

## Middle Triassic tetrapod footprints of southern South America

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**Abstract.** In South America, tetrapod footprints of Middle Triassic age were only described from the Cuyana (Cerro de las Cabras Formation) and Ischigualasto-Villa Unión (Los Rastros Formation) basins in west-central Argentina. They are scarce and remain mostly undescribed. Their significance and the putative trackmakers are identified and discussed within a phylogenetic context in the present contribution. Several groups of tetrapods are suggested to be represented, as non-mammalian therapsids, crurotarsal archosaurs and putative dinosaurs. The presence of crurotarsal archosaurs and non-mammalian therapsids in Cerro de las Cabras Formation suggests a tetrapod fauna more diverse than that documented by the known body fossil record. The ichnites described from the Los Rastros Formation are, until now, the only evidence of amniotes in the Ischigualasto-Villa Unión Basin during the deposition of these levels. They indicate the presence of putative dinosaurs, crurotarsal archosaurs and non-mammalian therapsids, which are already well represented in the rest of the sequence by skeletal remains.

**Resumen.** HUELLAS DE TETRÁPODOS DEL TRIÁSICO MEDIO DEL EXTREMO SUR DE AMÉRICA DEL SUR. En América del Sur, huellas de tetrápodos del Triásico Medio sólo se conocen en niveles de las cuencas Cuyana (Formación Cerro de las Cabras) e Ischigualasto-Villa Unión (Formación Los Rastros), en el centro-oeste de Argentina. Las huellas son escasas y la mayoría de los especímenes no están descriptos. En el presente trabajo el significado de estas huellas y sus supuestos generadores son discutidos en un contexto filogenético. Así, varios grupos de tetrápodos han sido identificados como terápsidos no mamalianos, arcosaurios crurotarsales y probables dinosaurios. La presencia de arcosaurios crurotarsales y terápsidos no mamalianos en niveles de la Formación Cerro de las Cabras sugiere una fauna más diversa que lo que indica el registro de restos fósiles esqueléticos conocidos para los mismos niveles. Las icnitas de la Formación Los Rastros son hasta el momento la única evidencia de amniotas en la Cuenca de Ischigualasto-Villa Unión durante la depositación de dichos niveles. Ellas indican la existencia de probables dinosaurios, arcosaurios crurotarsales y terápsidos no mamalianos, bien representados en el resto de la secuencia por restos esqueléticos.

**Key words.** Tetrapod footprints. Middle Triassic. Argentina. Phylogeny.

**Palabras clave.** Huellas de tetrápodos. Triásico Medio. Argentina. Filogenia.

### Introduction

In South America, Triassic tetrapod footprints were described mainly from Middle-Upper Triassic continental sequences of west-central Argentina and northern Patagonia (e.g. von Huene, 1931; Rusconi, 1952; Casamiquela, 1964; Bonaparte, 1966, 1997; Leonardi and Oliveira, 1990; Leonardi, 1994; Arcucci *et al.*, 1995; Manera and Calvo, 1999; Marsicano and

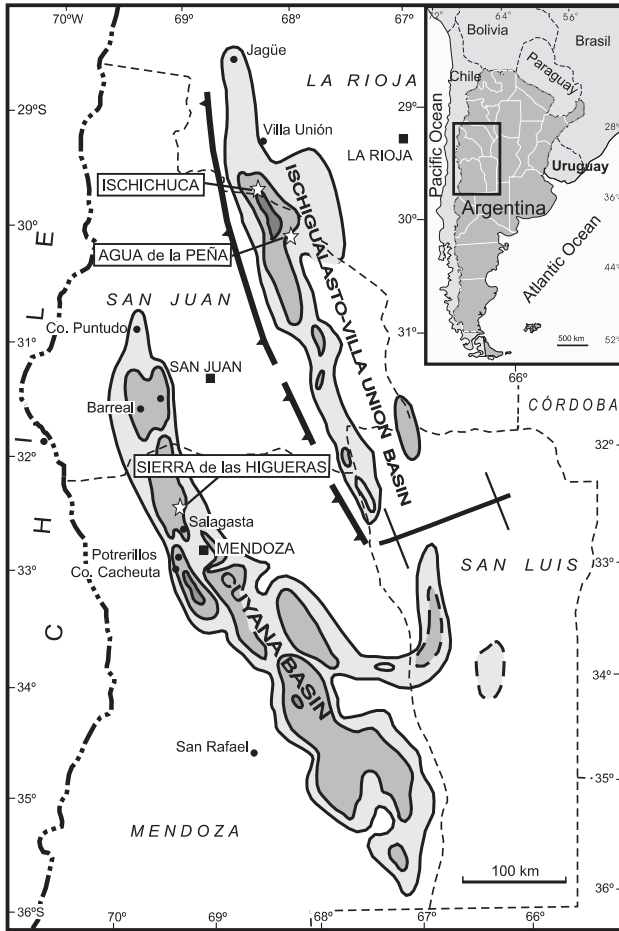
Barredo, 2000; Melchor *et al.*, 2002). Unlike the well known Triassic body-fossil record, which reveals taxonomically diverse tetrapod assemblages, footprints and trackways of this age are poorly known in this part of Gondwana mainly because they are scarce and most remain undescribed.

In Argentina, Middle Triassic footprint records are restricted to two sequences, the Cerro de las Cabras Formation (Cuyana Basin) and the Los Rastros Formation (Ischigualasto-Villa Unión Basin), both located in west-central Argentina. In the Cuyana Basin, the first report of the presence of tetrapod footprints was for the area of the Sierra de Uspallata (NW Mendoza), although the material was never figured or described (Rusconi, 1951, p. 48, 52) and is currently missing. Subsequently, a sparse track record was reported from the Cerro de las Cabras levels consisting of isolated "chirotheroid"

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**Figure 1.** Map of west-central Argentina showing the Triassic Cuyana and Ischigualasto-Villa Unión basins, and the location of the track-bearing sites (modified from Stipanovic and Marsicano, 2002) / Mapa del centro-oeste de Argentina donde se muestran las cuencas Cuyana y de Ischigualasto-Villa Unión, y las localidades con huellas (modificado de Stipanovic y Marsicano, 2002).

tracks (Rusconi, 1952; Peabody, 1955; Bonaparte, 1966) and several footprints attributed to "cynodonts" (Bonaparte, 1966; Romer, 1966; Leonardi, 1994).

In turn, in the Ischigualasto-Villa Unión Basin, the Los Rastros beds have yielded the first tetrapod footprints described from South America (von Huene, 1931). The specimen, recovered from the Hoyada de Ischigualasto, consists of two large trackways described as *Rigalites ischigualastianus* (von Huene, 1931) and attributed to large archosaurs (e.g. Bonaparte, 1966; Leonardi, 1994). Additional archosaur tracks were also recorded from the same unit (Stipanovic and Bonaparte, 1979; Arcucci *et al.* 1995, 1998; Melchor, 1998), from another locality (Quebrada de Ischichuca), but until now these ichnites have not been described or figured.

Tracks and trackways are an important source of information that provides, among other things, an estimation of the spatial and temporal distribution of tetrapod taxa (e.g. Lockley, 1986; Lockley *et al.*, 1994).

