

This article was downloaded by: [American Museum of Natural History]
[American Museum of Natural History]

On: 17 April 2007

Access Details: [subscription number 768489081]

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954

Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Historical Biology

An International Journal of Paleobiology

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title-content=t713717695>

Dinosaur origins: evidence from the footprint record

To cite this Article: , 'Dinosaur origins: evidence from the footprint record', *Historical Biology*, 19:1, 83 - 91

To link to this article: DOI: 10.1080/08912960600866920

URL: <http://dx.doi.org/10.1080/08912960600866920>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

© Taylor and Francis 2007

Dinosaur origins: evidence from the footprint record

CLAUDIA A. MARSICANO¹, NADIA S. DOMNANOVICH¹, & ADRIANA C. MANCUSO²

¹*Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria Pabellón II, C1428 DHE Buenos Aires, Argentina, and* ²*CRICYT-CONICET, Casilla de Correo 131, 5500 Mendoza, Argentina*

Abstract

Triassic tracks and trackways assigned to dinosaur trackmakers or closest relatives have been mentioned from several Middle to the latest Triassic successions from both northern and southern Pangea. At present, the earliest gondwanan records are those from the Middle Triassic Los Rastros Formation in west-central Argentina. A reanalysis of Los Rastros ichnites at the Ischichuca area, including new material, has revealed the presence of a more diverse ichnofauna than previously suspected. The ichnocoenosis includes several tracks and trackways of bipeds with functionally tridactyl digitigrade pes, well developed claws, and a parasagittal posture of the hindlimbs. Previously, some large tridactyl footprints from the Ischichuca area were allied to theropod dinosaurs, although no synapomorphies are preserved in the three-toed footprints that might discriminate among theropods, basal saurischians and basal ornithischian groups as their possible trackmakers. If the Ischichuca trackmakers are referred to a dinosaur taxon and/or to a close dinosaur sister-taxon, their presence in the Los Rastros levels suggests that derived dinosauriforms (including dinosaurs) had diverged and acquired their characteristic functionally tridactyl pes by at least the Middle Triassic, something that the body-fossil record has failed to document to date.

Keywords: *Footprints, Dinosauria, Triassic, Los Rastros Formation, Argentina*

Introduction

The Triassic represents a crucial time in the evolutionary history of dinosaurs: it records the origin and subsequent ascendancy of the group at the end of the period (Serenó 1997, 1999). Although the earliest dinosaur body-fossil records are rather scattered they show an already widespread distribution of the group with both ornithischian and saurischian representatives (e.g. Sereno 1999; Benton 2004; Langer 2004).

Skeletal remains attributed to Late Triassic dinosaurs are known from several areas in both Laurasia and Gondwana, and the oldest records are those from Africa and South America. Remains attributed to sauropodomorphs were described from the Karoo Basin of southern Africa (e.g. Raath et al. 1992; Yates and Kitching 2003), the Argana Basin of Morocco (*Azendohsaurus* Gauffre 1993) and the Morondava Basin of Madagascar (cf. *Azendohsaurus*, Flynn et al. 1999). Nevertheless, new material assigned to

Azendohsaurus recently discovered from Morocco poses doubts about the dinosaurian identity of the originally described specimen from Morocco (Jalil and Knoll 2002). In addition to the African records, fairly complete specimens are known from South America. The Paraná Basin of southern Brazil has yielded the putative basal sauropodomorphs *Saturnalia* (Langer et al. 1999) and *Guaibasaurus* (Bonaparte et al. 1999), and the herrerasaurid *Staurikosaurus* (Galton 1977). Basal ornithischians (*Pisanosaurus*) and basal saurischians (the herrerasaurid *Herrerasaurus* and *Eoraptor*) are known from the Carnian Ischigualasto Formation in west-central Argentina (e.g. Bonaparte 1970, 1982, 1997; Novas 1992; Rogers et al. 1993; Sereno et al. 1993).

Besides the body-fossil record, Triassic tracks and trackways assigned to dinosaur trackmakers or closest relatives have been mentioned from Middle to the latest Triassic horizons from both northern and southern Pangea. Several tridactyl and tetradactyl footprints from the Late Triassic Chinle Group (western USA)

Correspondence: C. A. Marsicano, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria Pabellón II, C1428 DHE Buenos Aires, Argentina. E-mail: clauamar@gl.fcen.uba.ar

have been interpreted as produced by theropods and sauropodomorphs (Lockley and Hunt 1995; Lucas et al. 2001; Lockley et al. 2001; Lucas 2003; Wilson 2005), whereas tridactyl tracks of bipeds from Carnian levels of the Newark Supergroup (Eastern USA) have been recognized as produced by theropod and ornithischian trackmakers (Olsen et al. 2002). Nevertheless, even older levels in Europe have yielded an extensive record of small tridactyl tracks and trackways of bipeds, and alleged facultative bipeds, that have been related to dinosaurs and/or dinosauriform trackmakers. Small tridactyl pes prints associated, in some cases, with very small manus prints are known from Middle Triassic beds from the eastern-southern border of the French Massif Central (Demathieu 1989; Courel and Demathieu 1995; Lockley and Meyer 2000). Likewise, several ichnites were described from the Middle Triassic Benker Sandstein (Northern Bavaria, Germany) where functionally tridactyl pedes of bipeds (*Grallator*) and quadrupeds (*Atreipus*) were postulated as produced by early dinosaurs and dinosauriforms, respectively (Haubold and Klein 2000, 2002). As occurs with the French material, the German prints are quite small, with a maximum length of 10 cm (Haubold and Klein 2000). Finally, isolated small tridactyl prints identified as dinosauriform tracks were recently described from the lower Middle Triassic (Anisian) of the southern Alps in Italy (Avanzini 2002).

