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Tetrapod footprints from the Triassic of Patagonia: reappraisal of the evidence

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Abstract. To date, the only known Triassic tetrapod footprints in Patagonia are those from the Los Menucos Basin, Río Negro province. The footprints occur at several levels in the Vera Formation in fine-grained tuffaceous sandstones interbedded with tuffaceous mudstones that contain a rich "*Dicroidium*-type Flora". A revision of the original material described by Casamiquela and study of undescribed specimens from the same locality are presented herein. Previous assumptions about the large number of tetrapod groups represented by the footprint assemblage are not corroborated by the available evidence. However, this new analysis supports former propositions about the relative abundance and high diversity of small therapsids, probably theriodonts. This footprint assemblage suggests a unique Late Triassic tetrapod fauna in northern Patagonia, in which archosaurs (basal archosaurs and dinosaurs) were not the dominant component as in most known Late Triassic Gondwanan tetrapod faunas. This unusual situation might be either the result of a taphonomic bias or the record of an endemic fauna actually dominated by therapsid taxa.

Resumen. HUELLAS DE TETRÁPODOS DEL TRIÁSICO DE PATAGONIA: REEVALUACIÓN DE LA EVIDENCIA. Hasta el presente, las únicas huellas de tetrápodos triásicas conocidas para Patagonia son aquellas de la Cuenca de Los Menucos en la provincia de Río Negro. Las huellas se registran en varios niveles de la Formación Vera en areniscas tobáceas de grano fino intercaladas con pelitas tobáceas que contienen una rica "Flora de *Dicroidium*". Una revisión del material original descrito por Casamiquela y el estudio de varios ejemplares inéditos de la misma localidad son discutidos en el presente trabajo. Hipótesis previas que proponían un gran número de grupos de tetrápodos representados por la asociación de huellas no es corroborado por la evidencia disponible en el presente estudio. Sin embargo, este nuevo análisis sí respalda propuestas anteriores que sostenían la relativa abundancia y alta diversidad de pequeños terápsidos, probablemente teriodontes, en la asociación. Las huellas sugieren una fauna de tetrápodos triásica poco común en el norte de Patagonia en la cual los arcosaurios (arcosaurios basales y dinosaurios) nos son el componente dominante como ocurre en la mayoría de las asociaciones de tetrápodos del Triásico Tardío de Gondwana. Esta situación inusual podría ser tanto el resultado de un bias tafonómico o el registro de una fauna endémica en efecto dominada por terápsidos.

Key words. Late Triassic. Argentina. Patagonia. Tetrapod footprints. Therapsids.

Palabras clave. Triásico Tardío. Argentina. Patagonia. Huellas de tetrápodos. Terápsidos.

Introduction

In southernmost South America, Triassic tetrapods are only known from two Late Triassic sequences that crop out in Patagonia, Argentina. One corresponds to the El Tranquilo Basin in southern Patagonia (Santa Cruz province), where several prosauropod skeletons and a unique specimen of an ornithischian dinosaur were described from the uppermost levels of its infilling (Casamiquela, 1980; Báez and Marsicano, 2001). The second record occurs in the Los Menucos Basin, located farther north, in the province of Río Negro. In this case, tetrapods are only represented by the ichnites of relatively small-sized animals (Casamiquela, 1964, 1975; Domnanovich, 2003). The tetrapod Patagonian record, thus, contrasts strikingly with the diverse Triassic faunas known from west-central Argentina, such as those from the Ischigualasto-Villa Unión Basin (e.g. Bonaparte, 1973, 1978, 1997; Báez *et al*., 1993; Lucas, 1998; Arcucci *et al*., 2004), particularly if only the skeletal evidence is considered.

The footprints and trackways from Los Menucos are recorded at several horizons in the volcaniclastic

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Vera Formation and were originally studied by Casamiquela (1964, 1975). This author described many different ichnotaxa that were referred to several groups of tetrapods (Casamiquela, 1964, 1975). Therefore, he suggested the presence in the ichnocoenosis of amphibians, "mammal-like reptiles", mammals, "thecodontians", lizards, chelonians and procolophonids, among others (Casamiquela, 1964, 1975). Subsequently, Casamiquela´s original ichnotaxa were reanalyzed and mostly attributed to therapsid trackmakers (Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994).

The aim of this paper is to restudy the Los Menucos ichnites, including all the original material described by Casamiquela, plus many undescribed specimens from the same locality, and to evaluate the possible trackmakers in a phylogenetic context. It is noteworthy that at present several studied specimens are in the slabs that pave the sidewalks along the shoreline of Nahuel Huapi Lake in the city of Bariloche, in the province of Río Negro (Domnanovich, 2003). In addition, some uncatalogued slabs are also housed in the Museum of Ingeniero Jacobacci town, in the same province (Domnanovich, 2003).

Institutional abbreviations. MLP: Facultad de Ciencias Naturales y Museo de La Plata, División Paleontología de Vertebrados, Buenos Aires, Argentina; CICRN: Centro de Investigaciones Científicas de Río Negro, Río Negro, Argentina.

Geological setting

The Triassic Los Menucos Basin is located in northern Patagonia, in the central region of the Río Negro province (figure 1). Its infilling consists of 150 m of nonmarine volcaniclastic rocks deposited by ephemeral river systems under explosive volcanic activity and developed over a local low gradient volcanic relief (Llambías, 1999; Kokogian *et al*., 2001; Labudía and Bjerg, 2001). The volcanism in the region during the Late Triassic is related to trans-arc extensional phenomena (Franzese and Spalletti, 2001; Macdonald *et al*., 2003) that produced the development of volcanic arcs on the active western margin of the continent and an important outpouring of silicic extensional volcanism (Macdonald *et al*., 2003).

The Triassic sequence (Los Menucos Group) is well exposed near the town of Los Menucos, approximately 40° 53′ S - 63° 11′ W; it unconformably overlies sedimentary and igneous paleozoic rocks and it is covered by Cretaceous sedimentary rocks and Tertiary volcanics (Labudía and Bjerg, 2001). The Triassic succession is lithostratigraphically divided into two units (figure 2), the Vera Formation and the overlying Sierra Colorada Formation (Stipanicic *et al*., 1968; Labudía *et al*., 1995; Labudía and Bjerg, 2001). The Vera Formation consists of tuffaceous sandstones and mudstones interfingered with volcanic rocks, whereas the Sierra Colorada Formation is exclusively rhyolitic (Stipanicic *et al*., 1968; Pesce, 1974; Rosenman, 1979; Labudía and Bjerg, 2001).

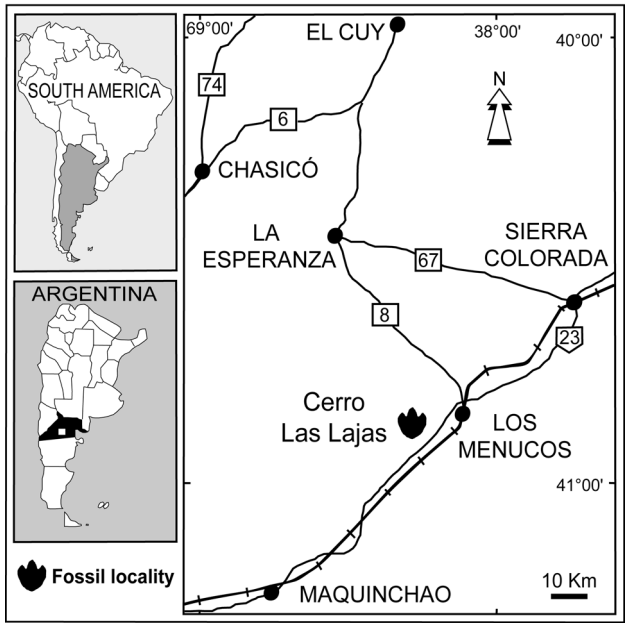

Figure 1. Location map of the Los Menucos area (modified from Kokogian *et al*., 2001) / *mapa del área de Los Menucos (modificado de Kokogian* et al*., 2001).*

As mentioned above, the footprints are recorded in the Vera unit from several levels of fine-grained tuffaceous pale yellowish brown and light brown sandstones interbedded with brown grayish mudstones bearing a rich "*Dicroidium*-type Flora" (Casamiquela, 1964; Stipanicic *et al*., 1968; Stipanicic and Methol, 1972; Pesce, 1974; Artabe, 1985, 1986; Labudía *et al*., 1995; Labudía and Bjerg, 2001). The sandstones containing the footprints are quarried for slabs; all studied material came from two quarries, the "Cantera Vieja" (= "La Vieja" *sensu* Leonardi and Henrique de Oliveira, 1990; = "Cantera Tscherig" *sensu* Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994) and the "Cantera Nueva" (= "La Cantera Nueva" *sensu* Leonardi and Henrique de Oliveira, 1990; = "La Nueva" *sensu* Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994). These quarries are located in the proximity of the Cerro Las Lajas, west of the town of Los Menucos, and they are still under excavation.

Recent radiometric analyses in volcanics from the Sierra Colorada Formation (222 ± 2 Ma, Rapela *et al*., 1996) place this sequence in the middle Carnian (*sensu* Gradstein *et al*., 1995), thus giving a minimum Carnian age to the Vera beds and to the track-bearing levels. This is in agreement with the Late Triassic age

previously assigned to the Vera unit based on its stratigraphic relationships, radiometric data and floral content (Stipanicic *et al*., 1968; Stipanicic and Methol, 1972; Labudía *et al*., 1995).