As an alternative to the traditional "phenetic correlation" method, a synapomorphy-based trackmaker identification has been recently proposed (Olsen *et al.*, 1998; Carrano and Wilson, 2001). It is focused on the recognition of shared derived characters present in the pedal skeleton of some body-fossil clades and the inferred structure of the pedal impressions of the ichnite (Carrano and Wilson, 2001). Additional features, such as body size and provenance, can be also used in association with synapomorphies as additional differentiae of trackmaker identity (Carrano and Wilson, 2001).

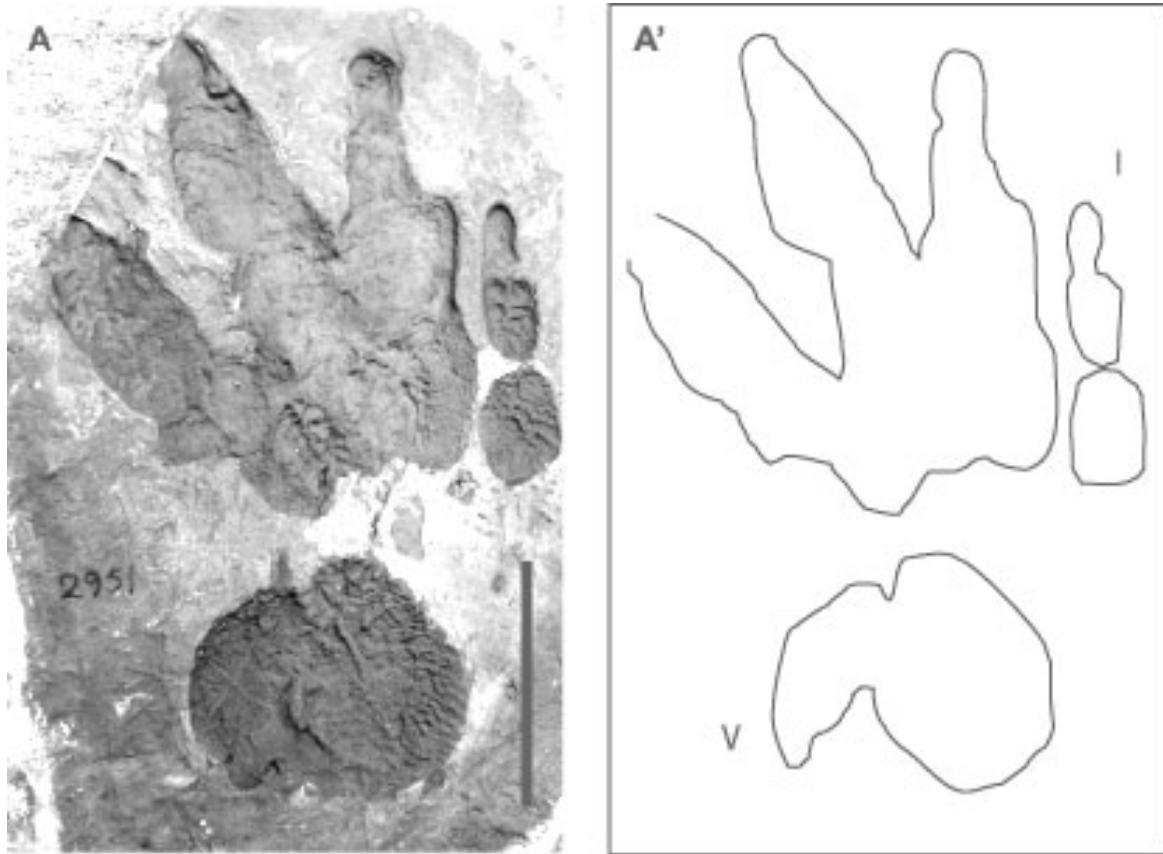
A description of most of the tetrapod ichnites recorded from Middle Triassic levels of Argentina is provided in the present contribution. In order to understand their significance, the putative trackmakers are discussed within a phylogenetic context. It is noteworthy that some of the trackways analyzed herein were considered the earliest evidence of the presence of members of the dinosaur clade, at least for Gondwana (Arcucci *et al.*, 1995; Carrano and Wilson, 2001).

*Abbreviations.* PVL: Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; MCNAM: Museo de Ciencias Naturales y Antropológicas "J.C. Moyano", Mendoza, Argentina.

## Geological setting

Between the end of the Paleozoic and the beginning of the Triassic several extensional depocenters were formed along the western margin of southern South America related to events associated with the pre-breakup of Gondwana (Uliana and Biddle, 1988). In central-western Argentina (Mendoza, San Juan and La Rioja provinces) two large depocenters, the Triassic Cuyana and Ischigualasto-Villa Unión basins, were filled by thick entirely nonmarine, predominately fluvial and lacustrine, successions (figure 1).

The Cuyana Basin is the largest basin and includes several sub-basins; its exposures are developed over 500 km mainly in the Mendoza Province (Kokogian and Mancilla, 1989; Kokogian *et al.*, 2001). The Triassic succession in the depocenter starts with coarse clastic facies of alluvial-fan deposits (Río Mendoza Formation) which interfinger with the tuffs, sandstones and mudstones of the Cerro de las Cabras Formation, that correspond to ephemeral streams and playa-lake deposits (Kokogian and Mancilla, 1989; López Gamundí *et al.*, 1994). Subsequently, the sequence grades up to cross-bedded sandstones, shales, bituminous shales, and tuffs of the Potrerillos Formation, all interpreted as deposited by braided-river systems with well developed flood plains. The fluvial Potrerillos Formation passes upwards into the widespread euxinic lacustrine shales of the Cacheuta Formation, which is suc-



**Figure 2.** A, and A', MCNAM 2951, "*Chirotherium higuense*" resp. / resp. "*C. barthii*", a pes print / huella de pie. Scale bar / Escala = 5 cm.

ceeded by the fluvial red beds of the Río Blanco Formation (Kokogian and Mancilla, 1989; López Gamundí *et al.*, 1994; Kokogian *et al.*, 2001). In Sierra de las Higueras locality, the track-bearing levels occur in quebrada de las Peñas, where a section of the Cerro de Las Cabras Formation is well exposed (Rolleri and Criado Roque, 1968; Carrara, 1970; Bellosi *et al.*, 2001). The footprints appear associated with mudcracks on the surface of several siltstone beds, which are intercalated with black shales bearing plant remains of the "*Dicroidium* type Flora" (Carrara, 1970; Bellosi *et al.*, 2001). The depositional environment of the track-bearing sequence was related to playa-lake deposits (Bellosi *et al.*, 2001). The Middle Triassic age of the Cerro de las Cabras Formation is based on its stratigraphic relationships (Kokogian *et al.*, 1993, 2001), palynological data (Zavattieri and Batten, 1996; Zavattieri, 2002) and the absolute age of basalts (Ramos and Kay, 1991) syntectonically emplaced in a nearby locality (Paramillos de Uspallata) to the track-bearing outcrops.

The Ischigualasto-Villa Unión Basin infilling is well exposed along the border between the San Juan and La Rioja provinces. At the base, the red beds of the Talampaya and Tarjados formations are unconformably covered by the Agua de La Peña Group

which is divided into five units. The tuffaceous fluvial/lacustrine sandstones and siltstones of the Chañares Formation grade upwards into the lacustrine black shales and deltaic sandstones of the Ischichuca/Los Rastros formations. This sequence passes into the fluvial sandstones, mudstones and tuffs of the Ischigualasto Formation, which, in turn, is covered by the fluvial red beds of the Los Colorados Formation (e.g. Stipanovic and Bonaparte, 1979; Lopez Gamundí *et al.*, 1989; Caselli *et al.*, 2001). The Los Rastros Formation is characterized by cyclic lacustrine-deltaic environments represented by thick deposits (600 m average thickness) that crop out in different localities with slight lateral facies variation (e.g. López Gamundí *et al.*, 1989; Milana and Alcober, 1994; Milana, 1999; Rogers *et al.*, 2001; Mancuso, 2003).

