



Large caviomorph rodent footprints of the Late Oligocene Vinchina Formation, Argentina

Verónica Krapovickas and Norma L. Nasif

ABSTRACT

Footprints and trackways provide valuable information about trackmaker behaviour, locomotion, spatial and temporal distribution, among others. Here we describe tetradactyl mammalian footprints and trackways recorded in Late Oligocene meandering fluvial deposits of the Vinchina Formation (Oligocene - Early Miocene). The morphological analysis of the footprints suggests that they were produced most likely by dinomyid caviomorph rodents or a close relative. The footprints, unlike any previously recorded, are designated to a new ichnospecies, *Tacheria troyana*. The occurrence of these footprints potentially extends the temporal record of dinomyids in Argentina to the Late Oligocene.

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KEY WORDS: trace fossil; Cenozoic; South America; dinomyid caviomorph rodents; Late Oligocene: La Rioja province

INTRODUCTION

The Vinchina Basin is a thick continental succession deposited under a wide variety of depositional systems (i.e., fluvial, lacustrine and eolian) that bears a diverse and exceptionally preserved ichnofauna. It documents several assemblages of Cenozoic South American trace fossils very different from any other recorded until now. The basin, mostly assigned to the Vinchina and Toro Negro Formations (Turner 1964; Ramos 1970), crops out at southern South America, at almost 29 degrees

South latitude, at northwestern Argentina, La Rioja province (Figure 1). Vertebrate body fossils are lacking at the Oligocene-Early Miocene Vinchina Formation. Conversely, fluvial and lacustrine faces of the unit host a rich invertebrate and vertebrate ichnofauna (Tripaldi et al. 2001; Krapovickas et al. 2009a; Melchor et al. 2010). The footprints studied herein are preserved in floodplain deposits of meandering fluvial systems together with other avian and mammalian trace fossils. They consist of tridactyl large cursorial birds, *Gruipeda* isp., *Macrauchenichnus* isp., small tridactyl rodent-like mam-

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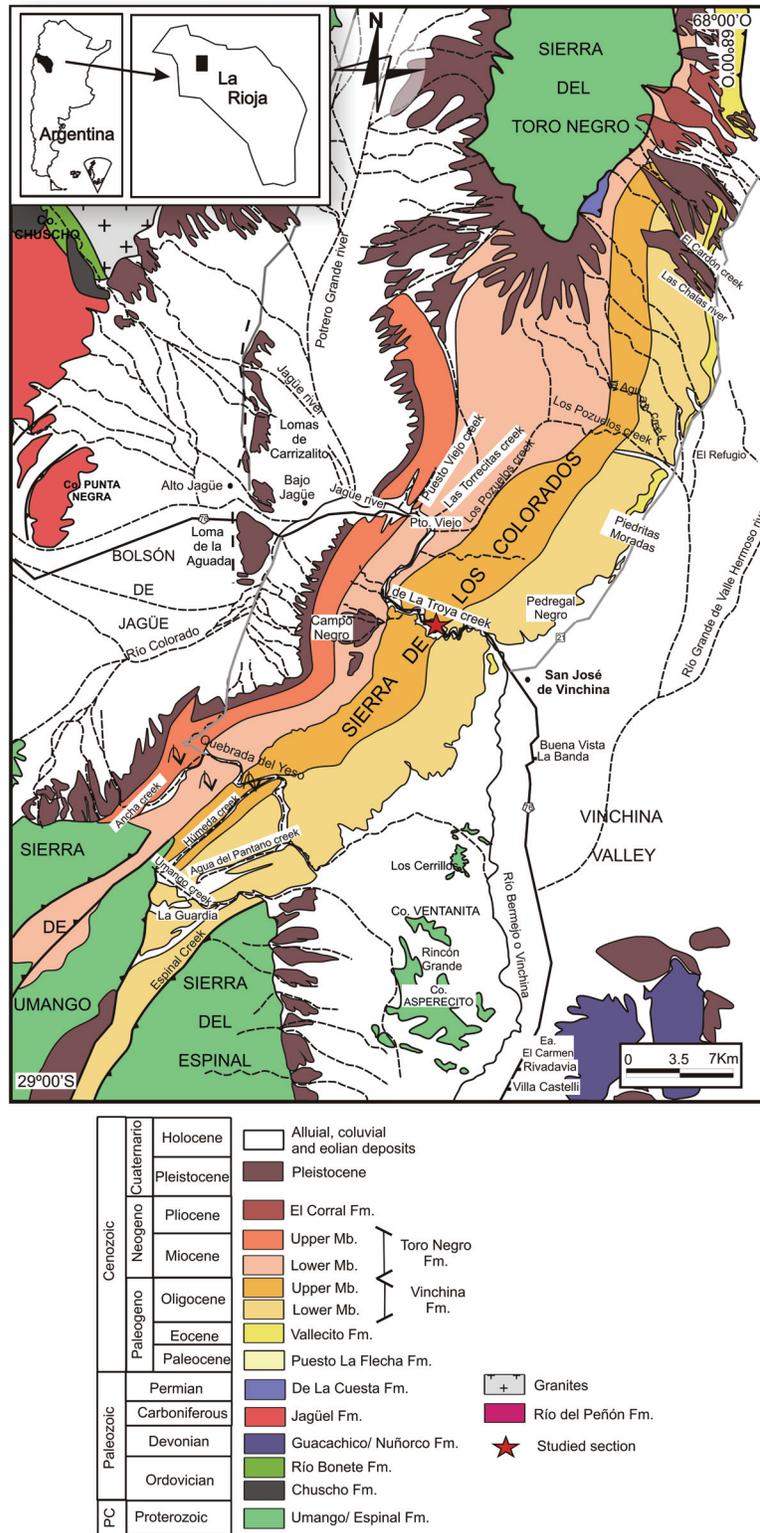


