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REVISION OF DINOSAUR ICHNOTAXA FROM THE LA MATILDE FORMATION (MIDDLE JURASSIC), SANTA CRUZ PROVINCE, ARGENTINA

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Abstract. An ichnological assemblage from the Middle Jurassic La Matilde Formation at Estancia Laguna Manantiales, Santa Cruz Province, Argentina, is exceptional both in diversity and abundance. It includes four dinosaurian ichnotaxa (*Wildeichnus*, *Grallator*, and the endemic *Delatorrichnus* and *Sarmientichnus*), the mammalian *Ameghinichnus*, several vertebrate tracks of uncertain ichnogeneric assignment and invertebrate and root cavities. Because of its importance, an updated ichnotaxonomic revision and a detailed study are needed. In this contribution, the dinosaur ichnogenera are revised and emended diagnoses of three of them are provided. Recorded together with ichnogenera originally named by Casamiquela —*Delatorrichnus*, *Sarmientichnus* and *Wildeichnus*— is the cosmopolitan *Grallator*. A few tracks of dubious assignment are described. *Casamiquelichnus* Coria and Paulina Carabajal, 2004, from the same locality, is a junior synonym of *Sarmientichnus*. The paleocommunity represented by the La Matilde ichnofauna was dominated by small-bodied species with high regenerative and resettling capacity.

Key words. Dinosaur tracks. Ichnotaxonomy. La Matilde Formation. Late Middle Jurassic. Argentina. South America.

Resumen. REVISIÓN DE LOS ICNOTAXONES DE DINOSAURIOS DE LA FORMACIÓN LA MATILDE (JURÁSICO MEDIO), PROVINCIA DE SANTA CRUZ, ARGENTINA. La asociación icnológica de la Estancia Laguna Manantiales, del Jurásico Medio de la Formación La Matilde, provincia de Santa Cruz, Argentina, es excepcional tanto por su diversidad como por su abundancia. La icnofauna de vertebrados de La Matilde incluye cuatro icnotaxones asignados a dinosaurios (*Wildeichnus*, *Grallator*, y los endémicos *Delatorrichnus* y *Sarmientichnus*), además de *Ameghinichnus* (un taxón relacionado con mamíferos), varias huellas de asignación incierta, además de trazas de invertebrados y raíces. Debido a su importancia, la asociación necesita un estudio detallado y una revisión icnotaxonómica actualizada. En esta contribución, se revisan los icnogéneros de dinosaurios y se enmienda la diagnosis de tres de ellos. Además de los icnogéneros nombrados originalmente por Casamiquela (*Delatorrichnus*, *Sarmientichnus* y *Wildeichnus*), se registra el icnogénero cosmopolita *Grallator*. Se describen algunas huellas de asignación icnogenérica incierta. *Casamiquelichnus* Coria y Paulina Carabajal, 2004, proveniente de la misma localidad, es considerado un sinónimo junior de *Sarmientichnus*. La paleocomunidad representada por esta icnofauna habría estado compuesta por especies de pequeño tamaño corporal con alta capacidad de regeneración y de recolonización.

Palabras clave. Huellas de dinosaurios. Icnotaxonomía. Formación La Matilde. Jurásico Medio superior. Argentina. América del Sur.

Current knowledge on the Jurassic dinosaur record from Argentina is relatively scarce considering that this region underwent geographical extension during this period, originating continental depositional basins suitable for the appearance of dinosaurs that are well-known in other areas of the world (*e.g.*, Bonaparte, 1996; Moreno and Benton, 2005; Rauhut, 2005, 2007). The Jurassic dinosaur-ichnofossil record from Argentina is not an exception. Tetrapod tracks in Jurassic rocks are restricted —in Argentina— to two geologic units, *i.e.*, the Cerro Cóndor Formation (late Late Jurassic–early Early Cretaceous), Chubut Province, which has yielded up to now only one tridactyl theropod footprint (Coria, 1989), and the La Matilde Formation, Santa Cruz Province, which carries a diverse assemblage of footprints (Casamiquela, 1960, 1961, 1964; de Valais and Melchor, 2003; de Valais *et al*., 2003; Coria and Paulina Carabajal, 2004; Melchor *et al*., 2004; de Valais, 2008, 2009).

Casamiquela (1964) mentioned a purported Triassic coelurosaurian footprint from Bajo Caracoles, northwestern Santa Cruz Province, Argentina (Leonardi, 1989, p. 166, 1994, p. 24), but the age of the section where the track was collected was later referred to the Jurassic (Panza and Haller, 2002). However, the lithology of the slab does not agree with that of the rocks exposed at the presumed source locality (Casamiquela, 2002). Therefore, the true nature and provenance of this track remains unknown.

Neorotodactylus leonardii Casamiquela, 1980, from the Early Jurassic Piedra Pintada Formation, Neuquén Province, Argentina, was originally presented as a reptilian footprint (Casamiquela, 1962, 1980). It was later reinterpreted as non-tetrapod by Leonardi (1994, p. 25), an opinion supported herein.

The ichnological assemblage from the La Matilde Formation (Santa Cruz Province, Middle Jurassic) is the most

diverse and abundant one coming from rocks of equivalent age anywhere in South America. It includes trace fossils of mammals, dinosaurs, invertebrates, and root cavities (Casamiquela, 1960, 1964, 1974a; de Valais and Melchor, 2003; de Valais *et al*., 2003; Coria and Paulina Carabajal, 2004; Melchor *et al*., 2004; de Valais, 2008, 2009). Because of the importance of this assemblage, an ichnotaxonomic revision of the dinosaur tracks is needed. The aim of this contribution is to present a comprehensive and updated ichnotaxonomic treatment of the Jurassic dinosaur-track assemblage from the La Matilde Formation. This review deals with published and unpublished material whether studied *in situ* or housed in different ichnological collections.

GEOLOGICAL SETTING

The La Matilde Formation interdigitates laterally and vertically with the Chon Aike Formation; together these units comprise the Bahía Laura Group (Stipanicic and Reig, 1956; Lesta and Ferello, 1972). The formation has been interpreted as deposited in a lowland setting associated with an active volcanic environment, with swamps and water bodies probably derived from adjacent floodplains (Mazzoni *et al*., 1981; Panza, 1998; Melchor *et al*., 2004).

Radiometric ages of the Chon Aike Formation (de Barrio *et al*., 1999), together with the faunal and floral fossil records of the La Matilde Formation (Stipanicic and Reig, 1956; Stipanicic and Bonetti, 1970), constrain the age of the unit to the 160–172 Ma interval (*i.e.*, Bajocian–Callovian, late Middle Jurassic).

The ichnofossiliferous site is located in Estancia Laguna Manantiales, 25 km to the northwest from the Petrified Forest Natural Monument at Jaramillo, Santa Cruz Province, Argentina (Fig. 1). The ichnofossil-bearing-unit lies here almost horizontal, with a measured thickness reaching 68 m (Melchor *et al*., 2004). It overlies the Aptian Bajo Tigre Formation of the Baqueró Group, from which it is separated by an angular unconformity (Andreis *et al*., 1992; Panza, 1998; Cladera *et al*., 2002). The analyzed section includes primary ashfall, reworked tuffs, welded tuffs, tuffaceous siltstones and fine-grained sandstones, and rhyolithic ignimbrites (Melchor *et al*., 2004).

Six different vertebrate ichnogenera from three track-bearing levels have been recognized from the Estancia Laguna Manantiales locality (de Valais and Melchor, 2003; Melchor *et al*., 2004). Two of them are mammalian in origin (*Ameghinichnus patagonicus* Casamiquela, 1961, and *A. manantialensis* de Valais, 2009), while the other four are dinosaurian (*Delatorrichnus goyenechei* Casamiquela, 1964, *Sarmientichnus scagliai* Casamiquela, 1964, *Wildeichnus navesi* Casamiquela, 1964, and *Grallator* isp.). Among the invertebrate ichnotaxa, the most abundant is *Hexapodichnus*