Description of the footprints and trackways

Morphotype A ("Shimmelia chirotheroides"*)*

Material. MLP 60-XI-31-1, a slab with a cast of a right pes and a right? manus impression (figure 3.A); MLP 60-XI-31-2, a slab with, apparently, a cast of a left pes impression; three isolated uncatalogued specimens (figure 3.B-C) in the sidewalks of the shoreline of the Nahuel Huapi Lake (Bariloche, Río Negro province).

Locality and horizon. "Cantera Vieja", Cerro Las Lajas, Los Menucos (aprox. 40° 53' S - 63° 11' W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).
Description. The slab MLP 60-XI-31-1 is a pale yellowish brown fine-grained sandstone which preserved two poorly defined footprints which are probably under prints. They correspond to a pes and a manus and, due to their relative size and position, they do not belong to the same pair. The pes is pentadactyl with digits I-IV anteriorly directed and digit V partially everted. Digit III is longer than II and IV, which are similar in length, and digit I is the shortest of the series; none of them presents claw marks. The manus track is tetradactyl with the digits of similar length and printed relatively spread out from each other.
Discussion. The specimens MLP 60-XI-31-1 (holotype) and MLP 60-XI-31-2 (paratype) were assigned to a new ichnotaxon, "*Shimmelia chirotheroides*", by Casamiquela (1964, pl. XV, fig. 2 and pl. XVI, fig. 1) who also suggested that they could belong to a primitive saurischian or derived prosauropod dinosaur. Subsequently, he related them to "pseudosuchian" archosaurs (Casamiquela, 1975). These tracks were also mentioned in the literature by other authors who also related them to "pseudosuchian" archosaurs (Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994). "Chirotheroid" footprints have often been regarded as crurotarsal archosaur prints (Parrish, 1989; Haubold, 1983, 1986; Demathieu and Wright, 1988; Courel and Demathieu, 1995; Haubold and Klein, 2000; Lockley and Meyer, 2000), although there is no evidence preserved in isolated "chirotheroid" tracks that might be used to distinguish among different crurotarsal archosaur taxa (see Sereno, 1991; Parrish, 1993).

As mentioned above, the pes and manus impressions in the holotype specimen do not belong to the same pair. The manus is comparatively large in relation to the pes and, moreover, its position (posteromedially to the pes) is unusual for this type of track in which the manus generally is imprinted in front of the pes (Peabody, 1955; Sarjeant, 1975; Lockley and Hunt, 1995). The isolated track in MLP 60-XI-31-2 and the footprints from Bariloche (see figures 3.B-C) although badly preserved, are considered here to represent the same morphotype.

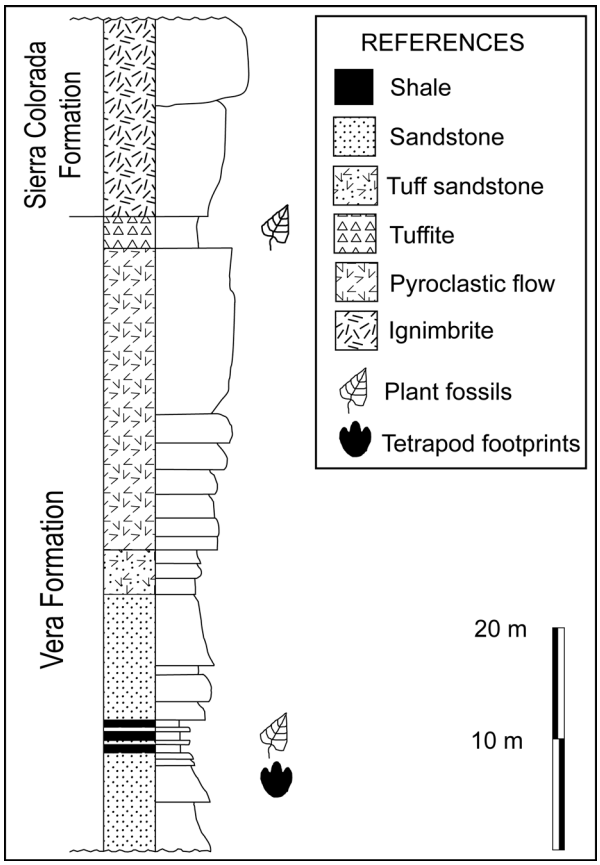

Figure 2. Generalized lithostratigraphic section of the Vera Formation, Los Menucos Group, showing the track-bearing levels (modified from Labudía *et al*., 1995) / *sección litoestratigráfica generalizada de la Formación Vera, Grupo Los Menucos, mostrando los niveles portadores de huellas (modificado de Labudía* et al*., 1995).*

Morphotype B ("Ingenierichnus sierrai"*)*

Material. MLP 60-XI-31-3, one slab, which preserves a cast of a trackway of 12 footprints with marks of body and tail drag (figure 4.A); two uncatalogued slabs with a trackway showing marks of body and tail drags (figure 4.B) housed in the Museum of Ingeniero Jacobacci (Río Negro province).

Locality and horizon. "Cantera Vieja", Cerro Las Lajas, Los Menucos (aprox. 40° 53' S - 63° 11' W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).
Description. The slab MLP 60-XI-31-3 is a pale yellowish brown fine-grained sandstone with a smooth-

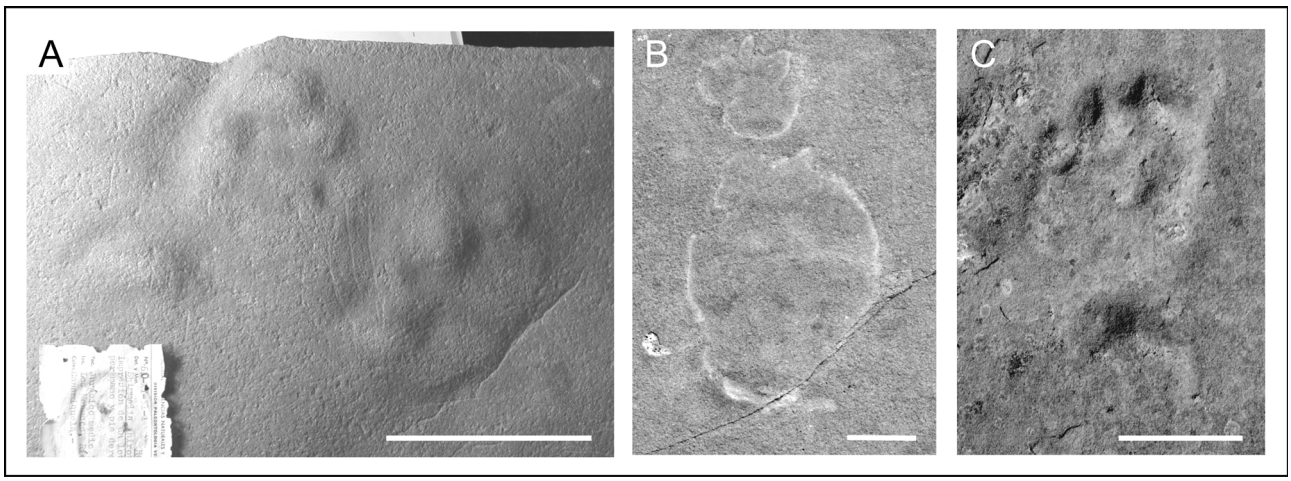

Figure 3. Morphotype A "***Shimmelia chirotheroides***". **A,** MLP 60-XI-31-1 (holotype), cast of a pes (right) and a manus impression, scale bar = 10 cm; **B,** natural mould of a manus-pes set and **C,** natural mould of a right pes impression, both specimens from the sidewalks of Bariloche, scale bar = 5 cm / *morfotipo A* "**Shimmelia chirotheroides**". ***A,*** *MLP 60-XI-31-1 (holotipo), calco de un pie (derecho) y la impresión de una mano, escala = 10 cm;* ***B,*** *molde de un par mano-pie y* ***C,*** *molde de un pie derecho, ambos especímenes de la avenida costanera de Bariloche, escala = 5 cm.*

ly preserved elongated trackway of a quadruped animal crossing its surface. It consists of twelve relatively small footprint impressions with a body drag throughout its length. Each impression shows a circular to oval outline and probably corresponds to the superposition of a manus and pes print. Thus, the more circular impressions might be interpreted as a total superposition and the elongate ones to a partial superposition (see Leonardi, 1987). In the midline of the trackway there is a broad, "sine-wave-shaped dragmark" (see Farlow and Pianka, 2000) as wide as the intermanus distance. Along the trackway, the body drag partially razes the footprints thus suggesting, together with its wideness, that it might correspond to both the belly and tail drag (see Farlow and Pianka, 2000).

The trackway pattern shows a regular progression of the trackmaker, with short steps, and small footprints relatively close to the midline of trackway. Moreover, the moderately low pace angulation (approximately 106º, table 1), and the shape of the body/tail drag indicate an elongated animal with a sprawling gait and having part of its body in continuous contact with the substrate surface during progression (see Boggs, 1987).