The Late Triassic Gondwanan dinosaur footprint record is more restricted than that of Laurasia and is known mainly from the Karoo Basin of southern South Africa (Ellenberger 1970, 1972, 1974; Raath et al. 1990; Lucas and Hancox 2001) and the Cuyana Basin (Portezuelo Formation) in central-western Argentina (Marsicano and Barredo 2004). However, earlier records were also mentioned and large tridactyl footprints related to theropods have been described from the Middle Triassic Los Rastros Formation, also from central-western Argentina (Arcucci et al. 1995; Forster et al. 1995; Marsicano et al. 2004).

In South Africa, tridactyl ichnites of bipeds are extensively known from the Late Triassic Molteno Formation, and they were interpreted as produced by different taxa of saurischian (prosauropods and theropods) and ornithischian dinosaurs (Ellenberger 1970, 1972, 1974; Raath et al. 1990; Lucas and Hancox 2001). Recently, a quite diverse Late Triassic track assemblage was described from central-western Argentina (Portezuelo Formation) and it includes several footprints and trackways that indicate the presence of middle-to-large sized sauropodomorphs and small-to-medium sized theropods (Marsicano and Barredo 2004).

As previously mentioned, the only Middle Triassic tridactyl tracks attributed to putative dinosaur trackmakers in Gondwana are those from Los Rastros

Formation of Argentina. A re-analysis of previously described tracks (Arcucci et al. 1995; Forster et al. 1995; Marsicano et al. 2004) as well as the description of recently discovered material from the same levels and locality is the aim of the present contribution. Moreover, an evaluation of the degree to which Middle-Late Triassic tridactyl footprints can be assigned to members of Dinosauria in a phylogenetic context is also discussed. It is important to remark that the Los Rastros ichnites might constitute the earliest evidence of members of that clade in the fossil record, at least for the southern Hemisphere (Carrano and Wilson 2001).

Los Rastros footprint record

In the Ischigualasto-Villa Unión Basin (San Juan and La Rioja provinces), the Middle Triassic Los Rastros Formation is represented by thick cyclic lacustrine-deltaic deposits (up to 600 m). They conformably overlie the tuffaceous sandstones and siltstones of the Chañares Formation, and are unconformably covered by the fluvial sandstones, mudstones and tuffs of the Ischigualasto Formation (e.g. Milana and Alcober 1995; Mancuso 2005). The Los Rastros Formation has long been known for its ichnological content (see Marsicano et al. 2004) and its outcrops are well exposed in the region, particularly in the Ischigualasto Provincial Park, the Quebrada de Ischichuca (Cerro Bola area), and the Talampaya National Park (Figure 1). Nevertheless, tridactyl footprints were previously recorded only from levels exposed at the Quebrada de Ischichuca locality, close to the base of the succession. The ichnites are preserved on multiple surfaces of laterally extended beds of calcareous siltstones and wackestones associated to a paleo-lake shoreline (Mancuso 2005).

Four different types of footprints showing a functionally tridactyl digitigrade pes are present in the Ischichuca area, three representing fully bipedal trackmakers and a fourth one which corresponds to a quadruped trackmaker:

Type 1

These ichnites are present, with different degrees of preservation, on the surface of calcareous siltstones. On the best preserved surface, all the footprints are present as natural molds and at least five trackways (measurements summarized in Table I) were identified on the surface associated with several isolated tridactyl prints (Figure 2). All trackways represent animals with full bipedal progression. The number of steps in the trackways varies from two and four and the prints are tridactyl with digit III projecting farther anteriorly than digits II and IV, which are, in contrast, of similar size. All the digits have narrow and pointed claws marks. In only two of the trackways the