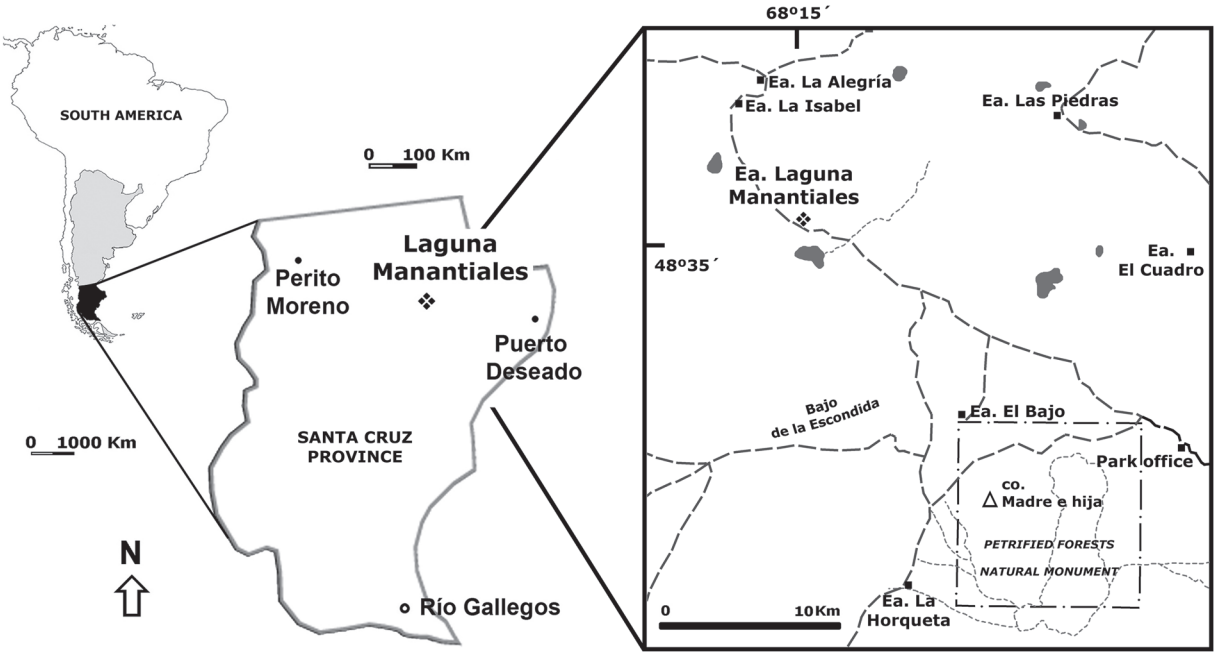

Figure 1. Location map of Estancia Laguna Manantiales, Santa Cruz Province, Argentina. The star indicates the ichnofossiliferous locality / *Mapa de localización de la Estancia Laguna Manantiales, provincia de Santa Cruz, Argentina. La estrella indica la localidad icnofosilífera.*

casamiquelai de Valais, Melchor and Genise, 2003, likely attributable to a pterygote insect. During the last few years, some other vertebrate tracks of dubious validity have further enriched the ichnological record (de Valais, 2008, 2009).

MATERIALS AND METHODS

The first ichnofossils recovered from the La Matilde Formation were collected during the 1960s by Casamiquela (1960, 1964); this collection was later enlarged by Bonaparte and others (Casamiquela, 2002; Melchor *et al*., 2004). Recent expeditions carried out by the author and colleagues yielded new specimens, increasing the data available from this locality.

The tracks examined, both as natural molds and casts, include published and unpublished material housed in several ichnological collections in Argentina. For those tracks not collected in the field, plaster replicas were prepared. All general measurements of the footprints (Tabs. 1–3) follow the conventions and methods of Leonardi (1987) and Thulborn (1990). In the case of tridactyl footprints, the conventions used are those of Olsen *et al*. (1998). Track and trackway measurements and collection numbers are shown in Tables 1–3.

In this contribution, the general ichnotaxomonic concepts of vertebrate trace fossils follow the criteria of Bertling *et al*. (2006) and de Valais and Melchor (2008).

***Institutional abbreviations*.** **MACN**, Colección de Paleontología de Vertebrados del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (**SC**, Colección de Santa Cruz), Buenos Aires Province, Argentina; **MJG**, Museo "Jorge Gerold", Ingeniero Jacobacci, Río Negro Province, Argentina; **MLP**, Museo de La Plata, La Plata, Buenos Aires Province, Argentina; **MPEF-IC**, Colección de Icnología del Museo Paleontológico "Egidio Feruglio", Trelew, Chubut Province, Argentina; **MPM-PIc**, Colección de Icnología del Museo Regional Provincial "Padre Manuel Jesús Molina", Río Gallegos, Santa Cruz Province, Argentina; **PVL**, Colección de Paleontología de Vertebrados del Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán Province, Argentina.

SYSTEMATIC PALEONTOLOGY

Ichnogenus ***Delatorrichnus*** Casamiquela, 1964

1964. *Delatorrichnus* Casamiquela, p. 134, pls. 1.3, 9; Casamiquela, 1966, p. 376, pls. 1–3; Haubold, 1971, p. 79, fig. 48.10; Bonaparte, 1983, p. 81, fig. 5.6; Leonardi, 1994, p. 26, pl. 4.1a,10, 18, 20, 22, 17.3–4; Casamiquela, 2002, p. 437; Melchor *et al*., 2004, p. 54, fig. 4.i–j; Milner *et al*., 2009, p. 11.

Type ichnospecies. *Delatorrichnus goyenechei* Casamiquela, 1964, from the upper Middle Jurassic La Matilde Formation, Santa Cruz Province, Argentina.

Emended diagnosis. Quadrupedal trackways with symmetric manus and pes impressions, with the manus impressions located medial to, and usually in contact with, the pes prints. Both manus and pes prints are longer than wide, with the pes nearly twice the size of the manus. Manus imprints are tridactyl or tetradactyl, have subparallel digit impressions, and are nearly rhomboid in outline, with the major axis almost parallel to the midline. Pes prints are tridactyl and display outward rotation from midline; digit impressions are robust and show low divarication angles. Digit III is the longest. Digital pads are absent. The trackway is relatively wide, with high pace angulation for both manus and pedes.

Remarks and comparisons. Quadrupedal ichnogenera composed of tridactyl pes prints associated with hand imprints have been recorded in the ichnofossil record in strata as old as Late Triassic (*e.g.*, Fraser and Olsen, 1996; Haubold and Klein, 2000, and references therein). Representative ichnogenera are *Atreipus* Olsen and Baird, 1986, *Banisterobates* Fraser and Olsen, 1996, *Anomoepus* Hitchcock, 1848, and *Hypsiloichnus* Stanford *et al*., 2004. *Delatorrichnus* can be distinguished from these ichnotaxa primarily by having medium-sized manus impressions (in relation to the pes impressions) that are usually in direct contact with —or nearly so— the pes prints. In addition, *Delatorrichnus* lacks certain characteristic features of the four ichnogenera mentioned above. *Atreipus* Olsen and Baird, 1986, differs from *Delatorrichnus* by having a lower length/width ratio, digital pad impressions, claw marks, and a substantial digit III projection (expressed as parameter P, see below). *Banisterobates* Fraser and Olsen, 1996, from the Triassic of Virginia (USA), is distinguished from *Delatorrichnus* by its tetradactyl pes print with a reduced digit I, a substantial digit III projection, and a poorly defined hand print with possibly three short digit impressions. Both *Anomoepus* Hitchcock, 1848, from the Early Jurassic Newark Supergroup in New England, USA, and *Hypsiloichnus* Stanford *et al*., 2004, from the Early Cretaceous of Maryland, USA, possess tridactyl pes prints but with digit I occasionally preserved (Gierliński, 1991), and a manus with five splayed digit imprints.

A manus-pes set from the Early Jurassic Zagaje Formation of Sołtyków, Poland, was compared with or included in *Delatorrichnus* (Gierliński and Sabath, 2002; Gierliński *et al*., 2004; Gierliński *et al*., 2005). Although the pes prints are morphologically similar, the hand print from Poland is smaller than the manus of *Delatorrichnus*, wider than long, and has splayed digit impressions. On the basis of these features, this set does not match the diagnosis of *Delatorrichnus*.

Pes impressions resembling *Delatorrichnus* —albeit without manus prints— were mentioned from the Kayenta Formation, Utah, USA (Lockley, 1986), but no further details are not available.