Discussion. The specimen MLP 60-XI-31-3 (holotype) was originally included in the new ichnotaxon "*Ingenierichnus sierrai*" by Casamiquela (1964, pl. XVII, fig. 4) who allied it to several different groups of tetrapods such as amphibians, "lizard-like" reptiles, crocodiles, "thecodonts", and theropod dinosaurs (Casamiquela, 1964, 1975). In the same publication, Casamiquela figured (1964, pl. XIX, fig. 3) a slab with a trackway of "*I. sierrai*" from the sidewalks of Bariloche which is at present in the collections of the Museum of Ingeniero Jacobacci. Subsequently, Leonardi recognized the holotype specimen as produced by a "lizard-like" reptile (Leonardi, 1994). The trackway probably corresponds to an undertrackway due to the lack of any detail in the footprints beyond their general outline.

The trackway was made by a quadruped animal with a sprawling gait, according to the low pace angulation. The shape of the body drag and the relatively long stride suggest an animal with short limbs and relatively long body, thus not able to maintain the belly away from the substrate. Trackways with a similar pattern have been described for extant salamanders (Peabody, 1959; Brand, 1996), Paleozoic

Table 1. Measures of Morphotype B "***Ingenierichnus sierrai***", MLP 60-XI-31-3. Parameters according to Leonardi (1987) / *medidas del Morfotipo B* "**Ingenierichnus sierrai**", *MLP 60-XI-31-3. Parámetros de acuerdo a Leonardi (1987).*

Measures	MLP 60-XI-31-3
Footprint length (cm) average	3.4
Footprint width (cm) average	2.8
Width of pace (cm) average	5.4
Pace angulation (degrees) average	106°
Pace length (cm) average	7.5
Stride length (cm) average	14.8
Trackway length (cm)	89
Trackway width (cm)	2.7
Speed (m/s)	1.03
Relative stride length (λ/h)	1.07

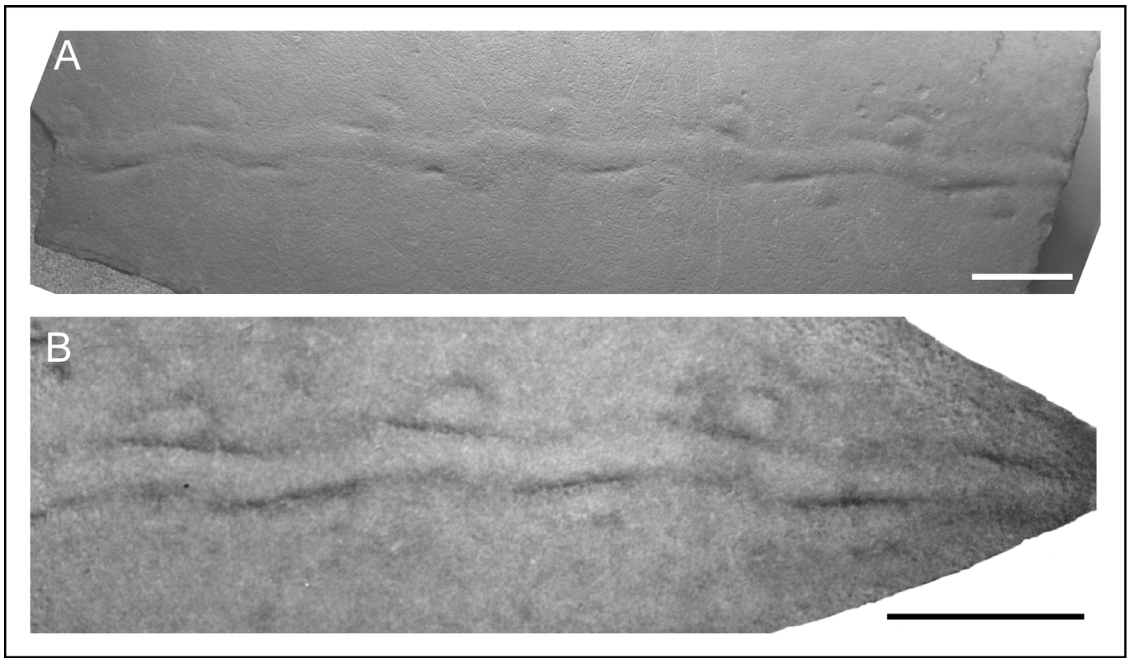

Figure 4. Morphotype B "***Ingenierichnus sierrai***". **A,** MLP 60-XI-31-3 (holotype), cast of a trackway of twelve footprints with marks of body and tail drag; **B,** cast of a trackway of the same morphotype housed in the collections of the Museum of Ingeniero Jacobacci. Scale bars = 10 cm / *morfotipo B "***Ingenierichnus sierrai***". **A,** MLP 60-XI-31-3 (holotipo), calco de una rastrillada de doce huellas con marcas de arrastre de cuerpo y cola; **B,** calco de una rastrillada asignada al mismo morfotipo de las colecciones del Museo de Ingeniero Jacobacci. Escalas = 10 cm.*

trackways assigned to amphibian trackmakers (Haubold, 1971; Scarboro and Tucker, 1995; Clack, 1997) and extant lizards (Peabody, 1948; Farlow and Pianka, 2000). Nevertheless, the lack of information about the morphology of the manus and pedes in the specimen from Patagonia prevents discrimination between a putative temnospondyl or a lepidosauriform trackmaker. Temnospondyl amphibians are well-known in the Upper Triassic of Argentina although lepidosauriforms are as yet unknown from the Triassic of Gondwana.

Morphotype C ("Calibarichnus ayestarani"*)*

Material. MLP 60-XI-31-4, one slab with an isolated manus-pes set preserved as a cast (figure 5.A); MLP 66-XI-15-2, one slab with a cast of manus-pes set (figure 5.B); MLP 93-XII-13-2, one slab with a cast of two superimposed footprint impressions (figure 5.C), one uncatalogued specimen with a manus-pes set (figure 5.E) housed in the Museum of Ingeniero Jacobacci (Río Negro province), a manus-pes set (figure 5.D) in the sidewalks along the shoreline of Nahuel Huapi Lake (Bariloche, Río Negro province).

Locality and horizon. "Cantera Vieja", Cerro Las Lajas, Los Menucos (aprox. 40° 53' S - 63° 11' W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).
Description. All analyzed material (MLP 60-XI-31-4, MLP 66-XI-15-2, MLP 93-XII-13-2) is preserved on slabs of pale yellowish brown fine-grained sandstones and they are very well impressed. All the tracks correspond to quadrupedal, semi-plantigrade, near-symmetrical, and pentadactyl animals with marked homopody. Each pes and manus impression shows two well defined pads (p1 and p2 in figure 5.A), one located just behind the digit impressions and other, anteroposteriorly elongated, behind the former; this latter pad probably represents a heel impression. The pedes impressions are somewhat longer than wide, whereas the manus prints are slightly wider than long. The manus are imprinted in front of the pedes and pedes digit impressions are anteriorly directed, subequal in size, similar in shape, and with the most external digits (I and V) slightly separated from the others (II, III, IV). All the digits have triangular and broad-based claw marks.
Discussion. The specimen in MLP 60-XI-31-4 is the holotype of "*Calibarichnus ayestarani*", Casamiquela, 1964 (pl. XVII, fig. 2) which was attributed to several tetrapod groups such as Chelonia (Casamiquela, 1964) and therapsids (Casamiquela, 1964, 1975; Haubold, 1971; Leonardi, 1994). The tracks in MLP 66-XI-15-2 were formerly assigned to a different ichnotaxon ("*Gallegosichnus garridoi*") by Leonardi (1994) which is also present in the Los Menucos assemblage (see below Morphotype F). Nevertheless, the general shape of the prints and the presence of well developed claw marks in MLP 66-XI-15-2 (figure 5.B) are here considered to include it in the Morphotype C group. The undescribed material in MLP 93-XII-13-2 (figure 5.C), in the uncatalogued

