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A REVIEW OF TRIASSIC TETRAPOD TRACK ASSEMBLAGES FROM ARGENTINA

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Abstract: This paper contains the first comprehensive ichnotaxonomic review of the Triassic tetrapod track record in Argentina, including previous accounts and new material recently discovered, and an analysis of its composition and stratigraphic distribution. Triassic footprints have been recorded from three basins: the Ischigualasto-Villa Unión and Cuyo basins in north-west Argentina, and the Los Menucos depocentre in northern Patagonia. Most are in successions of Middle Triassic age; a lower number are from the Late Triassic, and there are two records from Early Triassic rocks. The known track types include: *Brachychirotherium* isp., cf. *Brachychirotherium* isp., *Chirotherium barthii*, *Dicynodontipus* ispp., *Grallator* isp., *Rhynchosauroides* isp., *Rigalites ischigualastianus*, *Rigalites* isp., *Tetrasauropus* isp., and bird-like, chirotheriid and unidentified tridactyl footprints. The ichnogenera *Gallegosichnus* Casamiquela, 1964, *Calibarichnus* Casamiquela, 1964, *Palaciosichnus* Casamiquela, 1964 and *Stipanicichnus* Casamiquela, 1975 are considered to be synonyms of *Dicynodontipus* (Hornstein, 1876). In addition, the abandonment of the following ichnogenera (and single ichnospecies) that are based on poorly preserved material is suggested: *Ingenierichnus sierrai* Casamiquela, 1964, *Rogerbaletichnus aguilerai* Casamiquela, 1964 and *Shimmelia chirotheroides* Casamiquela, 1964. At least eight Triassic ichnofaunas can be recognized. The most peculiar is that of the Late Triassic Los Menucos depocentre, which is characterized by the dominance of therapsid footprints (*Dicynodontipus* ispp.). The track assemblages from the Cuyo Basin display the highest ichnodiversity, with five footprint types.

Key words: fossil footprints, Triassic, Argentina, tetrapod ichnofauna, ichnotaxonomy.

This paper presents a comprehensive ichnotaxonomic treatment of Triassic tetrapod track assemblages from Argentina. Our overview includes the revision of published and unpublished material in different museum collections (Museo de La Plata, Instituto Miguel Lillo, and Museo de Ciencias Naturales y Antropológicas 'Juan Cornelio Moyano'), as well as collection and *in situ* measurements of additional material resulting from fieldwork in the Cuyo and Ischigualasto-Villa Unión basins. This fieldwork was part of the revision of Triassic–Jurassic tetrapod tracks in Argentina by a group of researchers from the Museo Palaeontológico 'Egidio Feruglio' (Trelew), Universidad Nacional de La Pampa (Santa Rosa) and Museo Argentino de Ciencias Naturales (Buenos Aires). The ichnotaxonomic assessment of the numerous Triassic, seemingly 'endemic', ichnogenera erected by Casamiquela (1964) reveals that they can be dramatically reduced in number by assignment to previously described ichnotaxa. This analysis is completed by an account of the stratigraphic and temporal distribution of the ichnotaxa.

The scientific study of Triassic tetrapod tracks from Argentina dates back to the first third of the previous century and was inaugurated by the work of von Huene (1931), who described two trackways of a large quadrupedal animal found in the Ischigualasto area (San Juan province). The footprint-bearing succession was later named, for the presence of these trackways, the Los Rastros Formation (*rastros*, Spanish for trackways). The present state of knowledge of the Triassic tetrapod footprint record is relatively poor considering the geographical extent of continental basins of this age in Argentina, although some ichnofaunas have received greater attention (Melchor *et al.* 2001*c*; Marsicano *et al.* 2004; Marsicano and Barredo 2004). The published Triassic track record from Argentina contains numerous references to findings of vertebrate tracks, but detailed documentation, including ichnotaxonomic treatment, is scarce. Exceptions include the classic contributions by Rusconi (1951) and Casamiquela (1964, 1975), and the more recent compilations of South American tetrapod tracks by Leonardi

(1989, 1994). The monographic work of Casamiquela (1964) on Triassic and Jurassic footprints from Patagonia deserves special mention because of the detailed documentation of rich and well-preserved tetrapod track assemblages, which contain important palaeobiological information (e.g. Casamiquela 1964, 1975; Rainforth and Lockley 1996; de Valais and Melchor 2003). Extensive fieldwork in the Cuyo and Ischigualasto-Villa Unión basins during the 1960s yielded numerous records of tetrapod tracks (Romer 1966) and an important collection by Bonaparte from the Sierra de Las Peñas area of the Cuyo Basin (briefly reported in Bonaparte 1966). This material is housed at the Instituto Miguel Lillo (Tucumán province) and has remained essentially unpublished. Romer (1966) considered this ichnofauna comparable in diversity and abundance with that of the Connecticut Valley of the eastern United States, although recent surveys by us have yielded less optimistic results. In addition, the ichnotaxonomy of the Connecticut Valley ichnofauna by Hitchcock (1858, 1865) and Lull (1953) was considerably inflated, according to modern revisions (e.g. Olsen *et al.* 1992, 1998).

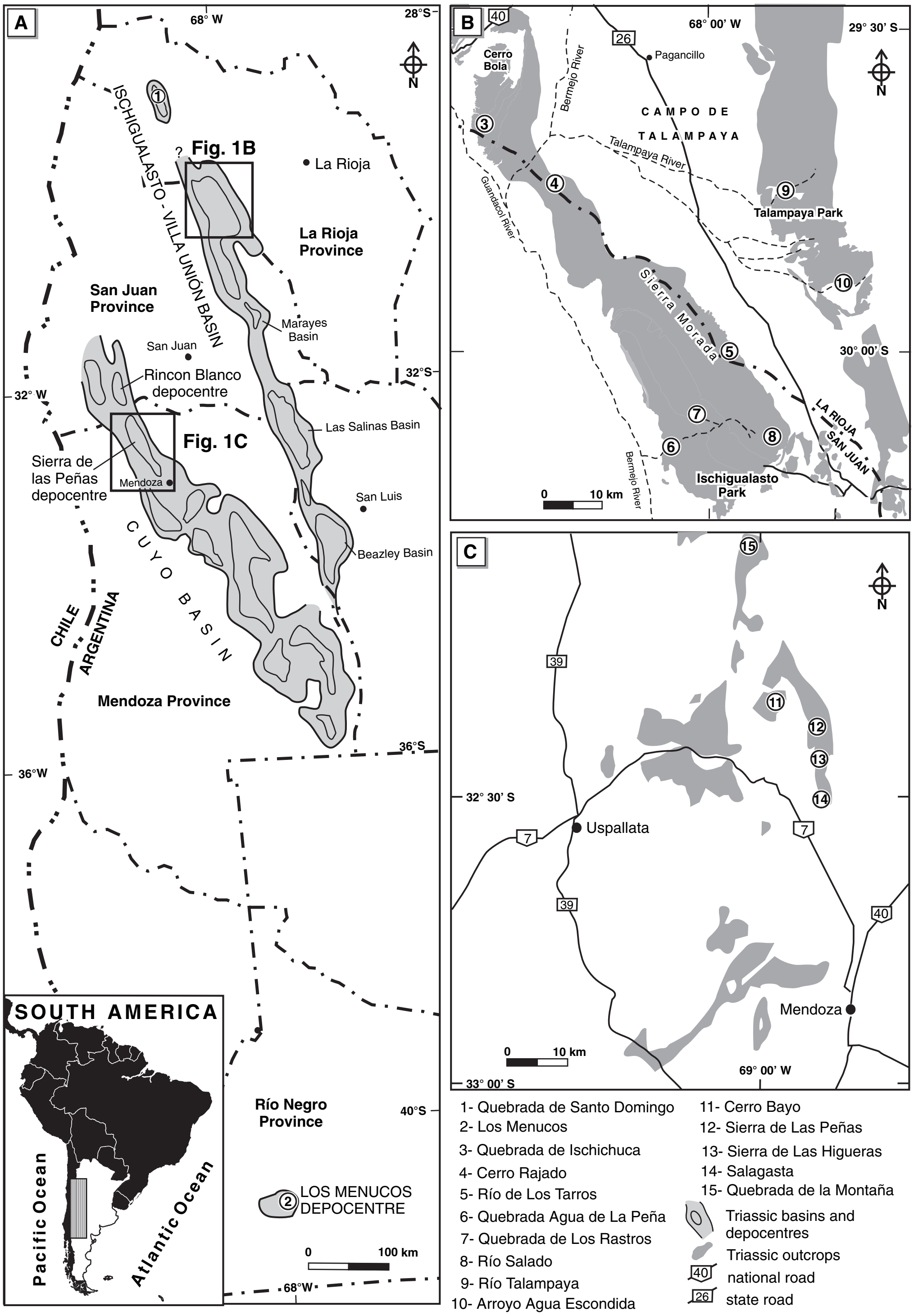
Two published track records of purported Triassic footprints from Argentina have since been reassigned to younger rocks. These are the footprints described by Lull (1942) under *Parabatrachopus argentina* Lull and *Anchisauripus australis* Lull, which actually come from the Early Cretaceous Los Jumes Formation, Sierra (mountains) de Las Quijadas, San Luis province (e.g. Yrigoyen 1975; Olsen and Padian 1986), and the supposed chirotheriid and lacertoid footprints identified by Casamiquela (in Cuerda *et al.* 1984) from the Quebrada del Jarillal Formation (Sierra de Mogna, San Juan province), which were re-interpreted as mammal footprints and the unit reassigned to the Neogene (Contreras and Gargiulo 1986). Leonardi (1989, p. 166; 1994, p. 24) made reference to some purported Triassic coelurosaurian footprints from Bajo Caracoles, north-west Santa Cruz province, Patagonia; however, the volcaniclastic succession where these tracks were collected appears to be of Jurassic age (Panza and Haller 2002).

Institutional abbreviations (all Argentina except where indicated). AC, Hitchcock Ichnology Collection, Pratt Museum of Natural History, Amherst College, Amherst, Massachusetts, USA; CICRN, Centro de Investigaciones Científicas de Río Negro, Río Negro; GHUNLPam, Universidad Nacional de La Pampa, La Pampa; INGEO, Instituto de Geología, Universidad de San Juan, San Juan; LAR-Ic, Agencia de Cultura de La Rioja, Colección de Icnología, La Rioja; LC, Geological Museum, Lafayette College, Easton, Pennsylvania, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MPEF Ic, Museo Palaeontológico 'Egidio Feruglio', Colección de Icnología, Chubut; MLP, Museo de La Plata, La Plata; MCNAM PV, Museo de Ciencias Naturales y Antropológicas 'Juan Cornelio Moyano', Palaeontología de Vertebrados, Mendoza; PVL, Instituto Miguel Lillo, Colección Palaeontología de Vertebrados, San Miguel de Tucumán.

STRATIGRAPHY AND PALAEOENVIRONMENTS

The Triassic footprint record from Argentina is restricted to three basins from the west of the country (Text-fig. 1A): the Ischigualasto-Villa Unión Basin (San Juan and La Rioja provinces, including the Santo Domingo depocentre), the northern part of the Cuyo Basin (Mendoza and San Juan provinces), and the Los Menucos depocentre (Río Negro province, Patagonia). These are part of the numerous rift basins developed on the western margin of south-west Gondwana during the Triassic Period (Uliana and Biddle 1988; Uliana *et al.* 1989; Tankard *et al.* 1995). The first two basins have a protracted history of sedimentation that spanned most of the Triassic, whereas the latter received sediments only in the Late Triassic (e.g. Spalletti 1999). The approximate palaeolatitude range for the footprint-bearing basins was estimated as 35–37° S (Ischigualasto-Villa Unión and north Cuyo Basin) and about 45° S for the Los Menucos depocentre (Prezzi *et al.* 2001). Text-figure 2 contains a summary of the stratigraphy of the Triassic track-bearing basins of Argentina along with a distribution of the main footprint taxa discussed in the text.

