

A NEW WIDE-GAUGE SAUROPOD TRACK SITE FROM THE LATE CRETACEOUS OF MENDOZA, NEUQUÉN BASIN, ARGENTINA

by BERNARDO JAVIER GONZÁLEZ RIGA* and JORGE ORLANDO CALVO†

*Laboratorio de Paleovertebrados, IANIGLA-CCT-CONICET-Mendoza, Avda. Ruiz Leal s/n, Parque Gral, San Martín (5500) Mendoza, Argentina/ICB, Universidad Nacional de Cuyo; e-mail: bgonriga@lab.cricyt.edu.ar

†Centro Paleontológico Lago Barreales, Universidad Nacional del Comahue, Buenos Aires 1400 (8300) Neuquén, Argentina; e-mail: jocalvo40@yahoo.com.ar

Typescript received 6 December 2007; accepted in revised form 19 May 2008

Abstract: Agua del Choique is a new Late Cretaceous sauropod track site from Mendoza Province, Neuquén Basin, Argentina. It is situated in the Loncoche Formation, late Campanian – early Maastrichtian in age, and is one of the youngest sauropod tracks site recorded in the world. Agua del Choique represents a lake setting and river-dominated delta deposits, and comprises at least 160 well-preserved tracks, located on a calcareous sandstone bed. A new ichnotaxon, *Titanopodus mendozensis* ichnogen. et ichnosp. nov., is erected for the footprints of this track site. *Titanopodus mendozensis* exhibits the following association of features: (1) wide-gauge trackway (manus and pes trackway ratios of 18–22 and 26–31 per cent respectively), (2) pronounced het-

eropody (manus-pes area ratio of 1:3), (3) outer limits of trackway defined, in some cases, by the manus tracks, and (4) manus impression with an asymmetrical crescent contour and acuminate external border. *Titanopodus mendozensis* is an excellent case study of the wide-gauge style of locomotion produced by Late Cretaceous derived titanosaurs that have no impression of manual phalanges. These features, and the fossil record from the Loncoche Formation, suggest that the trackmakers were, probably, middle size saltasaurine or aeolosaurine titanosaurs (14–16 m long).

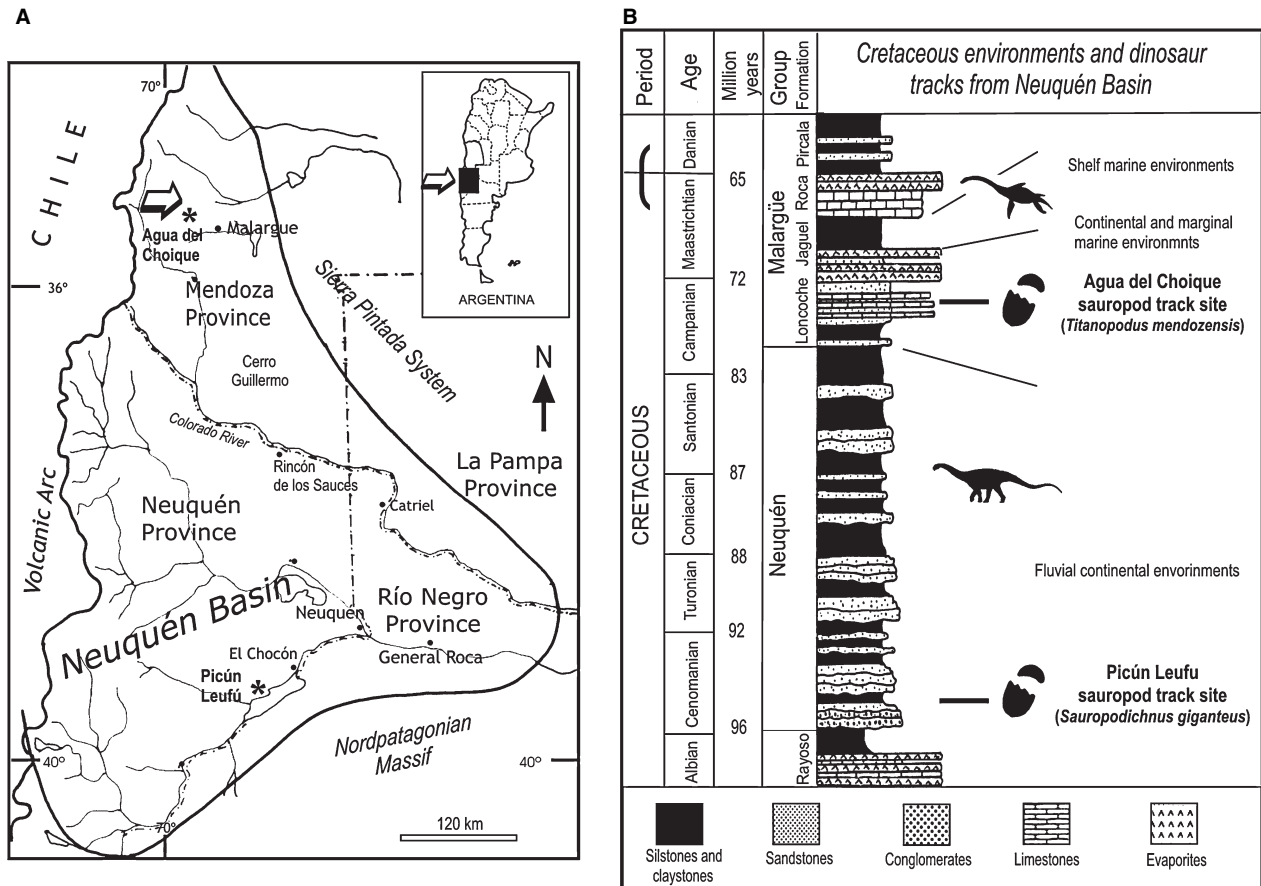
Key words: *Titanopodus mendozensis*, Late Cretaceous, Neuquén Basin, Argentina.

BRONTOPODUS footprints are the largest tracks known among sauropod ichnospecies and have been recorded from the Early Jurassic to Late Cretaceous on most continents. These tracks provide interesting information about the social behaviour and locomotion of sauropod dinosaurs, the largest terrestrial animals to have ever existed. Although this ichnological record is relatively abundant, most sauropod ichnospecies are poorly preserved and many are currently considered to be *nomina dubia* by Lockley *et al.* (1994). Important dinosaur track sites have been described in South America, particularly in Chile (Casamiquela and Fasola 1968; Moreno and Pino 2002; Moreno *et al.* 2004; Moreno and Benton 2005), Bolivia and Brazil (Leonardi 1989; Meyer *et al.* 2001; Lockley *et al.* 2002), with some sites preserving sauropod tracks.