Even though an absolute age can not be assigned to the Los Rastros levels, their stratigraphic relationships provide a relative constrain. An isotopic age of a bentonite in the lower part of the overlying Ischigualasto Formation (Rogers *et al.*, 1993) places this unit into the latest Ladinian-early Carnian, thus suggesting a minimum upper Middle Triassic age (Ladinian) for the underlying Ischichuca/Los Rastros sequence (Rogers *et al.*, 2001). Nevertheless,

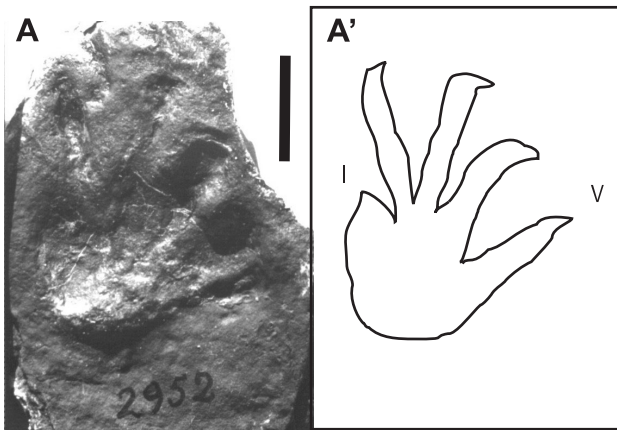


Figure 3. A, and A', MCNAM 2952, isolated foot print / huella aislada. Scale bar / Escala = 2 cm.

some authors have suggested a younger age (early Late Triassic) for the Los Rastros levels due to their palynological content (Zavattieri and Batten, 1996; Zavattieri, 2002). Therefore, a Middle Triassic-early Late Triassic age might be proposed to the whole sequence. It is important to remark that the track-bearing levels are close to the base of the sequence in the Quebrada de Ischichuca area, whereas at the Quebrada de los Rastros (Hoyada de Ischigualasto area) they were recorded near the top of the sequence.

### Footprints and trackways

#### *Cuyana Basin: Cerro de Las Cabras Formation*

**1. Material.** MCNAM 2951: one slab containing a cast of an isolated right pes impression (figure 2).

**Locality and horizon.** Quebrada del río las Peñas (aprox. 32° 30' S - 68° 45' W), Sierra de las Higueras, Mendoza province; Cerro de las Cabras Formation (Middle Triassic) (Rolleri and Criado Roque, 1968; Carrara, 1970; Zavattieri and Batten, 1996; Zavattieri, 2002).

**Description.** The footprint is preserved on a slab of a dusky brown siltstone; it is finely impressed, thus the scales of the pes are clearly visible. It is an asymmetric pentadactyl pes which is nearly complete as only the tip of the digit IV is missing. The digits I to IV are anteriorly directed, with digit III slightly longer than II and IV, which are similar in length. An average divarication angle of 25 degrees is present between digits III-II and III-IV. Digit V is short, strongly everted, and, as in the other digits, blunt claw marks are present. As previously mentioned, rounded tubercle-like scale impressions are clearly visible, particularly on the metatarsal-phalangeal pads of digits I and V.

**Remarks.** Rusconi (1952) studied this ichnite (MCNAM 2951) and a "manus" print (MCNAM 2952)

that were found close to each other but not forming the same set. In spite of this, Rusconi considered both to represent the same taxon and assigned them to a new "chirotheroid" taxon, "*Chirotherium higueraense*" (Rusconi, 1952). Subsequently, Peabody (1955) reassigned the specimen MCNAM 2951 to the Laurasian taxon "*Chirotherium barthii*" and considered the "manus" impression to belong to a completely different trackmaker (see below).

**2. Material.** MCNAM 2952: one slab containing a natural mould of an isolated footprint impression (figure 3).

**Locality and horizon.** Quebrada del río las Peñas (aprox. 32° 30' S - 68° 45' W), Sierra de las Higueras, Mendoza province; Cerro de las Cabras Formation (Middle Triassic) (Rolleri and Criado Roque, 1968; Carrara, 1970; Zavattieri and Batten, 1996; Zavattieri, 2002).

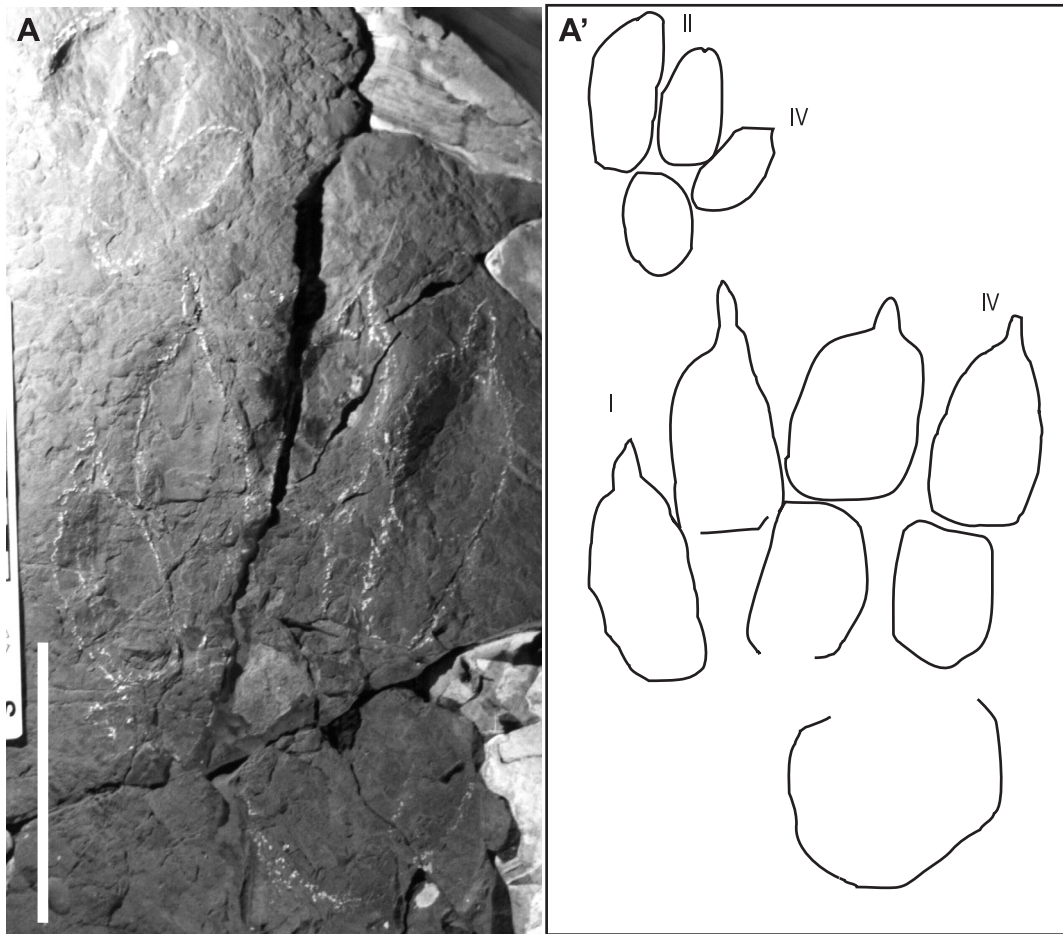
**Description.** The print is well preserved on a dusky brown siltstone. It corresponds to a small, plantigrade and pentadactyl right impression. All digits are elongated, straight, and the tips bear strongly laterally directed claw marks. Impressions of digits II and III are the longest and those of digits IV and V decrease in length successively; digit I seems to be the shortest of the series. A deep depression behind digits II and III is interpreted as a large sole/palm pad.