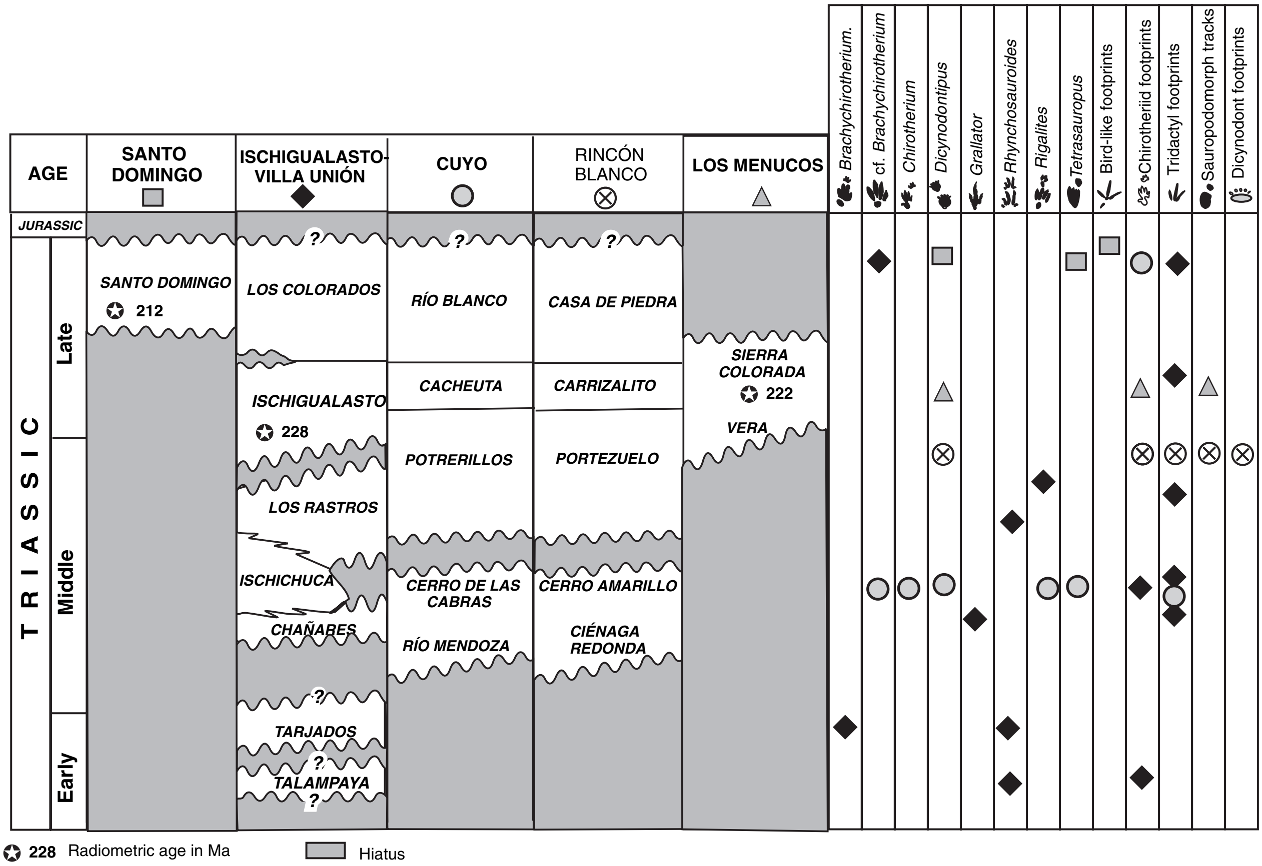
The footprint localities of the Ischigualasto-Villa Unión Basin are Quebrada (gulch) de Ischichuca, Cerro (hill) Rajado, Río (river) de los Tarros, Quebrada Agua de La Peña, Quebrada de Los Rastros and Río Salado (both in Ischigualasto Provincial Park), Río Talampaya, and Arroyo (creek) Agua Escondida (in Talampaya Park) (Text-fig. 1B, localities 3–10, respectively). Most of the stratigraphic units of the Ischigualasto-Villa Unión Basin contain tetrapod footprints. The thickness of the stratigraphic succession in different localities is variable, although it usually exceeds 2500 m (Text-fig. 3A). The track-bearing facies are, in ascending stratigraphic order: Talampaya Formation, sheet-flood and playa-lake deposits at Río Talampaya (López Gamundí *et al.* 1989); Tarjados Formation, ephemeral fluvial and loess deposits at Quebrada de Ischichuca; cross-bedded heterolithic fluvial channel deposits from the top of the unit at Arroyo Agua Escondida (where numerous footprints are exposed in cross-section); Chañares Formation, volcaniclastic shallow lacustrine deposits at Quebrada de Ischichuca; Ischichuca Formation, carbonate mudflats in a playa-lake setting at Quebrada de Ischichuca; Los Rastros Formation, upper delta plain deposits in a lacustrine delta at Quebrada de Los Rastros (Milana 1998; Melchor *et al.* 2003); Ischigualasto Formation,



TEXT-FIG. 1. Location maps. A, Triassic track-bearing basins in Argentina (inset shows general location). B, detail of main localities in the Ischigualasto-Villa Unión Basin. C, localities of the Sierra de Las Peñas depocentre of the northern Cuyo Basin. Modified from López Gamundí *et al.* (1994) and Spalletti *et al.* (1999).

high- to moderate-sinuosity fluvial deposits with abundant floodplain facies and concomitant pyroclastic sedimentation (Bellosi *et al.* 2001); Los Colorados Formation, ephemeral fluvio-lacustrine sediments at Río Salado (Melchor *et al.* 2001*b*) and Río de los Tarros (Caselli *et al.* 2001).

The Santo Domingo depocentre is provisionally considered to be an isolated half-graben that was genetically



TEXT-FIG. 2. Stratigraphical and geographical distribution of Triassic footprints in Argentina. Lithostratigraphical and chronostratigraphical framework modified from Spalletti *et al.* (1999), Marsicano and Barredo (2004) and Melchor *et al.* (unpublished); radiometric ages from Rogers *et al.* (1993), Rapela *et al.* (1996) and Coughlin (2001). Correlation of units from the Cuyo Basin follows the proposal of Stipanicic and Marsicano (2002).

linked to the Ischigualasto-Villa Unión Basin. This depocentre received more than 1800 m of sediments during Late Triassic times (Text-fig. 3B), which are recognized as the Santo Domingo Formation (Caminos and Fauqué 2001). The footprint locality at this depocentre is the Quebrada de Santo Domingo (Text-fig. 1A, locality 1), where it is exposed in the upper part of the formation. The Santo Domingo Formation is considered to be of Late Triassic age, as suggested by the presence of the Middle–Late Triassic Gondwana wood morphogenus *Rhexoxylon* (Caminos *et al.* 1995) and a $^{40}Ar/^{39}Ar$ step-heating analysis on albite from interbedded basalt flows, which yielded a plateau age of 212·5 ± 7·0 Ma (Coughlin 2001). Current work on the Santo Domingo Formation is aimed at refining the age of the footprint-bearing horizon by both geochronological and magnetostratigraphic methods. The results of these studies will be presented elsewhere; they are beyond the scope of this paper.

The Cuyo Basin has yielded Triassic footprints in two areas: the Sierra de Las Peñas (Mendoza province) and Rincón Blanco (San Juan province) depocentres (Text-fig. 1A). The footprint record from the first of these is plentiful, including the renowned Cerro Bayo, Sierra de Las Higueras, Sierra de Las Peñas, Salagasta and Quebrada de la Montaña occurrences. The material discussed herein (preliminarily described by Melchor *et al.* 2001*a*) comes from the first three localities (Text-fig. 1C, localities 11–13, respectively), which are in the Cerro de Las Cabras Formation. The succession exposed at Sierra de Las Peñas is composed of the two lower units of the Cuyo Basin (Text-fig. 3C). In particular, the Cerro de Las Cabras Formation was interpreted as the product of deposition in proximal to distal parts of shallow ephemeral lakes and mudflats sourced by sandy sheet-floods from the nearby highlands located to the west (Melchor *et al.* 2001*a*). The age of the Cerro de Las Cabras Formation was estimated by different authors to range between early Middle Triassic and late Middle Triassic (or possibly earliest Late Triassic), as discussed by Stipanicic and Marsicano (2002). Probable labyrinthodont footprints at the Salagasta locality were cited by Rusconi (1951), and Romer (1966) mentioned the presence of poorly preserved trackways at the Quebrada de la Montaña locality (Text-fig. 1C, localities 14 and 15, respectively).

The ichnofauna from the Rincón Blanco depocentre was recently described by Marsicano and Barredo (2004), although an ichnotaxonomic treatment is pending. The reported track occurrences include unspecified tetrapod footprints from the Middle Triassic Cerro Amarillo Formation (Barredo and Tunik 2000), and a moderately to poorly preserved and diverse ichnofauna from the overlying Late Triassic Portezuelo Formation (Barredo *et al.* 1999; Marsicano and Barredo 2000, 2004). The sedimentary filling of the depocentre is entirely siliciclastic and reaches *c.* 2300 m (Text-fig. 3E). Marsicano and Barredo (2004) determined that the ichnofauna of the Portezuelo Formation comprises large footprints and trackways attributed to basal sauropodomorphs (Type FB and Type B1 tracks), tridactyl tracks of possible theropods (Type B2 tracks), isolated chirotheriid tracks, and quadrupedal tracks assigned to small cynodonts (Type Q1 tracks) and large dicynodonts (Type Q2 tracks). The track-bearing horizons of the Portezuelo Formation have been interpreted as representing shallow lacustrine and ephemeral fluvial settings (Marsicano and Barredo 2004). The probable age of the Portezuelo Formation is early Late Triassic as constrained by regional stratigraphic correlations of the underlying Panul Formation and by the palynological and macrofloral content of the overlying Carrizalito and Casa de Piedra formations (Marsicano and Barredo 2004).

The Los Menucos depocentre (Text-fig. 1A, locality 2) is a restricted area of Triassic volcaniclastic sedimentation in northern Patagonia that has yielded abundant footprints and trackways that were extensively described by Casamiquela (1964, 1975, 1984). The volcaniclastic succession is *c.* 400 m thick and includes the Vera and Sierra Colorada formations (Text-fig. 3D). The material comes from flagstone quarries in the Vera Formation (defined by Labudía and Bjerg 2001) located near the town of Los Menucos. A Rb/Sr isochron for volcaniclastic rocks of this formation (Rapela *et al.* 1996) indicates that the age of the unit is 222 ± 2 Ma (Carnian). The depositional environment was characterized as comprising incipient fluvial systems associated with playa lakes (Kokogián *et al.* 1999).

SYSTEMATIC PALAEONTOLOGY

This section contains the identified ichnotaxa in alphabetical order, followed by forms that are left in open nomenclature. Material of uncertain assignation is also referred to under a separate heading.

BRACHYCHIROTHERIUM (Beurlen, 1950)

Type ichnospecies. Brachychirotherium hassfurtense Beurlen, 1950.

Diagnosis. Quadrupedal chirotheriids with plantigrade to semidigitigrade pes and manus posture. Roundish to oval pentadactyl pes impression with broad sole surface, pedal digit group I–IV almost as broad as long and showing a divarication angle of over 40 degrees, relatively short and blunt, moderately spread digits with strong, roundish pads and narrow claws, digits III and II longest, digit IV always preserved. Phalangeal segment of pedal digit V not separated or only moderately distinct from metatarsal-phalangeal pad, mostly oblique, anteriorly orientated and never turned backward. Compared with the pes, the pentadactyl manus impression is smaller, digit-group I–IV usually broader than long, otherwise like pes impression, although not documented in detail (translated from Karl and Haubold 1998, p. 41).

Brachychirotherium isp.
Text-figure 4A

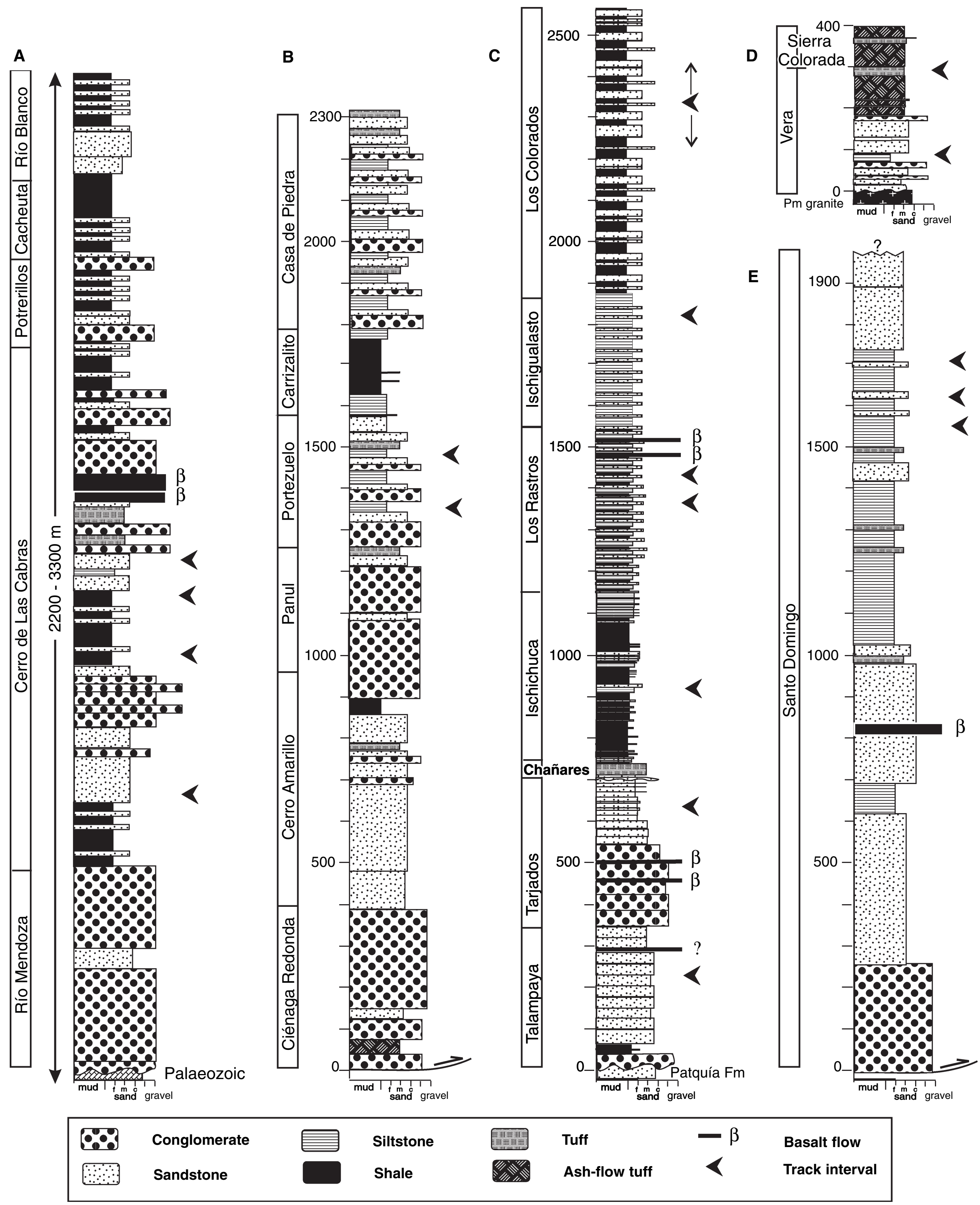
1999 *Brachychirotherium* isp.; Zavattieri and Melchor, p. 37, fig. 2.
2001*a* *Brachychirotherium* isp.; Melchor *et al.*, pp. 188, 192.