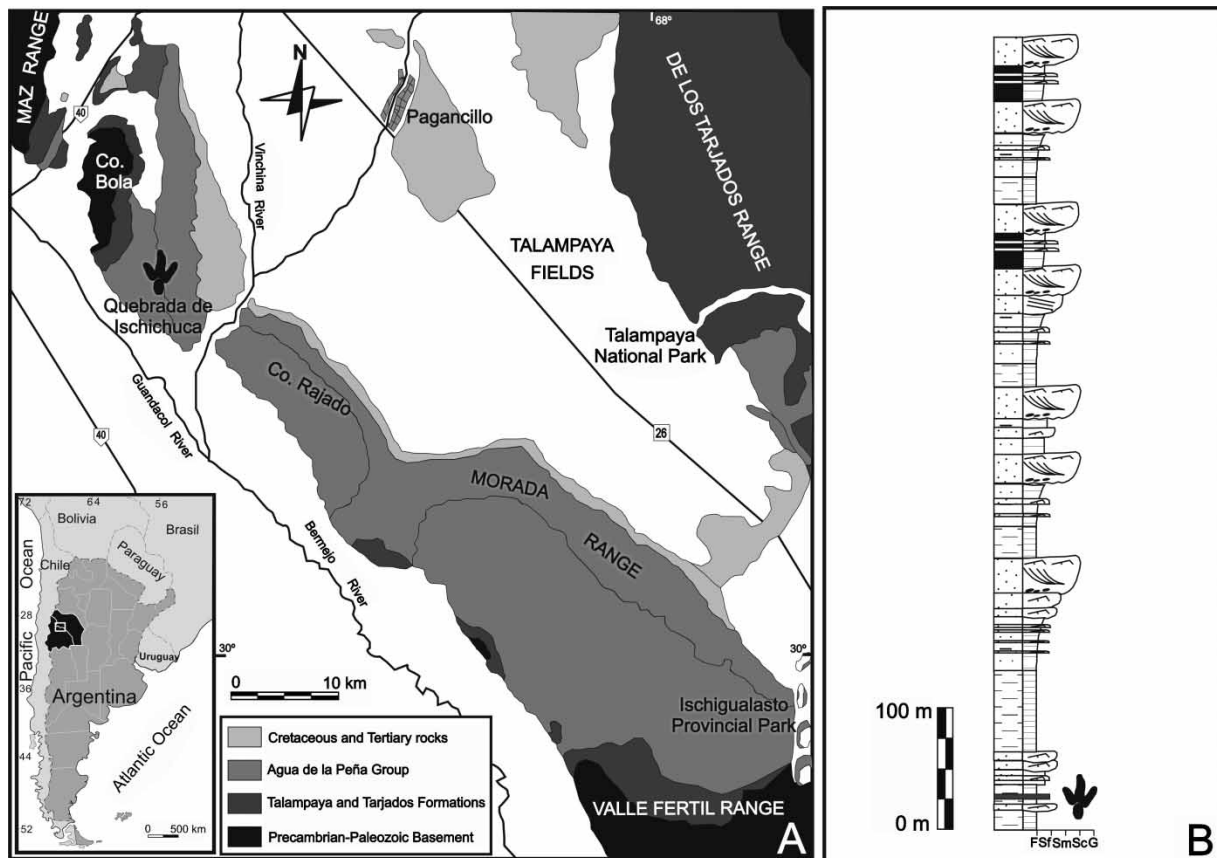


Figure 1. (A) Geological map of the Ichigualasto-Villa Unión Basin and (B) stratigraphic scheme of the Los Rastos Formation succession showing the position of the track-bearing horizons at the Ischichuca locality.

footprints have posteriorly a quite narrow metatarsal impression (Figure 2(B) and (B')) and are among the most deeply impressed prints on the surface, thus suggesting a preservational effect. As previously mentioned, the trackways correspond to bipeds with a symmetrical functionally tridactyl feet and fully

adducted hindlimbs indicated by the high pace angulation (approximately 160 degrees) in the trackways. Calculated measurements on the largest trackway suggest a medium-sized animal of approximately 108 cm hip height (Thulborn 1989; Henderson 2003).

Table I. Measurements of five trackways of **Type 1** registered on the surface shown in Figure 2(A). n.d., not datum. Parameters according to Leonardi (1987).

| Trackways Type 1 | Stride length (cm) | Pace length (cm) average | Pace angulation (degrees) average | Footprints | Width (cm) | Length (cm) |
|------------------|--------------------|--------------------------|-----------------------------------|------------|------------|-------------|
| 1 | 100 | 48 | 150 | 1 | 16 | 16 |
| | | | | 2 | 15 | 16 |
| | | | | 3 | 15 | 15.5 |
| | | | | 4 | 15 | 16 |
| 2 | 150 | 80 | 160 | 1 | 15 | 18 |
| | | | | 2 | 15 | 19 |
| | | | | 3 | 15 | 18 |
| 3 | 180 | 95 | 165 | 1 | 19 | 24 |
| | | | | 2 | 18 | 24 |
| | | | | 3 | 20 | 23 |
| 4 | 180 | 100 | 150 | 1 | 19 | 20 |
| | | | | 2 | 18 | 20 |
| | | | | 3 | 18 | 18 |
| 5 | n.d. | 100 | 165 | 1 | 24 | 27 |
| | | | | 2 | 24 | 28 |

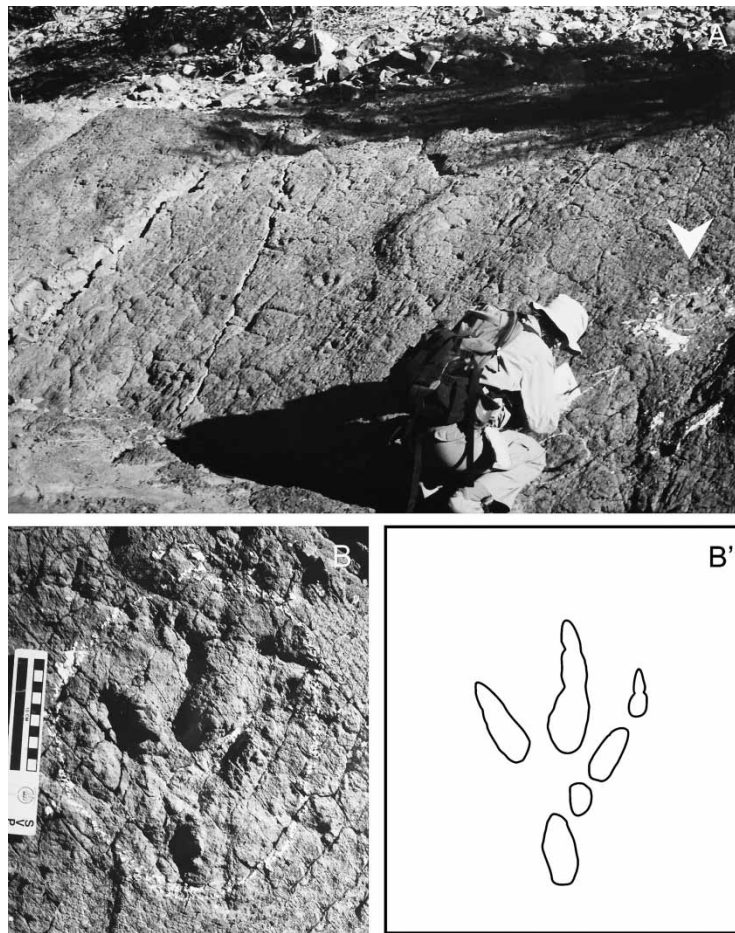


Figure 2. (A) General view of a track-bearing surface with several trackways of **Type 1**; (B) and (B') detailed photograph and interpretative line sketch of the pes impression pointed with an arrow in (A).