FIGURE 1. Geologic map of the Vinchina Basin at Vinchina, La Rioja province, Argentina, showing the location of the studied footprints. Modified from Ciccioli 2008.

mals, and small tridactyl to tetradactyl footprint with pronounced scratch marks. The overlying Toro Negro Formation (Miocene-early Pliocene) records a rich ichnofauna preserved at exposed sandbars and crevasse-splay deposits of anastomosed fluvial systems developed under a semi-arid climate (Krapovickas et al. 2009b). The invertebrate ichnofauna is composed of meniscate trace fossils (*Taenidium barretti* and *Scoyenia gracilis*), dwelling structures (*Palaeophycus tubularis*) and grazing trails (*Helminthopsis hieroglyphica*). The vertebrate ichnofauna includes avian (*Fuscinapeda sirin*, incumbent footprint, slender anisodactyl footprint) and mammalian footprints (*Macrauchenichnus rector*, cf. *Venatoripes riojanus*, small heteropod footprint, kidney-like footprints and oval impressions) (Krapovickas et al. 2009a, 2009b).

The accurate description of footprints and the identification of possible trackmakers expand the knowledge of their temporal and spatial distribution. Interestingly, the footprints of Cenozoic South American rodents or rodent-like mammals are uncommon in the geologic record. The scarce examples are mostly recorded since the Late Miocene to the Pleistocene of Argentina and were interpreted mainly as hydrochoerids and caviids (e.g., Angulo and Casamiquela 1982; Aramayo and M. de Bianco 2009; Krapovickas et al. 2009b). Here we present a new footprint ichnogenus and ichnospecies and analyze its putative trackmaker based on anatomical features of the postcranial skeleton that are transcribed to the footprint morphology and trackway pattern. In this context, we discussed its assignation to Dinomyidae (Rodentia, Hystricognathi, Caviomorpha) and the possible expansion of the temporal and spatial distribution of the family.

STRATIGRAPHIC AND SEDIMENTARY CONTEXT

The Vinchina broken-foreland basin, in northwestern Sierras Pampeanas, La Rioja province, Argentina (Figure 1), was filled by non-marine deposits mostly assigned to the Vinchina and Toro Negro Formations (Turner 1964; Ramos 1970). The stratigraphic scheme of the basin was recently modified by Ciccioli (2008) and Ciccioli et al. (2010). The basin infill is divided into five formational units (Figure 1). From bottom to top, they are: Puesto La Flecha (Paleocene-Early Eocene), Vallecito (Eocene), Vinchina (Oligocene-Early Miocene), Toro Negro (Miocene-Early Pliocene) and El Corral Formations (Pliocene).