Referred material. LAR-Ic 2 and 3.

Occurrence. Quebrada de Ischichuca, La Rioja province. Tarjados Formation (Early Triassic).

Description. The described specimens include one complete (LAR-Ic 2) and one incomplete (LAR-Ic 3) manus-pes set with typical chirotheriid morphology. The tracks are semiplantigrade, the pes is tetradactyl and the manus is pentadactyl. Digit impressions are broad and relatively short. In the pes, the impression of digit III is the longest followed by those of digits II, IV and I. Digit V is indistinguishable from the metatarsal impression, which is oblique in relation to the digit III impression. Claw marks were observed in digits I, II and probably in digit III. The pes is 137 mm long and 84 mm wide. The impressions of hand digits are broad and shorter than those of the pes; manus digits II and III are subequal in length, with IV and I successively shorter. Digit V is separated from the rest of the digits and laterally directed. The hand ranges from 53 to 58 mm long and 58 to 63 mm wide.

Remarks. These footprints are assigned to *Brachychirotherium* on the basis of their overall chirotheriid morphology, the presence of robust and wide digit impressions on the foot which join in a continuous sole, and the impression of digit V indistinguishable from a broad oblique metatarsal mark (Karl and Haubold 1998). In a recent review of the ichnogenus, including study of the original material described by Beurlen (1950), Karl and Haubold (1998) recognized only four valid ichnospecies: *B. hassfurtense* Beurlen, 1950, *B. thuringiacum* (Lilienstern, 1938),



TEXT-FIG. 3. Generalized lithological logs for the Triassic basins of Argentina with records of tetrapod footprints. A, succession in the Cuyo Basin after Bellosi *et al.* (2001). The section exposed at Sierra de Las Peñas includes only the two lower units. B, summary log for the Rincón Blanco depocentre (Marsicano and Barredo 2004). C, composite log for the Ischigualasto-Villa Unión Basin after Milana (1998), Kokogián *et al.* (1999), Caselli *et al.* (2001) and Melchor (2004). D, volcaniclastic filling of the Los Menucos depocentre (Labudía and Bjerg 2001). E, log for the Santo Domingo depocentre (E. Bellosi and RNM, unpublished data, 2004).

B. parvum (Baird, 1957) and *B. eyermani* (Hitchcock, 1889). The specimens described appear to be comparable with *B. parvum* (Baird, 1957). *Brachychirotherium* is attributed to Crurotarsi *sensu lato* (Karl and Haubold 1998), although Lockley and Hunt (1995) assigned them to Aetosauria and Olsen *et al.* (2002) to Rauisuchia, both groups belonging to Crurotarsi. The pes impression in LRA-Ic 2 is overprinted by a small lacertoid footprint ascribed to *Rhynchosauroides* (Text-figs 4A, 6B).

cf. *Brachychirotherium* isp.
Text-figure 4B–C, E

v1990 Chirotherian footprints; Leonardi and de Oliveira, p. 220, pl. 1, figs O, Q–R.
v?1994 Temnospondyli pes; Leonardi, p. 21.
v1994 *Chirotherium* isp.; Leonardi, pp. 24–25, pl. 2, figs 5–6.
v1994 Chirotheroid Leonardi, pp. 24–25, pl. 2, fig. 4.

Referred material. PVL 3441, 3448 and 3452 (from Río de Los Tarros), MCNAM PV-2952, and GHUNLPam 12492 (from Sierra de Las Higueras).

Occurrence. Río de Los Tarros, Talampaya Park, La Rioja province and Sierra de Las Higueras, Mendoza province; Los Colorados Formation (Late Triassic) and Cerro de Las Cabras Formation (Middle Triassic), respectively.

Description. This account is based on the best preserved material from the Río de Los Tarros locality (Text-fig. 4B). The tetradactyl and digitigrade pes imprints show low divarication between I and IV (*c.* 44 degrees). The pes length is 58 mm, and width is 44 mm (PVL 3448). The digits are short, robust, subequal in length and display marked subtriangular claw marks. The two central digits (III, 27 mm; II, 26 mm) and the two outer digits (I, 22 mm; IV, 20 mm) are subequal in length. Digit V is indistinguishable from the metatarsal impression. A probable shallow manus impression is present in PVL 3452 (Text-fig. 4C).

Remarks. This material is provisionally assigned to *Brachychirotherium* based on overall morphology, the relatively spread digits I–IV, the presence of an impression of digit V that is indistinguishable from the metatarsal impression, and possible quadrupedal tracks. These specimens are also similar to some of the ichnospecies of *Pseudotetrasauropus* Ellenberger, 1972. However, the material included by Ellenberger (1972) within *Pseudotetrasauropus* shows a large amount of morphological variability that warrants its assignation to more than one ichnogenus (Rainforth 2003; Nicosia and Loi 2003). The current usage of *Pseudotetrasauropus* is confusing and a revision is clearly needed (H. Haubold, pers. comm. 2001; Nicosia and Loi 2003), including re-study of the original material of Ellenberger (1972). An examination of the original description and drawings by Ellenberger (1972) suggest that some of the ichnospecies are comparable with *Tetrasauropus* Ellenberger, 1972. Lockley and co-workers (Lockley and Hunt 1995; Lockley *et al.* 1996; Lucas *et al.* 2001) have considered the slender forms under *Pseudotetrasauropus*, and the robust, massive forms under *Tetrasauropus*.

The specimen from Sierra de Las Higueras (MCNAM PV-2952 and GHUNLPam 12492, a plaster replica) is provisionally referred to this ichnogenus (Text-fig. 4E).

CHIROTHERIUM Kaup, 1835

Type ichnospecies. *Chirotherium barthii* Kaup, 1835.

Referred ichnospecies. *Chirotherium barthii* Kaup, 1835.

Diagnosis. Pedal digit III longest, digit IV longer than II, shorter in large ichnospecies, pes digit V slightly laterally behind digit group I–IV; palmar/plantar surface ratio in completely preserved footprints 1:2–1:3·5. Pace angulation usually 160–170 degress (Haubold 1971, p. 55).

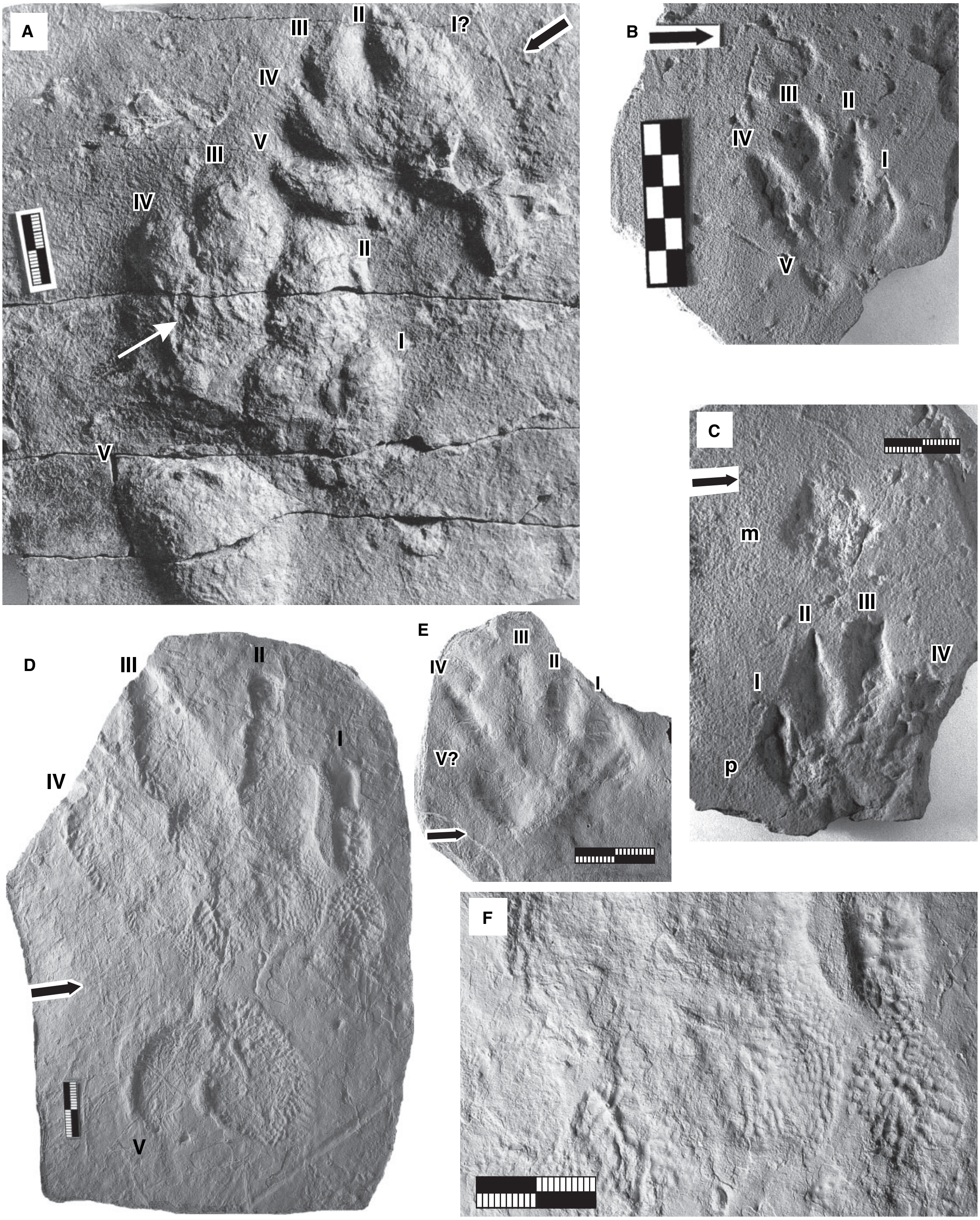
Chirotherium barthii Kaup, 1835
Text-figure 4D, F

v1951 *Chirotherium higuerensis* Rusconi, pp. 3–14, figs 1–2.
1955 *Chirotherium barthii*; Peabody, pp. 239–240 (= *Chirotherium higuerensis* Rusconi).
1957 *Chirotherium barthii*; Baird, pp. 501–502.
1964 *Chirotherium higuerensis*; Casamiquela, pp. 44–45.
1966 *Chirotherium barthii*; Bonaparte, p. 22.
1966 *Chirotherium higuerensis*; Bonaparte, pp. 28–29.
1967 *Chirotherium higuerensis*; Rusconi, pp. 234–236, pl. 33.
1971 *Chirotherium barthii*; Haubold, p. 55.
1990 '*Chirotherium higuerense*' Leonardi and de Oliveira, p. 217, pl. 1, fig. U (*lapsus calami*).
1990 '*Chirotherium bartill*' Kaup 1835; Leonardi and de Oliveira, p. 221 (*lapsus calami*).
1994 *Chirotherium barthii*; Leonardi, p. 21, pl. 2, fig. 1.

Referred material. MCNAM PV 2951 and GHUNLPam 12491 (plaster replica).

Occurrence. 2 km east of Puesto (settlement) Las Higueras (32°29′30″S, 68°53′30″W), Sierra de Las Higueras, north-east Mendoza province; Cerro de Las Cabras Formation (Middle Triassic).

Diagnosis. Trackways of large chirotheriid with narrow pattern, pace angulation 170 degrees, but with relatively



TEXT-FIG. 4. A, *Brachychirotherium* isp. (LAR-Ic 2), convex hyporelief. The white arrow indicates an overprinted *Rhynchosauroides* track (see Text-fig. 6B). B, cf. *Brachychirotherium* isp. (PVL 3448), concave epirelief. C, manus-pes couple of cf. *Brachychirotherium* isp. (PVL 3452), concave epirelief. D, *Chirotherium barthii* (GHUNLPam 12491, replica of MCNAM PV 2951), concave epirelief. E, footprint comparable with *Brachychirotherium* (GHUNLPam 12492, plaster replica of MCNAM PV 2952), concave epirelief. F, detail of skin impressions on the right side of the specimen pictured in D. Scale bars represent 20 mm in A and C–F, and 50 mm in B. Black arrows indicate direction of light. I–V, digits I–V; m, manus; p, pes.

short stride, ratio of stride to pes length 5:1, manus turned out more than pes; pes digit group I–IV relatively long, not short and broad as in other large chirotheriids; pes shows moderate development of specialized pads which are more or less localized under individual digital joints, large circular pad covers the base of digits II and III; digit IV shorter than III and equal to II in length; digit V with large rounded pad centering about the position of the metatarsal-phalangeal joint; maximum pes length below 25 cm; claws triangular in outline; pes digit V sometimes elongated posteriorly by broad metatarsal ridge (Peabody 1948, p. 364).