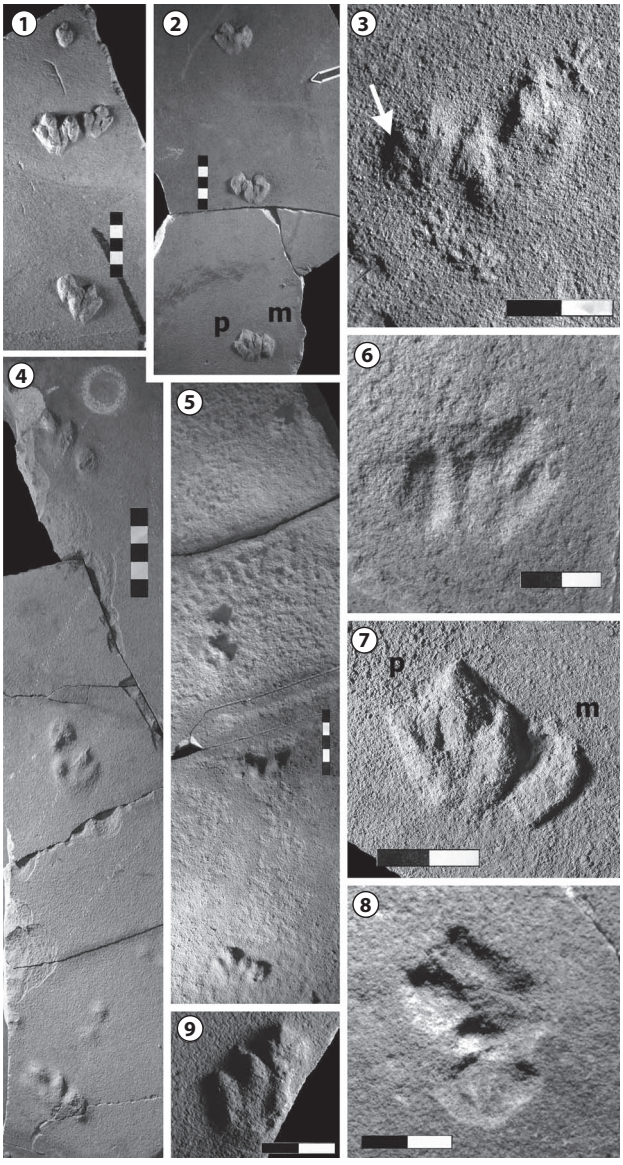

Figure 2. ***Delatorrichnus goyenechei*** from the La Matilde Formation. **1**, MLP 65-XI-12-1/1; **2**, MLP 60-X-31-6, holotype; **3**, PM-PIc-3958; the white arrow indicates the fourth manual digit impression; there are two manus-pes sets of ***Ameghinichnus patagonicus*** Casamiquela, 1961; **4**, MLP 65-XI-12-1/2; **5**, MPM-PIc-3782; **6**, MACN 18615; **7**, MLP 60-X-31-1; **8**, detail of the second manus-pes set of PVL 3690; **9**, MLP 65-XI-12-1/3. Scale bars: 2 cm in 3 and 6–9, and 5 cm in the rest. **m**, manus imprint; **p**, pes imprint / **Delatorrichnus goyenechei** *de la Formación La Matilde.* ***1,*** *MLP 65-XI-12-1/1;* ***2****, MLP 60-X-31-6, holotipo;* ***3,*** *PM-PIc-3958; la flecha blanca indica la impresión del cuarto dígito de la impronta de la mano; hay dos pares mano-pie de* **Ameghinichnus patagonicus** *Casamiquela, 1961;* ***4****, MLP 65-XI-12-1/2;* ***5****, MPM-PIc-3782;* ***6****, MACN 18615;* ***7****, MLP 60-X-31-1;* ***8****, detalle del segundo par mano-pie de PVL 3690;* ***9****, MLP 65-XI-12-1/3. Escala: 2 cm en 3 y 6–9, y 5 cm en el resto.* ***m****, impronta de mano;* ***p****, impronta de pie*

Delatorrichnus goyenechei Casamiquela, 1964

Figure 2

1964. *Delatorrichnus goyenechei* Casamiquela, p.134, pls. 1.3, 9; Casamiquela, 1966, p. 376, pls. 1–3; Haubold, 1971, p. 79, fig. 48 10; Bonaparte, 1983, p. 81, fig. 5.6.; Leonardi and de Oliveira Lima, 1990, p. 220, 225, pls. 1.D, 4.D; Leonardi, 1994, p. 26, pl. 4.1a,10,18,20,22, 17.3–4; Casamiquela, 2002, p. 437; Melchor *et al.*, 2004, p. 54, fig. 4.i,j.

Holotype. MLP 60-X-31-6, trackway with three manus-pes sets on two slabs, from the La Matilde Formation, Santa Cruz Province, Argentina (Fig. 2.2).

Paratypes. MLP 60-X-31-7, same locality.

Additional material. MPM-PIc-3782, 3958, MACN 18615, MLP 60-X-31-1 (two slabs with the same collection number), 65-XI-12-1/1, 65-XI-12-1/2, 65-XI-12-1/3, PVL 3677, 3690, 3682, one unnumbered MJG specimen, and at least one *in situ* trackway, same locality (Figs. 2.1, 2–8).

Diagnosis. Same as for ichnogenus.

Description. Specimens include four trackways produced by a quadrupedal trackmaker; the trackways contain eleven manus and twelve pes prints; there are also four isolated manus-pes sets. Table 1 summarizes their measurements.

Trackways are composed of manus-pes sets, with the pes print located external to and overstepping or slightly overprinting the manus. The pes prints are nearly symmetrical in relation to the major axis of the track, and have an average width and length of 25.2 mm and 29.1 mm, respectively. The average projection ratio of digit imprint III (parameter P of Olsen *et al.*, 1998) is 2.8 (parameter T= 26.2 mm and parameter R´= 18.4 mm). Pedal digit impressions are relatively thick and lack digital pads. Digit III is acuminate. Digit impressions display average lengths, in decreasing order, of 19.4 mm (III), 15.5 mm (IV), and 15.2 mm (II). Divarication angles subtended by II-III and III-IV are subequal, averaging 24º and 25º, respectively; the angle between II and IV averages 42º. Pes imprints show an outward rotation relative to the midline (mean 14º). Average pace angulation and stride length are 162º and 294.2 mm respectively.

Hand prints show rhomboid outlines with the major axis almost parallel to the midline. They have an average width of 12.9 mm and length of 18.4 mm. There are no clear distinctions between digit impressions; the imprint of digit I is clear only in MPM-PIc-3958 and MPM-PIc 3782, which are both tetradactyl (Fig. 2.3). Impressions of digits II, III and IV are relatively thick, subparallel, and closely appressed. Their average lengths, in decreasing order, are 6.1 mm (III), 4.6 mm (IV), 4.5 mm (II), and 2.5 mm (I). Average pace angulation is 172º and average stride length is 298 mm.

Remarks. At present, this ichnospecies has not been unambiguously recorded at any other locality.

Paleobiological implications. *Delatorrichnus* was originally attributed to a quadrupedal "coelurosaurian" dinosaur (Casamiquela, 1964, 1966), an opinion supported by other authors (*e.g.*, Thulborn, 1990; Haubold, 1971, 1984; Leonardi, 1994). More recently, its theropod affinities have been perceived as unlikely (Milner *et al*., 2009) and attribution to a basal, small ornithischian dinosaur appears more likely (Bonaparte, 1996; Gierliński and Niedźwiedzki, 2002). Based on track features (*e.g.*, high length/width ratio, thick pedal digit impressions, manus print associated with pes print; Moratalla *et al*., 1988), it is herein accepted as an ornithischian ichnotaxon.

In almost all specimens of *Delatorrichnus goyenechei*, the pes print is preserved with an associated hand print, except in the second set of MLP 60-X-31-1, probably because of preservation conditions. This consistent coupling of manus and pes prints indicates that the producer was an obligate quadruped.

Ichnogenus ***Grallator*** Hitchcock, 1858

Type ichnospecies. *Grallator parallelus* (Hitchcock, 1858), from the Early Jurassic Portland Formation, Massachusetts, USA.

Revised diagnosis. "Small (<15 cm long), bipedal, functionally tridactyl ichnite. Digit III projects relatively further anteriorly and the foot is more narrow than in *Eubrontes* and *Anchisauripus* (length/width ratio near or greater than 2). Hallux rarely impressed. Divarication of outer digits 10º–30º" (Olsen *et al*., 1998, p. 595).

Remarks and comparisons. Ichnogenera *Grallator*, *Anchisauripus*, and *Eubrontes* have been often distinguished mainly on the basis of their size rather than morphological differences (Olsen *et al*., 1998). Following the criteria of Bertling *et al*. (2006) and de Valais and Melchor (2008), the size of the track is not considered herein a valid or useful ichnogeneric criterion and should not be used to distinguish ichnogenera. A detailed analysis of these ichnogenera and their ichnospecies lies beyond the focus of this contribution.

Grallator prints differ from the ichnogenus *Atreipus* Olsen and Baird, 1986 by lacking a manus imprint (although not more than two sequential tracks were found in the La Matilde Formation) and the clear distinction of digital pads in digit III, which are usually coalesced in pes prints of *Atreipus* (Olsen and Baird, 1986).

Similarly, *Grallator* is distinguished from *Delatorrichnus* mainly by the absence of a manus imprint and by the presence of the digital pads in the pes prints.

***Table 1. Summary of measured track and trackway parameters of* Delatorrichnus goyenechei*. Linear measurements in millimeters and angles in degrees* / Resumen de los parámetros medidos de huellas y rastrilladas de *Delatorrichnus goyenechei*. Mediciones lineales en milímetros y ángulos en grados.**

	L	*W*	*I*	*II*	*III*	*IV*	*II-III*	*III-IV*	*II-IV*	*PA*	*SL*	*DM*
Delatorrichnus												
Manus												
Mean	*18,4*	*12,9*	*2,5*	*4,5*	*6,1*	*4,6*	…	…	…	*172*	*294,2*	…
Min	*13,5*	*12,4*	*2,5*	…	…	…	…	…	…	*152*	*258*	…
Max	*22,5*	*14*	*2,5*	…	…	…	…	…	…	*190*	*368*	…
n	*15*	*11*	*2*	*1*	*1*	*1*	…	…	…	*4*	*5*	…
Pes												
Mean	*29,1*	*25,2*		*15,2*	*19,4*	*15,5*	*23,8*	*24,7*	*42*	*161,5*	*297,8*	*14,3*
Min	*24*	*22*		*12,2*	*14,5*	*13,5*	*16*	*17*	*25*	*146*	*234*	*11*
Max	*33,1*	*28,4*		*17,6*	*21,6*	*19,6*	*32*	*39*	*52*	*170*	*375*	*18*
N	*16*	*14*		*8*	*10*	*10*	*8*	*9*	*9*	*4*	*4*	*6*

Abbreviations: **L**, *tracks length*; **W**, *track width*; **I**, *length of digit I*; **II**, *length of digit II*; **III**, *length of digit III*; **IV**, *length of digit IV*; **II-III**, *divarication angle between digits II and III*; **III-IV**, *divarication angle between digits III and IV*; **IV-V**, *divarication angle between digits IV and V*; **PA**, *pace angulation*; **SL**, *stride length*; **DM**, *divarication of the track from the midline* / abreviaturas: ***L***, largo de la huella; ***W***, ancho de la huella; ***I***, largo del dígito I; ***II***, largo del dígito II; ***III***, largo del dígito III; ***IV***, largo del dígito IV; ***II-III***, ángulo formado por los ejes de los dígitos II y III; ***III-IV***, ángulo formado por los ejes de los dígitos III y IV; ***IV-V***, ángulo formado por los ejes de los dígitos IV y V; ***PA***, ángulo de paso; ***SL***, largo del paso doble; ***DM***, divaricación de la huella respecto a la línea media.