Type 2

This type is preserved on an extensive wackestone surface which is laterally equivalent to the calcareous siltstones previously mentioned. Two large tridactyl footprints (approx. 42 cm length), which are successive steps of a trackway, are the only tracks of this type recorded in the Ischichuca locality, until now. The prints are tridactyl and relatively narrow with a posterior rounded metatarsal impression (Figure 3). Digit III is anteriorly directed and longer than digits II and IV, which are anterolaterally directed; digit IV is slightly longer than digit II; the average divarication angle between digits III–II and III–IV is approximately 35 degrees. The two footfalls in the trackway are on a nearly straight line and calculated measurements indicate the presence of a large-sized biped, approximately 168 cm hip height (see Thulborn 1989; Henderson 2003). These large tridactyl tracks were previously described and allied to theropod dinosaurs (Arcucci et al. 1995; Forster et al. 1995) and recently, one of them (Figure 3) was misinterpreted as the four toed foot of a “chirotheroid” track (Melchor and de Valais 2006).

Type 3

On the same surface where the tracks of Type 2 are preserved, but several meters W from them (approx. 6 m), there is a rather long trackway of a biped associated with some isolated tridactyl prints (Figure 4). These isolated footprints were apparently part of other perpendicular trackways (two) of the same type, but they are less deeply imprinted on the surface, and the structure of the trackways is not clear. All the prints of Type 3 are preserved as natural moulds. The trackway includes five consecutive steps of symmetric tridactyl prints (30 cm length; stride length approx. 200 cm) with somewhat indistinct pads (Figure 4(B) and (B')). Digit III is significantly longer than digits II and IV and it is anteriorly directed whereas digits II and IV are rather laterally projected; the average divarication angle between digits III–II and III–IV is approximately 45 degrees. All digit impressions present well-developed, pointed claw marks. In contrast with the footprints of bipeds previously described (Type 1 and 2), none of the observed prints have metatarsal impressions. The structure of the trackway suggests a medium-sized bipedal animal with a digitigrade

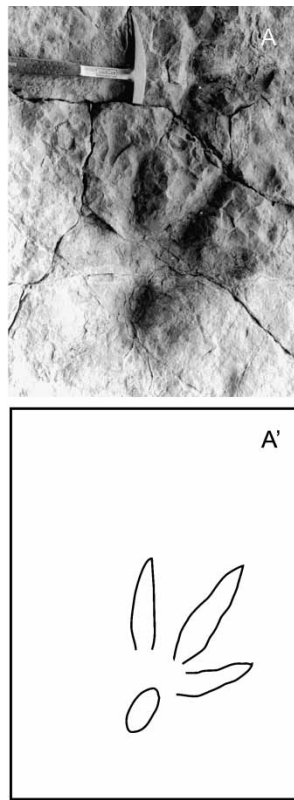


Figure 3. (A) and (A') photograph and interpretative line sketch of a tridactyl pes impression of **Type 2**.

tridactyl foot and a parasagittal hindlimb posture (pace angulation approximately 165 degrees). According to Thulborn's ratios (Thulborn 1989; Henderson 2003) the trackmaker's hip height is approximately 120 cm.

Type 4

This type is represented by several trackways (at least four between seven to nine steps) and they are also imprinted on the extensive wakestone surface as the trackways previously described, but approximately 20 m W from those of Type 3. The trackways (Figure 5) correspond to quadrupeds with functionally tridactyl semi-plantigrade pedes (approx. 40 cm length; average stride length of 120 cm). The prints are relatively narrow and the toe impressions are continuous with a posteriorly projected rounded metatarsal impression (?heel). The pads in the prints are not clear, probably because the tracks are deeply impressed on the surface. In most of the steps, the pedes have a small manus print oriented anterolaterally; the manus prints are quite small (approx. 14 cm length) with the digits not distinguishable and they are less impressed on the substrate than the pedes prints (Figure 5(B) and (B')). Nevertheless, in some of the trackways there are steps without any evidence of a manus print and this absence does not seem to be related to a preservational bias as all the trackways analyzed are well impressed on the