Description. An almost complete left hindprint mould, 185 mm long and 114 mm wide, displaying skin impressions on all metatarsal-phalangeal pads and on the second phalangeal pad of digits I and V (Text-fig. 4D). All measurements on this specimen follow the conventions of Peabody (1948). The digit length proportions are III > II > IV > V > I (113, 98, 90, 78 and 64 mm). Claw marks are triangular in digit I, rounded in digit II, while the rest of the digits cannot be observed. The impression of digit V is broad and posterolaterally recurved. The impression of digit I is slender, those of II, III and IV are wider than I, although in the case of digit II this may be due to extramorphological enlargement. Three pad impressions were recorded in digit I, while digits II, III and IV display four pad impressions. The angle of divarication between I and IV is 33 degrees. Skin impressions consist of patches of rounded to square or pentagonal scale marks, which range from *c.* 1·3 to 2·6 mm in diameter. Some apparently elongated and large scale impressions may not reflect the true skin morphology (Text-fig. 4F).

Remarks. We accept the assignment of this specimen to *Chirotherium barthii*, proposed by Peabody (1955) and also agreed upon by Haubold (1971) and Leonardi (1994). The footprint presents the general morphology of *C. barthii* and also displays features that were considered typical of the ichnogenus by Peabody (1948), namely: relatively long digit impressions, good development of digital pad impressions, similar relationship of digit length and presence of skin impressions. As the only available material is an isolated pes imprint, it is not possible to evaluate the trackway parameters that are considered to be diagnostic of the ichnogenus (Peabody 1948; Haubold 1971). An associated footprint (MCNAM PV-2952) found 0·5 m from MCNAM PV-2951, was considered to be its handprint by Rusconi (1951). However, Peabody (1955) claimed that this print looks more amphibian than reptilian, and that it is too small to be associated with the chirotheriid pes. Leonardi (1994) regarded this isolated impression as having been made by a temnospondyl. This footprint is tentatively considered here to be comparable with *Brachychirotherium* (Beurlen 1950).

DICYNODONTIPUS von Lilienstern, 1944

1876 *Chirotherium* Hornstein, p. 923.
1944 *Dicynodontipus* von Lilienstern, pp. 368–385, pls 22–23.
v*1964 *Calibarichnus* Casamiquela, pp. 145–147, pl. 17, fig. 2 (syn. nov.).
v*1964 *Palaciosichnus* Casamiquela, pp. 150–154, pl. 18 (syn. nov.).
v*.1964 *Gallegosichnus* Casamiquela, pp. 154–157, pls 15, fig. 1, 16, fig. 2, 19, fig. 1/2 (syn. nov.).
1969 *Dicynodontipus*; Haubold, p. 840.
1971 *Dicynodontipus*; Haubold, pp. 41–42, figs 26.1–6 (= *Chirotherium* Hornstein).
1971 *Calibarichnus*; Haubold, pp. 42–43, fig. 26.10.
1971 *Gallegosichnus*; Haubold, p. 43, fig. 26.8.
1971 *Palaciosichnus*; Haubold, p. 43, fig. 26.9.
1972 *Dicynodontipus*; Demathieu and Haubold, pp. 804, 808, 810–811, 815.
1972 *Calibarichnus*; Ellenberger, pl. 10, fig. 97.
1975 *Calibarichnus*; Casamiquela, pp. 563–564, pl. 4, fig. 2.
1975 *Gallegosichnus*; Casamiquela, pp. 565–566, pls 1, fig. 2; pl. 2, fig. 3.
1975 *Palaciosichnus*; Casamiquela, pp. 566–569, pl. 5.
v*.1975 *Stipanicichnus* Casamiquela, pp. 569–571, pl. 6 (syn. nov.).
v1975 *Dicynodontipus*; Conti *et al.*, p. 141, fig. 10.
1975 *Calibarichnus*; Ellenberger, p. 422, pl. 2, fig. 97.
1975 *Dicynodontipus*; Sarjeant, p. 294, fig. 14·11C.
v1977 *Dicynodontipus*; Conti *et al.*, pp. 50–52, figs 31–32, pl. 9, figs 2–4.
1984 *Dicynodontipus*; Haubold; pp. 139–141, 202; figs 91.2, 92; table 13.
1990 *Dicynodontipus* Leonardi and de Oliveira, p. 220, pls 2, fig. B, 6 fig. D.
1990 *Gallegosichnus*; Leonardi and de Oliveira, p. 224, pls 2, fig. A, 8, figs A–E.
1990 *Calibarichnus*; Leonardi and de Oliveira, p. 223, pls 2, fig. C, 6, fig. F.
1990 *Palaciosichnus*; Leonardi and de Oliveira, p. 224, pls 2, fig. G, 7, fig. C.
1990 Therapsid footprints; Leonardi and de Oliveira, pl. 2, fig. B–K.
1990 Theromorphoid footprints; Leonardi and de Oliveira, pl. 6.E.
1994 *Calibarichnus*; Leonardi, p. 23, pls 3, fig. 4, 16, fig. 4.
1994 *Palaciosichnus*; Leonardi, p. 23, pls 3, fig. 6, 16, fig. 9.
1994 *Gallegosichnus*; Leonardi, p. 23, pls 2·11, 3·1, 3·3, 16·1–3, 16·8.
1994 *Dicynodontipus*; Leonardi, p. 23.
1994 *Stipanicichnus*; Leonardi, p. 24, pl. 3, fig. 8.
?1996 *Dicynodontipus*; Retallack, pp. 311–312, figs 2–4, tables 1–3.
2000 *Dicynodontipus*; Lockley and Meyer, p. 64, fig. 3.11.
?2000 *Dicynodontipus*; Conti *et al.*; pp. 305–306, 308; figs 11.11-d, 11.18.
2000 *Gallegosichnus*; Sarjeant, p. 155, fig. 1.

2000 *Palaciosichnus*; Sarjeant, pp. 155–156, fig. 3.
2000 *Calibarichnus*; Sarjeant, p. 156, fig. 4.
2000 *Stipanicichnus*; Sarjeant, p. 156, fig. 5.
?2001 *Dicynodontipus*; Avanzini *et al.*, p. 97, fig. 4.
2001b *Dicynodontipus*; Melchor *et al.*, p. 58.
2004 Type Q1 tracks; Marsicano and Barredo, p. 322, fig. 7, table 3.

Type ichnospecies. *Dicynodontipus* geinitzi (Hornstein, 1876).

Revised diagnosis. Relatively narrow trackways, pace angulation at normal gait at least 100 degrees, at higher pace angulation manus impressions can be extensively overstepped, only at lower pace angulation manus impressions are positioned at short, distance anterior to the feet. Manus and pes showing the same shape, plantigrade, pentadactyl; short, anteriorly orientated digits, digit IV the longest, digit V slightly laterally and posteriorly shifted (modified from Haubold 1971, p. 41).

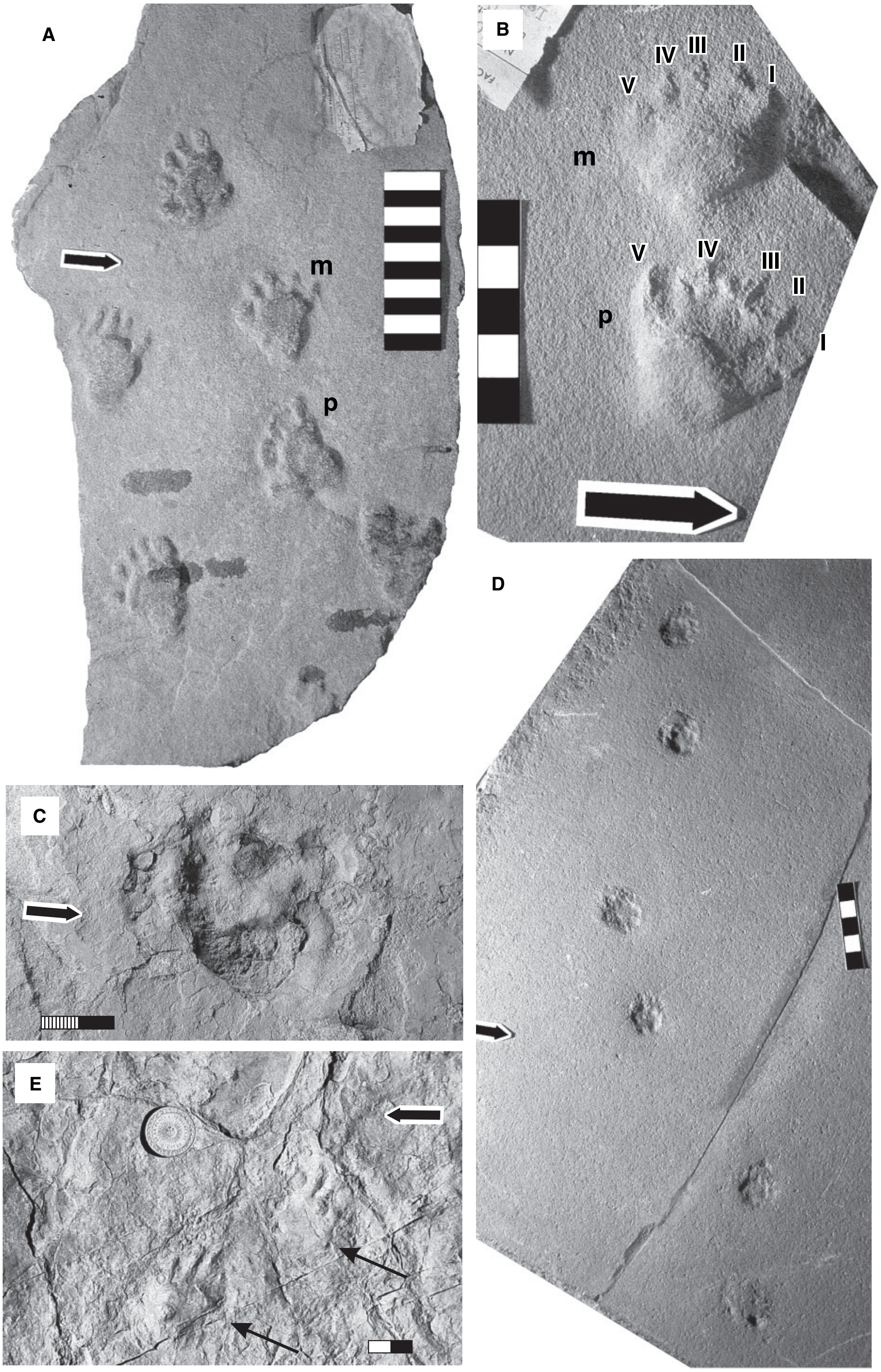
Remarks. The specimens from the Vera Formation were described and named by Casamiquela (1964, 1975) as belonging to four different ichnogenera and ichnospecies as follows: *Calibarichnus ayestarani* Casamiquela, 1964 (MLP 60-XI-31-4, Text-fig. 5B), *Gallegosichnus garridoi* Casamiquela, 1964 (MLP 60-XI-31-7, Text-fig. 5A; MLP 60-XI-15-3; 93-XII-13-1–13-3; 60-XI-31-9), *Palaciosichnus zettii* Casamiquela, 1964 (MLP 60-XI-31-6, Text-fig. 5D), and *Stipanicichnus bonetti* Casamiquela, 1975 (CICRN 1-X-72-3). The type material of the last of these could not be found at the published repository; for this reason we have used for comparison the description and photograph by Casamiquela (1975). Most of these monospecific ichnogenera were erected on the basis of a single specimen and distinguished only by subtle morphological differences. It is considered here that all the specimens mentioned herein can be referred to the common Triassic *Dicynodontipus* Lilienstern, 1944. The referred material displays the general morphology of that ichnogenus, namely: plantigrade and pentadactyl manus and pes of similar size, showing short, forward-pointing digits; digit IV is the longest; digit V is sometimes laterally separated from the rest of the footprint. Haubold (1971) questioned the validity of the ichnotaxa of Casamiquela (1964), remarking that subtle variations in 'theromorphoid' tracks are common and of little ichnotaxonomic value. Leonardi (1994) and Sarjeant (2000) also expressed their doubts about the ichnotaxonomic assignation of the Triassic 'theromorphoid' material described by Casamiquela (1964). Leonardi (1994) considered *Palaciosichnus* to be morphologically close to *Dicynodontipus* and cannot be retained. He also compared part of the material from the Sierra de Las Higueras (PVL 2737, 2738) with *Dicynodontipus*. The material herein described differs from *Therapsipus* Hunt *et al.*, 1993 on account of its smaller size, higher pace angulation and absence of a concave posterior margin, which is distinctive of that ichnogenus. The material assigned to *Dicynodontipus* by Retallack (1996) displays many features that differ from it, namely: wide trackway and relatively small pace angulation, fairly long digits and large digit divarication. In addition, the preservation of the tracks suggests that they are deep undertracks with extramorphological enlargement of digit imprints. For these reasons the ichnogeneric assignation of these tracks is in need of revision. The occurrence of *Dicynodontipus* in the Late Permian Val Gardena Sandstone (Conti *et al.* 1975, 1977, 2000; Avanzini *et al.* 2001) has been questioned (e.g. Haubold 2000), although we consider them to be morphologically comparable. These tracks are morphologically akin to *Dicynodontipus* but display a considerable size difference between manus and pes. *Dicynodontipus* has been recorded only from Europe and South America, although some of the Triassic–Jurassic ichnogenera from South Africa erected by Ellenberger (1972, 1974) may be comparable (e.g. *Eopentapodiscus* Ellenberger, 1974).