**Remarks.** The material was originally described as a "chirotheroid" manus print (Rusconi, 1952). However, there is no evidence in this isolated ichnite that can suggest whether it corresponds to a pes or manus impression. The presence of an asymmetric print, with a well defined palm/sole pad, and elongated, straight digits with laterally directed claw marks, prevents to ally this print to any known "chirotheroid" type of footprints. Peabody (1955) already considered it belonged to a different trackmaker to that of MCNAM 2951, and related it to an amphibian trackmaker. This assignment was also suggested by Leonardi (1994) who regarded it as a temnospondyl pes print, although the presence of a reduced digit I prevents to relate it to that group. Therefore, there is not enough available evidence in this isolated track to suggest its possible trackmaker affinities.

**3. Material.** PVL 2735: a slab containing a natural mould of a right manus-pes pair (figure 4); PVL 2736: a slab containing two very poorly impressed footprints.

**Locality and horizon.** Quebrada del río las Peñas (aprox. 32° 30' S - 68° 45' W), Sierra de las Higueras, Mendoza province; Cerro de las Cabras Formation (Middle Triassic) (Bonaparte, 1966; Rolleri and Criado Roque, 1968; Carrara, 1970; Zavattieri and Batten, 1996; Zavattieri, 2002).





**Figure 4.** A and A', PVL 2735, "*Rigalites* sp.", a manus-pes pair / *par pie-mano*. Scale bar / *Escala* = 10 cm.

**Description.** The specimen PVL 2735 is preserved on a dusky brown siltstone, and consists of a manus-pes pair of the same side of a digitigrade form, with the manus print significantly smaller than the pes (heteropody). The manus is less imprinted than the pes and located anteromedially to it. Digits II, III and IV are visible, all of similar length and anterolaterally projected. The hind footprint impression appears tetradactyl, although part of the slab containing the postero-lateral border of the ichnite, and thus the putative impression of digit V, is missing. Digits II, III and IV are nearly equally sized and slightly rotated outwards. Digit I is markedly shorter than the others and anteriorly directed; only a quite large round metatarsal impression is preserved posteriorly to digits III-IV. The average divarication angle is 15 degrees between digits I-II, II-III and III-IV.

The specimen PVL 2736 is poorly preserved and it is similar to PVL 2735.

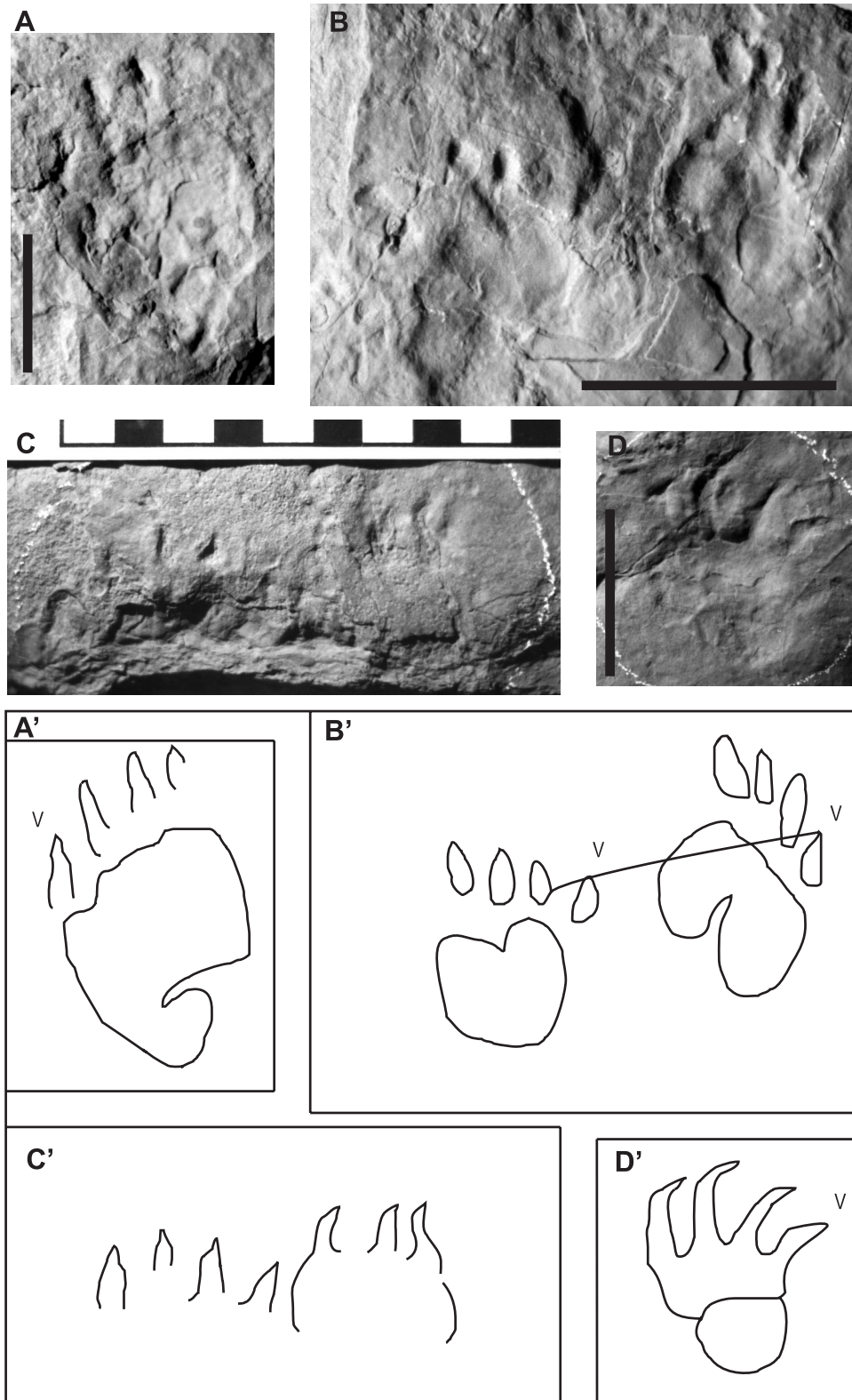
**Remarks.** The specimen was originally related to *Rigalites* sp. by Bonaparte (1966), an ichnotaxon already known from the Los Rastros levels (von Huene, 1931). Subsequently, this material was reassigned to *Chirotherium* sp. (Leonardi and Oliveira, 1990; Leonardi, 1994).

**4. Material.** PVL 2737-2741: several slabs containing natural moulds of small manus and pes prints (figures 5.A-D).

**Locality and horizon.** Quebrada del río las Peñas (aprox. 32° 30' S - 68° 45' W), Sierra de las Higueras, Mendoza province; Cerro de las Cabras Formation (Middle Triassic) (Bonaparte, 1966; Rolleri and Criado Roque, 1968; Carrara, 1970; Zavattieri and Batten, 1996; Zavattieri, 2002).