In Argentina there are two areas with numerous dinosaur tracks, one located in Neuquén Province (northern Patagonia), and the other in Salta Province (near eastern Puna). In Neuquén Province, dinosaur tracks have been found in Picún Leufú (Calvo 1991; Calvo and Mazzetta 2004) and in El Chocón areas (Calvo 1999), particularly

along the shore of Lake Ezquiél Ramos Mexía (Text-fig. 1A). These tracks were found in outcrops of the lower Candeleros Formation (early Cenomanian), a unit characterized by meandering rivers, poorly channelled ephemeral flows and playa-lake deposits (Calvo 1999). In Salta Province, theropod and ornithopod tracks have been described in the upper levels of the Yacoraite Formation (Maastrichtian), in littoral deposits related to continental environments (Alonso 1980; Alonso and Marquillas 1986). In Salta, sauropod footprints have not been recorded, and in Neuquén, only the ichnotaxon *Sauropodichnus giganteus* Calvo, 1991 has been described (Calvo 1999; Calvo and Mazzetta 2004).

In this context, the new track site described here, containing more than 160 sauropod tracks, is very important in light of its ichnotaxonomical, palaeoecological and palaeoenvironmental data. The purpose of this paper is to describe *Titanopodus mendozensis*, a new ichnotaxon from South America, and to present a new case study of wide-gauge sauropod trackway. In this paper, we have concentrated on ichnotaxonomy; for this reason, the palaeobiological and palaeoenvironmental interpretations,



TEXT-FIG. 1. A, location map of the Neuquén basin (Argentina) showing the Agua del Choique and Picún leufú track sites. B, Stratigraphic column of the Neuquén basin showing track levels (modified from González Riga 2002).

and the results from our study of the facies, microfossils and invertebrates, will be analyzed elsewhere.

The tracks were found in the Loncoche Formation, late Campanian – early Maastrichtian of the Neuquén basin. In this formation, diverse bone remains of fish and reptiles were found in several sites (Ranquil-Có, Calmu-Co) from the Mendoza Province (González Riga and Parras 1998; González Riga 1999; Previtera and González Riga 2008).

The senior author (BJGR), during an exploration of a project, found the dinosaur footprints described in this paper. This new track site was located in a secondary ravine near Agua del Choique, 14 km west of Malargüe City, Mendoza Province (Text-fig. 1A). These tracks are distributed in different trackways, most of them covered by detritus (González Riga and Calvo 2006, 2007). For this reason, our team worked 2 years in the track site removing sediments and preparing the footprints for studying. This discovery was made while conducting field-work for a project focused on the systematic, taphonomic and palaeoecologic aspects of dinosaurs, mammals and flora from the Late Cretaceous – Paleogene of Mendoza (Prámparo *et al.* 2006).

GEOLOGICAL SETTING

The Neuquén basin is located in northwestern Patagonia and extends from the active magmatic arc along the Andes to the west, and the Sierra Pintada System and the North Patagonian Massif to the northeast and southeast respectively (Text-fig. 1A). Within the thick Mesozoic succession of this basin, distinct orders of cyclicity are recorded, including marine and continental deposits related to transgressive–regressive episodes. The Late Cretaceous strata of these sequences correspond to the Neuquén and Malargüe groups and are included in the Riográndico Cycle (Legarreta and Gulisano 1989; Legarreta and Uliana 1991).

The Neuquén Group is a thick continental succession (maximum thickness 1300 m) deposited between the early Cenomanian to early Campanian. Conglomerates, sandstones and claystones deposited in alluvial fans, fluvial systems, and playa-lake environments are stacked in recurrent fining upward sequences (Leanza and Hugo 2001). Traditionally, it has been divided from the base to top, into the Río Limay, Río Neuquén and Río Colorado

subgroups (Leanza *et al.* 2004). However, the correlation and age range of these subgroups and subdivisions into formations have remained problematic, due to lateral facies changes associated with dynamic fluvial systems (González Riga and Astini 2007).

The Loncoche Formation was deposited during the late Campanian – early Maastrichtian (Text-fig. 1B). It is the lower unit of the Malargüe Group and unconformably overlies the Neuquén Group. The Loncoche Formation includes fluvial, lacustrine and marginal marine depositional environments (tidal flats, lagoon and sabkhas) produced by a marine incursion from the East that covered central-northern Patagonia (González Riga and Parras 1998). In Ranquil-Có and Calmu-Co areas, the Loncoche Formation has yielded a varied association of vertebrate bone assemblages (González Riga 1999; Previtera and González Riga 2008). These assemblages are associated with ancient tidally dominated deltas and show a mix of terrestrial vertebrates (dinosaurs and snakes), together with freshwater taxa (turtles, fish) and marine or littoral forms (plesiosaurs and rays).