Grallator isp.

Figure 3.2–7

2003. cf. *Grallator;* de Valais and Melchor, p. 53R–54R; Melchor *et al.,* 2004, p. 51, fig. 4.k.

Material. MPM 3496, 3497, 3498, 3499, MACN SC-3832 (two slabs with the same collection number).

Description. Specimens thus far recognized in the La Matilde Formation consist of five isolated and two associated, nearly symmetrical pes prints (Tab. 2). Average length and width are 74.2 mm and 47 mm, respectively, with an average length/width ratio of 1.6. The average of the projection ratio of digit imprint III (parameter P) is 1.9 (parameter T= 63.6 mm and parameter R´= 42.9 mm). Impressions of digits are mostly well-preserved, with very clear digital pad impressions with the formula x-2-3-4-x.

Digit impressions are of similar width, although digit III is slightly more robust. They display average lengths of 34.4 mm (II), 44.5 mm (III), and 53.5 mm (IV). On two tracks, digit IV imprints bear triangular claw marks. Average divarication angle between digit imprints II and IV is 37º; between II and III it is 11º, and 21º between digit imprints III and IV. No complete trackway are preserved, but the two associated pes prints display a pace length of 210 mm.

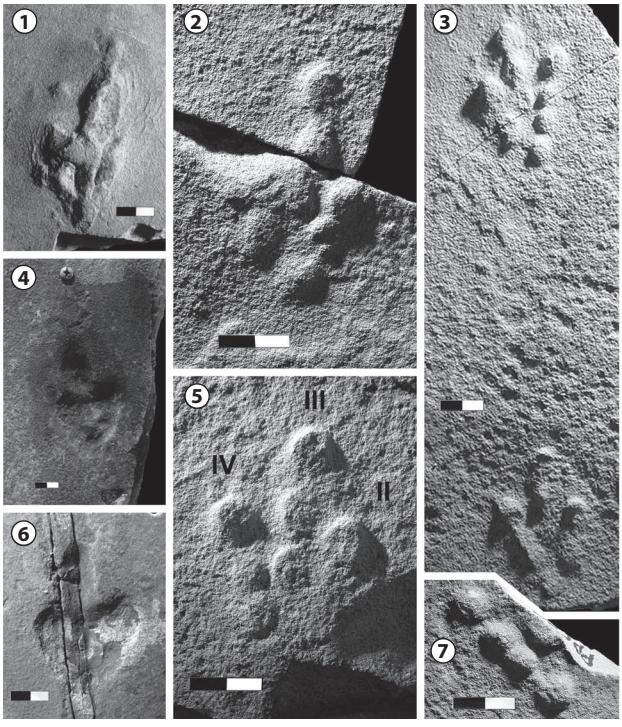

Figure 3. ***Grallator*** from the La Matilde Formation. **1**, MLP 60-X-31-12, ***Grallator***? isp.; **2**, MPMPic-3498; **3**, MPM-Pic-3497; **4**, MACN-SC 3832; **5**, MPM-Pic-3496; **6**, MACN-SC 3832; **7**, MACN-SC 3499. **2-7**, ***Grallator*** isp. Scale bars: 2 cm. **II**, imprint of digit II; **III**, imprint of digit III; **IV**, imprint of digit IV / **Grallator** *de la Formación La Matilde.* ***1****, MLP 60-X-31-12,* **Grallator***? isp.;* ***2****, MPMPic-3498;* ***3****, MPM-Pic-3497;* ***4****, MACN-SC 3832;* ***5****, MPM-Pic-3496;* ***6****, MACN-SC 3832;* ***7****, MACN-SC 3499.* ***2-7****,* **Grallator** *isp. Escala: 2 cm.* ***II****, impresión del dígito II;* ***III****, impresión del dígito III;* ***IV****, impresión del dígito IV.*

Remarks and comparisons. The specimens from the La Matilde Formation are assigned to *Grallator* (Hitchcock, 1858) on the basis of their relatively high length/width ratio, low total divarication, and moderate projection of digit III (Olsen *et al*., 1998).

Paleobiological implications. *Grallator* has been attributed to basal, small to medium-sized theropod dinosaurs (Arcucci, 1986; Olsen *et al*., 1998; Haubold and Klein, 2000; Gaston *et al*., 2003; Gand and Demathieu, 2005), possibly ceratosaurs (*sensu* Rainforth, 1997).

Grallator? isp.

Figure 3.1

1964. "Huella de terópodo celurosauroide"; Casamiquela, p. 138, pl. 10.5.

1990. *Wildeichnus navesi;* Leonardi and de Oliveira Lima, p. 224, pls. 1.A.

1994. *Coelurosauria indet.*; Leonardi, p. 27.

Material. MLP 60-X-31-12.

Description. This specimen is similar to the tracks referred above to *Grallator* isp. from the same locality, but it is characterized by having a cranially elongate (65.2 mm) digit III impression. The track is 88 mm long and 41.2 mm wide. Parameter P of Olsen *et al.* (1998) is 1.0 (parameters T= 100.7 mm and R´= 47.7 mm), and the divarication between digit imprints II-IV is 41°.

Remarks. MLP 60-X-31-12 has been mentioned as a "coelurosaur" track (Casamiquela, 1964; Leonardi, 1994), or even indistinguishable from *Wildeichnus navesi* (Leonardi and de Oliveira Lima, 1990). Herein it is reinterpreted as a track with an extraordinarily elongate digit impression III, which can be attributed to *Grallator* with reservations.

Ichnogenus ***Sarmientichnus*** Casamiquela, 1964

1964. *Sarmientichnus* Casamiquela, p. 130, pls. 2, 3, 10.4; Haubold, 1971, p. 73, fig. 46.7; Leonardi, 1994, p. 26, pls. 4.11, 7.2; Casamiquela, 2002, p. 435; Melchor *et al.*, 2004, p. 53, fig. 4.f–h.

1991. "Nueva icnita"; Coria, p. 405.

2004. *Casamiquelichnus* Coria and Paulina Carabajal, p. 394, fig. 2.

Type ichnospecies. *Sarmientichnus scagliai* Casamiquela, 1964, from the upper Middle Jurassic La Matilde Formation, Santa Cruz Province, Argentina.

Emended diagnosis. Bipedal trackways composed of functionally didactyl tracks with the major axis nearly parallel to the midline. Caudally orientated digit I and cranially orientated digit III impressions are directly in line with one another and usually are not clearly distinguishable from each other. No lateral digits are preserved. Digit III has a trian-

gular claw mark. Straight marks parallel to the midline are often present. The trackways are relatively narrow and have high pace angulation.

Remarks and comparisons. *Sarmientichnus* has been usually misinterpreted as a pes print, longer than wide, with a lateral digit impression (*e.g.*, Bonaparte, 1983, 1996; Novas, 2004), probably based on some specimens of the ichnogenus with a lateral deformation resembling an external digit imprint (*e.g.*, Fig. 4.2). In addition, specimen MLP 60-X-31-12, a tridactyl track that was assigned to *Sarmientichnus* (Casamiquela, 2002), is referred herein to *Grallator*? isp. (see above). After recent re-evaluation of the specimens, the lateral deformation is considered an outwards displacement of the sediment by the movement of digit III while the producer was moving forward.

Ichnogenus *Casamiquelichnus* Coria and Paulina Carabajal, 2004, was erected on the basis of a trackway comprising three pes prints and a fourth isolated track preserved in seven slabs catalogued together as MACN-SC 3380 (Fig. 4.5). It comes from the same track-bearing surface of the La Matilde Formation that produced *Sarmientichnus* specimens MPM-PIc-3777-3781 and 3959-3961. *Casamiquelichnus* displays morphological features similar to those of *Sarmientichnus*, *i.e.*, craniocaudally elongate traces (average width 20.3 mm) arranged in a bipedal trackway, and straight marks (average width 4.2 mm) parallel to the trackway axis. No complete pes print was preserved, so the total track length is unknown. The trackway displays a pace angulation of 167º and a stride length of 259.0 mm. The isolated track ("i4" *sensu* Coria and Paulina Carabajal, 2004) was originally described as a tridactyl pes print, but is reinterpreted herein as an incomplete, damaged track in which the entire contour is not visible. The caudal and well-preserved portion of this ichnite is morphologically similar to the other tracks included in MACN-SC 3380 and *Sarmientichnus*. On morphological grounds, *Casamiquelichnus* is herein considered as a junior synonym of *Sarmientichnus*.