**Description.** The specimens are preserved as isolated prints or manus-pes pairs on several dusky brown siltstone slabs. The manus and pes prints are morphologically quite similar (homopody) and they are plantigrade and tetradactyl. Palm and sole of both manus and pes impressions are preserved as two pads. One, transversely elongated, just posterior to the toes impressions and a second, slightly rounded and smaller, behind that. Four elongated subequal digits are present in the footprints, represented by oval impressions with pointed claw marks. They are anteriorly directed and nearly parallel to each other and in some cases (PVL 2737, 2741), the claw marks are somewhat laterally directed (e.g. figure 5.D).

**Remarks.** The specimens were first mentioned by



**Figure 5.** A and A', PVL 2737, "*Dicynodontipus*", scale bar / escala = 2 cm; B and B', PVL 2738, "*Dicynodontipus*", scale bar / escala = 5 cm; C and C', PVL 2737, "*Dicynodontipus*", scale bar / escala = 10 cm; D and D', PVL 2741, "*Dicynodontipus*", scale bar / escala = 5 cm.

Bonaparte (1966) and, subsequently, briefly described and figured by Leonardi (Leonardi and Oliveira, 1990; Leonardi, 1994) who assigned them to

the ichnotaxon *Dicynodontipus*, which has been generally related to "cynodont" trackmakers (see Haubold, 1971).

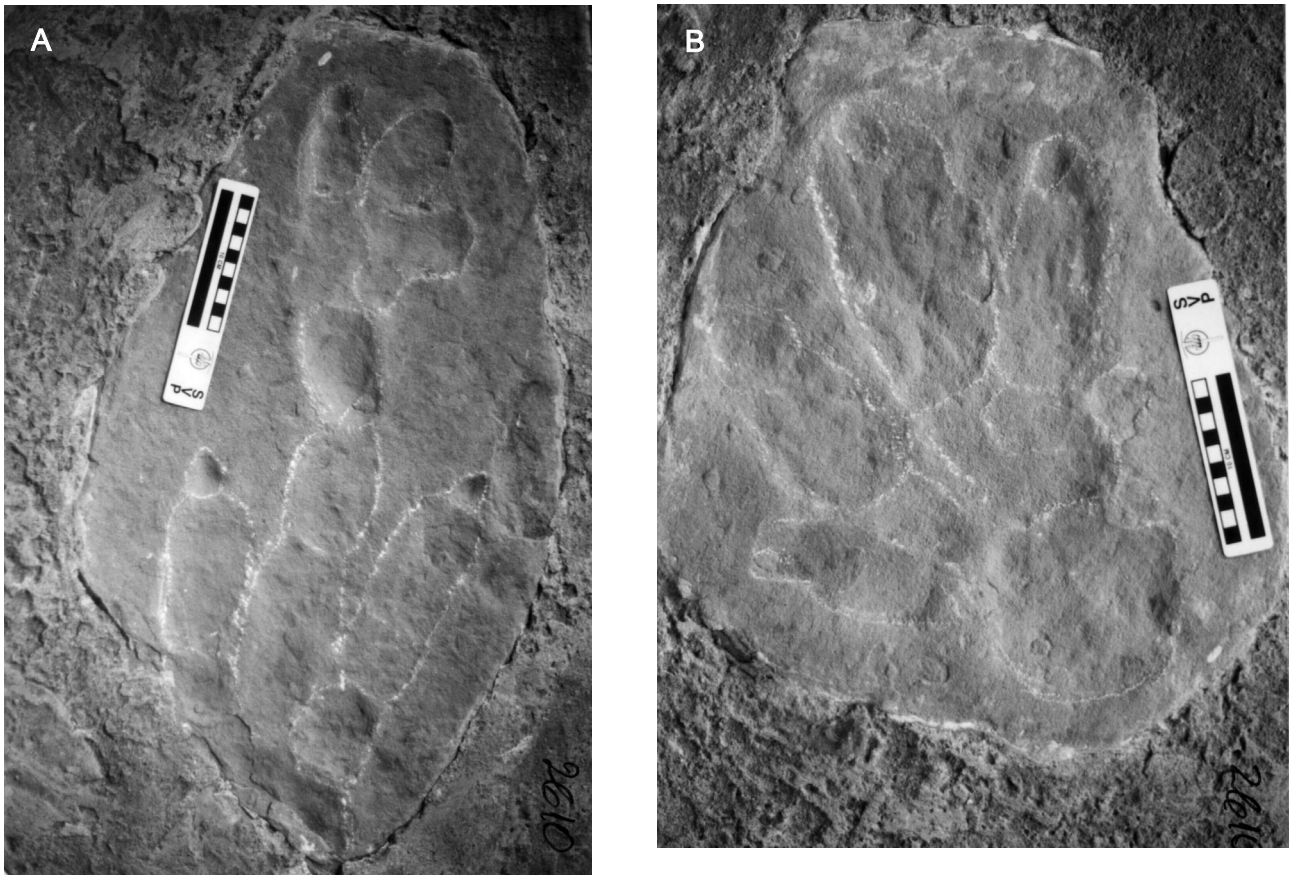


Figure 6. “*Rigalites ischigualastianus*” A, PVL 2610 a manus-pes pair / par mano-pie. B, a pes print / huella de pie. Scale bar / Escala= 10 cm.

#### *Ischigualasto-Villa Unión Basin: Los Rastros Formation*

**1. Material.** Originally, the specimen consisted of two trackways of a quadruped animal, of three and seven steps respectively and preserved as natural moulds. They were described and figured by von Huene, who considered them as a new ichnotaxon, *Rigalites ischigualastianus* (von Huene, 1931), and some authors (Frenguelli, 1948; Heim, 1949) partially photographed the specimen *in situ*. Subsequently, part of the prints (figure 6) were removed from the field (one right pes impression and a right manus-pes pair) and housed in the collections of the Instituto Miguel Lillo in Tucumán (PVL 2610). Currently, only one faint right pes print remains still *in situ* of the original described material.

**Locality and horizon.** Quebrada de los Rastros in Agua de la Peña, Hoyada de Ischigualasto (aprox. 29° 30' S - 69° 00' W), San Juan province; Los Rastros Formation (upper Middle Triassic-lower Late Triassic) (Zavattieri and Batten, 1996; Rogers *et al.*, 2001; Zavattieri, 2002).