Dicynodontipus ispp.
Text-figure 5A–E

Referred material. MLP 60-XI-31-4, 60-XI-31-6, 60-XI-31-7, 60-XI-31-9, 60-XI-15-3, 93-XII-13-1–93-XII-13-3 and CICRN 1-X-72-3 (from Los Menucos); PVL 2730, 2737, 2738 (two slabs with the same number), 2740 and 2741 (from Sierra de Las Higueras); MCNAM PV-3574 (from Sierra de Las Peñas); MCNAM PV -3575 (from Cerro Bayo); and LAR-Ic 1 (from Quebrada de Santo Domingo).

Occurrence. Los Menucos in Río Negro province, Sierra de Las Higueras (2 km east of Puesto Las Higueras, 32°29′30″S, 68°53′30″W), Sierra de Las Peñas (near Puesto Las Peñas, 32°27′03″S, 68°53′25″W) and Cerro Bayo (unnamed quarry, 32°24′07″S, 68°57′12″W) in Mendoza province; Rincón Blanco creek (31°29′S, 69°16′W) in San Juan province: and Quebrada de Santo Domingo (28°31′S, 68°44′W), north-west La Rioja province. These localities belong to the Vera Formation (Carnian) in Río Negro province, Cerro de Las Cabras Formation (Middle Triassic) in Mendoza province, Portezuelo Formation (?Carnian) in San Juan province, and Santo Domingo Formation (Late Triassic) in La Rioja province, respectively.

Description. The referred material consists of isolated footprints, manus-pes sets and trackways, which show a similar overall morphology. Both pes and manus are pentadactyl with a broad, subcircular to subtriangular sole and short digit impressions that commonly lack claw marks (Text-fig. 5A–E). The pes is slightly larger than the manus. Footprint size commonly varies between 36 and 55 mm long and 35 and 43 mm wide, although two specimens (MLP 60-XI-31-6 and CICRN 1-X-72-3; Text-fig. 5D) are about half that size (25–27 mm long and 21–24 mm wide).



TEXT-FIG. 5. *Dicynodontipus* ispp. A, MLP 60-XI-31-7, holotype of *Gallegosichnus garridoi* Casamiquela, 1964, convex hyporelief. Note paint spots on the lower part of the slab. B, MLP 60-XI-31-4, holotype of *Calibarichnus ayestarani* Casamiquela, 1964, convex hyporelief. C, LAR Ic-1. D, MLP 60-XI-31-6, holotype of *Palaciosichnus zettii* Casamiquela, 1964, concave epirelief. E, field photograph of specimen MCNAM PV 3574 (two small footprints arrowed), concave epirelief. Scale divisions represent 10 mm. Black arrows indicate direction of light. I–V, digits I–V; m, manus; p, pes.

The tracks from the Cerro de Las Cabras Formation are poorly preserved, isolated footprints or manus-pes sets and seem to have a slightly different morphology, which could be related to contrasting taphonomic conditions (Text-fig. 5E). The footprints are *c.* 40 mm long and of similar width. Digit impressions are slender and longer than in the remaining material of the ichnogenus, the order of length from longest to shortest being IV, III, II, V and I. The sole is subcircular to oval. The footprints described as 'Type Q1 tracks' by Marsicano and Barredo (2004) are considered morphologically similar to those of the Cerro de Las Cabras Formation.

Specimens from the Vera Formation are better preserved and also include isolated trackways (Text-fig. 5A–B). The trackways display moderately high pace angulation, ranging from 95 to 150 degrees. Digit impressions are subequal in length, relatively shorter, broader and display a more triangular sole than those from the Cerro de Las Cabras Formation. The single footprint described from the Santo Domingo Formation (Text-fig. 5C) is more similar to those of the Vera Formation than the Cerro de las Cabras Formation.

Remarks. The morphological differences outlined will probably warrant recognition of more than one ichnospecies of *Dicynodontipus* from the Triassic of Argentina. For example, the specimens MLP 60-XI-31-6 (Text-fig. 5D) and CICRN 1-X-72-3 (formerly named as *Palaciosichnus* and *Stipanicichnus*, respectively) share similar trackway parameters and are smaller than the rest of the specimens. The remaining material from the Vera Formation is fairly abundant and well preserved, which ensures a detailed redescription and ichnotaxonomic treatment.

GRALLATOR (Hitchcock, 1858)

Type ichnospecies. Grallator parallelus (Hitchcock, 1858).

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

Grallator isp.
Text-figure 6A

v2001*a* *Grallator* isp. Melchor *et al.*, pp. 188, 192.

Referred material. MPEF Ic 223, a plaster cast of one uncollected isolated footprint.

Occurrence. Quebrada de Ischichuca, La Rioja province; Chañares Formation (Middle Triassic).

Description. Measurements of this track follow the conventions of Olsen *et al.* (1998). It is a single, nearly symmetrical, well-preserved tridactyl footprint. The total length:width ratio is 1·85 (length 87 mm, width 47 mm) and the length of the phalangeal part of the foot (parameter T of Olsen *et al.* 1998) is 80·5 mm. Digit impressions are of similar width, although digit III appears more robust and bears distinct claw marks. Pad impressions are clear, especially in digit III. Relative digit lengths are IV > III > II (59, 44 and 29 mm). The projection ratio of digit III (P of Olsen *et al.* 1998) is 1·6, while the length of the rear of the phalangeal part of the foot is 48 mm (R of Olsen *et al.* 1998). The impression of digit IV projects slightly further than that of digit II. The divarication between digits II and IV is 35 degrees.

Remarks. This footprint is assigned to *Grallator* (Hitchcock, 1858) on the basis of its small size, relatively large length:width ratio, low total digit divarication and moderate projection of digit III (Olsen *et al.* 1998). This track can also be compared with *Atreipus* Olsen and Baird, 1986. The main differences is the absence of associated manus impression (although no trackway was found) and the clear distinction of phalangeal pads in digit III, which are usually coalesced in *Atreipus* pes impressions (Olsen and Baird 1986). Leonardi (1989) mentioned the finding of a small 'coelurosaur' footprint by Bonaparte in 1981 at the same locality. It is not clear if this finding is related to the footprint described here or to some of the fairly common tridactyl footprints that are found in the overlying Ischichuca Formation at this locality (see tridactyl footprints, below).

RHYNCHOSAUROIDES Maidwell, 1911

Type ichnospecies. Rhynchosauroides rectipes Maidwell, 1911.

Revised diagnosis. Pentadactyl heteropod footprints, pes often tridactyl and digitigrade. Relationship of digit lengths: IV > III > II. Digits slender and slightly curved. Manus smaller than pes and semiplantigrade, plantigrade or digitigrade. Pes pace angulation 110 degrees (modified from Demathieu 1970, 1985).

Rhynchosauroides isp.
Text-figure 6B–D

v2001*a* ?*Rhynchosauroides* isp.; Melchor *et al.*, pp. 188, 192.
v2003 *Rhynchosauroides* isp.; Melchor *et al.*, fig. 7.

Referred material. INGEO-PV 041 and 040 (from Ischigualasto Park), LAR-Ic 4 (from Quebrada de Ischichuca), and one uncollected trackway (from Talampaya Park).

Occurrence. Ischigualasto Provincial Park, San Juan province, and Quebrada de Ischichuca and Talampaya Park, La Rioja province. These localities belong to the Los Rastros Formation (Middle Triassic), Ischichuca Formation (Middle Triassic) and Talampaya Formation (Early Triassic), respectively.

Description. The material from Los Rastros Formation is a short trackway (Text-fig. 6D) preserved as natural casts and composed of three manus-pes sets. It was described in detail by Melchor *et al.* (2003) and partially collected: INGEO-PV 041 is the third manus-pes set and INGEO-PV 040 is a plaster cast of the second set. The manus and pes are tridactyl with curved digit impressions. The manus lies on the midline and is always arranged behind and towards the midline in relation with the pes. The pace angulation is high (pes 124 degrees, manus 175 degrees). Imprints of pes digits display increasing length from II to IV; the pes oversteps the manus and is less marked than the manus impression. The hind print wider than long, with a total divarication of 11 degrees.

LAR-Ic 4 is an isolated pes imprint of lacertoid morphology (Text-fig. 6B), which overprints a larger *Brachychirotherium* pes track (LAR-Ic 2, Text-fig. 4A). It is 21 mm long and 22 mm wide and displays four curved digit impressions of increasing length from 6 to 13 mm.

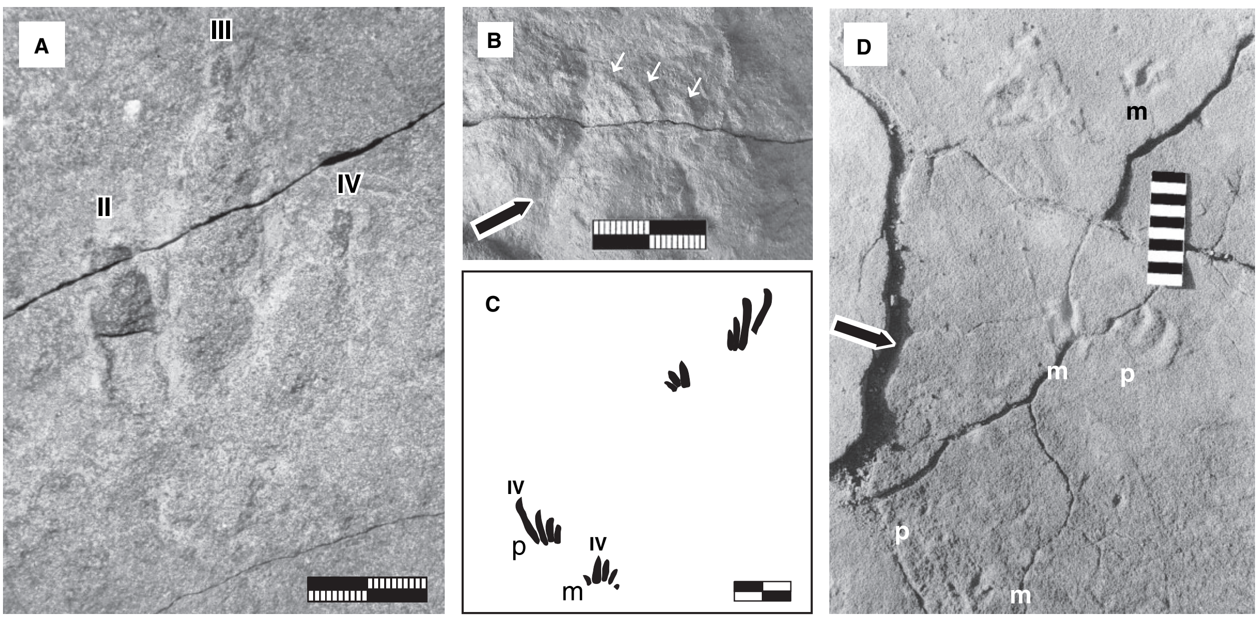
The trackway from Talampaya Park was found on the bottom of a wave-rippled sandstone bed in the tourist trail of the park ('Los Cajones' stop) and remains uncollected. It is composed of two consecutive manus-pes couples (Text-fig. 6C) preserved as positive hyporelief. The pes impression appears tetradactyl and the manus is pentadactyl; both are digitigrade. The footprints, especially the pes print, show a marked increase in the length of the digits from I to IV. The pes impression oversteps that of the manus and is rotated outward (*c.* 15–20 degrees). The manus is placed closer to the midline and appears not to be rotated or has a slight inward rotation. The pes impression is 20 mm long and 11 mm wide and the manus impression is 10 mm long and 11 mm wide.

Remarks. The overall morphology and the rest of the features described suggest the referral of these tracks to *Rhynchosauroides* Maidwell, 1911, although they are not well preserved. This track morphology had been attributed to the Sphenodontidae (Baird 1957) or the Prolacertidae (Avanzini and Renesto 2002; Diedrich 2002). The specimens described here are the first record of *Rhynchosauroides* from South America (Leonardi 1994).

RIGALITES von Huene, 1931

Type ichnospecies. Rigalites ischigualastianus von Huene, 1931.