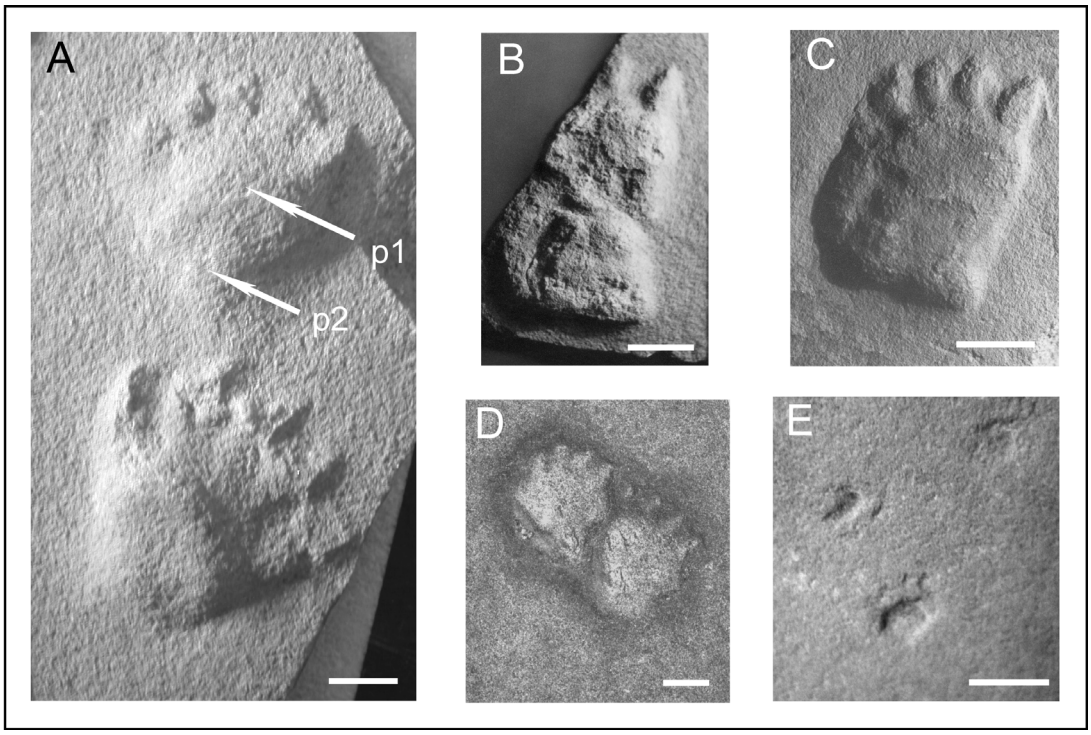

Figure 5. Morphotype C "***Calibarichnus ayestarani***". **A,** MLP 60-XI-31-4 (holotype), a cast of a manus-pes set (manus above, pes below), p1 and p2 pad impressions, scale bar = 1 cm; **B,** MLP 66-XI-15-2, a cast of a manus-pes set; **C,** MLP 93-XII-13-2, a cast of two superimposed footprint impressions; **D,** cast of a manus-pes set from the sidewalks of Bariloche; **E,** natural mould of a manus-pes set housed in the collections of the Museum of Ingeniero Jacobacci. B-E scale bars = 2 cm / *morfotipo C "***Calibarichnus ayestarani***". **A,** MLP 60-XI-31-4 (holotipo), calco de un par mano-pie (mano arriba, pie abajo), p1 y p2 impresiones de almohadillas, escala = 1 cm; **B,** MLP 66-XI-15-2, calco de un par mano-pie; **C,** MLP 93-XII-13-2, calco de dos huellas superpuestas; **D,** calco de un par mano-pie de la avenida costanera de Bariloche; **E,** molde de un par mano-pie de las colecciones del Museo de Ingeniero Jacobacci. B-E escala = 2 cm.*

slab of the collections of the Museum of Ingeniero Jacobacci (figure 5.E) and in the sidewalks of Bariloche (figure 5.D) are here considered indistinguishable from the holotype specimen.

The morphology of the prints (near-symmetrical, marked homopody and pentadactyly) relates the trackmaker to non-mammalian therapsids (e.g. Haubold, 1971; Olsen and Galton, 1984; Leonardi and Henrique de Oliveira, 1990; Hunt *et al*., 1993; Leonardi, 1994; Retallack, 1996; Lockley and Meyer, 2000). Within this clade (*sensu* Sidor and Hopson, 1998; Rubidge and Sidor, 2001), the presence of nearly equal sized toes indicates a relatively derived form with an erect gait (Hopson, 1995; Peters, 2000). Moreover, the presence of a well developed heel impression (calcaneal heel *sensu* Hopson, 1995) and the Late Triassic age of the track-bearing levels suggest that the trackmaker might be allied with the eutheriodontian group (see Jenkins, 1971; Hopson, 1994, 1995).

Morphotype D ("Rogerbaletichnus aguilerai"*)*

Material. MLP 60-XI-31-5, one slab containing a natural mould of a trackway with four manus-pes sets, two complete and two incomplete impressions with evidence of limb-drags (figure 6) one slab, housed in the Museum of Ingeniero Jacobacci (Río Negro Province), containing a natural mould of a trackway with four manus-pes sets with evidence of limb-drags.

Locality and horizon. "Cantera Nueva", Cerro Las Lajas, Los Menucos (aprox. 40° 53' S - 63° 11' W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).
Description. The trackway is on the surface of a light brown very-fined sandstone preserved as a natural mould and faint small symmetrical ripple marks are superimposed on the footprints. The material indicates the presence of a quadrupedal plantigrade animal that drags the limbs during progression. The trackway consists of four manus-pes sets where the pedes prints are larger than those of the manus (table 2) and partially overprint the posterior half of the former. The manus impressions are slightly rotated inwards and are, apparently, tetradactyl with the digit impressions anteriorly directed. The digit impressions are similar in shape and size, with the first inner digit shorter than, and somewhat separated from, the others (II, III and IV). The pedes impressions are an-

Table 2. Measures of Morphotype D "***Rogerbaletichnus aguilerai***", MLP 60-XI-31-5, and Morphotype E "***Palaciosichnus zettii***", MLP 60-XI-31-6. Parameters according to Leonardi (1987) / *medidas del Morfotipo D* "**Rogerbaletichnus aguilerai**", *MLP 60-XI-31-5, y Morfotipo E* "**Palaciosichnus zettii**", *MLP 60-XI-31-6. Parámetros de acuerdo a Leonardi (1987).*

Measures	MLP 60-XI-31-5		MLP 60-XI-31-6	
	Manus	Pes	Manus	Pes
Footprint length (cm) average	—-	6.4	2.8	2.9
Footprint width (cm) average	6.4	5.3	2.4	2.6
Foot angulation (degrees) average	23°(-)	0°	26°(+)	0°
Width of pace (cm) average	8.1	11.1	5	4.2
Pace angulation (degrees) average	123°	116°	145°	153°
Pace length (cm) average	17.1		16.8	
Stride length (cm) average	35.5		30.8	
Trackway length (cm)	72.3		42.8	
Trackway width (cm)	22.5		9.8	
Dist. manus-pes (cm) average	— —-		6.4	
Limb drag width (cm) average	3.3		— —-	
Speed (m/s)	2.16		4.35	
Relative stride length (λ/h)	1.38		2.7	

teriorly directed and the digit impressions are subequal in size although they are poorly preserved due to partial superposition over the manus prints. Arc-shaped limb drags are present along the trackway, produced by the forelimbs (figure 6). The limb drag marks show striations that run parallel to the margins. These may represent toe drag traces.

The trackway starts with an incomplete left manus print followed by three alternating complete manus-pes sets and ends with an incomplete left pes print. The trackway pattern is broad (low pace angulation, see table 2) and shows short steps suggesting a trackmaker with a relatively short body. Also, the pattern of the limb drags, in an open laterally convex arc, indicates an animal that had its elbows-out, at least for the forelimbs, and laterally flexed the vertebral column during progression (see Smith, 1993).

Discussion. The specimen MLP 60-XI-31-5 (holotype) was originally described by Casamiquela (1964, pl. XVII, fig. 3) as a new ichnotaxon, "*Rogerbaletichnus aguilerai*", and which he related to Chelonia (Casamiquela, 1964). In the original publication, Casamiquela assigned an uncatalog specimen as paratype (1964, pl. XIV, figs. 5 and 6) which was part of the same trackway of the holotype (Casamiquela, 1964). This specimen is at present housed in the collections of the Museum of Ingeniero Jacobacci. The trackmaker of "*R. aguilerai*" was interpreted as a possible cynodont (Casamiquela, 1975) or anomodont therapsid (Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994).

The trackway denotes the progression of a quadrupedal animal with a sprawling gait evidenced by the relative breadth of the trackway and the shape of the limb drag traces. Trackways that show a similar degree of drag to the limbs as that analyzed above are, hitherto now, known for South America. In general, the described trackways frequently preserve only isolated toe dragmarks and they were mentioned for extant amphibians (Peabody, 1948, 1959), paleozoic trackways attributed to amphibians and basal amniotes (Haubold, 1971; Demathieu *et al*., 1992; Haubold *et al*., 1995), and chelonians (Ellenberger, 1974; Bernier *et al*., 1982; Wright and Lockley, 2001). According to the Late Triassic age of the material, temnospondyl amphibians and turtles could be proposed as possible trackmakers. However, the reduction of the manus digits in the specimen to four, if it is not a preservational effect (Peabody, 1959; Brand, 1979, 1996; McKeever and Haubold, 1996), cannot be used as a character to distinguish between these tetrapod groups. Even though temnospondyls have a four digit manus, the same condition has been also described for Triassic turtles such as *Proterochersis* from west-central Argentina (Rougier *et al*., 1995). Another possibility is that the trackmaker may correspond to a Late Triassic non-mammalian therapsid