**Description.** All footprints were preserved as deeply impressed natural moulds on the surface of a fine-

grained sandstone as two trackways showing a quadrupedal progression. One of the trackways consisted of 3 consecutive sets of manus-pes prints, and the another was composed by 7 sets; in both trackways a right manus-pes pair was the first step of the preserved series. The manus impressions (aprox. 25 cm length) are smaller than those of the pes (aprox. 40 cm length) and are printed just in front of the corresponding pes and, sometimes, they are partially overprinted by the pes print. The manus are tetradactyl with digits II, III and IV nearly equal sized and anteriorly directed; digit V is somewhat smaller and strongly posteriorly everted. Blunt claw marks are present on digits II, III and IV. Generally, the pes impressions are also tetradactyl but, apparently, functionally tridactyl with a digit I considerably small (half size of digit III), and sometimes it appears to be not printed (von Huene, 1931, Figure IX). In the material housed in the Instituto Miguel Lillo (PVL 2610), one of the pes prints (figure 6.B) also preserves a very reduced, anteriorly directed, digit V impression. Digits II, III and IV are elongated with digit III slightly longer than digits II and IV, which are nearly of the same size. Both manus and pes prints are slightly rotated outwards and the track-



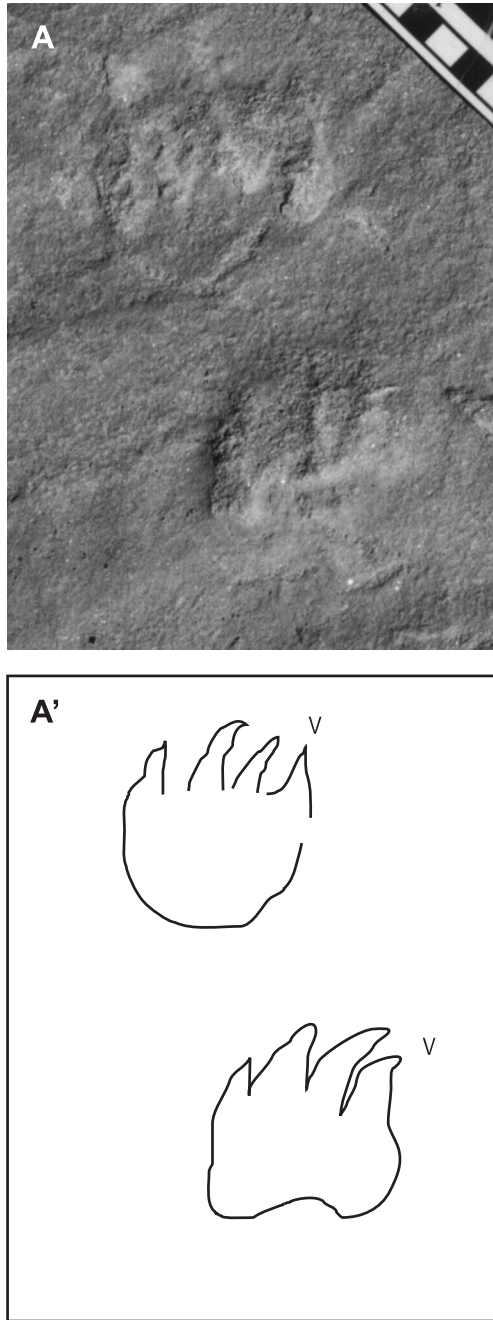


Figure 7. A and A', manus-pes pair / *par mano-pie*, scale bar / *escala* = 1 cm.

ways showed a relatively wide pace angulation (average 160 degrees) and a narrow pace width (von Huene, 1931, Figure IX).

**Remarks.** The specimen was originally related to ornithischian dinosaurs (von Huene, 1931) and, subsequently, to rauisuchid archosaurs (Reig, 1961; Bonaparte, 1966, Leonardi and Oliveira, 1990; Leonardi, 1994) and "protosuchian" crocodylomorphs (Haubold, 1971).

**2. Material.** A left manus-pes pair preserved as casts on the surface of a light greenish gray fine-

grained sandstone (figure 7). This specimen remains *in situ*.

**Locality and horizon.** Quebrada de los Rastros in Agua de la Peña, Hoyada de Ischigualasto (aprox. 29° 30' S - 69° 00' W), San Juan province; Los Rastros Formation (upper Middle Triassic-lower Late Triassic) (Zavattieri and Batten, 1996; Rogers *et al.*, 2001; Zavattieri, 2002).

**Description.** The prints correspond, apparently, to a left manus-pes pair; they have the same size and morphology (homopody) and are semiplantigrade and tetradactyl. The impressions appear not to be rotated, thus, the digits are anteriorly directed; they are elongated, nearly parallel to each other and all bear pointed claw marks.

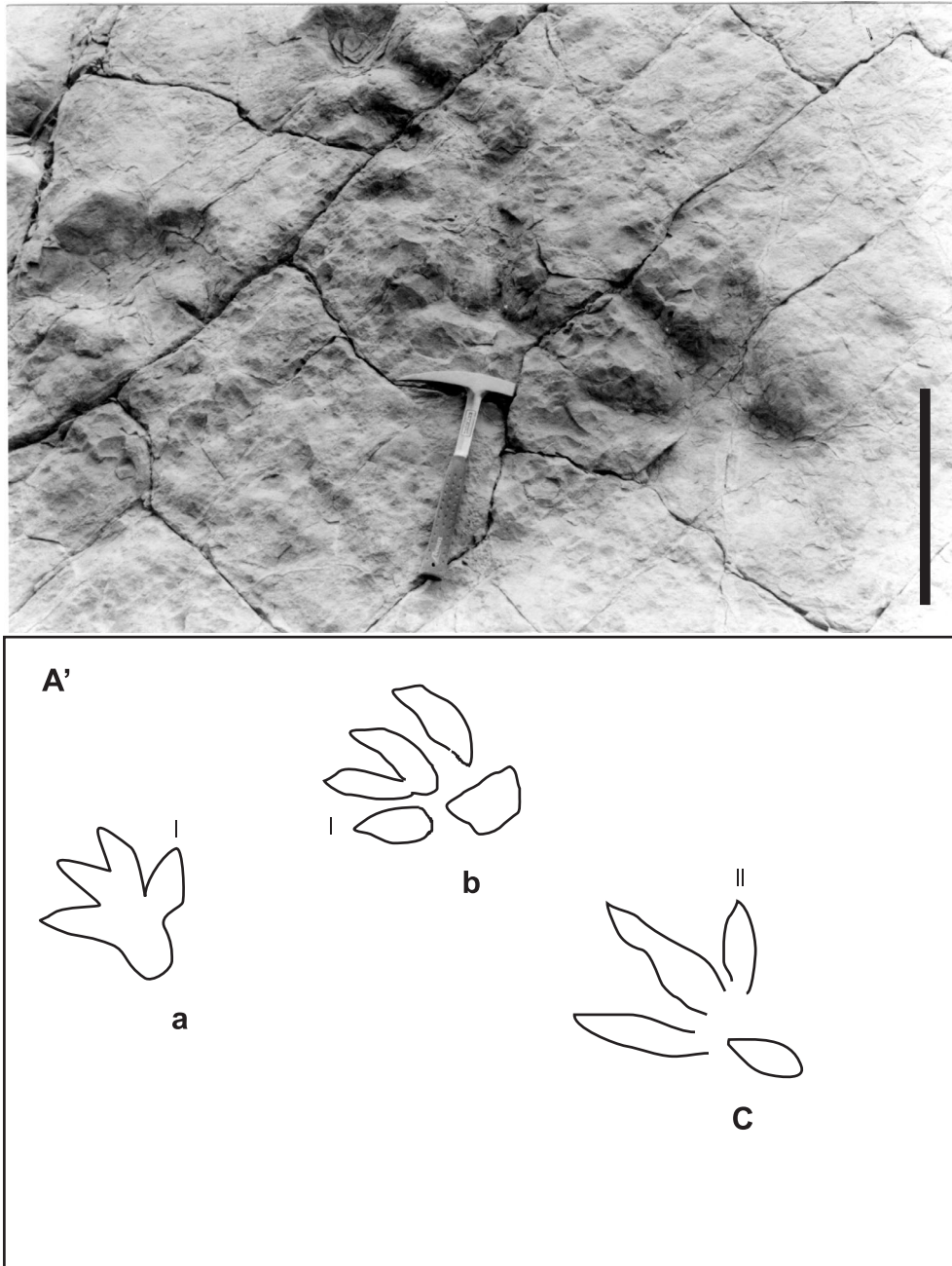
**Remarks.** The tracks are preserved in an equivalent level to that bearing the *Rigalites* holotype material, and associated with invertebrate trail marks and oscillation ripple marks.