Diagnosis. Quadrupedal trackway, stride length:pes length ratio 6:1–8:1, manus partially and proximally overstepped by the pes, pace angulation over 160 degrees. Pes tetradactyl, functionally tridactyl, digit I reduced, digit III longest, base of digits I–IV plantigrade. Manus smaller than pes, pentadactyl, sometimes lacking digit impressions I and V, sole narrowly extended to the rear. Manus axes turned outward. All digits can show pointed claws; foot



TEXT-FIG. 6. A, *Grallator* isp., field photograph from Quebrada de Ischichuca, convex hyporelief. B, *Rhynchosauroides* isp. pes print (LAR-Ic 4) on the same specimen as Text-figure 4A, rotated 180 degrees. White arrows indicate digit impressions. C, drawing of uncollected *Rhynchosauroides* isp. trackway from Talampaya Park. D, field photograph of trackway of *Rhynchosauroides* isp. (plaster casts INGEO-PV 040 and 041 were extracted from this trackway), concave epirelief. m, manus; p, pes. Scale divisions represent 10 mm. Black arrows indicate direction of light. II–V, digits II–V; m, manus; p, pes.

length ~35 cm, palmar surface about half of plantar surface (translated from Haubold 1971, p. 63).

Rigalites ischigualastianus von Huene, 1931
Text-figure 7A

*1931 *Rigalites ischigualastianus* von Huene, p. 112, pl. 9.
1966 *Rigalites ischigualastianus*; Bonaparte, p. 29.
1967 *Regalites ischigualastensis*; Rusconi, p. 235 (*lapsus calami*).
1970 *Rigalites ischigualastianus*; Haubold, p. 63, fig. 37.1.
1990 *Rigalites ischigualastianus*; Leonardi and de Oliveira, p. 221, pl. 3, fig. G.
1990 *Rigalites ischigualastensis*; Thulborn, p. 203, fig. 6.39e (*lapsus calami*).
1994 *Rigalites ischigualastianus*; Leonardi, p. 20, pl. 2.2.

Neotype. A holotype was not designated. As the original material is no longer in place (Marsicano *et al.* 2004), we designate the plaster cast PVL 2610 (Text-fig. 7A), housed at the Instituto Miguel Lillo, as the neotype.

Additional material. Plaster casts of single manus-pes sets of the type trackways housed at the Museo de La Plata (Argentina), and Tübingen (Germany). The casts from Germany were not seen.

Type locality. Quebrada de Los Rastros, Ischigualasto Provincial Park, San Juan province; Los Rastros Formation (Middle–Late Triassic).

Diagnosis. As for ichnogenus.

Description. This account is based on the original description of von Huene (1931) and on measurements of replicas housed in museum collections of Argentina. The trackways are 3–6 m long and belong to a large quadrupedal animal. The pes is tetradactyl and plantigrade to semiplantigrade, 340–390 mm long, showing long and broad impressions of digits I, II and III that bear triangular claw marks; digit IV is extremely reduced and often not preserved. The divarication between digits I and III is 30 degrees. The pentadactyl manus is about half the size of the pes and always set very close to and in front of the pes. It displays broad and short digit impressions. Impressions of manus digits I, II and III are directed forward, while the IV/V? is posteriorly directed. The pace angulation is high (close to 180 degrees).

Remarks. The tracks have a clear crocodylomorph or crurotarsian morphology (cf. Olsen and Padian 1986) and have been assigned to the Pseudosuchia (Bonaparte 1966, 1969), in particular to the Rauisuchidae (Leonardi 1994, p. 20; Bonaparte 1997, p. 96). Additional interpretations of the identity of the trackmaker were reviewed by Thulborn (1990, p. 202). This ichnogenus was included in the morphofamily Batrachopodidae Lull 1904 by Haubold (1971), an opinion supported by Leonardi (1994). It is considered that *Rigalites* is morphologically comparable with *Batrachopus* (Hitchcock 1845), although it is rather larger than specimens commonly included in this ichnogenus (Olsen and Padian 1986). Some forms of *Brachychirotherium* are also close to *Rigalites*, though a detailed comparison is beyond the scope of this paper. Certain Triassic tracks described by Ellenberger (1972) from South Africa could be comparable with *Rigalites*, but the taxonomy of that ichnofauna is in need of major revision.

Rigalites isp.
Text-figure 7B–C

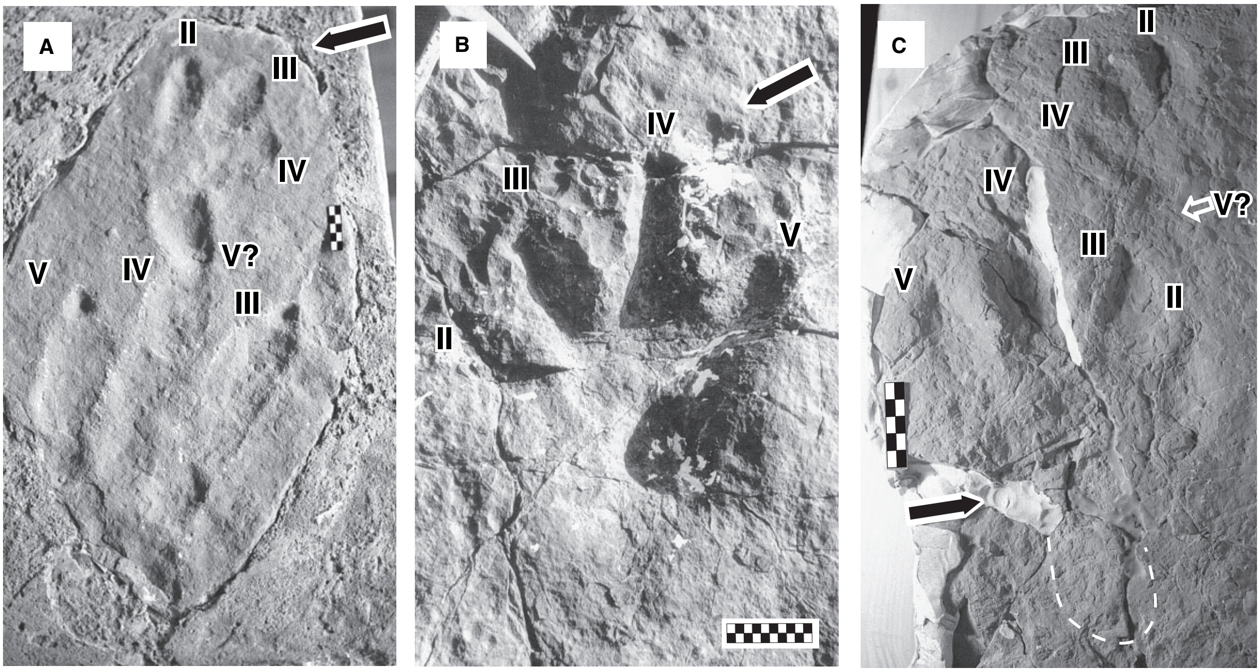
1966 cf. *Rigalites* isp.; Bonaparte, p. 28.
v.1995a 'Tridactyl footprints'; Arcucci *et al.*, p. 1.
v.1995b 'Theropod tracks'; Arcucci *et al.*, p. 16A.
v.1999 *Eubrontes* isp.; Zavattieri and Melchor, p. 37, fig. 2.
v2001a *Rigalites* isp.; Melchor *et al.*, pp. 188, 193.

Referred material. PVL 2735 from Sierra de Las Higueras; a trackway measured in the field and a plaster cast of a pes from this trackway (GHUNLPam 12489), from Quebrada de Ischichuca.

Occurrence. Sierra de Las Higueras, Mendoza province, and Quebrada de Ischichuca, La Rioja province; Cerro de Las Cabras Formation (Middle Triassic) and Ischichuca Formation (Middle Triassic), respectively.

Description. PVL 2735 is a manus-pes set in a moderate state of preservation. The pes is tetradactyl, 230 mm long and 160 mm wide. The angle of digit impressions I–IV is 28 degrees and there is a shallow rounded 'heel' (probable metatarsal + digit V). The manus impression is tetradactyl, 90 mm long and 83 mm wide. The manus is rotated outward and the presumed digit V points backwards (Text-fig. 7C, white arrow). The trackway from the Ischichuca Formation is *c.* 7 m long, quadrupedal and poorly preserved (cf. Marsicano *et al.* 2004). It contains five manus-pes sets, but only a single pes track displays details of its morphology (GHUNLPam 12489). This track is 410 mm long, 410 mm wide and tetradactyl; digit IV is the longest, then V, III and II (Text-fig. 7B).

Remarks. Leonardi (1994) assigned PVL 2735 to either *Chirotherium* isp. or a prosauropod. The tracks described herein are included in *Rigalites* because of the presence of a large tetradactyl pes print, a tetradactyl manus with outward rotation and an impression of digit V(?) pointed backwards (von Huene 1931). These features seem to be characteristic of the family Batrachopodidae and the footprints can be also compared with *Brachychirotherium* and *Batrachopus*. The footprints from the Ischichuca Formation were referred to as tridactyl theropod footprints by Arcucci *et al.* (1995*a*, *b*) and as *Eubrontes* isp. by Zavattieri and Melchor (1999), but further detailed examination demonstrated that the pes is tetradactyl (Melchor *et al.* 2001*a*).



TEXT-FIG. 7. *Rigalites* footprints. A, neotype of *Rigalites ischigualastianus* (PVL 2610), a plaster replica of a single manus-pes set from the type material housed at the Instituto Miguel Lillo (Tucumán, Argentina), concave epirelief. B, field photograph of *Rigalites* isp. pes from Quebrada de Ischichuca, concave epirelief. C, PVL 2735, manus-pes set of *Rigalites* isp. from Sierra de Las Peñas, concave epirelief. Probable metatarsal imprint outlined by dashed white line. White arrow indicates the impression of manus digit V. Scale bars represents 50 mm in A and C and 100 mm in B. Black arrows indicate direction of light. II–V, digits II–V.

The tracks are deeply impressed in carbonate micrite sediment, which is linked to the progression of the trackmaker in a substrate with a high water content. Bonaparte (1966) mentioned the presence of large footprints (*c.* 500 mm long) that are comparable with *Rigalites* from the same locality as specimen PVL 2735.

TETRASAUROPUS Ellenberger, 1972

Type ichnospecies. Tetrasauropus unguiferus Ellenberger, 1972.

Revised diagnosis. After the description and illustrations of Ellenberger (1972, p. 67), this ichnogenus was diagnosed to refer quadrupedal and plantigrade footprints. Pes rounded to subtriangular, more asymmetrical than in *Pseudotetrasauropus*, commonly shows marked external ridge. Digit imprints I–IV form an ample crescent with anterior convexity, digit V is projected forward more than digit I. Pes displays marked claw marks that curve laterally or vertically depending on ichnospecies. Sole and posterior part of pes digits not very different from *Pseudotetrasauropus*, but heel (metatarsals III–V) is best impressed. Manus, similar to pes, about 20 per cent smaller. Manus impressions arranged in regular fashion in trackways, with pace greater than double that of pes. Manus impressions less deeply imprinted than pes impressions.

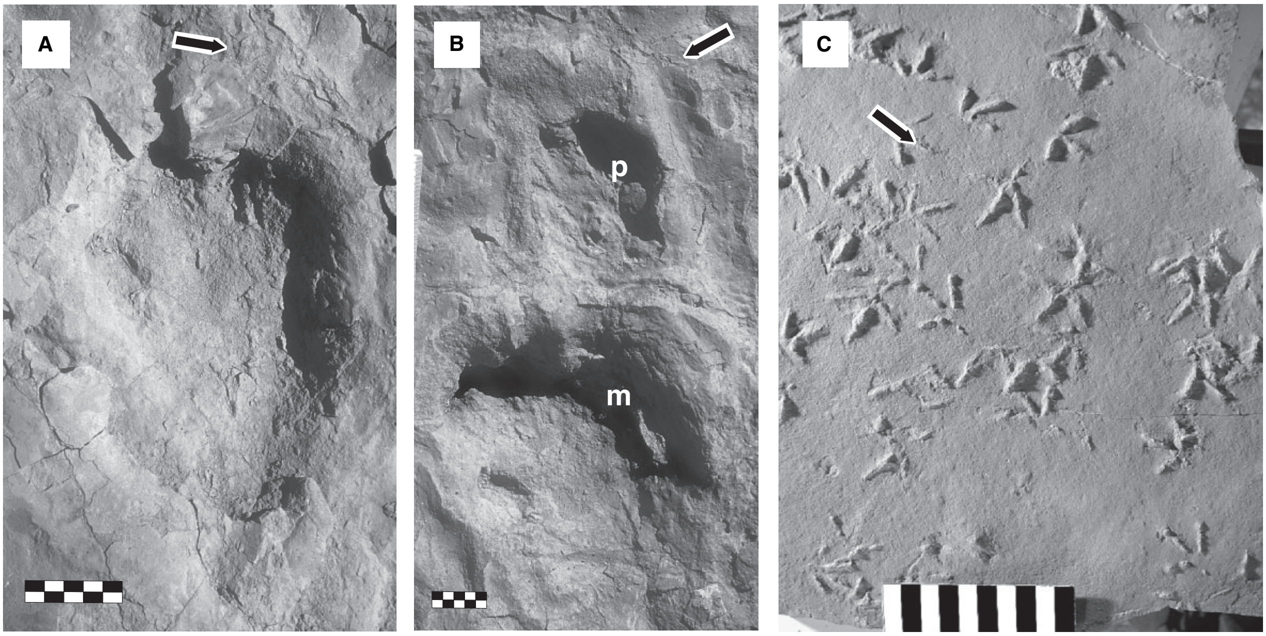
Remarks. The type ichnospecies, *T. unguiferus*, has been attributed to Prosauropoda (Ellenberger 1972; Haubold 1984; Lockley and Hunt 1995), whereas the additional ichnospecies, *T. gigas*, has been attributed to Sauropoda (Ellenberger 1972). The two species are probably not cogeneric; Olsen and Galton (1984) referred *T. gigas* to *Brachychirotherium* and Lockley and Meyer (1999) proposed to include it under *Pentasauropus*. The subequal length pes digits preclude the species' referral to *Brachychirotherium* or *Chirotherium* (Rainforth 2003).

