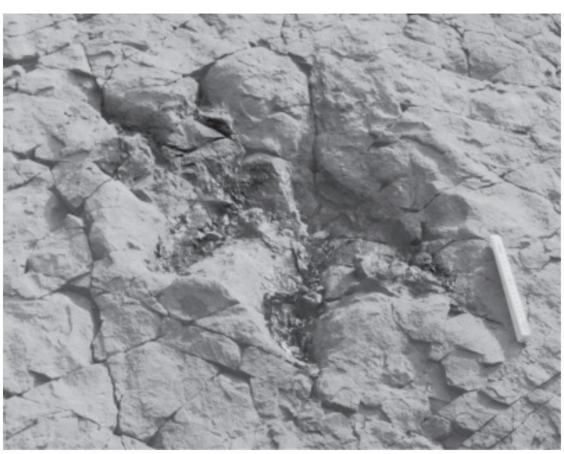

FIG. 8. Photo showing the first footprint of trackway 12 (left corner) superposed to one of the footprints of trackway 13 (centre). Ruler is 23 cm long.

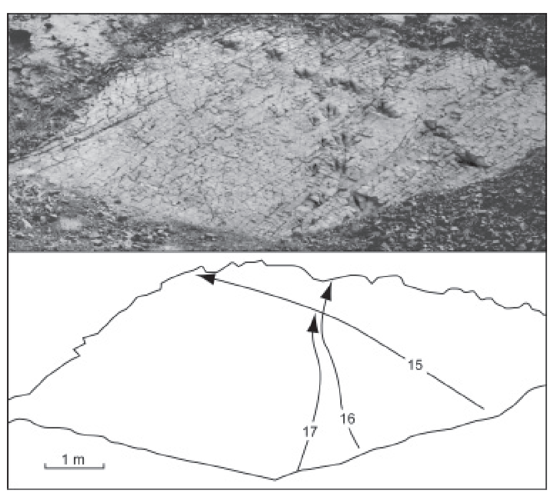

FIG. 9. Photo and schematic view of trackways 16 and 17 crossing the deeper trackway 15.

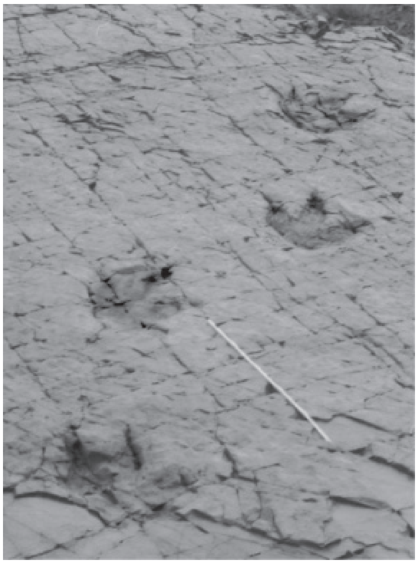

FIG. 10. Photo of a portion of trackway 22. Ruler is 70 cm long.

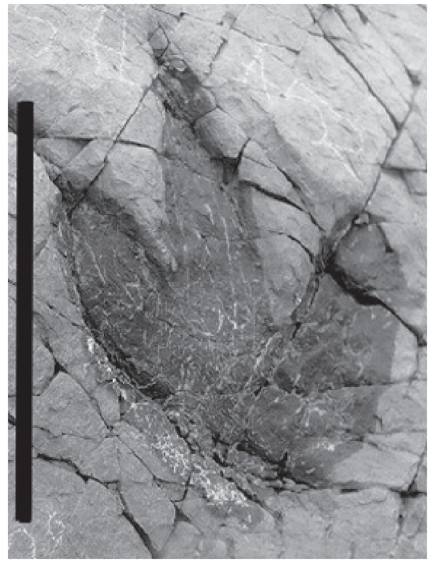

FIG. 11. Photo of the fifth footprint of trackway 22. Scale is 50 cm long.

TABLE 1. MEASUREMENTS OF THE FOOTPRINTS AT SITE III OF THE CHACARILLA FORMATION.

Trackway	N	L (cm)	W (cm)	II/L	IV/L	P (cm)	A (°)	S (cm)	H (cm)	Speed (cm/s)	Speed (km/h)	S/H
Small theropod footprints												
17	6	23	21	0.2	0.2	116	180	232	104	3.1	11.2	2.2
18†	2	16	13	0.5	0.5	61	-	-	72	-	-	-
Average		19.5	17	0.3	0.3	88.5	180	232	88	3.1	11.2	2.2
St. Dev		5	6	0.2	0.2	39	-	-	-	-	-	-
Large theropod footprints												
3†	8	33	21	0.5	0.5	119	180	234	162	2.0	7.2	1.6
4†	8	34	22	0.5	0.5	120	180	241	167	2.1	7.6	1.6
5	6	31	29	0.3	0.3	117	178	234	152	2.2	7.9	1.7
6	1	55	37	0.3	0.3	-	176	-	270	-	-	-
8	3	50	44	0.2	0.3	155	176	285	245	1.7	6.1	1.3
10	6	35	25	0.3	0.3	115	180	230	172	1.9	6.8	1.5
12	9	40	36	0.3	0.3	132	180	252	196	1.8	6.5	1.4
13	5	63	46	0.3	0.3	138	180	265	309	1.2	4.3	0.9
15	7	60	45	0.3	0.3	160	180	307	294	1.6	5.8	1.1
16	6	65	45	0.3	0.3	125	180	273	319	1.2	4.3	0.9
22	8	60	53	0.3	0.3	152	180	322	294	1.0	3.6	1.1
24	2	28	15	0.3	0.3	90	-	-	137	-	-	-
25	2	50	45	0.3	0.3	145	-	-	245	-	-	-
26*	7	60	50	0.2	0.2	172	175	330	294	1.0	3.6	1.1
Average		47	37	0.3	0.3	134	179	270	232	1.6	5.8	1.3
St. Dev		13	12	0.1	0.1	23	2	36	66	0.4	1.6	0.3