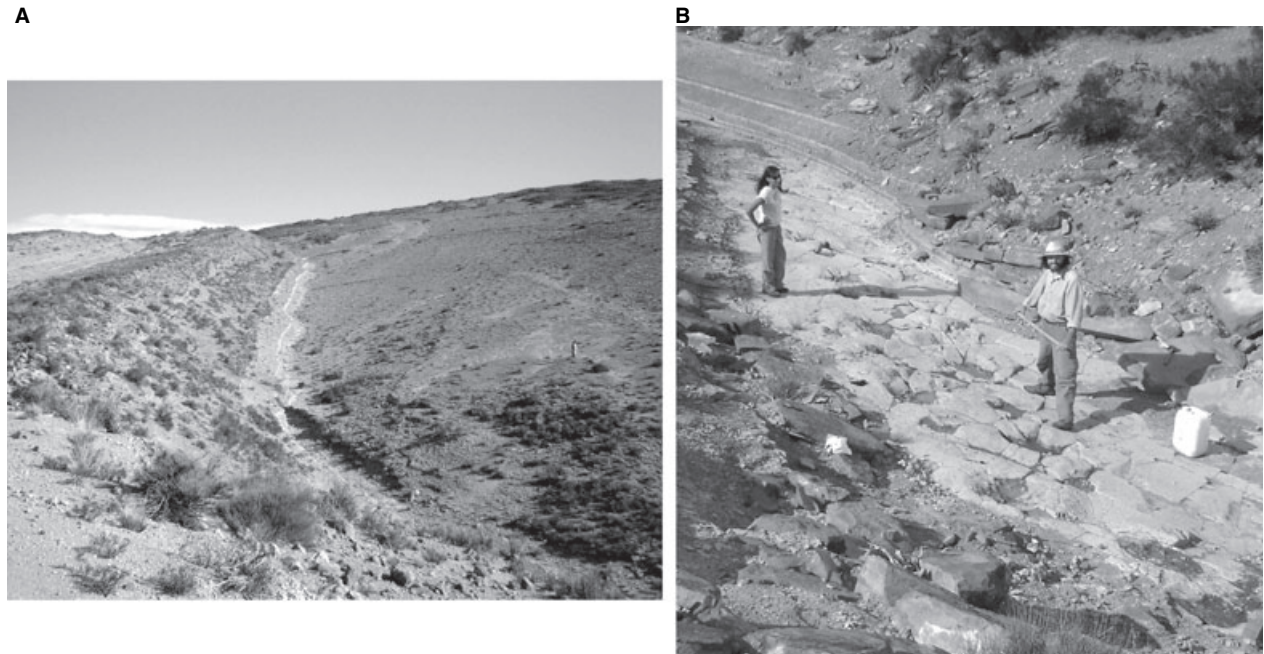
The upper section of the Neuquén (Anacleto Formation) and the Malargüe Groups outcrop in the Agua del Choique area. The Anacleto Formation (early Campanian) is composed of reddish siltstones and claystones and some tabular sandstones. These facies were deposited in sporadic channels, mantiform tractive processes and extensive floodplain developed in fluvial systems.

The Malargüe Group unconformably overlies the Anacleto Formation and includes the Loncoche, Jagüel, Roca

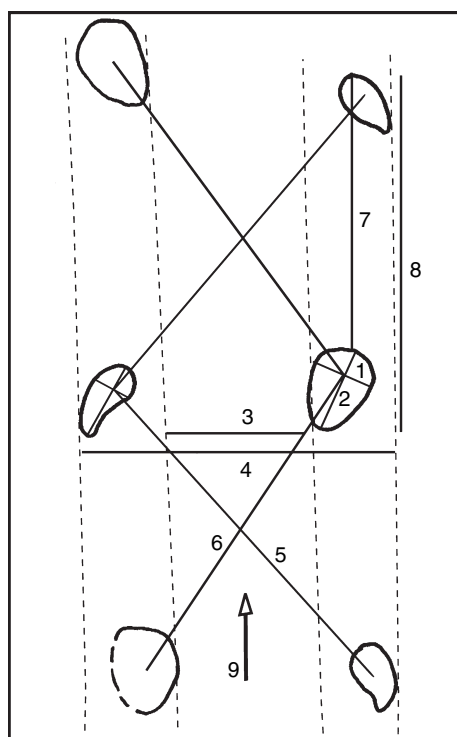
and Pircala formations. The Loncoche Formation is composed of claystones, sandstones and calcareous sandstones, with some intercalations of bioclastic limestones with abundant bivalves and scarce vertebrates remains. In this area, Parras *et al.* (1998) recognized two depositional environments: the first is attributed to a river-dominated delta and lake setting and the second corresponds to a river-dominated delta transitional to a tide-dominated delta.

The footprint horizon is located in the middle section of the formation and dips 12 degrees towards the north-east (Text-fig. 2). It corresponds to yellowish grey, calcareous sandstone facies interbedded with yellow oolitic limestones and green claystones. The footprint horizon extends across three localities: A, B and C. Area A (geographic reference: 35°26'55,2''S; 69°44'2,0''W) includes *c.* 160 tracks in four principal trackways (AC-1 to AC-4 in this paper). Area B is located 234 m to south of the Area A, whereas Area C is located 150 m south to the Area B. In this paper, we focus on a description of the trackways contained within Area A.

Fossil preservation and terminology. In the Agua del Choique track site, the footprint depth (*c.* 5–30 cm) varies over very short distances, while prominent rims around the ichnites are abundant. These features suggest important variations in the consistency of the original calcareous sediments, presumably in relation to their high or low water content. This aspect was carefully analyzed during the collection of measurement data, following the recom-



TEXT-FIG. 2. Photographs of Agua del Choique track site (Mendoza Province, Argentina): A, outcrop of the Loncoche Formation in the track site. B, Trackway AC-1.



TEXT-FIG. 3. Measurements of sauropod tracks used in this paper (based on Farlow *et al.* 1989). 1, pes footprint width. 2, pes footprint length. 3, inner trackway width. 4, outer trackway width. 5, manus pace. 6, pes pace. 7, manus-pes distance. 8, length of manus-pes set. 9, direction of the gait. For more explanations see Table 1.

mendations of Lockley *et al.* (2002). Finally, calcareous geodes are developed in the bottom of the tracks of most trackways. This mineral structure is useful to localize the ichnites in the track site and requires further study.

In this paper (Text-fig. 3), we follow the terminology of Farlow *et al.* (1989) and Romano *et al.* (2007).

Institutional abbreviations. IANIGLA-PV, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, colección Paleovertebrados.

SYSTEMATIC PALAEOLOGY

Genus *TITANOPODUS* ichnogen. nov.

Derivation of name. From *titan* (latin) meaning giant, *podus*, foot.

Diagnosis. Sauropod tracks of medium size (footprint length about 50 cm) characterized by a wide-gauge trackway [manus and pes trackway ratios (MTR and PTR) of 18–22 and 26–31 per cent respectively]; manus tracks

without claw impressions and strongly rotated outward (25–48 degrees), with asymmetrical crescent shape and acuminate and thinner external border; pes tracks with subtriangular to subcircular shape, longer than wide, and rotated slight negative (outward); pronounced heteropody (manus/pes area ratio of 1:3); outer limits of trackway defined, in some cases, by manus tracks; manus-pes distance about 1.7 times pes track length; stride length around 4.9 times pes track length; step angle 92–110 degrees; tail drag marks absent.

Type ichnospecies. *Titanopodus mendozensis* by monotypy.

Titanopodus mendozensis ichnospecies nov.