Tetrasauropus isp.
Text-figure 8A–B

v.2001*b* cf. *Brachychirotherium* isp.; Melchor *et al.*, p. 58.

Referred material. Two uncollected trackways with three and at least four manus-pes sets (from Sierra de Las Peñas), respectively; one uncollected trackway and various isolated footprints, and MPEF Ic 234, a plaster cast of a manus-pes set (from Quebrada de Santo Domingo).

Occurrence. Sierra de Las Peñas (near Puesto Las Peñas: 32°27′03″S, 68°53′25″W), Mendoza province; and Quebrada de Santo Domingo (38°31′35″S, 68°43′50″W), La Rioja province; Cerro de Las Cabras Formation (Middle Triassic) and Santo Domingo Formation (Late Triassic), respectively.



TEXT-FIG. 8. Typical footprints from the Santo Domingo Formation. A, field photograph of hind print of *Tetrasauropus* isp., preserved in concave epirelief. B, field photograph of a manus-pes couple attributed to *Tetrasauropus* isp., preserved in concave epirelief. C, bird-like footprints (LAR Ic-5), convex hyporelief. Scale divisions represent 10 mm. Black arrows indicate direction of lighting. m, manus; p, pes.

Description. The specimens are moderately to poorly preserved. The pes is large, subtriangular, tetradactyl and plantigrade, and deeply imprinted (Text-fig. 8A–B). The pes is up to 300 mm long and 135 mm wide. The impressions of the digits are short. The manus is smaller and subcircular, measuring 120–150 mm in diameter and showing at least three short digit impressions. The manus imprint is often less deeply impressed and preserved as a rounded featureless mark (Text-fig. 8B). A single trackway from Quebrada de Santo Domingo has a pes pace angulation of 149 degrees.

Remarks. This ichnogenus seems to be a frequent component of the ichnofauna of both localities. The material is assigned to *Tetrasauropus* on the basis of comparison with the specimens from South Africa described by Ellenberger (1972), and following the recent usage of that ichnotaxon (i.e. *T. unguiferus*) by Lockley and Hunt (1995) and Lockley *et al.* (1996).

Bird-like footprints
Text-figure 8C

2002 Bird-like footprints; Melchor *et al.*, pp. 936–938, fig. 1

Referred material. About 30 slabs with several hundred footprints (LAR-Ic 5–8).

Occurrence. Quebrada de Santo Domingo (28°32′S, 68°45′W), near Alto Jagüé, north-west La Rioja province; Santo Domingo Formation (Late Triassic).

Description. These bird-like footprints were described by Melchor *et al.* (2002) and their ichnotaxonomy will be dealt with in detail elsewhere (de Valais and Melchor, in prep.). They are bipedal tracks with high pace angulation (mean, 170 degrees; range, 150–182 degrees). The footprints are tetradactyl or tridactyl, depending on the presence or absence of the impression of digit I or hallux. When impressed, the hallux is directed backwards. The digits are slender with claw marks, and the relative digit length is III > IV > II > I. The imprints are almost symmetrical, wider than long, and the digits converge in a rounded sole. The average divarication of digits II–IV is 115 degrees (range, 87–137 degrees).

Remarks. These footprints display the overall morphology and almost all the features that characterize modern bird footprints. They are envisaged as the footprints of an unknown Triassic theropod (Melchor *et al.* 2002). They are morphologically related to *Trisauropodiscus* Ellenberger, 1972 from South Africa, although this ichnotaxon is poorly documented and seems to lack an opposed hallux imprint. Another track genus with purported avian affinity is *Plesiornis* Hitchcock, 1858. However, the latter ichnotaxon shows low divarication between digit II and IV, a U-shaped outline and relatively thick digits (e.g. Hitchcock 1858, p. 102; Gierlinski 1996).

Chirotheriid footprints
Text-figure 9A–B

Description and remarks. This group includes poorly preserved material from three basins: the Ischigualasto-Villa Unión, Rincón Blanco and Los Menucos depocentre. A manus-pes set discovered in 1964 by J. F. Bonaparte (Stipanicic and Bonaparte 1972; Bonaparte 1997, p. 41), near Río Talampaya (in Talampaya Park, La Rioja province), comes from the Talampaya Formation and its poor preservation prevents an ichnotaxonomic assignation. A second occurrence of chirotheriid footprints corresponds to two isolated pes imprints from playa lake facies of the Ischichuca Formation at Quebrada de Ischichuca (Melchor *et al.* 2001*a*). They are 100–150 mm long and display a broad, oblique, metatarsal-digit V imprint and the imprints of digits IV, III and II with a marked marginal crease (Text-fig. 9B).

Marsicano and Barredo (2004) report two isolated footprints of chirotheriid footprints (their fig. 9) from the Portezuelo Formation of the Rincón Blanco depocentre.

The chirotheriid specimens from the Los Menucos depocentre were originally assigned by Casamiquela (1964) to a new ichnogenus and ichnospecies *Shimmelia chirotheroides*. This ichnotaxon was created on the basis of two slabs containing three poorly preserved footprints: MLP 60-XI-31-1, a natural cast of a manus-pes set, as the holotype (Text-fig. 9A), and MLP 60-XI-31-2, a natural cast of an isolated left foot, as the paratype. These slabs come from the Vera Formation (Carnian) at Cantera Vieja (Los Menucos, Río Negro province) and were extracted from the pavements of Costanera Avenue in San Carlos de Bariloche. The first specimen is a deep undertrack of very low relief. The probable pes imprint displays four (?) larger digits and a fifth digit (probable digit V) directed laterally. The possible tetradactyl manus print is fairly large relative to the pes. It is located behind the pes and rotated outwards (Text-fig. 9A). This material displays a morphology that resembles chirotheriid footprints; however, its poor preservation impedes any ichnotaxonomic treatment. As a result, *Shimmelia chirotheroides* Casamiquela, 1964 is considered a *nomen nudum*.

Chirotheriid footprints have been noted from the Rincón Blanco depocentre, Cuyo Basin (Marsicano and Barredo 2000) and the Los Colorados Formation, Ischigualasto-Villa Unión Basin (Marsicano *et al.* 2000). In the latter case, three small pentadactyl, digitigrade, chirotheriid footprint forms were recognized. No further information on these has been published.

Tridactyl footprints
Text-figure 9E

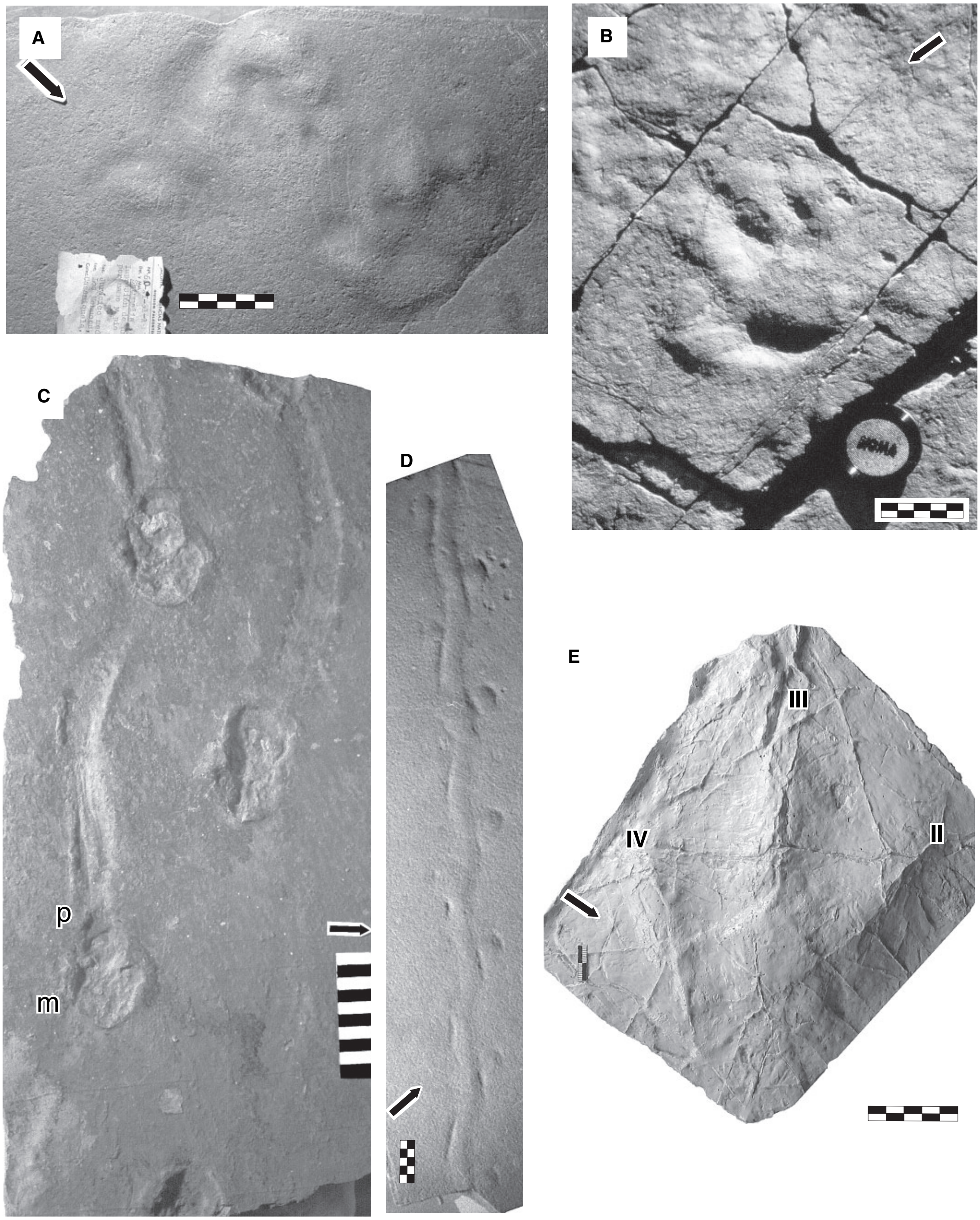
Description and remarks. There are several references to tridactyl footprints from the Ischigualasto-Villa Unión (including the Santo Domingo depocentre) and Cuyo (including the Rincón Blanco depocentre) basins, although their ichnotaxonomic assignation is imprecise because of their poor preservation or inadequate documentation. The records from the first basin belong to four formations: (1) The Chañares Formation (Quebrada de Ischichuca), a trampled surface with many tridactyl bipedal footprints *c.* 150 mm long. (2) The Ischichuca Formation (Quebrada de Ischichuca), long trackways (up to 15 m) showing deeply impressed, bipedal tridactyl footprints *c.* 150–250 mm in length. They have a high pace angulation (130 degrees) and the stride length is 1830 mm. At least five trackways were recorded from carbonate mudflat facies. The single catalogued specimen is a plaster cast (GHUNLPam 12490, Text-fig. 9E) of a right footprint undertrack 175 mm long and 170 mm wide displaying an apparently rounded sole. The relative length of the digits is III > II > IV (85 mm, 70 mm, 65 mm). Digit II projects anteriorly further than digit IV, which is separated from the sole. The total divarication (II–IV angle) is 75 degrees. The poor preservation of this footprint precludes an ichnotaxonomic assessment; however, it is comparable with *Anchisauripus* Lull, 1904 because of the subequal length and width, although the divarication angle is too high in comparison with the common values for this ichnotaxon (Olsen *et al.* 1998). (3) The Los Rastros Formation, two locations within Ischigualasto Provincial Park (Piedra Pintada and Quebrada Agua de La Peña, mentioned by Alcober 1993 and Contreras and Bracco 1998, 2004), tridactyl footprints, some of which were considered comparable with *Anchisauripus* isp. (Contreras and Bracco 1998, 2004). (4) The Ischigualasto Formation (Cerro Rajado), one tridactyl footprint from the upper section of the formation (Contreras and Bracco 1998, 2004). The Santo Domingo depocentre at Quebradade, Santo Domingo yielded isolated, poorly preserved tridactyl footprints less than 100 mm long.

The occurrences in the Cuyo Basin are restricted to two localities. At Sierra de Las Peñas, two isolated, poorly preserved footprints from the Cerro de Las Cabras Formation were reported by Melchor *et al.* (2001*b*). These are 60–80 mm long and about the same width. A single footprint and a short trackway described as 'Type B2 tracks' by Marsicano and Barredo (2004) from the Portezuelo Formation (Rincón Blanco depocentre) are also considered as belonging to this informal group.

Tracks of dubious assignation

Description and remarks. This section includes some specimens that have been formally named by Casamiquela (1964), as well as other unpublished and published (Marsicano and Barredo 2004) footprints that display no distinct morphology. In particular, it is considered that both *Rogerbaletichnus* Casamiquela, 1964 (Text-fig. 9C) and *Ingenierichnus* Casamiquela, 1964 (Text-fig. 9D) potentially provide useful palaeoecological information, as claimed by that author. However, the poor preservation of the material and the scarce detailed morphological data that can be extracted from the footprints concerned rule out any ichnotaxonomic treatment. These ichnotaxa are considered to be 'phantom taxa' (*sensu* Haubold 1996) and we suggest that they should be abandoned.