**3. Material.** A trackway of seven steps with the prints as natural moulds of a quadruped animal on the surface of a grayish orange limestone (figure 8.a-b). This specimen remains *in situ*.

**Locality and horizon.** Quebrada de Ischichuca (aprox. 29° 45' S - 68° 15' W), Cerro Bola, Guandacol locality, La Rioja province; Los Rastros Formation (upper Middle Triassic-lower Late Triassic) (Zavattieri and Batten, 1996; Rogers *et al.*, 2001; Zavattieri, 2002).

**Description.** The trackway is composed of, apparently, 7 manus-pes pairs, although some of them are quite faint preventing an accurate evaluation of the number of steps in the trackway. Moreover, there are also some very poorly preserved footprints, apparently of similar morphology, associated in the same surface. The footprints correspond to a quadruped plantigrade animal with manus and pes impressions quite different from each other (heteropody). The pes prints are larger than those of the manus (maximum length approximately 35 cm), and they are, apparently, pentadactyl with short and robust digit impressions ending in blunt tips. Digits are near equally sized, with digit III slightly longer than the others, and digit V strongly everted and reduced to a large elongate postero-laterally directed metatarsal pad; the divarication angle between digits I-II, III-II and III-IV is between 60-70 degrees. The manus impressions are situated anterolaterally to those of the pes. Manus prints (approximately 22 cm in length) are nearly rounded and shallower than those of the pes. The manus are pentadactyl with four anterolaterally directed short digits with the digit V posterolaterally directed. As mentioned above, the structure of the trackway is not clear and the measurements between successive impressions





**Figure 8.** A and A', Ischichuca area trampling surface showing: **a**, and **b**, two pes prints of a trackway of a quadruped trackmaker; **c**, a tridactyl print of a biped trackmaker. Scale approximately 30 cm. / *A and A'*, Superficie de pisoteo en el área de Ischichuca donde: **a**, y **b**, dos impresiones de pies de una rastrillada de un cuadrúpedo; **c**, una huella tridáctila de un bípedo. Escala aproximadamente 30 cm.

vary along the trackway. Nevertheless, the trackway pattern shows that the manus and pes impressions are quite separated to the midline (wide trackway), with a moderately low pace angulation (approximately 90 degrees).

**Remarks.** This material, still *in situ*, is associated on the same surface with the large tridactyl tracks described below. Previously, this specimen was only briefly mentioned by Arcucci *et al.* (1998).

**4. Material.** Two consecutive tridactyl prints as nat-

ural moulds on the surface of a grayish orange limestone (figure 8.c). This specimen remains *in situ*.

**Locality and horizon.** Quebrada de Ischichuca (aprox. 29° 45' S - 68° 15' W), Cerro Bola, Guandacol locality, La Rioja province; Los Rastros Formation (upper Middle Triassic-lower Late Triassic) (Zavattieri and Batten, 1996; Rogers *et al.*, 2001; Zavattieri, 2002).

**Description.** The material consists of two consecutive steps of large-sized digitigrade tridactyl footprints (approx. 42 cm long) with somewhat indistinct

pads. The first of the series is a left pes and is better preserved than the right one, which is partially obscured by the ichnites of the trackway described above. The digit III is projected farther anteriorly than digits II and IV, which are anterolaterally directed and nearly equal in length; the divarication angle between digits III-II and III-IV is, approximately, 40 degrees. The trackway corresponds to a functionally tridactyl large-sized biped with the footfalls on a nearly straight line.

**Remarks.** This material was only previously mentioned by Arcucci *et al.* (1995, 1998) who suggested that its trackmaker could belong to the theropod dinosaur clade (Arcucci *et al.*, 1995). Associated with these tracks there is a poorly preserved trackway with the footprints deeply impressed in the substrate. The footprints are narrow and only the general contour is visible. The trackway is quite narrow and has very high pace angulation, thus suggesting a fully erect gait for its maker, which was relatively smaller than the previously described.

### Trackmakers affinities

The Cerro de las Cabras succession yielded two different types of tracks. One group includes the isolated right pes print MCNAM 2951 and the manus-pes pair PVL 2735 which correspond to the "chirotheroid" footprint type. This type of tracks has been often regarded as crurotarsal archosaur prints (Parrish, 1989; Haubold, 1983, 1986; Demathieu and Wright, 1988; Courel and Demathieu, 1995; Lockley and Meyer, 2000). Both specimens represent quadruped animals with marked heteropody and a plantigrade symmetrical pes and manus with reduced digits I and V. The MCNAM 2951 pes print presents a very small everted digit V. The small size of digit V is generally considered as a more derived condition than that in which digit V is better developed, because digit V reduction is related to a more erect gait of the trackmaker (e.g. Parrish, 1989; Haubold, 1983, 1986; Lockley and Meyer, 2000). Both specimens (MCNAM 2951 and PVL 2735) were previously discussed in the literature and allied to different groups of basal archosaurs, as rauisuchids, "protosuchians" and "pseudosuchids", among others (Rusconi, 1952; Peabody, 1955; Reig, 1961; Bonaparte, 1966; Leonardi and Olivera, 1990; Leonardi, 1994). Nevertheless, and considering recent phylogenetic analyses on basal archosaurs (Sereno, 1991; Parrish, 1993), there is no evidence preserved in isolated "chirotheroid" ichnites that might be used to distinguish among different crurotarsal archosaur groups. To date in the Cuyana Basin, archosauriforms are only represented by one incomplete skeleton (Reig, 1961; Desojo *et al.*, 2002), which

was recorded from younger levels (Cacheuta Formation) than those bearing the ichnites.

The remaining tracks from the Cerro de las Cabras Formation (PVL 2737-41) described herein represent completely different trackmakers. These footprints also denote quadrupedal progression of a plantigrade animal but, in this case, the manus and pes impressions are similar (homopody), with four short, nearly equal-sized and anteriorly directed digits. Recent analyses of synapsid relationships and locomotion and limb structure in nonmammalian therapsids (Hopson, 1994, 1995; Sidor and Hopson, 1998; Blob, 2001) provide a context to interpret the probable trackmakers. They represent small animals with symmetrical, anteriorly-directed manus and pes. This morphology suggests, together with the Triassic age of the track-bearing levels, that the trackmaker might be related to non-mammalian therapsids. Nevertheless, the lack of information about the trackway pattern prevents any discussion about the gait and posture of the trackmaker and, therefore, its more likely phylogenetic position within that group. These materials from Las Higueras were previously assigned to cynodonts (Leonardi and Oliveira, 1990; Leonardi, 1994) although, as discussed above, this assessment can not be supported. Even though skeletal remains of non-mammalian therapsids are unknown from Las Higueras area, several specimens were described from equivalent levels at the more southern Potrerillos area (Bonaparte, 1978; Abdala, 1996).