Derivation of name. From Mendoza Province, Argentina, where the track site is located.

Type material. Original manus and pes tracks *in situ*, trackway AC-1, Agua del Choique track site.

Repository. Cast of manus-pes set from trackway AC-1 is housed under the abbreviation IANIGLA-PV 052.

Reference material. Trackway AC-4 from the site of the type material.

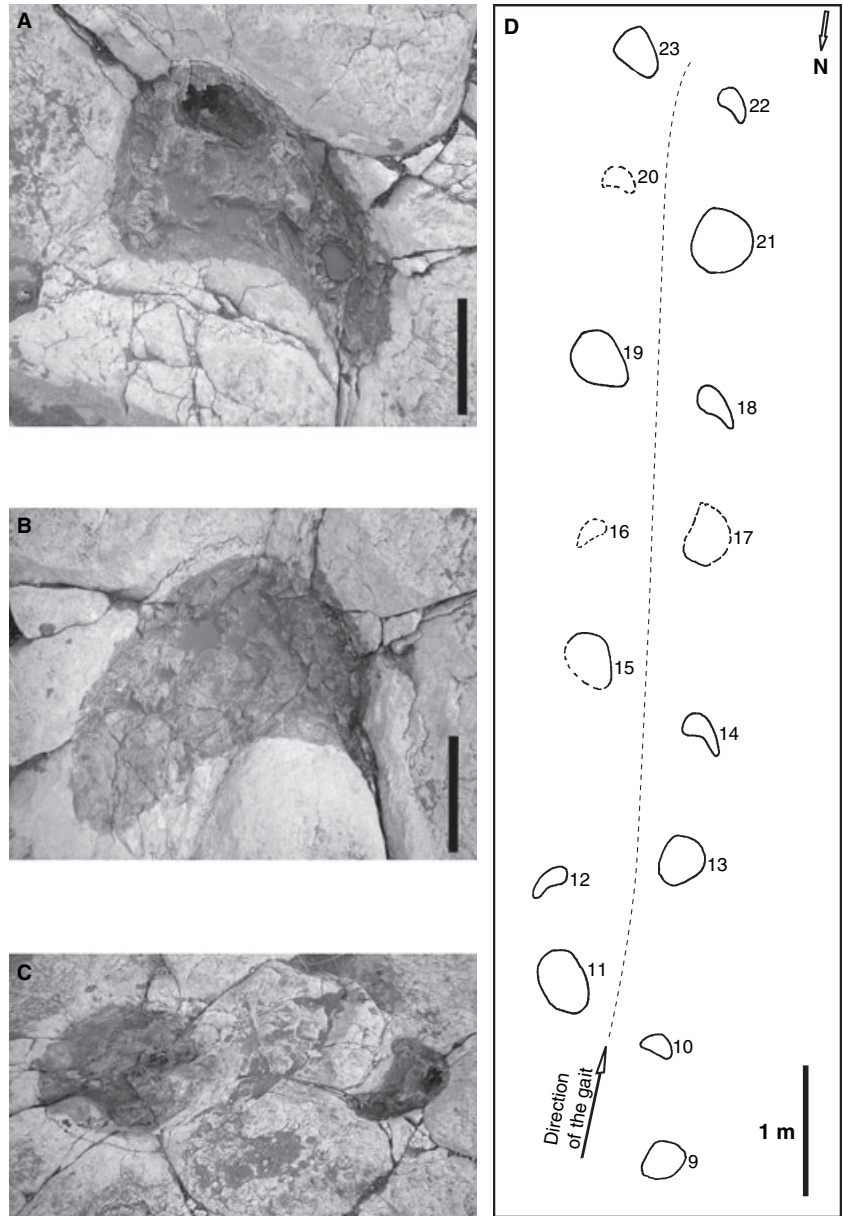
Type horizon and locality. Loncoche Formation (late Campanian – early Maastrichtian), Agua del Choique track site, Malargüe Department, Mendoza Province, Argentina.

Description

In the northern area of the Agua del Choique track site, we recognized four trackways of sauropods. The best preserved, trackways AC-1 and AC-4, we describe and figured herein.

The trackway AC-1 is 18.5 m long and includes 27 tracks (Text-fig. 2B). The midline is oriented toward the southwest (193–224 degrees) and both manus and pes prints are well separated from the midline, as in other wide-gauge trackways (Farlow 1992; Lockley *et al.* 1994). The total width of the trackway is about 125 cm, and the inner trackways width is about 40 cm. We analyze this feature following the MTR and PTR proposed by Romano *et al.* (2007). These indices are defined as the ratio of the track width measured transversely to the midline (side width; SW) relative to the total width of the trackway (overall width; OW) as follow: $TR = SW/OW \times 100$. In our case, the trackway AC-1 shows a MTR and PTR values of 22.09 and 31.32 per cent respectively. These values indicate that *Titanopodus* has a very wide-gauge trackway in comparison with the most known trackways recorded in the world (Romano *et al.* 2007). Moreover, in the case of the trackway AC-4 described below, the MTR and PTR reach values of 17.54 and 26.75 per cent respectively.

TEXT-FIG. 4. *Titanopodus mendozensis* ichnogen. et ichnosp. nov. Field photographs of right manus (A), left manus (B) and manus-pes track set (C), all from the trackway AC-1. D, map of the trackway AC-1. Scale bar represents 10 cm in A and B.



Manus tracks of AC-1 are elongated and have a typical crescent shape, with a posteriorly concave contour. This morphology is similar in part to those described for *S. giganteus* (Calvo 1991, 1999) and several unnamed ichnotaxa (e.g. Lockley *et al.* 2002; Day *et al.* 2004). However, the manus prints described, are assigned to a new ichnogenus *Titanopodus*, which shows a peculiar morphology for sauropod tracks: an asymmetrical crescent contour with an acuminate external border that is thinner than the internal one (Text-fig. 4A–B). This shape is present in well-preserved footprints (e.g. pes tracks number 12, 14, 16, 18, 22 of the Text-fig. 4D). Manus tracks are strongly rotated outward, ranging between 25 and 48 degrees. This value, measured between the transverse axis of the manus (as compared to a perpendicular line running to the midline), is larger than that of *Brontopodus birdi* (Farlow *et al.* 1989). There are no indications of digits or manual claw impressions.