The ichnospecies *Ingenierichnus sierrai* Casamiquela, 1964 was created on the basis of two slabs: MLP 60-XI-31-3 (holotype, a trackway with more than 13 manus-pes sets; Text-fig. 9D) and MLP 60-XI-31-2 (paratype, a shorter trackway). They are from the Vera Formation (Carnian) at Cantera Vieja (Los Menucos, Río Negro province, and were removed from the pavements of Costanera Avenue, San Carlos de Bariloche, Río Negro province). Casamiquela (1984) mentioned the finding of a new



TEXT-FIG. 9. Chirotheriid and miscellaneous footprints. A, MLP 60-XI-31-1, holotype of '*Shimmelia chirotheroides*' Casamiquela, 1964, convex hyporelief. B, field photograph from the Ischichuca Formation at Quebrada de Ischichuca, concave epirelief. C, MLP 60-XI-31-5, holotype of *Rogerbaletichnus aguilerai* Casamiquela, 1964, concave epirelief. D, MLP 60-XI-31-3, holotype of *Ingenierichnus sierrai* Casamiquela, 1964, convex hyporelief. E, plaster cast of a tridactyl bipedal footprint from the Ischichuca Formation (GHUNLPam 12490), convex hyporelief. Scale divisions represent 10 mm. Black arrows indicate direction of light. II–V, digits II–V; m, manus; p, pes.

unpublished trackway, which displays a lacertoid morphology that he considered to belong to this ichnogenus.

The ichnospecies *Rogerbaletichnus aguilerai* Casamiquela, 1964 was erected on the basis of a single specimen (MLP 60-XI-31-5), a trackway with three complete manus-pes sets (Text-fig. 9C), from the Vera Formation at Cantera La Nueva (Los Menucos, Río Negro province). The trackway consists of rounded footprints bearing short and blunt digits and displays two conspicuous characteristics: the manus is related to a prominent, curved drag mark and the manus overprints the pes (Text-fig. 9C). Leonardi (1994) consigned the probable phalangeal formula of the trackmaker; however, we were unable to recognize any phalangeal pads on the specimens.

Recently, Manera de Bianco and Calvo (1999) reported the occurrence of large footprints from the Los Menucos depocentre. These are quadrupedal trackways consisting of a subtriangular pes (410 mm long by 300 mm wide) and a subcircular manus (150 mm by 120 mm). Manera de Bianco and Calvo (1999) suggested that they may belong to Prosauropoda. We have not examined this material.

Some of the material collected from the Los Colorados Formation at Río de los Tarros by Bonaparte (PVL 3451, 3435) is akin to *Brachychidrotherium* (Beurlen, 1950), although it is poorly preserved. Isolated and commonly incomplete footprints from the same locality (e.g. PVL 3439, 3445, 3450) are indeterminate (Leonardi 1994). Contreras and Bracco (1998) mentioned uncollected footprints of Cynodontia in this formation at the Río Salado locality (Ischigualasto Provincial Park) that can be referred to *Dicynodontipus* Lilienstern, 1944.

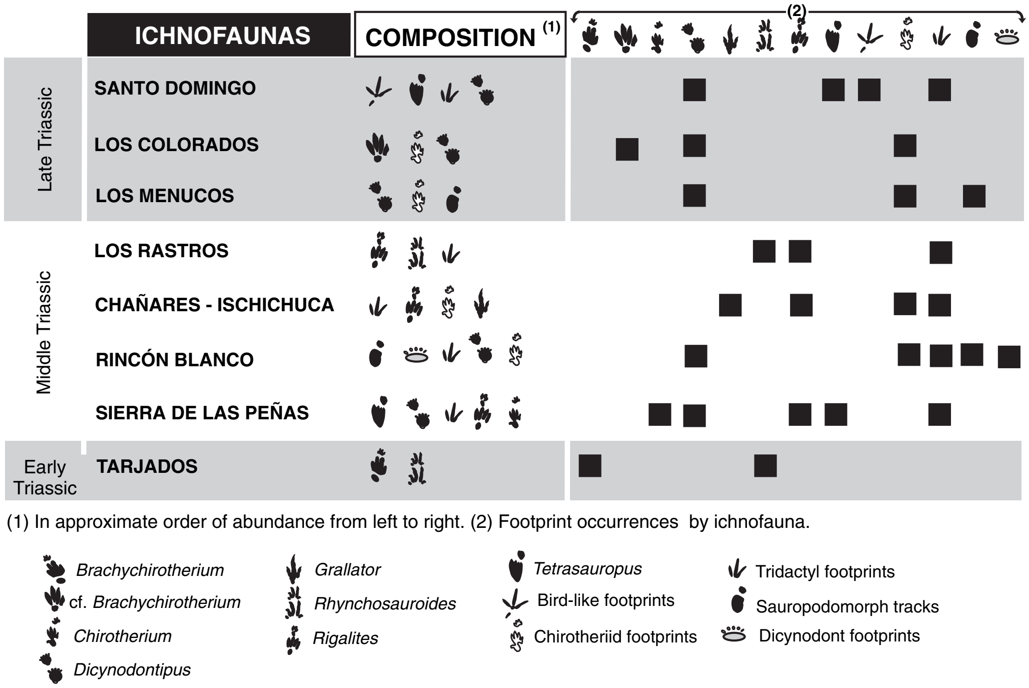
A number of trackways and tracks, mostly undertracks, described by Marsicano and Barredo (2004) from the Rincón Blanco Basin are difficult to assign to ichnotaxa. In particular, 'Type FB trackways' and 'Type B1 tracks' are considered taphonomic and preservational variants of the same type of quadrupedal trackway. The differences pointed out by Marsicano and Barredo (2004) between these track types can be explained by different substrate consistency and by the 'undertrack fallout' phenomenon (Goldring and Seilacher 1971). These tracks are considered to be comparable with *Tetrasauropus* Ellenberger, 1972. Another footprint type described by Marsicano and Barredo (2004) from the same basin, referred to as 'Type Q2 tracks', comprises large (*c.* 35 cm wide and long), rounded tracks arranged in narrow quadrupedal trackways, and is the only known occurrence of this type of footprint in the Triassic of Argentina. They are morphologically close to *Pentasauropus* Ellenberger, 1972 from South Africa, but their poor to moderate preservation state precludes positive identification. Marsicano *et al.* (2004) have described a poorly preserved manus-pes couple from the Ischigualasto Formation at Quebrada Agua de La Peña (Ischigualasto-Villa Unión Basin), which consists of rounded tetradactyl tracks. They were found at approximately the same stratigraphic interval as the original finding of *Rigalites* (Marsicano *et al.* 2004).

DISCUSSION

Stratigraphic distribution and composition of the track assemblages

The stratigraphic distribution of Triassic footprints in Argentina is summarized in Text-figure 2. About one-third of the total track occurrences are in Upper Triassic deposits and two-thirds in the Middle Triassic, and there are couple of records in Lower Triassic rocks. Tetrapod tracks appear preferentially in certain environmental settings, namely: Late Triassic assemblages in ephemeral fluvial settings, Middle Triassic ichnofaunas in playa lakes or shallow, freshwater lake deposits, and the Early Triassic ichnofauna in ephemeral fluvial and loess deposits. At present, eight ichnofaunas (track assemblages from a single unit and from intervals with homogeneous environmental conditions) can be recognized with confidence (Text-figure 10). Most of these are the only evidence of the tetrapod fauna that existed during the deposition of the track-bearing successions; only the Los Colorados and Chañares formations contain an abundant bone record (Bonaparte 1997). Between these assemblages a few ichnocoenoses (groups of vertebrate traces produced by a single community of organisms) are identified with confidence. They are found in the Santo Domingo, Chañares-Ischichuca, Sierra de Las Peñas and Tarjados ichnofaunas.

The most common track types are tridactyl footprints (including *Grallator*), chirotheriid footprints (including *Chirotherium* and *Brachychirotherium*) and 'therapsid' footprints (*Dicynodontipus* and ?*Pentasauropus*). These seem to span most of the Middle and Upper Triassic. *Rigalites* is restricted to three Middle Triassic ichnofaunas. The ichnogeneric diversity of the ichnofaunas ranges from two to five; the most diverse are the Sierra de Las Peñas and Rincón Blanco ichnofaunas, followed by those of Chañares-Ischichuca and Santo Domingo. The Tarjados ichnofauna contains *Brachychirotherium* and *Rhynchosauroides*, which are two morphotypes commonly found associated in the European Late Triassic (Karl and Haubold 1998). The Chañares-Ischichuca and Los Rastros ichnofaunas share the presence of *Rigalites* and tridactyl footprints. The Sierra de Las Peñas ichnofauna is compositionally closer to the Santo Domingo ichnofauna, especially because of the presence of *Tetrasauropus*, *Dicynodontipus* and tridactyl footprints. *Tetrasauropus* has been attributed tentatively to prosauropods (Ellenberger 1972; Lockley and Hunt 1995, p. 91), although this assignation should be revised as some (Lockley *et al.* 1994) or even most (Rainforth 2002, 2003) purported Late Triassic prosauropod tracks have been reinterpreted as having been produced by other groups of animals. The Los Menucos ichnofauna is unusual by comparison with other Late Triassic track assemblages (Haubold 1984; Lockley and Hunt 1995) because of the dominance of therapsid and the apparent absence of tridactyl dinosaur footprints. Moreover, the purported occurrence of prosauropod tracks in this ichnofauna requires confirmation. The reasons for the particular composition of the Los Menucos ichnofauna are unknown. A possible explanation is sedimentation under conditions of environmental stress that might have restricted the tetrapod fauna that inhabited the region. In particular, the track-bearing facies and associated flora of the Vera Formation suggest sedimentation



TEXT-FIG. 10. Composition and temporal distribution of the eight Triassic tetrapod ichnofaunas from Argentina. The composition of individual ichnofaunas is represented in order of abundance and also by track type.

strongly influenced by explosive volcanism in a semi-arid climate (Spalletti *et al.* 1999; Bellosi *et al.* 2001).

There have been a few attempts to propose Triassic tetrapod ichnofacies (e.g. Lockley and Conrad 1989; Lockley *et al.* 1994). A tetrapod ichnofacies is considered to be a recurrent track assemblage that occurs in definite sedimentary facies (e.g. Lockley *et al.* 1994). It is considered that the definition of tetrapod or invertebrate ichnofacies should not be restricted to definite time intervals. This procedure will emphasize the palaeoenvironmental or lithofacies-dependent aspect of tetrapod ichnofacies, possibly to the detriment of ichnostratigraphic applications. However, it will facilitate the definition of broader and common tetrapod ichnofacies.

Comparison with Late Triassic ichnofaunas elsewhere

The track types recorded from the Triassic of Argentina are broadly similar to those recorded in successions of the same age in eastern North America (Lockley and Hunt 1995), Europe (Haubold 1984; Lockley and Meyer 2000) and South Africa (Ellenberger 1972; Olsen and Galton 1984). However, some significant differences are apparent. (1) Other track assemblages are more diverse. This contrasting ichnodiversity might be a reflection of either a different degree of study or a larger sample size. (2) The ichnogenus *Rigalites*, present in Argentina, has been not identified from other continents. However, further detailed studies may reveal possible relationships with *Brachychirotherium* and other Triassic ichnotaxa. (3) The presence of Late Triassic bird-like footprints in the Santo Domingo Formation (Melchor *et al.* 2002) is remarkable. The morphologically closest tracks are some of the footprints included in *Trisauropodiscus* Ellenberger, 1972. The ichnotaxonomy of these tracks will be discussed elsewhere.

In spite of the overall similarity with other Triassic ichnofaunas, the Triassic track assemblages from Argentina contain at least three morphotypes that are present in South Africa, as described by Ellenberger (1972, 1974): bird-like tracks (?*Trisauropodiscus*), ?*Pentasauropus* and *Tetrasauropus*. The taxonomic status of these ichnogenera is uncertain, but the footprint morphologies are distinctive and characteristic. This similarity may suggest a greater affinity between the Triassic Gondwana track assemblages of South Africa and Argentina than between assemblages from other parts of the world.

CONCLUSIONS

Despite the fact that scientific study of Triassic tetrapod tracks from Argentina began more than 70 years ago, the present state of knowledge is rudimentary owing to the scarcity of studies. The ichnotaxonomic revision presented in this paper has shown that many of the seemingly endemic ichnotaxa from Argentina are comparable with well-known Triassic tetrapod track types and that other ichnotaxa were erected merely on the basis of scarce and poorly preserved material. Eight ichnofaunas have been recognized, the most diverse (including five track types) are those of the Sierra de Las Peñas and Rincón Blanco, followed by those of Chañares-Ischichuca and Santo Domingo (each with four track types). The most common track types are tridactyl footprints, chirotheriid footprints and 'therapsid' footprints. More studies on individual ichnocoenoses are needed in order to evaluate the contribution of the Triassic track record in Argentina to the definition of tetrapod ichnofacies.

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NOTE ADDED IN PROOF

Recent palaeomagnetic work by Vizan *et al.* (2005) has suggested that the age of the Santo Domingo Formation is within the range Late Triassic–Early Jurassic.

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