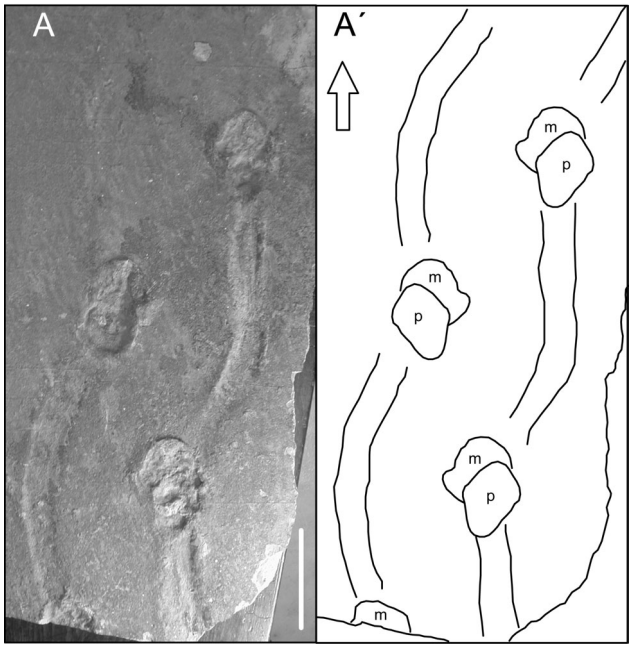

Figure 6. Morphotype D "***Rogerbaletichnus aguilerai***". **A** and **A´**, holotype (MLP 60-XI-31-5), a trackway of four manus-pes sets with limb-drags as a natural mould; **m,** manus and **p,** pes. Scale bar = 10 cm / *morfotipo D* "**Rogerbaletichnus aguilerai**". ***A y A´****, holotipo (MLP 60-XI-31-5), una rastrillada de cuatro pares mano-pie como molde con marcas de arrastre de miembros;* ***m,*** *mano y* ***p,*** *pie. Escala = 10 cm.*

as was previously proposed (Casamiquela, 1964; Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994) although, the lack of details in the trackway does not allow us to confirm the attribution of its trackmaker to this group of tetrapods. In any case, the trackway pattern and the apparent sinuous progression strongly suggests a quite primitive progression of its trackmaker.

Morphotype E ("Palaciosichnus zettii"*)*

Material. MLP 60-XI-31-6 (figure 7.A), a slab with a natural mould of a trackway of six steps (three manus-pes sets), MLP 60-XI-31-2, a slab with a cast of a trackway of five footprints (two manus-pes sets and one isolated print) all preserved as underprints; several uncatalogued slabs with trackways (figure 7.B) housed in the Museum of Ingeniero Jacobacci (Río Negro province) preserved as a natural mould; six trackways in the slabs of the sidewalks along the shoreline of Nahuel Huapi Lake (Bariloche, Río Negro province).

Locality and horizon. "Cantera Vieja", Cerro Las Lajas, Los Menucos (aprox. 40° 53′ S - 63° 11′ W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).
Description. The specimens are preserved on slabs of pale yellowish brown fine-grained sandstones. The MLP 60-XI-31-6 consists of a well preserved trackway of three manus-pes sets starting with a right manus-pes pair. It corresponds to a quadrupedal, pentadactyl, semi-plantigrade animal. All the tracks are very similar (homopody), with the manus prints a little larger than those of the pedes. In each set the manus is imprinted in front of the pes, and is slightly rotated outwards, whereas the pedes are anteriorly directed. All the footprints have several small rounded palm/sole pad impressions and five very short subparallel toes. In all the prints, digit III is the longest, II and IV are of similar length and digits I and V are the shortest of the series.

The size of the footprints relative to the stride length and the narrowness of the trackway with the slightly laterally placed position of the manus suggest an animal with a parasagittal gait, holding the elbows beneath the body during progression (table 2).
Discussion. The specimen was originally described as the new ichnotaxon "*Palaciosichnus zettii*" (Casamiquela, 1964, pl. XVIII) and related to different groups of therapsids (Casamiquela, 1964, 1975; Haubold, 1971, Leonardi, 1994). In the original publication, Casamiquela figures several undescribed slabs from the sidewalks of Bariloche (Casamiquela, 1964 pl. XX, XXI and XXII), apparently still in place, which are here considered to represent the same morphotype. Another undescribed specimen is housed in the Museum of Ingeniero Jacobacci (figure 7.B).

The trackway of MLP 60-XI-31-6 shows a quadrupedal animal with homopody and an upright posture that probably relate it to non-mammalian

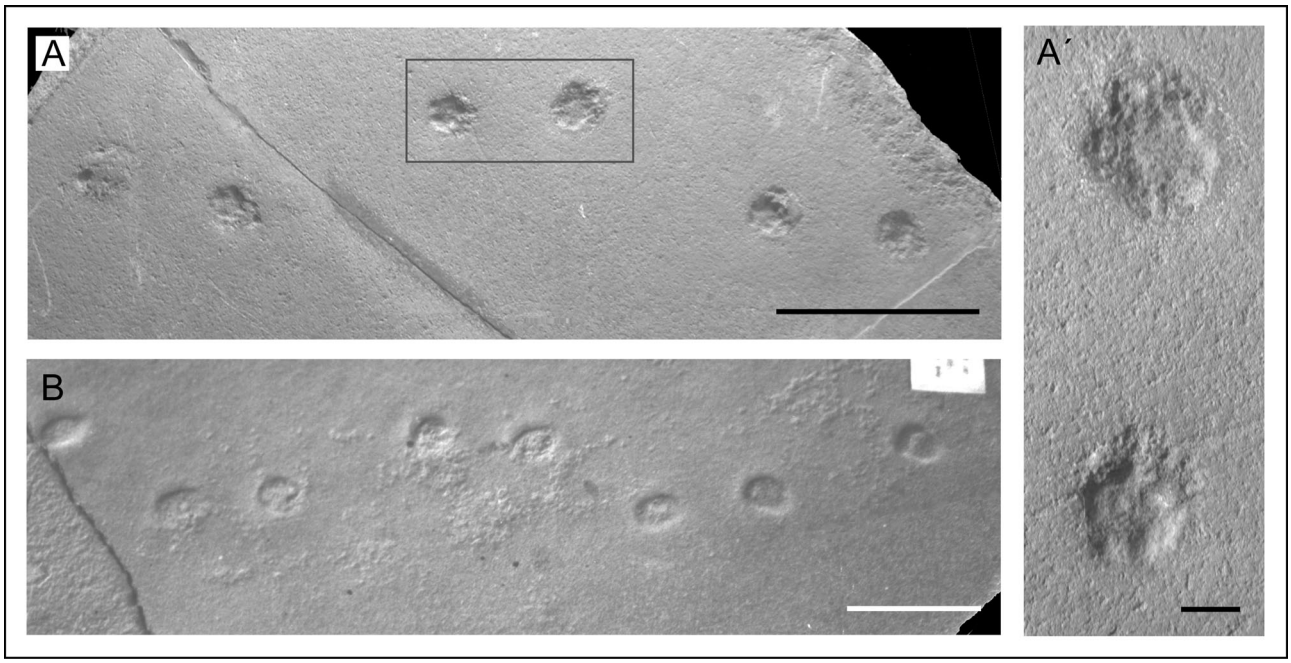

Figure 7. Morphotype E "***Palaciosichnus zettii***". **A** and **A´**, holotype (MLP 60-XI-31-6); **A,** a natural mould of a trackway of three manus-pes sets, scale bar= 10 cm; **A´,** detail of one of the manus-pes set of the same trackway, scale bar = 1 cm; **B,** a natural mould of a trackway housed in the collections of the Museum of Ingeniero Jacobacci, scale bar= 10 cm / *morfotipo E* "**Palaciosichnus zettii**". ***A y A´****, holotipo (MLP 60-XI-31-6);* ***A,*** *molde de una rastrillada de tres pares mano-pie, escala = 10 cm;* ***A,*** *detalle de un par mano-pie de la misma rastrillada, escala = 1 cm;* ***B,*** *molde de una rastrillada de las colecciones del Museo de Ingeniero Jacobacci, escala = 10 cm.*

therapsids (e.g. Haubold, 1971; Olsen and Galton, 1984; Hunt *et al*., 1993; Retallack, 1996; Lockley and Meyer, 2000). According to recent phylogenetic hypotheses of therapsid relationships (Sidor and Hopson, 1998; Rubidge and Sidor, 2001), the presence of nearly equal-sized toes and the upright posture of the limbs in the trackmaker suggest the presence of a derived therapsid (Jenkins, 1971; Hopson, 1994, 1995; Pough *et al*., 1999; Peters, 2000; Blob, 2001). The trackway pattern also suggests that the trackmaker was running during the imprinting of the trackway and the speed was estimated using Alexander's formula (Alexander, 1976; see table 2). The resulting speed is relatively high (4.35 m/s) and the stride length is 2.7 times the estimated trackmaker hip height (relative stride length) thus indicating a trotting/running gait for the trackmaker (Alexander, 1976; Thulborn, 1989, 1990; McKeever, 1994). This result was based on the assumption that *h* (hip height) was about four times the pes length (mean estimated for erect reptiles *sensu* Thulborn, 1989, 1990). If calculation of hip height (*h*) is considered less than four times the pedes length (see McKeever, 1994), judging from reconstructions of Triassic cynodonts (e.g. Jenkins, 1971; Benton, 2000), the calculated values indicate an even faster gait for the trackmaker. Therefore, the trackway suggests the presence of quite a small animal that could have developed a derived, fast gait such as galloping. As no synapomorphies are preserved in Late Triassic eutheriodontian footprints that might discriminate between non-mamalian eutheriodonts and mammals as possible trackmakers, mammalian affinities cannot be rejected for the "*Palaciosichnus*" trackmaker.

The MLP 60-XI-31-2 slab contains one isolated track (see above, discussion of Morphotype A) and a poorly preserved small trackway of five steps. This small trackway is equivalent to that discussed above, and also shows an animal that developed a fast running gait.