Pes tracks are bigger than those attributed to the manus (Table 1) and are subtriangular to subcircular in shape (Text-fig. 4C). Pedal claw impressions are absent, and some pes tracks show an elongated and distorted contour, mainly in the deeper footprints. The absence of pedal digit impressions is probably related to the physical conditions (humidity, texture and composition) of the sediments and has been described in other tracks assigned to titanosaurs (Calvo 1991; Calvo and Mazzetta 2004).

The trackway AC-1 shows a pronounced heteropody (c. 1/3), indicating that the manual area is only 32.4 per cent of the pes area (Table 1). Moreover, we observe that the pes pace angulation (110 degrees) is larger than that of the manus (104 degrees).

The trackway AC-4 includes 71 ichnites extending for 46.2 m (Text-fig. 4A–B). This trackway exhibits a sinuous midline oriented toward the south (176 degrees), southwest (224 degrees),

TABLE 1. Measurements of the trackway AC-1, Agua del Choique tracksite, Mendoza, Argentina.

Track number	Foot shape	Width (cm)	Length (cm)	MPD (cm)	MPL (cm)	HI (%)	Manus stride (cm)	Pes stride (cm)	Manus step angle	Pes step angle
9	right pes	42	34	80	112	46,70	238	232	(10-12-14) = 101°	(9-11-13) = 107°
10	right manus	29	23							
11	left pes (*)	43	65							
12	left manus	32	17							
13	right pes	46	55							
14	right manus	32	19	85	122	24,03	243	237	(12-14-16) = 104°	(11-13-15) = 110° (13-15-17) = 119°
15	left pes (*)	–	–							
16	left manus	29	21	69	107	–	240	221	(16-18-20) = 113°	(15-17-19) = 104°
17	right pes	53	50							
18	right manus	39	23	88	137	33,38				
19	left pes	35	49	–	–	–	224	227	(18-20-22) = 98°	(17-19-21) = 112°
20	left manus (*)	–	–							
21	right pes	36	42	91	133	33,73	236	229	104°	110°
22	right manus	34	15							
23	left pes	32	40	86	131	37,18	236	229	104°	110°
24	left manus	28	17							
Average	manus	32,2	19,6	80,4	123,6	32,4 %	236	229	104°	110°
	pes	42,4	46			~1/3,08				

MPD, manus-pes distance (measured between the anterior margin of both manus and pes tracks); MPL, length of manus-pes set (measured between the anterior margin of the manus and the posterior margin of the pes); HI, heteropody index, estimated as the length manus \times width manus/length pes \times width pes \times 100; *shape distorted.

south (172 degrees) and finally, to the southwest (253 degrees). It exhibits manus tracks with an asymmetrical crescent contour rotated outward (about 34 degrees); however, the external border is less acuminate than observed for track in the trackway AC-1. Moreover, the stride values (253 cm for the manus and 246 cm for the pes) are larger than those from the trackway AC-1.

In the trackway AC-4 of *Titanopodus*, the outer limits of the trackway is defined by manus tracks (Text-fig. 5), whereas in the trackway AC-1 this condition is present in tracks 11–14. In contrast, in *B. birdi* the outer limits are defined by the pes tracks (Farlow *et al.* 1989).

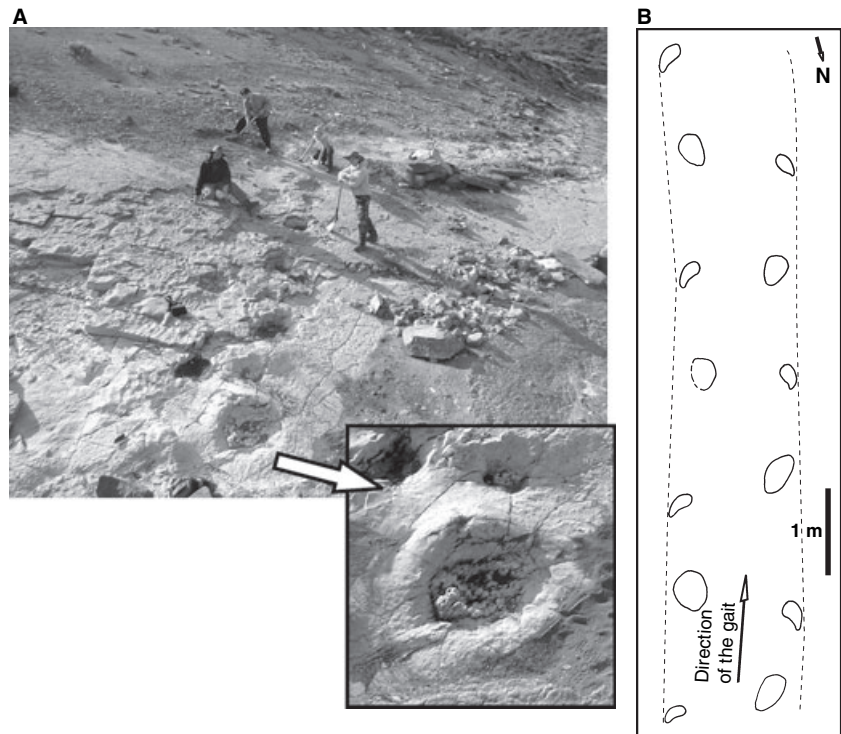
In *Titanopodus* tracks we observe some variations both in the left and right stride values, indicative of some change in the

direction of travel. If we consider that the pes length is around 50 cm in trackway AC-4, we calculate an acetabular high of 201 or 295 cm using the formulas of Alexander (1976) and Thulborn (1990) respectively. These values suggest that the trackmaker could be a sauropod somewhere between 14 and 16 m in total length.

DISCUSSION

Farlow (1992), Farlow *et al.* (1989), Lockley *et al.* (1994) and Wilson and Carrano (1999) recognized two different

TEXT-FIG. 5. *Titanopodus mendozensis* ichnogen. et ichnosp. nov. A, field photographs of the trackway AC-4 showing pes tracks with prominent rims. B, map of the trackway AC-4.



types of sauropod trackways: 'narrow-gauge' and 'wide-gauge'. These types of trackways were based on two well-known ichnotaxa: *Parabrontopodus* (Lockley *et al.* 1994) and *Brontopodus* (Farlow *et al.* 1989). *Brontopodus* are wide-gauge trackways displaying left and right tracks widely spaced from the midline, with manus prints positioned closer to the midline than pes prints and no associated pollex claw impressions. In contrast, *Parabrontopodus* are narrow-gauge trackways where both manus and pes prints fall very close to, or intersect the trackways midline and are associated with pollex claw impressions.