Characichnos Whyte and Romano, 2001, is represented by tracks composed of two to four elongate, parallel hypichnial ridges (or epichnial grooves), straight, gently curved or sinuous. It was interpreted as swimming tracks (Whyte and Romano, 2001). All specimens *Sarmientichnus* can be distinguished from *Characichnos* because they display in a unique long trace with no evidence of elongation.

Sarmientichnus scagliai Casamiquela, 1964

Figures 4–5

1964. *Sarmientichnus scagliai* Casamiquela, p.130, pls. 2, 3, 10.4; Haubold, 1971, p. 73, fig. 46.7; Bonaparte, 1983, p. 81, fig. 5.6B; Leonardi, 1994, p. 26, pls. 4.11, 17.2; Casamiquela, 2002, p. 435; de Valais and Melchor, 2003, p. 53R; Melchor *et al.,* 2004, p. 53, fig. 4.f–h.

1991. "Nueva icnita"; Coria, p. 405.

2004. *Casamiquelichnus navesorum* Coria and Paulina Carabajal, p. 394, fig. 2.

Holotype. MLP 60-X-31-1A, isolated trace, from the La Matilde Formation, Santa Cruz Province, Argentina (Fig. 4.1).

Paratypes. MLP 60-X-31-1B, 60-X-31-2A, 60-X-31-2B (natural cast of 60-X-31-1B), same locality (Figs. 4.2–4).

Table 2. Summary of measured track and trackway parameters of **Grallator** ***isp. and*** **Wildeichnus navesi**. ***Linear measurements in millimeters and angles in degrees*** **/ resumen de los parámetros medidos de huellas y rastrilladas de** ***Grallator*** **isp.** ***y Wildeichnus navesi***. **Mediciones lineales en milímetros y ángulos en grados.**

	L	*W*	*I*	*II*	*III*	*IV*	*II-III*	*III-IV*	*II-IV*	*I-III*	*PA*	*SL*
Grallator												
Mean	*74,2*	*47*	…	*34,4*	*44,5*	*53,5*	*11,3*	*21,2*	*35,3*	…	…	…
Min	*67*	*41,3*	…	*33,3*	*42,1*	*51*	*9*	*18*	*34*	…	…	…
Max	*84*	*55*	…	*35,5*	*48,2*	*58*	*13*	*23*	*37*	…	…	…
n	*6*	*5*	…	*2*	*4*	*4*	*4*	*5*	*3*	…	…	…
Wildeichnus												
Mean	*45,8*	*31,5*	*6,6*	*22,1*	*31,2*	*21,8*	*30*	*34,7*	*61,7*	*72,5*	*165*	*468,3*
Min	*33,4*	*26,7*	*7,4*	*15,1*	*21,3*	*13,3*	*15*	*18*	*50*	*68*	*147*	*297*
Max	*55*	*35*	*5,8*	*34,8*	*36,6*	*29*	*47*	*52*	*100*	*77*	*173*	*559*
n	*23*	*26*	*2*	*16*	*25*	*16*	*23*	*25*	*24*	*2*	*4*	*6*

Abbreviations: ***I-III****, divarication angle between digits I and III; the rest as in Table 1* / abreviaturas: **I-III**, ángulo formado por los ejes de los dígitos I y III; el resto como en la Tabla 1.

Additional material. MACN-SC-3823, 3380, MPM-PIc-3777, 3778, 3779, 3780, 3781, 3959, 3960, 3961, same locality (Figs. 4.5–7 and 5).

Diagnosis. Same as for ichnogenus.

Description. Specimens include eight trackways consisting of 37 tracks produced by a bipedal trackmaker, plus eleven isolated tracks. Their measurements (Tab. 3) were taken as indicated in Figure 4.8.

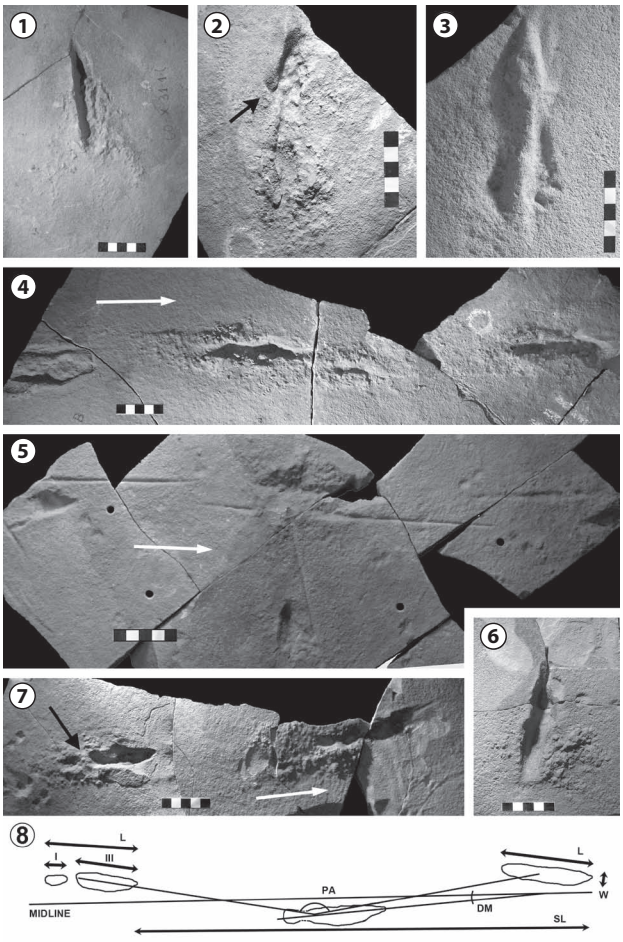

Figure 4. ***Sarmientichnus scagliai*** from the La Matilde Formation. **1**, MLP 60-X-31-1A, holotype; **2**, detail of the last footprint of MLP 60-X-31-1B, paratype; the black arrow indicates a lateral deformation of the sediment; **3**, MLP 60-X-31-2B, paratype; **4**, MLP 60-X-31-1B, paratype; **5**, MACNSC-3380; **6**; MPM-PIc-3779; **7**, detail of the second and third footprint of MPM-PIc-3778; the black arrow indicates the joint between the impressions of the digits I and III; there are at least two manus-pes set of ***Ameghinichnus patagonicus*** Casamiquela, 1961, at the left side of the photograph; **8**, diagram with the conventions of footprint and trackway measurements used on ***Sarmientichnus*** in this paper; for abbreviations, see Table 1. The white arrows in 4, 5, and 7 indicate the moving direction of the trackmaker. Scale bars: 5 cm / **Sarmientichnus scagliai** *de la Formación La Matilde.* ***1****, MLP 60-X-31-1A, holotipo;* ***2****, detalle de la última huella de MLP 60-X-31-1B, paratipo; la flecha negra indica una deformación lateral del sedimento;* ***3****, MLP 60-X-31-2B, paratipo;* ***4****, MLP 60-X-31-1B, paratipo;* ***5****, MACNSC-3380;* ***6****, MPM-PIc-3779;* ***7****, detalle de las segunda y tercera huella de MPM-PIc-3778, la flecha negra indica la unión de las impresiones de los dígitos I y III; hay al menos dos pares mano-pie de* **Ameghinichnus patagonicus** *Casamiquela, 1961, en el lado izquierdo de la foto;* ***8****, diagrama con las convenciones de las medidas a huellas y rastrilladas usadas sobre* **Sarmientichnus** *en el presente trabajo; para las abreviaturas, ver la Tabla 1. La flecha blanca en 4, 5 y 7 indica el sentido de avance del productor. Escala: 5 cm.*

Trackways are composed of large, normally deeply impressed (up to 20 mm depth) tracks, in many cases with lateral and medial creases or sediment collapsed into the interior of the tracks. The more complete traces display digit I and III impressions forming a continuous, single, linear depression. Some well-preserved specimens appear to be anisodactyl, with the impressions of digits I (probably only the basal portions) and III separated by a "ridge" or a structure preserved as positive epichnia when the track is preserved as negative epichnia (Fig. 4.7). Some shallow tracks have only the impression of digit III (Figs. 4.5–6). Average lengths of digit I and III impressions are 27.3 mm and 68.4 mm respectively, while the angle between these impressions is close to 170º. Digit III impressions may bear blunt triangular claw marks. Some tracks display a lateral deformation considered an outside displacement of the sediment by the movement of the digit III while moving forward (Fig. 4.2).

Trackways are relatively narrow. Stride length and pace angulation average 465 mm and 173º respectively. Footprints show almost no rotation relative to midline, with an average angle of -4°.

Most specimens reveal deformations of the sediment behind and along both sides of the track. These rough structures are preserved as positive epichnia when the pes print is preserved as negative epichnia; they consist of small, subrounded to irregular mounds of sediment, with the highest concentrations near the track (*e.g.*, Figs. 4.1, 4.6).

In some cases, the specimens bear straight and narrow marks of relatively constant width (average 5.4 mm), parallel to the midline. The lengths of these marks are quite variable, ranging from a few centimeters to equaling the whole stride length (*e.g.*, Figs. 5.2–3). The marks arise from the caudal tips of the footprints.

Remarks. *Casamiquelichnus navesorum* Coria and Paulina Carabajal, 2004, is herein considered a junior synonym of *Sarmientichnus scagliai* Casamiquela, 1964, which is the only ichnospecies of the ichnogenus.