Morphotype F ("Gallegosichnus garridoi"*)*

Material. MLP 60-XI-31-7, a slab containing a trampled surface, including seven footprints as casts (figure 8.A); MLP 60-XI-31-8, a slab which preserves a cast of a trackway of six steps plus two isolated footprints and a tail drag (figure 8.B); MLP 60-XI-31-9, a slab with a cast of part of a trackway of two (left- right) manus-pes sets and an isolated left set; MLP 66-XI-15-1, a slab with a cast of a left manus-pes set and, apparently, an incomplete right set (figure 8.C); MLP 66-XI-15-3, a slab containing a cast of a complete left manus-pes set? (figure 8.D); MLP 93-XII-13-1, a slab which preserves a cast of a probable isolated right pes footprint (figure 8.E); MLP 93-XII-13-3 (**a** and **b**), a large slab with a natural mould of two trackways, one (**a**) of thirteen steps and the other (**b**) of twelve steps (figure 9); four uncatalogued specimens housed in the Museum of Ingeniero Jacobacci town (Río Negro province) (figures 8.F-G); several slabs of uncatalogued specimens in the sidewalks of the shoreline of the Nahuel Huapi Lake (Bariloche, Río Negro province) (figure 8.H).

Locality and horizon. "Cantera Vieja", Cerro Las Lajas, Los Menucos (aprox. 40° 53' S - 63° 11' W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).

Description. All material previously mentioned is preserved on slabs of fine-grained pale yellowish brown sandstones and, in general, they are very well impressed. They correspond to quadrupedal, plantigrade animals with two well defined pads in both the manus and pedes prints (p1 and p2 in figure 8.A). One pad is located just behind the digits and another anteroposteriorly elongated (probably a heel impression) posterior to the former. The manus and pedes tracks are pentadactyl, and quite similar in size (homopody), although the pedes tracks are slightly longer than wide whereas the manus tracks are somewhat wider than long. The manus tracks are imprinted in front of the pedes tracks and are rather rotated inwards; the digits are anteriorly directed, similar in shape, with digit IV slightly longer than the others and the most lateral digits (I and V respectively) slightly separated from the others (II, III, IV). The pedes impressions are anteriorly directed with the digit impressions subequal in size with digit III somewhat longer than the others and digits I and V shorter than all remaining digits. In the manus prints the digit imprints are more spread out than in the pedes prints. None of the studied footprints shows claw marks.

The trackway pattern visible in slabs MLP 60-XI-31-8 (figure 8.B) and a and b in MLP 93-XII-13-3 (figure 9), indicate a regular progression of the trackmakers, with short steps (measurements summarized in table 3), and the manus and pedes prints rather close to the midline of trackway (relatively narrow trackway). Moreover, the pace angulation (between 104° and 124°, table 3) indicates an animal with a sprawling to semi-erect gait. In the specimen MLP 60-XI-31-8, a narrow tail dragmark is preserved along the midline of the trackway (figure 8.B).

Discussion. The ichnites in MLP 60-XI-31-7 (holotype), MLP 60-XI-31-8 (paratype) and in MLP 60-XI-31-9 (paratype) were originally included in "*Gallegosichnus garridoi*" (Casamiquela, 1964, pl. XV, fig. 1 and pl. XVI, fig. 2) and related to several different groups of synapsids (Casamiquela, 1964; Haubold, 1971; Casamiquela, 1975; Leonardi, 1994). The undescribed slab MLP 93-XII-13-3 preserves three trackways, two of them (**a** and **b**) are here recognized as the same type as the material described above. The third trackway (**c**) was originally also assigned by Leonardi to "*G. garridoi*" (Leonardi and Henrique de Oliveira, 1990; Leonardi, 1994), although the manus prints are rotated outwards in contrast to the trackways **a** and **b** where the manus

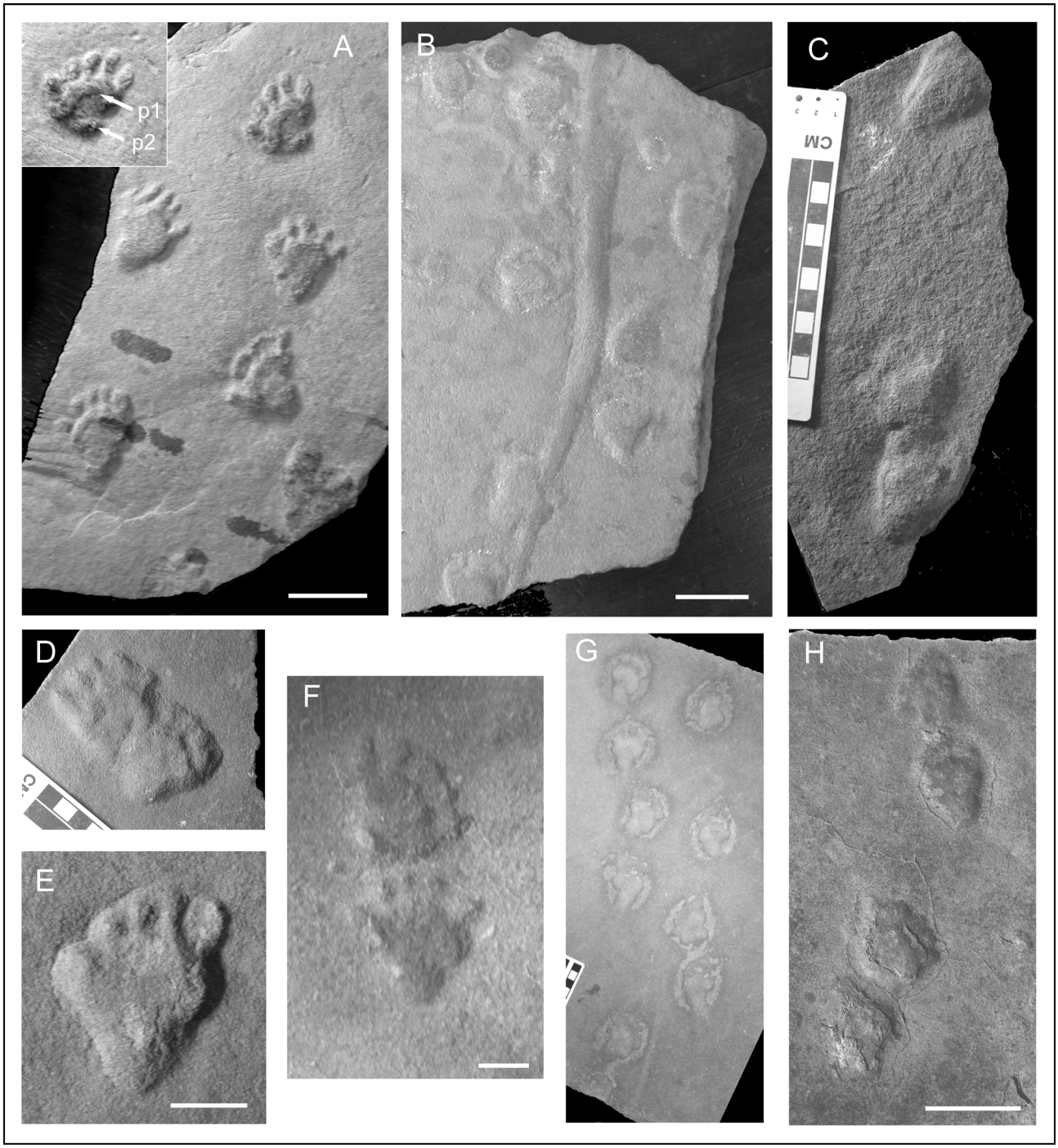

Figure 8. Morphotype F "***Gallegosichnus garridoi***". **A,** holotype (MLP 60-XI-31-7), a cast of a trampling surface, including seven footprints, and a detail of one of the footprint (upper left corner) showing the p1 and p2 pad impressions, scale bar = 5 cm; **B,** paratype (MLP 60-XI-31-8), a cast of a trackway of six steps with a tail drag plus two isolated footprints, scale bar = 5 cm; **C,** MLP 66-XI-15-1, a cast of a left manus-pes set and, apparently, an incomplete right set; **D,** MLP 66-XI-15-3, a cast of a complete left manus-pes set?; **E,** MLP 93-XII-13-1, a cast of a probable isolated right pes footprint, scale bar = 2 cm; **F,** a cast of a manus-pes set housed in the collections of the Museum of Ingeniero Jacobacci, scale bar = 2 cm; **G,** a cast of a trackway of the same morphotype housed in the collections of the Museum of Ingeniero Jacobacci; **H,** a cast of two manus-pes set from the sidewalks of Bariloche, scale bar = 5 cm / *morfotipo F* "**Gallegosichnus garridoi**". ***A,*** *holotipo (MLP 60-XI-31-7), calco de una superficie de pisoteo, que incluye siete huellas, y detalle de una de las huellas (ángulo superior izquierdo) donde se muestran las impresiones de las almohadillas p1 y p2, escala = 5 cm;* ***B,*** *paratipo (MLP 60-XI-31-8), calco de una rastrillada de seis pasos con arrastre de cola y otras dos huellas, escala = 5 cm;* ***C,*** *MLP 66-XI-15-1, calco de un par mano-pie izquierdo y, aparentemente, un par derecho incompleto;* ***D,*** *MLP 66-XI-15-3, calco de un par ? mano-pie izquierdo;* ***E,*** *MLP 93-XII-13-1, calco de una huella aislada de un probable pie derecho, escala = 2 cm;* ***F,*** *calco de un par mano-pie de las colecciones del Museo de Ingeniero Jacobacci, escala = 2 cm;* ***G,*** *calco de una rastrillada del mismo morfotipo de las colecciones del Museo de Ingeniero Jacobacci;* ***H,*** *calco de dos pares mano-pie de la avenida costanera de Bariloche, escala = 5 cm.*