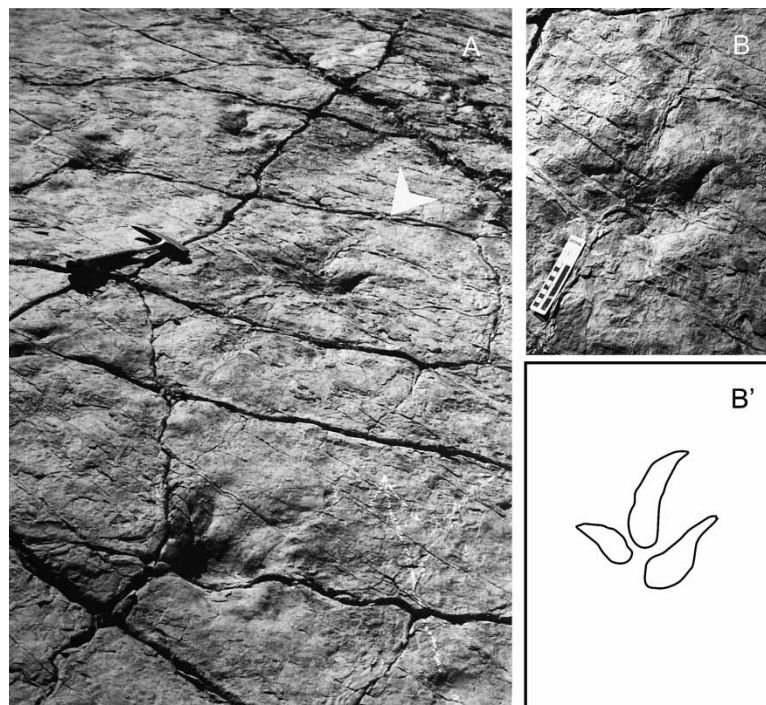


Figure 4. (A) photograph of a trackway of **Type 3**; (B) and (B') detailed photograph and interpretative line sketch of the tridactyl pes impression pointed with an arrow in (A).

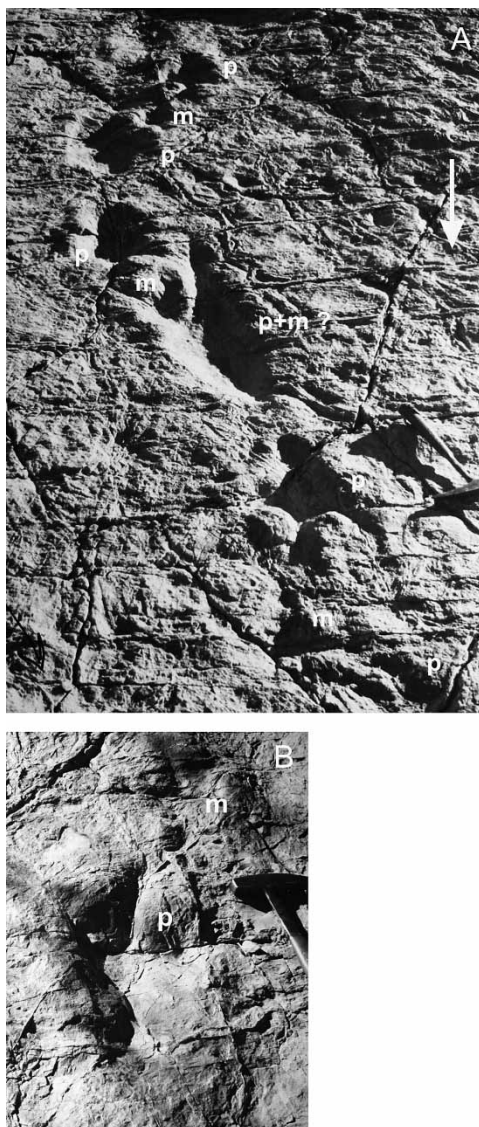


Figure 5. (A) photograph of a trackway of **Type 4**; (B), photograph of the manus and pes impression pair corresponding to the first step of the trackway in (A); m = manus and p = pes, arrow indicates the direction of the movement.

original surface. The observed trackway pattern denotes a regular progression of the trackmaker, with short steps; the prints are almost on a straight line (pace angulation approx. 150 degrees) thus indicating a quadruped with an erect gait that might alternatively adopt a bipedal posture.

Discussion

Inferences about the spatial and temporal distribution of tetrapod groups based on footprints depend on the identification, with some reliability, of the maker of the ichnites (e.g. Lockley et al. 1994; Carrano and Wilson 2001). Recently, a new approach to this practice, synapomorphy-based trackmaker identification (Olsen et al. 1998; Carrano and Wilson 2001), has been proposed as an alternative to the widely used method based on general similarity between a track

and the pedal structure of a known body-fossil taxon. The synapomorphy-based technique is focused on the identification of osteological derived character states in the ichnites that allow the recognition, albeit at a coarse taxonomic level, of a particular body-fossil clade and independently from the defined body-fossil distributions (see Olsen et al. 1998; Carrano and Wilson 2001; Wilson 2005).

Recent phylogenies of ornithodiran archosaurs and included clades (e.g. Sereno 1991, 1997, 1999; Benton 1999, 2004; Carrano 2000) suggest that digitigrade pedal posture, obligate bipedalism and parasagittal posture characterize the members of the ornithodiran clade. Nevertheless, and due to the incompleteness of some basal ornithodirans, optimization of the last two conditions on a phylogeny of Archosauria are only unambiguously reconstructed at Dinosauriformes (see Carrano 2000). Within Ornithodira, only dinosaurs are distinguished by the presence of a symmetric tridactyl foot (e.g. Parrish 1989; Sereno 1991, 1997; Sereno and Arcucci 1993, 1994; Farlow and Chapman 1997). Although, the presence of a functionally tridactyl pes in the recently described dinosauriform *Silesaurus* from the Late Triassic of Poland (Dzik 2003) suggests that this condition may indeed diagnose a more inclusive clade of derived dinosauriforms (including Dinosauria; see Langer and Benton in press). Moreover, a functionally tridactyl pes would also diagnose a larger clade of derived dinosauriforms according to alternative phylogenetic hypotheses of basal Dinosauria proposed by several authors (e.g., Gauthier 1986; Brinkman and Sues 1987; Novas 1992; Fraser et al. 2002). Under these hypotheses, *Herrerasaurus* (and *Eoraptor*), which have a full symmetric tridactyl foot, are considered as derived dinosauriforms closer to Dinosauria than to other Ornithodirans. Nevertheless, more recent analyses of early dinosaur evolution support previous assumptions about the dinosaurian nature of *Herrerasaurus* and *Eoraptor* (Langer 2004; Langer and Benton in press).