In the last year, the discovery of new track sites (e.g. Santos *et al.* 1994; Lockley *et al.* 2002, 2006) indicates that the diversity of sauropod tracks and trackways is more complex than previously suspected. For example, Day *et al.* (2004) recognized at least four types of sauropod trackways: (1) narrow-gauge trackways with well-developed manus claw impressions considered to be formed by non-titanosauriform sauropods; (2) intermediate-gauge trackways with well-developed or reduced manus claw impressions, considered to be formed by brachiosaurs and the most basal titanosaurs; (3) fully wide-gauge trackways, with reduction of the manus claw and other manual phalanges, considered to be formed by basal titanosaurs; (4) fully wide-gauge trackways with no indication of the presence of any manual phalanges, considered to be produced by advanced titanosaurs.

Later on, Romano *et al.* (2007) studied different sauropod trackways and proposed a new parameter named

'trackway ratio'. These authors defined provisionally three categories of gauge after the values of the trackway ratio: more than 50 per cent (narrow), 36–49 per cent (medium) and less than 36 per cent (wide).

Taxonomically, about a dozen sauropod ichnogenera have been named, although only a few are considered valid (Lockley *et al.* 1994; Wright 2006). However, we think that it is important to recognize ichnotaxa that represent different types of the four trackways described above. In this context, we consider the description of *T. mendozensis* to be a new ichnotaxon that represents a fully wide-gauge trackway produced by advanced titanosaurs from the latest Cretaceous (type 4 after Day *et al.* 2004).

Tracks of *Titanopodus* have a typical ichnological structure assigned to sauropod dinosaurs. A series of features observed both in the manus tracks and in the trackway pattern allow us to erect this new ichnotaxon. First, the crescent outline of the manus impressions is present in most sauropod tracks (e.g. Farlow *et al.* 1989; Lockley 1991; Santos *et al.* 1994). However, a strongly asymmetrical contour with an acuminate and thinner external border has not been described in other formal ichnotaxa. For example, in *B. birdi* from the Lower Cretaceous of Texas and Arkansas (Farlow *et al.* 1989), the manus has a 'double-crescent shape', a structure very different to *Titanopodus*. In *S. giganteus* from the Late Cretaceous (Albian–Cenomanian) of Neuquén Province, Argentina (Calvo 1991, 1999) the manus has a crescent shape, but does not have an asymmetrical contour like *Titanopodus*.

Other relevant Cretaceous sauropod trackways are present in Spain, Germany and Bolivia. In Spain, *Brontopodus oncalensis* from the Lower Cretaceous (Berriasian) of Soria (La Revilleja track site) has irregular to pentagonal manus tracks (Meijide Fuentes *et al.* 2004). In Germany, *Rotundichnus muenchehagensis* from the Lower Cretaceous (Berriasian) of the Bückeberg Formation (Münchehagen track site) has manus with symmetrical crescent shape, and a heteropody index of 1:2 (Hendricks 1981; Lockley *et al.* 2004), indicating a larger 'manus-pes area ratio' than those of *Titanopodus*.

In Bolivia three important Late Cretaceous (?Campanian–Maastrichtian) track sites (Toro Toro, Cal Orco and Humaca) have been described (Leonardi 1984, 1989; Lockley *et al.* 2002), all of which are assigned to titanosaurs, the only group of sauropods recorded for this time. The Bolivian tracks show some differences with respect to *Titanopodus*, i.e. they exhibit a relatively high manus/pes ratio (1:1, 1:2 and 1:2–1:3 in Toro Toro, Cal Orco and Humaca sites respectively). In this context, Lockley *et al.* (2002) claimed that the relatively small manus of some of the tracks from Humaca are, in part, an artefact of preservation, and all Bolivian sauropod tracks assigned to adult individuals, show a relatively high manus/pes ratio. In contrast, at the *Titanopodus* track site, relatively large manii have not been observed, and so all the trackways measured indicate a ratio for the manus/pes of 1:3. Other differences between the Bolivian tracks and *Titanopodus* are related to the trackway width. The large Bolivian titanosaur tracks from Toro Toro and Cal Orco exhibit a moderate wide-gauge trackway (MTR and PTR values of 31.56 and 36.24 per cent respectively), whereas the Cal Orco footprints shows a medium gauge trackway. Moreover, the smaller tracks from Humaca (tentatively assigned to subadults or juveniles for Lockley *et al.* 2002) show a medium gauge trackway (PTR ratio of 45.30 per cent). In contrast, the trackways AC-1 and AC-4 of *Titanopodus*, assigned to individuals of relatively medium size (14–16 m long), shows a very wide-gauge trackway (MTR and PTR of 18–22 and 26–31 per cent respectively).

Morphologically, the Bolivian footprints show both differences and similarities with respect to *Titanopodus*. For example, some manus impressions of Toro Toro exhibit an asymmetrical crescent shape with an acuminate and thinner external border, like is present in *Titanopodus*. However, we recognized differences of heteropody value and digit morphology between *Titanopodus* and the unnamed ichnotaxon of Toro Toro. For examples, the manus tracks of Toro Toro shows three sharper claw traces while those of the Humaca site exhibit five blunt digit impressions. In contrast, the manus of *Titanopodus* have neither claw nor digit impressions.

In general lines, the crescent shape is related to the unique morphology of the sauropod manus, which forms

a semi-tubular and U-shaped structure due to the vertical orientation of the metacarpals (McIntosh 1990; Upchurch 1994; Wilson and Sereno 1998; Wilson 2002). Functionally, a semi-tubular manus and a parallel radius and ulna may have limited tensional stresses in the forearm, and might constitute part of the larger number of mechanisms responsible for gigantism in sauropods (Bonnar 2003). In the trackways described herein no evidences of manual phalanges are found. This aspect is in agreement with the skeletal remains of the Late Cretaceous titanosaurs, which have no phalangeal facets in the metacarpals (González Riga 2003). This character is considered as synapomorphy of Titanosauridae (Salgado *et al.* 1997; Calvo *et al.* 2007) or Litostrotia clades (Upchurch *et al.* 2004; González Riga *et al.* 2009).