Table 3. Measures of Morphotype F "***Gallegosichnus garridoi***", MLP 93-XII-13-3 and MLP 60-XI-31-8. Parameters according to Leonardi (1987) / *medidas del Morfotipo F "***Gallegosichnus garridoi***", MLP 93-XII-13-3 y MLP 60-XI-31-8. Parámetros de acuerdo a Leonardi (1987).*

Measures	MLP 93-XII-13-3						MLP 60-XI-31-8	
	Trackway a		Trackway b		Trackway c			
	Manus	Pes	Manus	Pes	Manus	Pes	Manus	Pes
Footprint length (cm) average	5.7	5.1	4.2	5.3	— —-	5.7	4.6	5.3
Footprint width (cm) average	6.3	3.1	6.3	4.8	4.2	4.4	4.8	4.7
Foot angulation (degree) average	52°(-)	17°(+)	57°(-)	16°(-)	24°(+)	7°(+)	23°(-)	8°(+)
Width of pace (cm) average	6.3	11.5	5.3	8.5	8.1	6.3	8.3	2.7
Pace angulation (degree) average	145°	117°	148°	123°	133°	137°	—-	108°
Pace length (cm) average	17.5		15.9		15.7		13.3	
Stride length (cm) average	35.7		31.4		39.3		26.6	
Trackway length (cm)	118.8		99.4		99.7		41.5	
Trackway width (cm)	16.4		16.7		15.1		13.5	
Dist. manus-pes (cm) average	— —-		— —-		— —-		5.5	
Speed (m/s)	2.65		2.49		2.9		1.65	
Relative stride length (λ/h)	1.7		1.65		1.72		1.25	

prints are rotated inwards. This condition suggests a different position of the fore limbs during progression in the trackmaker of trackway **c**, with the manus rotated outwards and thus, possibly, the elbows held underneath the body (Jenkins, 1971). The undescribed specimens from Bariloche and Jacobacci were previously partially figured by Casamiquela (Casamiquela, 1964 pl. XIX, figs. 1 and 2) and Leonardi (Leonardi, 1994 pl. XVI, fig. 1).

All the specimens described above denote an animal with a quadrupedal progression, homopody and pentadactyly; this morphology relates them to non-mammalian therapsids (e.g. Haubold, 1971; Olsen and Galton, 1984; Hunt *et al*., 1993; Retallack, 1996; Lockley and Meyer, 2000). The presence of a heel pad (calcaneal heel *sensu* Hopson, 1995) in the prints suggests a relatively derived non-mammalian therapsid trackmaker (Jenkins, 1971; Hopson, 1995), probably a eutheriodont (*sensu* Sidor and Hopson, 1998; Rubidge and Sidor, 2001). The inward rotation of the manus suggests an elbows-out gait (Smith, 1993), and the shape of the digits might indicate a basal position of the trackmaker within that clade (see Jenkins, 1971; Hopson, 1994, 1995; Sidor and Hopson, 1998; Peters, 2000). In the three known trackways (MLP 60-XI-31-8 and, a and b in MLP 93-XII-13-3), the speed of the trackmakers was estimated (Alexander, 1976; see above discussion of Morphotype E). In the three cases, the animals were walking, although the relative speeds (table 3) are slightly different. The speed of the trackmaker in MLP 60-XI-31-8 shows that progression was comparatively much slower than in trackways **a** and **b**. This trackway is the only one with a tail dragmark preserved and the relatively low pace angulation and the higher manus-pes distance are also consistent with slower progression by its trackmaker (see Peabody, 1959).

Morphotype G ("Stipanicichnus bonetti*")*

Material. CICRN 1-X-72-3, one slab containing a natural mould of a trackway of eleven footprints with five complete manus-pes sets and one isolated pes print (figure 10).

Locality and horizon. "Cantera Vieja", Cerro Las Lajas, Los Menucos (aprox. 40° 53' S - 63° 11' W), Río Negro province, Argentina; Vera Formation (Los Menucos Group), Late Triassic (Labudía *et al*., 2002).
Description. The trackway is well impressed on a slab of a fine-grained sandstone and it corresponds to a quadrupedal, plantigrade, pentadactyl animal. All the footprints are similar in size (homopody). As mentioned above, the trackway consists of four manus-pes sets and one isolated print. In each set, the manus is imprinted medially and slightly anterior to the corresponding pes print. The manus tracks are somewhat rotated inwards whereas the pedes tracks are more anteriorly directed and the interpedes distance is greater than that of the manus tracks spacing. The sole pads are posteriorly elongated which probably denotes the presence of a heel impression. In general, all the digits are subequal, similar in shape and have pointed claw-marks medially directed. The manus digits are more spread out than those of the pedes, in particular digits I and V are

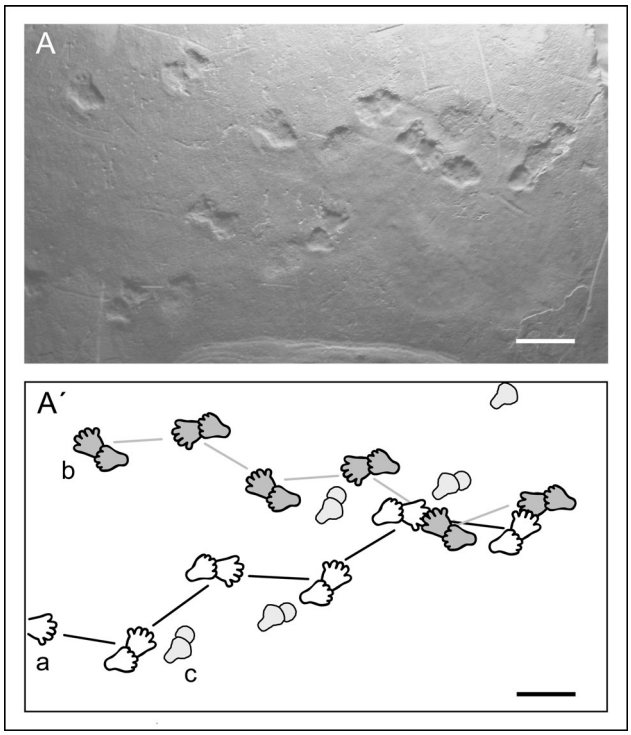

Figure 9. Morphotype F "***Gallegosichnus garridoi***". **A** and **A´**, MLP 93-XII-13-3; **A,** a natural mould of three trackways (**a, b** and **c**), two of them correspond to the Morphotype F (**a** and **b**). Scale bar = 10 cm / *morfotipo F* "**Gallegosichnus garridoi**". ***A y A´,*** *MLP 93-XII-13-3; A, molde de tres rastrilladas* ***(a, b y c)****, dos de ellas corresponden al Morfotipo F* ***(a y b)****. Escala = 10 cm.*

more separated than the inner ones. The trackway starts with a left manus-pes set followed by four alternating manus-pes sets and ends with an incomplete right pes print. It shows regular progression by the trackmaker with very short steps and footprints particularly widely separated from the midline of the trackway (broad trackway). Moreover, the very low pace angulation (table 4) indicates an animal with a sprawling gait (*sensu* Leonardi, 1987).

Discussion. The specimen in CICRN 1-X-72-3 is the holotype material of *Stipanicichnus bonetti* Casamiquela, 1975 (pl. 6), which was related to Cynodontia (Casamiquela, 1975). Subsequently, the same specimen was allied to "Therapsida or Mammalia" (Leonardi, 1994).

The morphology of the prints (e.g. homopody) relates the trackmaker to non-mammalian therapsids (e.g. Haubold, 1971; Olsen and Galton, 1984; Leonardi and Henrique de Oliveira, 1990; Hunt *et al*., 1993; Leonardi, 1994; Retallack, 1996; Lockley and Meyer, 2000). Moreover, within that group the presence of a probable heel impressions (calcaneal heel *sensu* Hopson, 1995) might be correlated with relatively derived therapsids (Jenkins, 1971; Hopson, 1995). Nevertheless, the marked broadness of the trackway suggests a sprawling posture for both the forelimbs and hindlimbs. Moreover, the pattern observed in the trackway is very peculiar due to the sideways orientation of the footprints. This arrangement of the prints has been related to animals that walked, probably uphill, across a steep surface (McKeever, 1994). The lack of information about the environmental context where the trackway CICRN 1-X-72-3 was imprinted does not allow us to corroborate this hypothesis.