The Los Rastros levels have yielded a relatively more diverse ichnofauna than the one from the Cuyana Basin. This sequence has also yielded tracks that can be related to non-mammalian therapsids (figure 7). However, as they consist of isolated prints, a more accurate assignation of the trackmaker within that group is not possible. Skeletal remains of this group of synapsids are very well known in the basin and several taxa have been described from the Chañares, Ischigualasto and Los Colorados formations (e.g. Abdala, 1996; Bonaparte, 1997).

"Chirotheroid" footprints are also present in the Los Rastros sequence and are represented by two different specimens, von Huene's *Rigalites* material (PVL 2610) and the trackway described from the Ischichuca area (figures 8.a-b). They represent animals with quadrupedal progression and a plantigrade symmetrical pes and manus with reduced digits I and V. As previously discussed, this type of footprints has long been regarded as crurotarsal archosaur tracks (Parrish, 1989; Haubold, 1983, 1986; Demathieu and Wright, 1988; Courel and Demathieu, 1995; Lockley and Meyer, 2000). The configuration of the *Rigalites* trackways suggests a large animal with a relatively narrow, functionally tridactyl foot and an erect gait. These features suggest a track-

maker with a foot with a consolidated metatarsus and a parasagittal posture of the limbs (see Parrish, 1986). Within the crurotarsal clade, ornithosuchids and basal suchids were assumed to have derived upright postures (Serenó, 1991; Parrish, 1986, 1993). In Ornithosuchidae and some suchids, such as prestosuchids and some raiusuchids, digits I and V are reduced and digit V is anteriorly projected, thus producing a more symmetrical foot (Parrish, 1986). In contrast, several basal suchids present a L-shaped metatarsal V resulting in an everted digit V, not present in the *Rigalites* tracks.

Both ornithosuchids and basal suchids are very diverse in the Ischigualasto-Villa Unión Basin (e.g. Sereno, 1991; Parrish, 1993; Bonaparte, 1997; Arcucci *et al.*, in press). Basal suchids were already diversified in the underlying Chañares Formation (e.g. *Lewisuchus* and *Gracilisuchus*) and represented by several taxa in the overlying Ischigualasto (e.g. *Saurosuchus*) and Los Colorados (e.g. *Fasolasuchus*) formations. In turn, ornithosuchids are known from the overlying Los Colorados Formation (e.g. *Riojasuchus*). To date, only large suchian forms, comparable to that of the *Rigalites* trackmaker, have been described from the basin infilling and the stratigraphical distribution of the group suggests that they had already diverged during Los Rastros deposition.

The crurotarsal achosaur that produced the Ischichuca trackways was a quite different animal to that discussed above. It was functionally tetradactyl, with more robust, nearly equally sized toes, and a strongly divergent digit V. These features, together with the relatively wideness of the trackway, suggest the presence of an animal with a less erect gait and a more primitive foot structure than that of the *Rigalites* trackmaker.

As mentioned above, large tridactyl tracks (figure 8.c) of a medium-to-large-sized biped animal are also present in the Ischichuca area. The pes prints show a functionally tridactyl digitigrade pes with a long anteriorly directed digit III. The trackway has a very high pace angulation as the footfall pattern is on a nearly straight line. These features are also present in another trackway of a biped mentioned from the same levels which, in contrast, presents a quite narrow pes impression. These large tridactyl footprints were discussed by Arcucci *et al.* (1995) who suggested that the trackmaker could be allied to theropod dinosaurs. According to current ornithodiran phylogenetic relationships and included clades (e.g. Sereno, 1991, 1999; Benton, 1999), obligate bipedalism and digitigrade pedal posture characterize the Ornithodira and, within this group, a symmetric tridactyl pes distinguishes the members of the dinosaur clade (Parrish, 1989; Sereno, 1991; Farlow and Chapman, 1997). However, no synapomorphies that

might help to discriminate between theropod and basal ornithischian groups as possible trackmakers are present in three-toed footprints (Olsen *et al.*, 1998). Some authors have proposed that theropod tracks can be identified by the asymmetrical arrangement of the digits, with a distinct divergence of digit IV from II and III (e.g. Carrano and Wilson, 2001). The poor preservation of the material here described and the fact that the trackway of the large biped only consists of one clearly preserved print prevent to ascertain the arrangement of the digits in the trackmakers.

Basal theropod body fossils (*Herrerasaurus* and *Eoraptor*) as well as ornithischians (e.g. *Pisanosaurus*) were already described from the overlying Carnian Ischigualasto Formation (Rogers *et al.*, 1993; Sereno, 1999), although recently the inclusion of some of these taxa within Dinosauria was considered doubtful (Fraser *et al.*, 2002). Instead, *Herrerasaurus* and *Eoraptor* were suggested to represent dinosauriforms, closer to Dinosauria than other ornithodiran taxa (Fraser *et al.*, 2002). Therefore, and according to the previously discussed evidence, the biped Ischichuca trackmaker might be a basal dinosaur or a derived ornithodiran close to dinosaur origin.

## Discussion

In order to understand the significance of the tracks and trackways described above, trackmakers were identified and discussed within a phylogenetic context. Thus, and even to a coarse taxonomic level, several tetrapod taxa are suggested to be represented by those ichnites.

In the Cuyana Basin, tetrapods are almost restricted to temnospondyl amphibians as amniotes are fairly rare and mainly represented by non-mammalian cynodonts (Báez *et al.*, 1993; Marsicano, 1999; Marsicano *et al.*, 2000; Desojo *et al.*, 2002). To date, only a skeleton of an archosauriform, closely related to the crown-group archosaurs (Desojo *et al.*, 2002), was described from the upper part of the sequence (Late Triassic). Therefore, the presence of several ichnites referred to crurotarsal archosaurs and non-mammalian therapsids in the Middle Triassic Cerro de las Cabras Formation suggests a more diverse tetrapod fauna in older levels than those bearing the younger, rather monotonous body fossil record (e.g. Báez *et al.*, 1993).

To date, the thick fluvial-lacustrine deposits of the Los Rastros Formation are nearly devoid of tetrapod skeletal remains. The only record corresponds to a temnospondyl palate mould (Contreras *et al.*, 1997). In contrast, both the underlying Chañares Formation and the overlying Ischigualasto and Los Colorados formations are extensively known by their tetrapod

record which has been long considered unique among known Triassic Pangean tetrapod faunas (e.g. Romer, 1973; Bonaparte, 1978, 1997; Rogers *et al.*, 1993; Sereno and Arcucci, 1994; Martínez *et al.*, 1996; Arcucci and Marsicano, 1998; Lucas, 1998; Arcucci *et al.*, in press). Therefore, the presence of putative non-mammalian therapsids, crurotarsal and ornithodiran archosaurs in the Los Rastros levels fills the gap in their records as both groups were already well known in the rest of the sequence. So far, the ichnites described herein provide the only evidence of amniotes in the basin during Los Rastros depositional time.

As mentioned above, the large tridactyl footprints from the Ischichuca area have been considered the earliest evidence of the presence of members of the Dinosauria, at least, for Gondwana (Arcucci *et al.*, 1995; Carrano and Wilson, 2001). If the trackmaker is referred to a dinosaur taxon, or a dinosaur sister-taxon, its presence in the Los Rastros beds implies an earlier distribution of members of that clade in Gondwana than that provided by the body fossil record. This supports previous assumptions that the initial radiation of dinosaurs and close relatives might have occurred in the Middle Triassic, probably during the Anisian (Sereno, 1999; Carrano and Wilson, 2001).

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