N: number of footprints; **L**: footprint length; **W**: footprint width; **II/L**: digit II-footprint length ratio; **IV/L**: digit IV- footprint length ratio; **P**: pace length; **A**: pace angle; **S**: stride length; **H**: hip height calculated using the correction factor of Thulborn (1984): either 4.5 or 4.9 times the footprint length for small or large theropods respectively. Speed is calculated with the formula developed by Alexander (1976) in MKS units; **speed**: $2.817\ L^{1.67}H^{-1.17}$; **†:** Theropods with morphology A, in which the length of digits II and IV is half the length of digit III; *****: Length of the footprint without considering the metatarsal impression.

5. Discussion

There are two dinosaur groups with tridactyl footprints: theropods and ornithopods. Diagnostic features which permit the discrimination between both groups are the marked differences of footprint length/width ratio, the lower interdigital angles and lower trackway pace angulations, and the presence of an indentation along the medial edge of digit two just distal to the 'heel' apex seen in theropods as opposite to ornithopods (Fig. 4). However, these characters do not allow the identification of a specific trackmaker, due to the weak correlation between footprint morphology and skeletal features (Farlow and Chapman, 1997).

The ichnofauna identified in site III of Quebrada Chacarilla is composed of about 80% theropods and 20% ornithopod footprints. Therefore, it is distinct from other Late Jurassic-Early Cretaceous tracksites, such as San Salvador and Baños del Flaco, which present a mostly small theropod and a small ornithopod-small theropod-narrow gauge sauropod ichnocoenosis respectively (Moreno and Pino, 2002; Moreno *et al.,* 2004; Moreno and Benton, 2005). This variation is difficult to interpret since many factors are involved in the preservation of the various tracksites, being dinosaur behaviour, distribution, palaeogeography and chronological differences among the most important. In this respect, much more work is needed in order to identify possible ichnofacies and chronological accuracy.

The general orientation of the trackways in site III is similar to the direction of water flow (NE-SW).

Based on the proportions of the digital impressions, two morphotypes have been recognized: Morphotype A, with a prominent digit III (lateral digits II and IV about a half of digit III length), which is comparable to tracks attributed to 'coelurosaurs' in South America (Leonardi, 1989; Calvo, 1991; Leonardi and Spezzamonte, 1994). Within this morphotype we observed two trackways (3 and 4) that are walking parallelly at a similar speed (~7 km/h), and have a regular separation between both trackways, suggesting that both individuals were walking in a synchronized manner (Fig. 7).

Morphotype B, with lateral digits (II and IV) about a third of digit III, is similar to the ichnogenus *Abelichnus* (Calvo, 1991, 1999; see Figs. 10-11), where claw impressions are very prominent and the digit impressions occupy most of the length of the tracks, and may be tentatively referred to that ichnotaxon. However, the pace angulation recorded is 180° in contrast to ~150° for *Abelichnus*.

Morphotype B includes one of the largest theropod ichnites known in South America. These ichnites are comparable in size (mean hip height ~3 m) with carcharodontosaurids such as *Giganotosaurus*, as was previously referred (Calvo and Mazzetta, 2004) from the early Late Cretaceous of Argentina (Coria and Salgado, 1995; Calvo and Coria, 1998; Novas *et al.,* 2005). However, theropod remains of this size have not yet been found on the western portion of Gondwana. Consequently, the Chacarilla footprints represent the first evidence of their existence in that area. In addition, a trackway of seven tetradactyl footprints (trackway 26) with metatarsal impression is included in this morphotype. The particular morphology of these footprints suggests a quasi-plantigrade locomotion (Kuban, 1989) and presents independent evidence that these theropods powered the early stance phase by femoral retraction, rather than by knee flexion as in living birds (Gatesy *et al.,* 1999). Subtracting the posterior footprint elongation from the total footprint length (1 m), we obtain similar dimensions (60 cm long, 53 cm wide) as those as in other trackways of morphotype B (Fig. 6).

The average speed estimated for all the trackways is 5.8 km/h, which is consistent with a walking gait. The only trackway that has a trotting gait is 17, with an estimated speed of 11.2 km/h.

6. Conclusions

The ichnofossils from the Chacarilla Formation as a whole, but particularly in site III, are a unique record of dinosaurian fauna which inhabited a flood plain environment of a meandering river in the north of Chile during the Early Cretaceous (as indicated by the presence of large ornithopod footprints characteristical of this period). Here, described some of ichnites from site III, which show a main direction NE-SW, and therefore are parallel to the direction of the water flow. Two theropod morphotypes were recognized, including some of the largest of South America, which indicate that large theropods lived on the western portion of Gondwana in earlier times than the suggested by the oldest carcharodontosaurid record (early Late Cretaceous). In addition, among these large theropods traces we found two parallel trackways with similar speed and footprint morphology, which are evidence of synchronized walking, a behaviour previously not described for these big animals.

The quality, abundance and time span of the footprint record of the Chacarilla Formation makes it potentially useful for the study of paleogeographic, behavioural and evolutionary patterns during the Late Jurassic and Early Cretaceous. This should be addressed in future research.

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