Paleobiological implications. Casamiquela (1964) attributed *Sarmientichnus* to a medium-sized theropod dinosaur trackmaker. Coria and Paulina Carabajal (2004), in reference to MACN-SC 3380, accepted the assignment by Casamiquela (1964), but Haubold (1971) claimed it to belong to an indeterminate group. Herein, a theropod origin is accepted for *Sarmientichnus*.

The straight and narrow marks have been previously suggested as a drag mark made by the claw of digit III (Coria and Paulina Carabajal, 2004), or by digits II and/or IV (Melchor *et al.*, 2004). These marks are parallel to the midline (Figs. 4.5, 5.2) and in some specimens they extend from the caudal end of the tracks, but never from the distal tip of digit III imprints or from the sides of the tracks (Figs. 5.2–3). They are interpreted herein as the dragging marks of digit I, supporting the idea that digit I would have carried a relative big claw. Until now, none of the known theropods has a pedal morphology matching *Sarmientichnus* tracks.

The small irregular mounds of sediment around the tracks in most of the specimens look like a spatter of soft sediment produced by the trackmaker while moving on the substrate under some particular condition. This deformation and the depth of the tracks suggest that the trackmaker walked on soft and probably water-saturated volcanic ash (Melchor *et al.*, 2004).

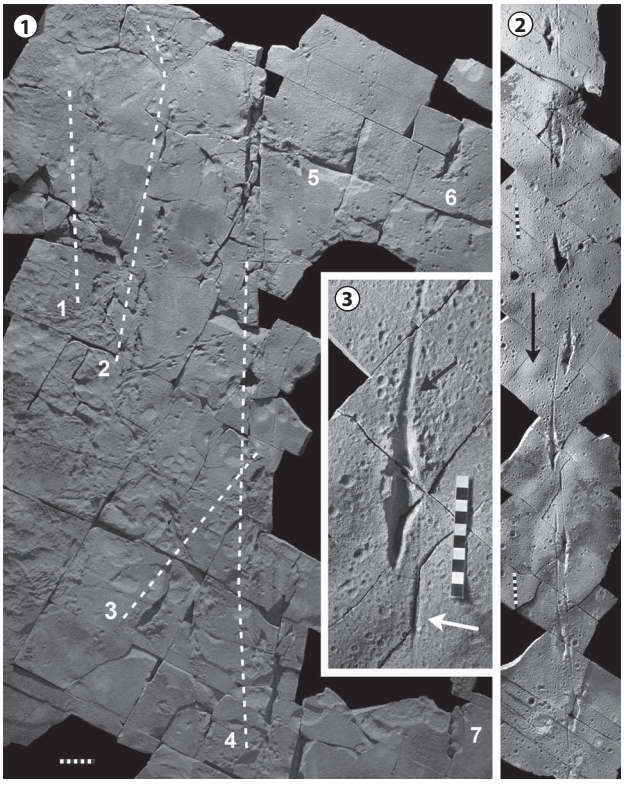

Figure 5. ***Sarmientichnus scagliai*** from the La Matilde Formation. **1**, mosaic with associated trackways MPM-PIc-3777, 3778, 3779, 3780, 3961, 3959 and 3960, numbered 1 to 7 following this order. The dotted lines indicate the trackways; the numbers 1 to 4 lie at the beginnings of their respective trackways. There are several tracks and trackways of ***Ameghinichnus patagonicus*** Casamiquela, 1961 on this surface; **2**, MPM-PIc-3781; the black arrow indicates the moving direction of the trackmaker; **3**, detail of the fifth pes print of MPM-PIc-3781; the white arrow indicates the drag mark of digit I from the previous footstep; the grey arrow indicates the drag mark of digit I of the same track. Scale bar: 10 cm / **Sarmientichnus scagliai** *de la Formación La Matilde.* ***1****, mosaico con las rastrilladas asociadas MPM-PIc-3777, 3778, 3779, 3780, 3961, 3959 y 3960, mencionadas del 1 al 7 siguiendo este orden. Las líneas puntuadas indican las rastrilladas; la ubicación del 1 al 4 indica el inicio de cada rastrillada. Hay varias huellas y rastrilladas de* **Ameghinichnus patagonicus** *Casamiquela, 1961 sobre la superficie;* ***2****, MPM-PIc-3781; la flecha negra indica el sentido de avance del productor;* ***3****, detalle de la quinta huella de MPM-PIc-3781; la flecha blanca indica la marca de arrastre del dígito I relacionado con el paso anterior; la flecha gris indica la marca de arrastre del dígito I de la misma huella. Escala: 10 cm.*

The paleobiology of the producer of *Sarmientichnus* is especially interesting on the basis of the extraordinary morphology of their tracks. Imprint features resemble some aspects of those in swimming tracks (*e.g.*, Coombs, 1980; Whyte and Romano, 2001; Ezquerra and Pérez-Lorente, 2003; Milner *et al.*, 2006), but *Sarmientichnus* lacks the typical elongate morphology of swimming tracks. Besides, they occur along with other similar sized tracks on the same surface (*e.g.*, Fig. 5.1). Casamiquela (1964) interpreted them as produced by a running animal, an opinion supported herein.

Neoichnological studies are currently conducted in the provinces of La Pampa and Río Negro (Argentina) in order to analyze morphological and behavioral similarities between *Sarmientichnus* and extant bird tracks.

Ichnogenus ***Wildeichnus*** Casamiquela, 1964

1964. Wildeichnus Casamiquela, p. 126; Haubold, 1974, p. 69, fig. 42.9; Leonardi, 1994, p, 25, pls. 4.1b,13,14,15,21, 17.1; Casamiquela, 2002, p. 434; Melchor *et al.,* 2004, p. 53, fig. 4.c–d.

Type ichnospecies*. Wildeichnus navesi* Casamiquela, 1964, from the late Middle Jurassic La Matilde Formation, Santa Cruz Province, Argentina.

Emended diagnosis*.* Bipedal trackways composed of asymmetric, functionally tridactyl tracks with a length/width ratio of about 1.5. Hallux is rarely impressed; when preserved, it is medially directed. Divarication angles between II and IV digit imprints are greater than 50º. The trackways have high pace angulation.

Remarks and comparisons*. Wildeichnus* differs from *Grallator*, *Eubrontes*, *Anchisauripus*, and the pes imprints of *Anomoepus* (disregarding the size of the tracks) by its higher total divarication (an average of 62º *vs*. less than 40°), a lower length/width ratio (about 1.5 *vs* about 2), parameter P of Olsen *et al*. (1998) higher than 2, and the similar width of digit II, III, and IV impressions.

Tracks comparable to *Wildeichnus* are scarce. Abundant, small, tridactyl pes prints have been recorded from the Middle Jurassic of eastern Utah that have high total divarication angles of 56°–73°, and an average length/width ratio of 1.4 (Lockley *et al*., 2007). Lockley *et al*. (2007) referred these tracks to cf. *Wildeichnus*.

Several small, tridactyl tracks from the Late Triassic of Queensland, Australia, referred to cf. *Grallator*, display slen-

der digit impressions, a length/width ratio near 1.4, and a total divarication angle of 70º (Thulborn, 1998). In agreement with the ichnogeneric diagnosis of *Grallator* by Olsen *et al*. (1998), those specimens are instead referred herein to *Wildeichnus*.

A trackway composed of tridactyl footprints from the Lower Jurassic Navajo Sandstone, USA, has been referred to cf. *Wildeichnus* (Rainforth, 1997), an assignment accepted herein.

Two tridactyl tracks from the Middle Jurassic of the Holy Cross Mountains, Poland (Gierliński *et al*., 2009) —from the Bałtów Coral Limestones (Gierliński, 2008; Gierliński *et al*., 2009) and from the Wierzbica Oolite and Platy Limestones—, are nearly symmetric, with total divarication angle greater than 50º. Both were assigned to *Wildeichnus* (Gierliński, 2008; Gierliński *et al*., 2009), an assignment also accepted herein.

Wildeichnus navesi Casamiquela, 1964

Figure 6

1964. *Wildeichnus navesi* Casamiquela: 126, pls. 1, 10; Haubold, 1974, p. 69, fig. 42.9; Bonaparte, 1983, p. 81, fig. 5.6A; Leonardi and de Oliveira Lima, 1994, p. 220 and 224, pls. 1.B,C,G,N, 4.D, 5.G; Leonardi, 1994, p. 25, figs. 4.1b, 13, 14, 15, 21, 17.1; Casamiquela, 2002, p. 435; de Valais and Melchor, 2003, p. 53R; Melchor *et al.*, 2004, p. 53, fig. 4.c–d.

Holotype. MLP 60-X-31-5, isolated left pes print from the La Matilde Formation, Santa Cruz Province, Argentina.

Paratypes. MLP 60-X-31-7B, 60-X-31-9, 60-X-31-11, PVL 2302B, 2305, same locality (Fig. 6.1).

Additional material. MLP 65-XI-12-1/2, 65-XI-12-1 (at least four slabs with the same number), two unnumbered MLP specimens, MPEF-IC 1029, PVL 3700, 3701, 3723, 2305, MACN-SC-3381, unnumbered MACN-SC specimens, MPM-PIc-3783, 3784, 3785, 3786, 3787, 3788, 3962, 3963, 3964, same locality (Figs. 6.2–12).