The ichnological features of *Titanopodus* indicated that the trackmakers were sauropods of wide-gauge trackways and middle size (14–16 m long). In the Campanian–Maastrichtian strata of the world, the only sauropod species known represent derived titanosaurs. For this reason, we conclude that *Titanopodus* was made by derived titanosaurs (e.g. Aeolosaurini or Saltasaurini species, very abundant in the Neuquén Basin). It is important to consider that in other sites at or near Mendoza Province, the Formation Loncoche has several records of bones and teeth belonging to derived titanosaurs (González Riga 1999; Previtara and González Riga 2008). Finally, in contrast to other track sites in South America (like Toro Toro and Cal Orco from Bolivia), *Titanopodus* indicates that not all titanosaurs had both a large manus and low degree of heteropody.

Acknowledgements. The Agua del Choique track site was discovered while developing project PIP 5132 of CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina). We thank the financial support provided via project PIP 5222 of CONICET, project 2007–2009 of the Universidad Nacional de Cuyo (Mendoza, Argentina) and project PICT 2005–33984 of the ANPCYT (Agencia Nacional de Promoción Científica y Tecnológica, Argentina). We thank Dra. Mercedes Prámparo, who worked with the authors in the preservation of the track site, Lic. Elena Previtara, Lic. Cecilia Pirrone and Rodolfo Giménez for their field support, Dra. Ana Parras for their geological studies that facilitated our explorations. Constructive comments of the editor, Dr Oliver Rauhut, and reviewers significantly improve this paper. We thank to Dr Michael Caldwell for reviewing this paper and improving the English. Finally, we are grateful to IANIGLA (Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza) for their important field support, and the Municipalidad de Malargue for their collaboration.

REFERENCES

- ALEXANDER, R. M. 1976. Estimates of the speed of dinosaurs. *Nature*, **261**, 129–130.

- ALONSO, R. N. 1980. Icnitas de dinosaurios (Ornithopoda: Hadrosauridae) en el Cretácico superior del norte de Argentina. *Acta Geológica Lilloana*, **15**, 55–63.
- and MARQUILLAS, R. 1986. Nueva localidad con huellas de dinosaurios y primer hallazgo de aves en la Formación Yacoraita (Maastrichtiano) del norte argentino. *Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía*, **2**, 33–42.
- BONNAN, M. E. 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. *Journal of Vertebrate Paleontology*, **23**, 595–613.
- CALVO, J. O. 1991. Huellas de dinosaurios en la Formación Río Limay (Albiano–Cenomaniano?), Picún Leufú, Provincia del Neuquén, República Argentina (Ornithischia–Saurischia: Sauropoda–Theropoda). *Ameghiniana*, **28**, 241–258.
- 1999. Dinosaurs and other vertebrates of the Ezequiel Ramos Mexía área, Neuquén–Patagonia Argentina. 13–15. In TOMIDA, Y., RICH, T. and VICKERS-RICH, P. (eds). *Proceedings of the Second Gondwanan Dinosaur Symposium. National Science Museum Monographs*, **15**, 296 pp.
- and MAZZETTA, G. V. 2004. Nuevos hallazgos de huellas de dinosaurios en la Formación candeleros (albiano–Cenomaniano), Picún leufú, Neuquén, Argentina. *Ameghiniana*, **41**, 545–554.
- GONZÁLEZ RIGA, B. J. and PORFIRI, J. A. 2007. *Muyelensaurus pecheni* gen. et sp. nov., a new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Archivos do Museu Nacional*, **65**, 485–504.
- CASAMIQUELA, R. M. and FASOLA, A. 1968. Sobre pisadas de dinosaurios del Cretácico Inferior de Colchagua (Chile). *Departamento de Geología de la Universidad de Chile*, **30**, 1–24.
- DAY, J. J., NORMAN, D. B., GALE, A. S., UP-CHURCH, P. and POWELL, H. P. 2004. A idle Jurassic Dinosaur trackway site from Oxfordshire, UK. *Palaeontology*, **47**, 319–348.
- FARLOW, J. O. 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. *Zubia*, **10**, 89–138.
- PITTMAN, J. G. and HAWTHORNE, J. M. 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U.S. Gulf Coastal Plain. 371–394. In GILLETTE, D. D. and LOCKLEY, M. G. (eds). *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, 454 pp.
- GONZÁLEZ RIGA, B. J. 1999. Hallazgo de vertebrados fósiles en la Formación Loncoche, Cretácico Superior de la provincia de Mendoza, Argentina. *Ameghiniana*, **36**, 401–410.
- 2002. Estratigrafía y Dinosaurios del Cretácico Tardío en el extremo sur de la Provincia de Mendoza, República Argentina. Unpublished PhD thesis, Universidad Nacional de Córdoba, Córdoba, Argentina, 280 pp.
- 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. *Ameghiniana*, **40**, 155–172.
- and ASTINI, R. 2007. Fossil preservation of large titanosaur sauropods in overbank fluvial facies: a case study in the Cretaceous of Argentina. *Journal of South American Earth Sciences*, **23**, 290–303.
- and CALVO, J. O. 2006. Primer estudio sobre huellas de dinosaurios en la provincia de Mendoza, Argentina. *Actas del Noveno Congreso Argentino de Paleontología y Bioestratigrafía*, **1**, 284.
- — 2007. Huellas de dinosaurios saurópodos en el Cretácico de Argentina. In DÍAZ-MARTÍNEZ, E. and RÁBANO, I. (eds). *4th European Meeting on the Palaeontology and Stratigraphy of Latin America, Cuadernos del Museo Geominero*, **8**, 173–179.
- and PARRAS, A. M. 1998. Paleambiente y Paleontología de la Formación Loncoche (Cretácico Superior) en Ranquil-Có, sur de la provincia de Mendoza, Argentina. *Actas del Séptimo Congreso Argentino de Paleontología y bioestratigrafía*, **1**, 81.
- PREVITERA, E. and PIRRONE, C. 2009. *Malarguesaurus florenciae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cretaceous Research*, **30**, 135–148.
- HENDRICKS, A. 1981. Die Saurierfahrten von Múnchehagen bei Rehburg-Loccum (NW-Deutschland). *Abhandlung Landesmuseum Naturkunde Münster*, **43**, 1–22.
- LEANZA, H. A., APESTEGUIA, S., NOVAS, F. and DE LA FUENTE, M. S. 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapods assemblages. *Cretaceous Research*, **25**, 61–87.
- and HUGO, C. A. 2001. Cretaceous red beds from southern Neuquén Basin (Argentina): age, distribution and stratigraphic discontinuities. *Asociación Paleontológica Argentina, Publicación Especial*, **7**, 117–122.
- LEGARRETA, L. and GULISANO, C. 1989. Análisis estratigráfico secuencial de la cuenca Neuquina (Triásico Superior–Terciario inferior). In CHEBLI, G. and SPALLETTI, L. (eds). *Cuencas Sedimentarias Argentinas. Correlación Geológica*, **6**, 221–243.
- and ULIANA, M. A. 1991. Jurassic–Cretaceous marine oscillations and geometry of back-arc basin fill, central Argentine Andes. *International Association of Sedimentology, Special Publication*, **12**, 429–450.
- LEONARDI, G. 1984. Le impromte fossili di dinosauri. 165–186. In BONAPARTE, J., COLBERT, J., CURIE, P., DE RICQLES, A., KIELAN-JAWOROWSKA, Z., LEONARDI, G., MORELLO, N. and TAQUET, P. (eds). *Sulle orme dei dinosauri*. Errizo Editrice, Venice, 250 pp.
- 1989. Inventory and statistics of the South American dinosaurian Ichnofauna and its paleobiological interpretation. 165–178. In GILLETTE, D. and LOCKLEY, M. (eds). *Dinosaur Tracks and Traces*. Cambridge University Press, Cambridge, 454 pp.
- LOCKLEY, M. G. 1991. *Tracking Dinosaurs: A New look at an Ancient World*. Cambridge University Press, New York, 238 pp.
- FARLOW, J. O. and MEYER, C. A. 1994. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia*, **10**, 233, 248.
- HOUCK, K., YANG, S., MATSUKAWA, M. and LIM, S. 2006. Dinosaur-dominated footprint assemblages