According to the previously discussed evidence, all tracks and trackways of types 1, 2 and 3 considered herein to represent bipeds with symmetrical functionally tridactyl foot and fully adducted hindlimbs (parasagittal posture) might correspond to true dinosaur trackmakers even though, the possibility that they represent derived ornithodirans close to dinosaur origin cannot be ruled out. In contrast, the configuration and general shape of the ichnites of the Type 4 suggest a relatively large quadruped with a relatively narrow, functionally tridactyl semi-plantigrade foot and a parasagittal posture of the limbs. Comparable ichnites to Type 4 from the same unit, but from somewhat younger levels and different locality, were previously discussed and related to crurotarsal archosaurs with characteristic symmetrical, narrow (consolidated metatarsus) foot and an erect gait,

as ornithosuchids and some suchians (see Marsicano et al. 2004).

As mentioned above, the large tridactyl footprints identified herein as Type 2 were previously allied to Theropoda by other authors (Arcucci et al. 1995; Forster et al. 1995). Nevertheless and it is important to remark at this point, that no synapomorphies are preserved in the three-toed footprints that might discriminate among theropods, basal saurischian and basal ornithischian groups as possible trackmakers (see Olsen et al. 1998). Furthermore, the bipeds from Ischichuca might be equally representing different groups of basal dinosaurs and/or dinosauriform trackmakers close to dinosaur origin.

If at least one of the Ischichuca trackmakers is referred to a dinosaur taxon, its presence in the Los Rastros levels suggests that dinosaurs had diverged by at least the Middle Triassic (Figure 6). Instead, if all the tracks are assigned to a clade of derived dinosauriforms with symmetrical functionally tridactyl foot, their presence in the Los Rastros levels implies a Middle Triassic age for the diversification of

this lineage. Besides, the footprint record discussed herein supports previous notions that the early history of dinosaurs and their closest relatives might have occurred significantly earlier than is indicated by the body-fossil record alone, probably during the early Middle Triassic (e.g. Sereno 1999; Carrano and Wilson 2001).

As previously discussed, the ichnological record can be used, among other things, to make inferences about the spatial and temporal distribution of tetrapod taxa and, also, as a possible means of tetrapod diversity. In some cases, it complements the skeletal record but can offer new insights in others (Lockley 1998). In the context of the present discussion, our current knowledge of basal dinosaurs and close relatives based exclusively on the skeletal record suggests their sudden appearance by the early Late Triassic (Carnian) with a limited diversification both in diversity and abundance. Nevertheless, if the known footprint record is considered a different scenario is depicted about the timing of their appearance and early diversification. The ichnological record indicates the presence of a diverse and widespread fauna of animals with a bipedal parasagittal posture and tridactyl digitigrade pes during the Middle Triassic in both Laurasia and Gondwana, a condition that the body-fossil record has failed to document thus far.

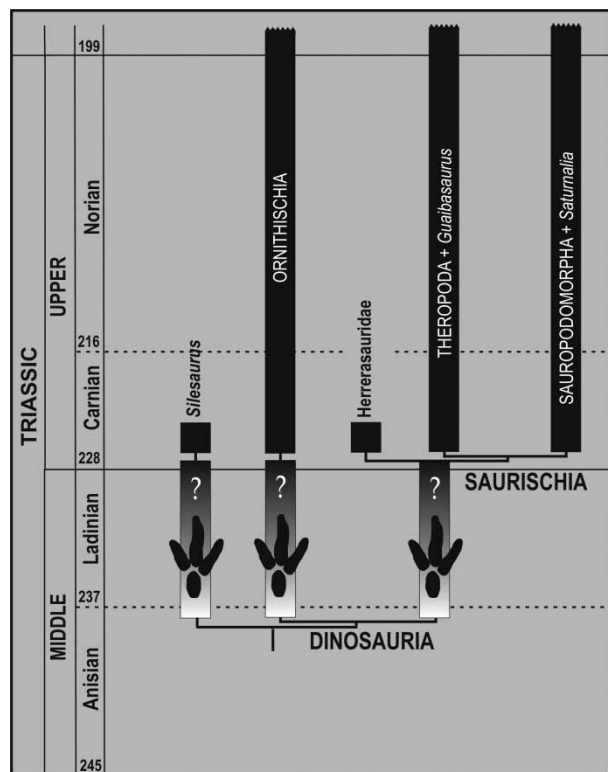


Figure 6. Calibrated phylogeny of early dinosaurs and its sister-taxon. Black bars indicate the Triassic dinosaur body-fossil record. The extension of the temporal ranges due to the incorporation of the ichnological data is represented by the lighter grey bars and the uncertainty about the affinities of the tridactyl footprints from Ischichuca is indicated by a question mark. In any case, the addition of the ichnological data to the phylogeny implies the extension of the early diversification of dinosaurs and/or their closest relatives well into the Middle Triassic. Figure based on Langer and Benton in press. Time scale from Gradstein et al. (2005).

Acknowledgements

CM greatly acknowledge Diego Pol and Max Langer for inviting her to participate in the I Symposium of Early Dinosaur Evolution helded in Rio de Janeiro (Brasil) during August 2005. We specially thank Jeff Wilson (University of Michigan, USA), Diego Pol (Museo Paleontológico Egidio Feruglio, Argentina) and Marco Avanzini (Museo Tridentino di Scienze Naturali, Italy) for their critical reading of the manuscript and pertinent comments. Funding for this work was provided by PIP-CONICET 5120 to CM. Additional financial support was provided by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

References

- Arcucci A, Forster C, Abdala F, May C, Marsicano C. 1995. "Theropod" tracks from the Los Rastros Formation (Middle Triassic), La Rioja Province, Argentina. *Journal of Vertebrate Paleontology* 15:16A.
- Avanzini M. 2002. Dinosauriomorph tracks from the Middle Triassic (Anisian) of the Southern alps I (Valle di Non—Italy). *Bollettino della Società Geologica Italiana* 41:37–40.
- Benton M. 1999. *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philos Trans R Soc Lond B* 354:1423–1446.
- Benton M. 2004. Origin and relationships of Dinosauria. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. 2nd ed. Berkeley: University of California Press. p 7–24.