Diagnosis. Same as for ichnogenus.

Description. The specimens include six bipedal trackways containing 21 tracks, and ten isolated tracks, moderately to poorly preserved (Tab. 2).

Wildeichnus navesi tracks are tridactyl, although in two cases a medially directed hallux impression is preserved (Fig. 6.5). The angles formed by the impressions of the hallux and digit III are 68º and 77º in these two specimens. Average width of the footprints is 31.5 mm, and the average length is 45.8 mm, rendering a length/width ratio of 1.45. Digit impressions are slender, each with comparable width and subparallel margins, usually with unclear digital pad marks. Digit III impression sometimes carries a narrow claw mark. Average lengths of digit impressions are, in decreasing order, 31.2 mm (III), 22.1 mm (II), 21.8 mm (IV), and 6.6 mm (I). Average angle subtended by digits II-III is 30º, by III-IV is 35º, and 62º by digits II-IV. The footprints display almost no rotation relative to the midline. Average pace angulation is 165º, and average stride length is 468 mm. Parameter P of Olsen *et al*. (1998) shows an average of 2.2 (R= 33.2 and T= 48).

Remarks and comparisons. The tridactyl tracks from the Middle Jurassic of eastern Utah (Lockley *et al*., 2007) are morphologically quite similar to the specimens included in *W. navesi*. However, it was not possible to measure parameter P or compare trackway measurements because of the scarce available information. Therefore, it was not possible to confirm whether or not the Utah sample is ichnospecifically similar to the La Matilde specimens.

Rainforth (1997) presented tracks and trackways from

***Table 3. Summary of measured track and trackway parameters of* Sarmientichnus scagliai*. Linear measurements in millimeters and angles in degrees* / resumen de los parámetros medidos de huellas y rastrilladas de *Sarmientichnus scagliai*. Mediciones lineales en milímetros y ángulos en grados.**

	L	*W*	*I*	*III*	*I-III*	*PA*	*SL*	*DM*	*Ldr*	*Wdr*
Sarmientichnus										
Mean	*105,7*	*22,6*	*28*	*68*	*170,5*	*173,4*	*466*	*-4,3*	*217,8*	*5,4*
Min	*86*	*16,7*	*15,1*	*53,8*	*151*	*167*	*294*	*-6*	*395*	*2,9*
Max	*134,6*	*39*	*51*	*84,4*	*180*	*194*	*597*	*0*	*42,8*	*8*
n	*26*	*33*	*19*	*12*	*11*	*15*	*16*	*7*	*12*	*12*

Abbreviations: ***Ldr****, length of drag mark of digit I;* ***Wdr****, width of drag mark of digit I; others as in Table 1* / abreviaturas*:* **Ldr**, largo de la marca de arrastre del dígito I; **Wdr**, ancho de la marca de arrastre del dígito I; el resto como en la Tabla 1.

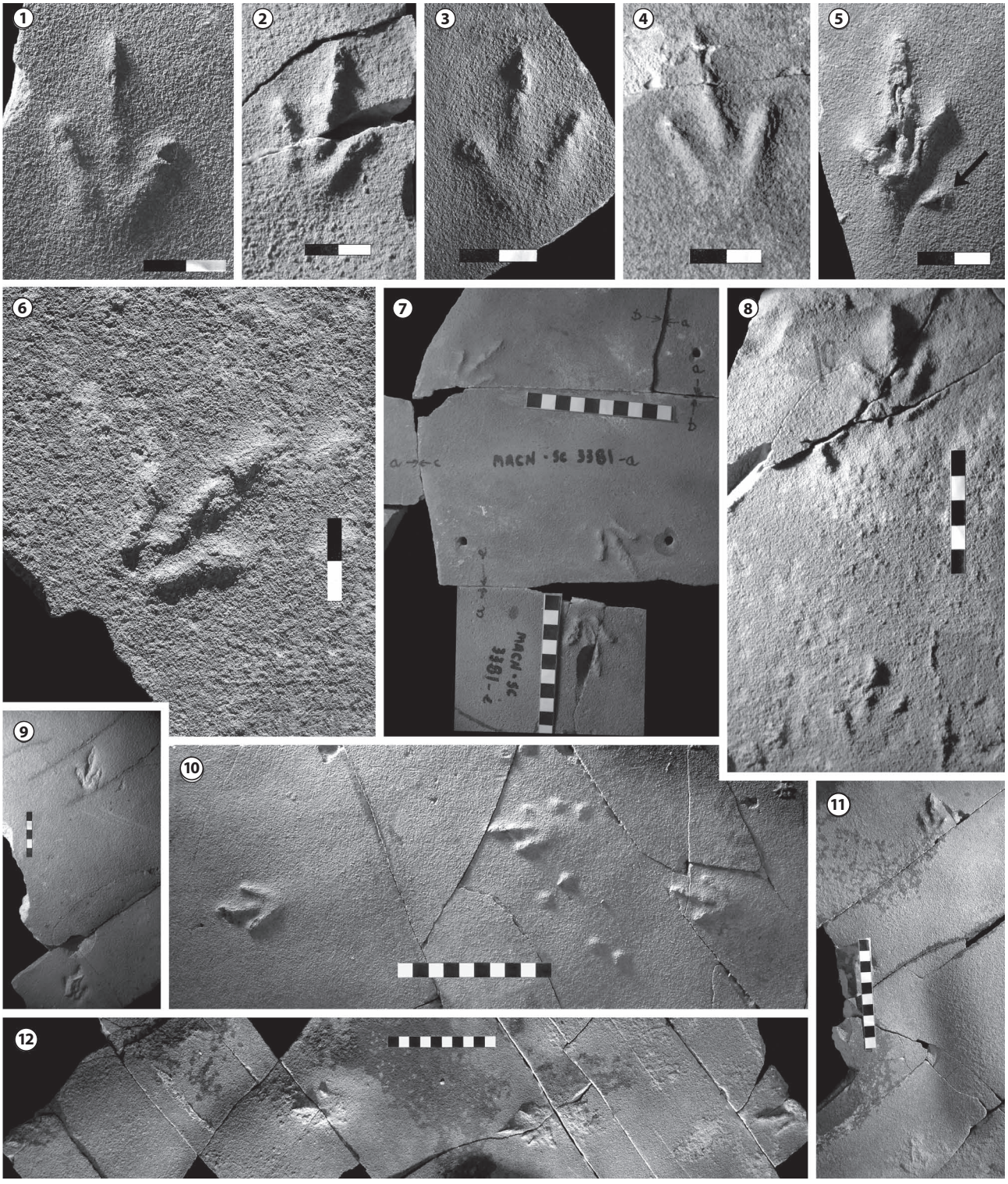

Figure 6. ***Wildeichnus navesi*** from the La Matilde Formation. **1**, MLP 60-X-31-11, paratype; **2**, MPM-PIc-3784; **3**, MPEF-Ic 1029; **4**, PVL 2302; **5**, MPM-PIc 3786; the black arrow indicates the hallux impression; **6**, MLP 65-XI-13-1; **7**, MACN-SC-3381; **8**, MPM-PIc 3964; **9**, PVL 3701; **10**, MLP 65-XI-12-1/2; **11**, MPM-PIc-3788; **12**, MPM-PIc 3787. Scale bars: 2 cm in 1–4, 5 cm in 5, 6 and 8, and 10 cm in 7 and 9. **I**, imprint of digit I; **II**, imprint of digit II; **III**, imprint of digit III; **IV**, imprint of digit IV / **Wildeichnus navesi** *de la Formación La Matilde.* ***1****, MLP 60-X-31-11, paratipo;* ***2****, MPM-PIc-3784;* ***3****, MPEF-Ic 1029;* ***4****, PVL 2302;* ***5****, MPM-PIc 3786; la flecha negra indica la impression del hálux;* ***6****, MLP 65-XI-13-1;* ***7****, MACN-SC-3381;* ***8****, MPM-PIc 3964;* ***9****, PVL 3701;* ***10****, MLP 65-XI-12-1/2;* ***11****, MPM-PIc-3788;* ***12****, MPM-PIc 3787. Escala: 2 cm en 1–4, 5 cm en 5, 6 y 8, y 10 cm en 7 y 9.* ***I****, impresión del dígito I;* ***II****, impresión del dígito II;* ***III****, impresión del dígito III;* ***IV****, impresión del dígito IV.*

the Jurassic of the Navajo Sandstone (USA) with an average length/width ratio of about 1.4, an average total divarication angle of 60º and general morphologies comparable to *W. navesi*. Even though the specimens are only moderately well preserved and information is limited, they appear to agree with *W. navesi*.

Based on their morphologies, tridactyl tracks from the Late Triassic of Queensland, Australia (Thulborn, 1998), are also assigned herein to this ichnospecies.

The scarcity of available information about two small tracks from the Middle Jurassic of Poland (Gierliński, 2008; Gierliński *et al*., 2009) precludes any definitive ichnospecific assignment.