- from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong County, South Korea: Evidence and implications. *Cretaceous Research*, **27**, 70–101.
- SHULP, A. S., MEYER, C. A., LEONARDI, G. and KERUMBA MAMANI, D. 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research*, **23**, 383–400.
- WRIGHT, J. L. and THIES, D. 2004. Some observations on the dinosaur tracks at Münchehagen (Lower Cretaceous), Germany. *Ichnos*, **2**, 261–274.
- MCINTOSH, J. S. 1990. Sauropoda. 345–401. In WEISHAMPEL, D., DOBSON, P. and OSMOLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.
- MEIJIDE FUENTES, F., FUENTES VIDARTE, C. F., MEIJIDE CALVO, M. and MEIJIDE FUENTES, M. 2004. Rastro de un dinosaurio saurópodo en el Weal de Soria (España). *Brontopodus oncalensis* nov. icnsp. *De Celtiberia*, **98**, 501–516.
- MEYER, C. A., HIPPLER, D. and LOCKLEY, M. G. 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia—facts and implications. 7th International Symposium on Mesozoic Terrestrial Ecosystems. *Asociación Paleontológica Argentina, Publicación Especial*, **7**, 133–138.
- MORENO, K. and BENTON, M. 2005. Occurrence of sauropod dinosaur tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*). *Journal of South American Earth Sciences*, **20**, 253–257.
- BLANCO, N. and TOMLINSON, A. 2004. Nuevas huellas de dinosaurios del Jurásico Superior en el norte de Chile. *Ameghiniana*, **41**, 535–543.
- and PINO, M. 2002. Huellas de dinosaurios (Theropoda–Ornitopoda–Sauropoda) de la Formación Baños del Flaco, VI Región, Chile: paleoambiente y paleoetología. *Revista Geológica de Chile*, **29**, 191–206.
- PARRAS, A., CASADÍO, S. and PIREZ, M. 1998. Secuencias depositacionales del Grupo Malargüe (límite Cretácico–Paleógeno), sur de la provincia de Mendoza, Argentina. *Publicación Especial de la Asociación Paleontológica Argentina*, **5**, 181–192.
- PRÁMPARO, M. B., GONZÁLEZ RIGA, B. J., CERDEÑO, E., CALVO, J. O., REGUERO, M. and PREVITERA, E. 2006. Enfoque multidisciplinario para el estudio de nuevos hallazgos paleontológicos en el Cretácico y Paleógeno del sur de Mendoza. *Actas del noveno Congreso Argentino de Paleontología y Bioestratigrafía*, **1**, 263.
- PREVITERA, M. E. and GONZÁLEZ RIGA, B. J. 2008. Primer hallazgo de vertebrados fósiles en la Formación Loncoche (Cretácico Superior) en el área de Calmu-Co, Mendoza, Argentina. *Ameghiniana*, **45**, 349–359.
- ROMANO, M., WHYTE, M. and JACKSON, S. J. 2007. Trackway ratio: a new look at trackway gauge in the analysis of quadrupedal Dinosaur trackways and its implications for Ichnotaxonomy. *Ichnos*, **14**, 257–270.
- SALGADO, L., CORIA, R. A. and CALVO, J. O. 1997. Evolution of Titanosaurid Sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana*, **34**, 3–32.
- SANTOS, V. F. dos., LOCKLEY, M. G., MEYER, C. A., CARVALHO, J., GALOPIM DE CARVALHO, A. M. and MORATALLA, J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia*, **10**, 5–13.
- THULBORN, A. 1990. *Dinosaur tracks*. Chapman and Hall, London, 410 pp.
- UPCHURCH, P., BARRET, P. M. and DODSON, P. 2004. Sauropoda. 259–324. In WEISHAMPEL, D., DOBSON, P. and OSMOLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.
- 1994. Manus claw function in sauropod dinosaurs. *Gaia*, **10**, 161–171.
- WILSON, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society*, **136**, 217–276.
- and CARRANO, M. T. 1999. Titanosaurs and the origin of ‘wide gauge’ trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, **25**, 252–267.
- and SERENO, P. 1998. Early evolution and higher-level phylogeny of Sauropod dinosaurs. *Journal of Vertebrate Paleontology*, **18**(Suppl. 2), 1–68.
- WRIGHT, J. L. 2006. Steps in understanding Sauropod biology. 252–284. In CURRY ROGERS, K. A. and WILSON, J. A. (eds). *The Sauropods, evolution and paleobiology*. University of California Press, Berkeley, 349 pp.