- Bonaparte JF. 1970. Annotated list of the South American Triassic tetrapods. *Proceedings II Gondwana Symposium* (Pretoria). p. 665–681.
- Bonaparte JF. 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 2:362–371.
- Bonaparte JF. 1997. El Triásico de San Juan—La Rioja, Argentina y sus dinosaurios. Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires.
- Bonaparte JF, Ferigolo J, Ribeiro AM. 1999. A new early Late Triassic saurischian dinosaur from Rio Grande do Sul state, Brazil. In: Tomida Y, Rich TH, Vickers-Rich P, editors. *Proceedings of the Second Dinosaur Symposium*. National Science Museum Monograph. Vol. 15. p 89–109.
- Brinkman DB, Sues H-D. 1987. A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. *Palaeontology* 30: 493–503.
- Carrano MT. 2000. Homoplasy and the evolution of dinosaur locomotion. *Paleobiology* 26:489–512.
- Carrano MT, Wilson JA. 2001. Taxon distributions and the tetrapod track record. *Paleobiology* 27:564–582.
- Courel L, Demathieu G. 1995. Tentative stratigraphic correlation using ichnological data from continental sandstone series and marine faunas in the middle Triassic of Europe. *Albertina* 15:83–91.
- Demathieu GR. 1989. Appearance of the first Dinosaur Tracks in the French Middle Triassic and their probable significance. In: Carpenter K, Currie PJ, editors. *Dinosaur systematics: Approaches and perspectives*. Cambridge University Press. p 201–207.
- Dzik J. 2003. A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 23:556–574.
- Ellenberger P. 1970. Les niveaux paléontologiques de premier apparition des Mammifères Primordiaux en Afrique du Sud et leur Ichnologie: Etablissement de zones stratigraphiques détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias Supérieur à Jurassique). In: Haughton SH, editor. *II Symposium on Gondwana Stratigraphy and Palaeontology*. Pretoria: Council for Scientific and Industrial Research. p 343–370.
- Ellenberger P. 1972. Contribution à la classification des pistes de vertèbres du Trias: Les types du Stormberg d’Afrique du Sud (I partie). *Palaeovertebrata* 104:1–152.
- Ellenberger P. 1974. Contribution à la classification des pistes de vertèbres du Trias: Les types du Stormberg d’Afrique du Sud (II partie): Le Stormberg Supérieur-I. Le biome de la zone B/1 ou niveau de Moyeni: Ses biocénoses). *Palaeovertebrata* 141:1–202.
- Farlow J, Chapman R. 1997. The scientific study of dinosaur footprints. In: Farlow J, Brett-Surman M, editors. *The complete Dinosaur*. Bloomington: Indiana University Press. p 519–553.
- Flynn J, Parrish M, Ratokosamimanana B, Simpson W, Whatley R, Wyss A. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286:763–765.
- Forster CA, Arcucci AB, Marsicano CA, Abdala F, May CL. 1995. New vertebrate material from the Los Rastros Formation (Middle Triassic), La Rioja Province, northwestern Argentina. *Journal of Vertebrate Paleontology* 15:29A.
- Fraser N, Padian K, Walkden G, Davis L. 2002. Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. *Palaeontology* 45:79–95.
- Galton PM. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur from Brazil, with notes on the Herrerasauridae and Poposauridae. *Paläontologische Zeitschrift* 51:234–245.
- Gauffre F-X. 1993. The prosauropod dinosaur *Azendohsaurus laaroussii* from the Upper Triassic of Morocco. *Palaeontology* 36:897–908.
- Gauthier J. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. *The origin of birds and the evolution of flight*. San Francisco: California Academy of Sciences. p 1–55.
- Gradstein FM, Ogg JG, Smith AG. 2005. *A geologic timescale 2004*. Cambridge University Press.
- Haubold H, Klein H. 2000. Die dinosauroiden Fährten *Parachirotherium—Atreipus—Grallator* aus dem unteren Mittelkeuper (Obere Trias: Ladin, Karn, ?Nor) in Franken. *Hallesches Jahrbuch für Geowissenschaften*, part B, 22:59–85.
- Haubold H, Klein H. 2002. Chirotherien und Grallatoriden aus der Unteren bis Oberen Trias Mitteleuropas und die Entstehung der Dinosauria. *Hallesches Jahrbuch für Geowissenschaften*, part B, 24:1–22.
- Henderson DM. 2003. Footprints, trackways, and hip heights of bipedal dinosaurs—testing hip height predictions with computer models. *Ichnos* 10:99–114.
- Jalil N-E, Knoll F. 2002. Is *Azendohsaurus laaroussii* (Carnian, Morocco) a dinosaur? *Journal of Vertebrate Paleontology* 22:70A.
- Langer MC. 2004. Basal Saurischia. In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria*. 2nd ed. Berkeley: University of California Press. p 25–46.
- Langer MC, Abdala F, Richter M, Benton MJ. 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes rendus de l’Académie des Sciences, Paris. Sciences de la Terre et des Planètes* 329:511–517.
- Langer MC, Benton MJ. Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology*. In press.
- Leonardi G, editor. 1987. *Glossary and manual of Tetrapod Footprint Palaeoichnology*. Brasília: Departamento Nacional de Produção Mineral.
- Lockley MG. 1998. The vertebrate track record. *Nature* 396:429–432.
- Lockley M, Hunt AP. 1995. *Dinosaur tracks*. New York: Columbia University Press.
- Lockley M, Hunt AP, Meyer C. 1994. Vertebrate tracks and the ichnofacies concept: Implications for paleoecology and palichnostratigraphy. In: Donovan S, editor. *The paleobiology of trace fossils*. Wiley and Sons. p 241–268.
- Lockley M, Meyer C. 2000. *Dinosaur tracks and other fossil footprints of Europe*. New York: Columbia University Press.
- Lockley MG, Wright JL, Hunt AP, Lucas S. 2001. The Late Triassic sauropod track record comes into focus: old legacies and new paradigms. *New Mexico geological society guidebook, 52nd Field Conference, Geology of the Llano Estacado*. p 181–190.
- Lucas S. 2003. Triassic tetrapod footprint biostratigraphy and biochronology. *Albertina* 28:75–84.
- Lucas S, Hancox J. 2001. Tetrapod-based correlation of the nonmarine Upper Triassic of Southern Africa. *Albertina* 25:5–9.
- Lucas S, Hunt AP, Lockley MG. 2001. Tetrapod footprint ichnofauna of the Upper Triassic Redonda Formation, Chinle Group, Quay County, New Mexico. *New Mexico geological society guidebook, 52nd Field Conference, Geology of the Llano Estacado*. p 177–180.
- Mancuso A. 2005. *Tafonomía en ambientes lacustres: Estudio integral de las asociaciones fósiles de las secuencias lacustres del Triásico Medio de la Cuenca de Ischigualasto-Villa Unión (formaciones Chañares, Los Rastros e Ischichuca)*. Unpublished PhD Thesis. Universidad de Buenos Aires, Argentina.
- Marsicano CA, Barredo S. 2004. A Triassic tetrapod footprint assemblage from southern south America: Palaeobiogeographical and evolutionary implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 203:313–335.
- Marsicano CA, Arcucci AB, Mancuso A, Caselli AT. 2004. Middle Triassic tetrapod footprints of southern South America. *Ameghiniana* 41:171–184.
- Melchor R, de Valais S. 2006. A review of Triassic tetrapod track assemblages from Argentina. *Palaeontology* 49:355–379.
- Milana JP, Alcober OA. 1995. Modelo tectosedimentario de la Cuenca triásica de Ischigualasto, San Juan, Argentina. *Revista de la Asociación Geológica Argentina* 49:217–235.