Paleobiological implications. *Wildeichnus* was originally attributed to a "coelurosaurid" theropod because "coelurosaurids" were then considered the smallest theropods (Casamiquela, 1964). Casamiquela (1974a) more specifically attributed this ichnogenus to *Herbstosaurus pigmaeus* Casamiquela, 1974 (Casamiquela, 1974b), from the Middle to Late Jurassic Lotena Formation, Neuquén Province, Argentina, first interpreted as a small theropod but presently perceived as a pterosaur (Ostrom, 1978). Later, the tracks of *Wildeichnus* were attributed to the activity of a ceratosaurian theropod (*sensu* Rainforth, 1997). The general features of this ichnogenus (asymmetric track, slender digit imprints with three of them cranially oriented, narrow trackways) reveal a theropod origin (Lockley *et al*., 2007). As *Wildeichnus* tracks meet these criteria, the most parsimonious attribution seems to be theropods. However, information available is not enough to assign *Wildeichnus* tracks to a more inclusive group within Theropoda.

The track maker of *Wildeichnus* was probably related in some way to the trackmaker of *Grallator*; both were small theropods. The former could represent a juvenile stage of the latter (Rainforth, 1997), or else they could be phylogenetically closely related lineages.

Both *Piatnitzkysaurus* Bonaparte, 1979 and *Condorraptor* Rauhut, 2005, from the Middle Jurassic in Chubut Province, Argentina, have been described as medium-sized theropods that are phylogenetically closely related (Rauhut, 2005). The tracks included in *Wildeichnus* and *Grallator* demonstrate the existence of smaller theropods during the same period and in close geographic proximity, increasing the known diversity of Middle Jurassic dinosaurs from Argentina beyond that provided by the current record of body-fossils alone. However, it is necessary to point out the possibility that both ichnotaxa could represent juvenile specimens.

Specimens of uncertain ichnotaxonomic placement

Material. MPM-PIc-3965 (Fig. 7.1).

Description. This ichnite is 88 mm long and 128 mm wide, with four short and thick digit imprints. At least three digits bear clear claw marks measuring up to 18 mm long. There are no digital pad impressions. Divarication between the outermost digit imprints is 108º, and the internal angles, beginning from the left side of the track, are: 22º, 44º, and 45º. The lengths of the digit impressions, including the claw marks, in the same order, are 41 mm (incomplete), 53 mm, 66 mm, and 49 mm.

Remarks. *Brasilichnium* Leonardi, 1981, from the Botucatu Formation, Paraná Basin, Brazil, includes heteropod tracks, with tetradactyl, ectaxonic pes and nearly mesaxonic manus imprints; manus prints displaying claw marks, with the central digit impressions being the largest (Fernandes and Carvalho, 2008). MPM-PIc-3965 differs from *Brasilichnium* because its digit impressions are subequal in length and the angles between the digit imprints are smaller.

The track resembles the manus print of the ichnogenus *Otozoum* Hitchcock, 1847 (Rainforth, 2003, fig. 4). Both have similar length/width ratio, are tetradactyl with short and broad digits, and have total divarication angles greater than 100º. Nevertheless, the track from the La Matilde Formation bears long and sharp claw marks that do not occur in *Otozoum*. In addition, no associated pes print was preserved.

Material. MPEF-IC 1008, plaster cast of an uncollected track, probably an undertrack (Fig. 7.2).

Description and remarks. MPEF-IC 1008 appears to be a tridactyl ichnite 121 mm wide and 288 mm long, with no

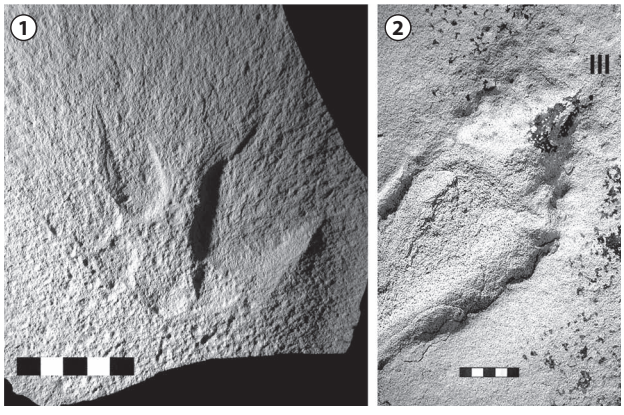

Figure 7. Specimens of uncertain ichnotaxonomic assignment from the La Matilde Formation. **1**, MPM-PIc-3965; **2**, *in situ* track; **III**, imprint of digit III. Scale bar: 5 cm / *especímenes de asignación icnotaxonómica incierta de la Formación La Matilde.* ***1****, MPM-PIc-3965;* ***2****, huella* in situ*;* ***III****, impresión del dígito III. Escala: 5 cm*

clear distinction between the digit impressions. No digital pads or claw marks are preserved. The lack of morphological details precludes ichnotaxonomic assignment.

DISCUSSION

For the time being, the La Matilde ichnofauna from Estancia Laguna Manantiales includes four dinosaurian ichnotaxa (*Delatorrichnus goyenechei*, *Sarmientichnus scagliai*, *Wildeichnus navesi*, and *Grallator* isp.), in addition to the mammalian ichnotaxa *Ameghinichnus patagonicus* Casamiquela, 1961 and *A. manantialensis* de Valais, 2009, and some tracks of uncertain ichnotaxonomic assignment.

Among the dinosaurian components of the La Matilde ichnofauna, two ichnotaxa are endemic (*i.e.*, *Delatorrichnus* and *Sarmientichnus*). In contrast, the site has yielded some tracks referred to the cosmopolitan ichnogenus *Grallator* (*e.g.*, Demathieu, 1990; Olsen *et al.*, 1998; Haubold and Klein, 2000; Gaston *et al.*, 2003). The remaining ichnotaxon, *Wildeichnus*, is not as widespread as *Grallator* but has been reported from other ichnological localities of the world, including the Late Jurassic of eastern Utah, USA (Lockley *et al.*, 2007; Rainforth, 1997), the Middle Jurassic of the Holy Cross Mountains, Poland (Gierliński, 2008; Gierliński *et al.*, 2009), and the Late Triassic of Queensland, Australia (Thulborn, 1998). These findings geographically and temporally stretch the record of this ichnogenus. A track resembling the manus print of *Otozoum* (MPM-PIc-3965) is also very similar to specimens in the Navajo Sandstone (Rainforth, 1997).

In addition, de Valais (2009) reviewed three other Jurassic ichnological assemblages with specimens referred to *Ameghinichnus* from the upper Towaco Formation from the Newark basin, New Jersey (Olsen and Rainforth, 2001), the upper Elliot Formation of the Karoo basin, South Africa (Ellenberger, 1970), and the Zagaje Formation from Sołtyków, Poland (Gierliński *et al.*, 2004).

Several authors compared the La Matilde ichnofauna with the Botucatu ichnofauna from the Late Jurassic–Early Cretaceous Botucatu Formation of southern Brazil (*cf.*, Leonardi and de Oliveira Lima, 1990; Leonardi, 1994). The two assemblages share similar paleoecological characteristics, suggesting paleocommunities with comparable biological traits (*e.g.*, similar locomotory characteristics for *Ameghinichnus* and *Brasilichnium*, small body size) and community structures *(i.e.*, the two are composed of small-sized animals, including dinosaurs, mammals or mammal-like reptiles, and arthropods). These arguments were based on the shared presence of tracks referred to small-sized dinosaurs, mammals or mammal-like reptiles and trackways of arthropods, preserved in purported eolian deposits in paleodesert environments (Leonardi, 1980, 1994; Leonardi and de Oliveira Lima, 1990; Bonaparte, 1996). However, new evidence indicates that the La Matilde Formation should be reinterpreted not as a paleodesert but as a fluvial system, with swamps and water bodies probably derived from adjacent floodplains associated to an active volcanic environment (Mazzoni *et al.*, 1981; Panza, 1998; Melchor *et al.*, 2004). This volcanic activity may have acted as a selective trend towards smaller-sized forms among the producers of the La Matilde ichnofauna. This does not mean that only small taxa were living in the area, but they probably were the component of the fauna capable of moving back into —and repopulate— a volcanically devastated area sooner and faster than large taxa do.

A paleoecological frame showing paleocommunities including small elements with theropods, mammals or non-mammalian therapsids, and arthropods as the basis of the trophic pyramid, was discussed elsewhere (*e.g.*, La Matilde Formation, Casamiquela, 1974a; Middle Jurassic Curtis Formation, Utah, USA, Lockley *et al.*, 2007).

Generalist or r-strategist species (*e.g.*, small and simple taxa) would have greater chances than specialist or k-strategist species (*e.g.*, large and complex taxa) of surviving under such rigorous environmental conditions as those subject to strong volcanic activity. This would result in a paleocommunity including populations of different species with high capacity of regenerating and resettling in damaged and periodically vacant environments.

Towards the Middle Jurassic, almost all Triassic vertebrate ichnogenera in Argentina disappeared (*Grallator* is a notable exception). Dinosaurian ichnotaxa represented by *Sarmientichnus*, *Wildeichnus*, *Delatorrichnus*, *Grallator*, and some indeterminate ichnites, are more diverse than earlier in the Jurassic, and true mammal tracks, represented by *Ameghinichnus*, appear in the record for the first time. Dinosaur ichnotaxa suggest a higher diversity of Jurassic dinosaurs in Argentina than reflected by the osteological record only.

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