Discussion

With the exception of Patagonia, Triassic ichnites attributed to non-mammalian therapsids are generally scarce in Argentina. They were mentioned from the Ischigualasto-Villa Unión Basin (Marsicano *et al*., 2004) and the Cuyana Basin (Bonaparte, 1966; Romer, 1966; Leonardi, 1994; Marsicano and Barredo, 2004; Marsicano *et al*., 2004) in west-central Argentina. In other Gondwanan areas, footprints attributed to this group of tetrapods are also scanty and were described from Late Triassic and Early Jurassic levels of Southern Africa (Ellenberger, 1970, 1972, 1974; Lockley *et al*., 2004), the Lower Triassic of Antarctica (Macdonald *et al*., 1991) and the Lower Triassic of Australia (Retallack, 1996).

The Middle Triassic Cerro de Las Cabras (Cuyana Basin) and Los Rastros formations (Ischigualasto-Villa Unión Basin) have mainly yielded small isolated tracks (Bonaparte, 1966; Romer, 1966; Leonardi, 1994; Marsicano *et al*., 2004) that were recently reviewed and tentatively assigned to non-mammalian therapsids (Marsicano *et al*., 2004). No clear evidence of a calcaneal heel impression is present in the material from central-western Argentina, in contrast to

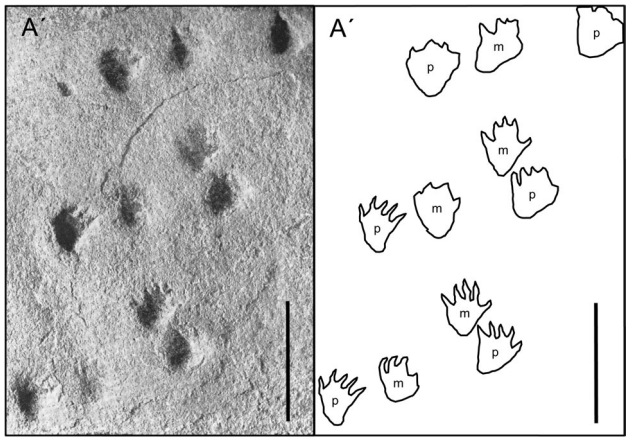

Figure 10. Morphotype G "***Stipanicichnus bonetti***". **A** and **A´,** holotype (CICRN 1-X-72-3), a natural mould of a trackway of eleven footprints (from Casamiquela, 1975); **m,** manus and **p,** pes. Scale bar = 10 cm / *morfotipo G* "**Stipanicichnus bonetti**". ***A y A´,*** *holotipo (CICRN 1-X-72-3), molde de una rastrillada de once huellas (tomado de Casamiquela, 1975);* ***m,*** *mano y* ***p,*** *pie. Escala = 10 cm.*

Table 4. Measures of Morphotype G "***Stipanicichnus bonetti***", CICRN 1-X-72-3. Parameters according to Leonardi (1987) / *medidas del Morfotipo G "***Stipanicichnus bonetti***", CICRN 1-X-72-3. Parámetros de acuerdo a Leonardi (1987).*

Measures	CICRN 1-X-72-3	
	Manus	Pes
Footprint length (cm) average	2.3	2.4
Footprint width (cm) average	2.4	1.9
Foot angulation (degrees) average	15°(-)	13°(+)
Width of pace (cm) average	1.2	2.9
Pace angulation (degrees) average	116°	61°
Pace length (cm) average	3.5	
Stride length (cm) average	7.1	
Trackway length (cm)	19.3	
Trackway width (cm)	8.4	
Dist. manus-pes (cm) average	1.7	
Speed (m/s)	0.46	
Relative stride length (λ/h)	0.74	

the condition observed in almost all of the footprints from Los Menucos. Only in the Morphotype E ("*Palaciosichnus zettii*") is the impression of a calcaneal heel absent, although this apparent semiplantigrade condition might be the result of unusually fast progression developed by the trackmaker during the imprint of the trackway.

In the Upper Triassic Portezuelo Formation (Cuyana Basin) two types of tracks attributed to non-mammalian therapsid trackmakers were studied and, in both cases, they are represented by isolated footprints and trackways (Marsicano and Barredo, 2004). One type (Type Q1 in Marsicano and Barredo, 2004) was related to cynodont trackmakers; the described trackway displays an animal developing a rather fast running gait and the prints lack the heel impression present in the specimens from Patagonia. The other type (Type Q2 in Marsicano and Barredo, 2004) corresponds to large rounded footprints that were attributed to members of the dicynodont anomodont clade, probably kannemeyerids (Marsicano and Barredo, 2004). This type of print is, until now, not present in the assemblage from Los Menucos.

In Gondwana, relatively well preserved footprints of non-mammalian therapsids (Eucynodontia) were described from the lower part of the Early Jurassic Clarens Formation in the Karoo Basin (Ellemberger, 1970, 1972; Olsen and Galton, 1984). All these South African footprints mainly consist of isolated material and were reassigned to the Jurassic Patagonian ichnotaxon "*Ameghinichnus*" by Olsen and Galton (1984). These prints are fairly similar to those from Los Menucos (see Ellemberger, 1970, 1972), particularly to the specimens of morphotypes C ("*Calibarichnus ayestarani*") and F ("*Gallegosichnus garridoi*"). In the Lower Triassic of the Sydney Basin (Australia) a relatively wide trackway of short steps was attributed to an anomodont therapsid trackmaker (Retallack, 1996), although the footprints show quite long subequal and relatively spread-out digits that differ strikingly from the Los Menucos material.

In Laurasia, similar footprints to those of Morphotype F ("*Gallegosichnus garridoi*") were described from the Lower Triassic of Germany and England ("*Dicynodontipus geinitzi*" in Haubold, 1971, pp. 41). They closely resemble those from Los Menucos, particularly in the morphology and orientation of the manus-pes sets: the inward rotation of the manus, the anteriorly directed pedes and the presence of conspicuous heel impressions.

"Chirotheroid" footprints are extensively known in the Triassic footprint assemblages of Pangea. They were described from several basins in southern Africa (e.g., Haubold, 1984; Olsen and Galton, 1984), North America (e.g., Lockley and Hunt, 1995), Europe (e.g., Courel and Demathieu, 1995; Haubold and Klein, 2000; Lockley and Meyer, 2000), and South America (Leonardi, 1994). In Argentina, they are also known from the Middle Triassic Cerro de las Cabras (Rusconi, 1952; Peabody, 1955; Bonaparte, 1966; Marsicano *et al*., 2004) and Los Rastros formations (von Huene, 1931; Marsicano *et al*., 2004), and the Upper Triassic Los Colorados (Bonaparte, 1997; Arcucci *et al*., 2000, 2004) and Portezuelo formations (Marsicano and Barredo, 2004); all these footprints resemble, in general, the ones described herein (Morphotype A) although, as noted above, a chirotherid affinity for Morphotype A is by no means certain.

Trackways comparable to those originally described as "*Ingenierichnus*" (Morphotype B) by Casamiquela are unknown from Triassic sequences of Argentina. Moreover, the broad continuous "sine-wave-shaped dragmark" produced during the progression of the animal was not previously recorded from lower Mesozoic sequences of Gondwana. A similar situation occurs with the material originally assigned to "*Rogerbaletichnus*" (Morphotype D). Similar tracks with conspicuous and persistent limb dragmarks were neither described for Lower Mesozoic sequences of Argentina nor for other Gondwanan areas.

Faunal significance of Los Menucos assemblage

Nearly all of our knowledge about the Triassic tetrapod faunas in southernmost South America comes from two Late Triassic successions in Patagonia: the El Tranquilo Group in Santa Cruz province and the Los Menucos Group. Whereas the

El Tranquilo has yielded exclusively dinosaur remains (prosauropods and ornithischians), the situation represented by the Los Menucos ichnites is completely different.

Until now, all well known Late Triassic Gondwanan tetrapod faunas have been archosaur-dominated (crurotarsal archosaurs and dinosaurs), such as those recorded in the Ischigualasto and Los Colorados formations in central-western Argentina (e.g. Bonaparte, 1971,1997; Arcucci *et al*., 2004), the upper part of the Santa María Supersequence in southern Brazil (Schultz *at al*., 2000; Zerfass *et al*., 2003), and the Elliot-Clarens succession in southern South Africa (e.g., Kitching and Raath, 1984; Olsen and Galton, 1984; Lucas, 1998; Lucas and Hancox, 2001).

The present analysis of Los Menucos tracks, which relied on a relatively large number of specimens, supports the existence of a terrestrial tetrapod fauna characterized by rather small animals. The dominant component of the fauna was largely the non-mammalian therapsids, probably eutheriodonts, both in terms of taxonomic diversity and relative abundance. Nevertheless, the presence of mammals in the assemblage cannot be ruled out. Therefore, the Los Menucos assemblage was unique, relative to other coeval Gondwanan tetrapod faunas, in which archosaurs (basal archosaurs and dinosaurs) are not the dominant component. This unusual situation might be either taphonomically biased toward small, predominantly terrestrial tetrapods or the record of an endemic fauna actually dominated by therapsids. The likelihood of a preservational bias as an explanation is difficult to assert because no taphonomic studies of the collected material are available.

The second interpretation is that the assemblage really represents an endemic fauna. The deposition of the Los Menucos succession was controlled by volcanic processes and deposited by ephemeral river systems under explosive volcanic activity, conditions that probably continuously changed the configuration of the landscape (see Lockley, 1990). This scenario might contributed to the development of an endemic fauna which reflects the instability of the landscape in which the animals lived.

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