- Novas F. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. *Palaeontology* 35:51–62.
- Olsen P, Smith JB, McDonald NG. 1998. Type material of the type species of the classic theropod footprint genera *Eubrontes*, *Anchisauripus*, and *Grallator* (Early Jurassic, Hartford and Deerfield Basins, Connecticut and Massachusetts, USA). *Journal of Vertebrate Paleontology* 18:586–601.
- Olsen PE, Kent DV, Sues H-D, Koeberl C, Huber H, Montanari A, Rainforth EC, Fowell SJ, Szajna MJ, Hartline BW. 2002. Ascent of dinosaurs linked to an iridium anomaly at the Triassic-Jurassic boundary. *Science* 296:1305–1307.
- Padian K. 1997. Phylogeny of dinosaurs. In: Currie PJ, Padian K, editors. *Encyclopedia of dinosaurs*. California: Academic Press. p 546–551.
- Parrish JM. 1989. Phylogenetic patterns in the manus and pes of early Mesozoic archosauriform reptiles. In: Gillette DD, Lockley MG, editors. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press. p 249–258.
- Raath MA, Kitching JW, Shone RW, Rossouw GJ. 1990. Dinosaur tracks in Triassic Molteno sediments: the earliest evidence of dinosaurs in South Africa. *Palaeontologia Africana* 27:89–95.
- Raath MA, Oesterlen PM, Kitching JW. 1992. First record of Triassic Rhynchosauria (Reptilia: Diapsida) from the Lower Zambezi Valley, Zimbabwe. *Palaeontologia Africana* 29:1–10.
- Rogers R, Swischer C III, Sereno P, Monetta A, Forster C, Martínez R. 1993. The Ischigualasto tetrapod Assemblage (Late Triassic, Argentina) and K/40 Ar/39 dating of dinosaur origins. *Science* 260:794–797.
- Sereno PC. 1991. Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology* 11:1–53.
- Sereno PC. 1997. The origin and evolution of dinosaurs. *Annu Rev Earth Planet Sci* 25:435–489.
- Sereno P. 1999. The evolution of dinosaurs. *Science* 284: 2137–2147.
- Sereno P, Arcucci A. 1993. Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *Journal of Vertebrate Paleontology* 13:385–399.
- Sereno P, Arcucci A. 1994. Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, *gen. nov.* *Journal of Vertebrate Paleontology* 14:53–73.
- Sereno P, Forster CA, Rogers RR, Monetta AM. 1993. Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature* 361:64–66.
- Thulborn RA. 1989. The gaits of dinosaurs. In: Gillette DD, Lockley MG, editors. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press. p 39–50.
- Wilson J. 2005. Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. *Paleobiology* 31:400–423.
- Yates AM, Kitching JW. 2003. The earliest known sauropod dinosaur and the first steps towards sauropod locomotion. *Proc R Soc Lond Ser B* 270:1756–1758.