The Vinchina Formation is a thick red-bed succession of 5100 m thick, essentially composed of reddish sandstone, mudstone and intra- and extraformational conglomerate with abundant desiccation cracks (Turner 1964; Tripaldi et al. 2001). This sedimentary succession is interpreted as having been deposited by different fluvial styles (anastomosed, meandering and braided channels) with minor intercalations of shallow lacustrine and eolian deposits of semiarid climate conditions (Turner 1964; Tripaldi et al. 2001). The unit is divided in two members (Ramos 1970). The Lower Member (2156 m thick) consists of thick beds of medium to coarse sandstone with interbedded intra- and extraformational conglomerate and mudstone. It is separated from the Upper Member by a low-angle erosive surface (Tripaldi et al. 2001). Amalgamated sandstone beds with common intraformational conglomerate characterize the Upper Member (4428 m thick) (Tripaldi et al. 2001). The material studied herein is exposed at de la Troya creek, more precisely at the base of the Upper Member of the Vinchina Formation, in the lowermost 350 m. The footprints are recorded in laminated and massive mudstone with desiccation cracks and raindrop imprints deposited in overbank floodbasin areas of meandering fluvial systems (Figure 2) (Tripaldi et al. 2001). The succession ends at the contact with the overlying Toro Negro Formation that constitutes a high relief erosional unconformity surface (Ciccioli 2008).

The age of the Vinchina Formation is actually considered Oligocene to Early Miocene since new stratigraphic relationships and K40/Ar40 radiometric dating were reported for the Vinchina Basin (Ciccioli et al. 2005; Tedesco 2007; Ciccioli 2008; Ciccioli et al. 2010). Previously, Tabbutt et al. (1987) suggested an Upper Miocene age for the Vinchina Formation based on a zircon fission-track age of 7.3 ± 1.2 Ma of uncertain stratigraphic position. Ciccioli (2008) reported for the middle part of the Vinchina Formation in the northern part of the studied area (Los Pozuelos creek) a 25.3 ± 0.9 Ma K40/Ar40 dating. These data are consistent with the 8.6 ± 0.3 Ma and 6.8 ± 0.2 Ma K40/Ar40 dating of two vitric tuffs of the middle-Upper part of the overlying Toro Negro Formation (Ciccioli et al. 2005). Trace fossil studied herein are preserved near the base of the Upper Member of the Vinchina Formation, below the 25.3 ± 0.9 Ma K/Ar dating, consequently considered Late Oligocene in age.

SYSTEMATIC ICHNOLOGY

Tacheria igen. nov.



FIGURE 2. Outcrop photographs of the Vinchina Formation at the studied area. 1. Meandering fluvial system facies that record the studied footprints. 2. General view of the tracking surface.

Etymology. Refers to “the hands” (greek ΤΑ ΧΕΡΙΑ, the hands), how the traces are known by the local inhabitants of Vinchina.

Geographic and stratigraphic location. Preserved at the Vinchina Formation at La Troya creek, nearby San Jose de Vinchina town, La Rioja province, Argentina.

Type ichnospecies. *Tacheria troyana*

Diagnosis. As is a monospecific ichnogenus, the diagnosis is the same as for the ichnospecies.

Tacheria troyana isp. nov.

2007 “huellas cuadrúpedas tetradáctilas” Melchor et al., p. 54.

2009a “large tetradactyl rodent-like footprints” Krapovickas et al.

2009b “large tetradactyl rodent-like footprints” Krapovickas et al.

2010 “large tetradactyl footprints” Melchor et al., p. 7.

Etymology. Refers to La Troya creek, place where the holotype material was found.

Holotype. The set manus-pes Tw1-1 included in one trackway (Tw1) with four footprints sets (Figures 3 and 4). Material preserved in situ.

Paratypes. Trackway 2 (Tw2) and four isolated sets of manus-pes footprints (F1-F4).

Referred material. One set of manus-pes footprints (Figure 5).

Comment. The referred material comes from Cenozoic deposits of the Quebrada del Jarillal Formation at Sierra de Mogna (Middle-Late Miocene), San Juan province, Argentina. The footprints were originally described and illustrated by Casamiquela R.M. in Cuerda et al. (1984, plate XV, figure 2 and plate XVI, figures 1, 2) and later also documented by Leonardi (1994, plate XIX, figure 11). Unfortunately, the material was never numbered and was not possible to located by the authors.

Diagnosis. Tetradactyl manus and pes impressions of sub-equal size with long and robust digits with strong elongated claws. Lateral digits (II-V) are shorter than central digits (III-IV). Elongated phalangeal–metapodial pad impressions are present. Trackways are narrow (footprint impressions near to the midline), and the pes are placed more lateral to the midline than the manus. Footprints are usually digitigrade although plantigrade footprints can occur.

Description. Footprints produced by quadrupeds with homopody. Forefoot and hind foot impressions are tetradactyl and digitigrade to plantigrade. In both the manus and pes, digits are long and robust, with strong elongated and slight curved

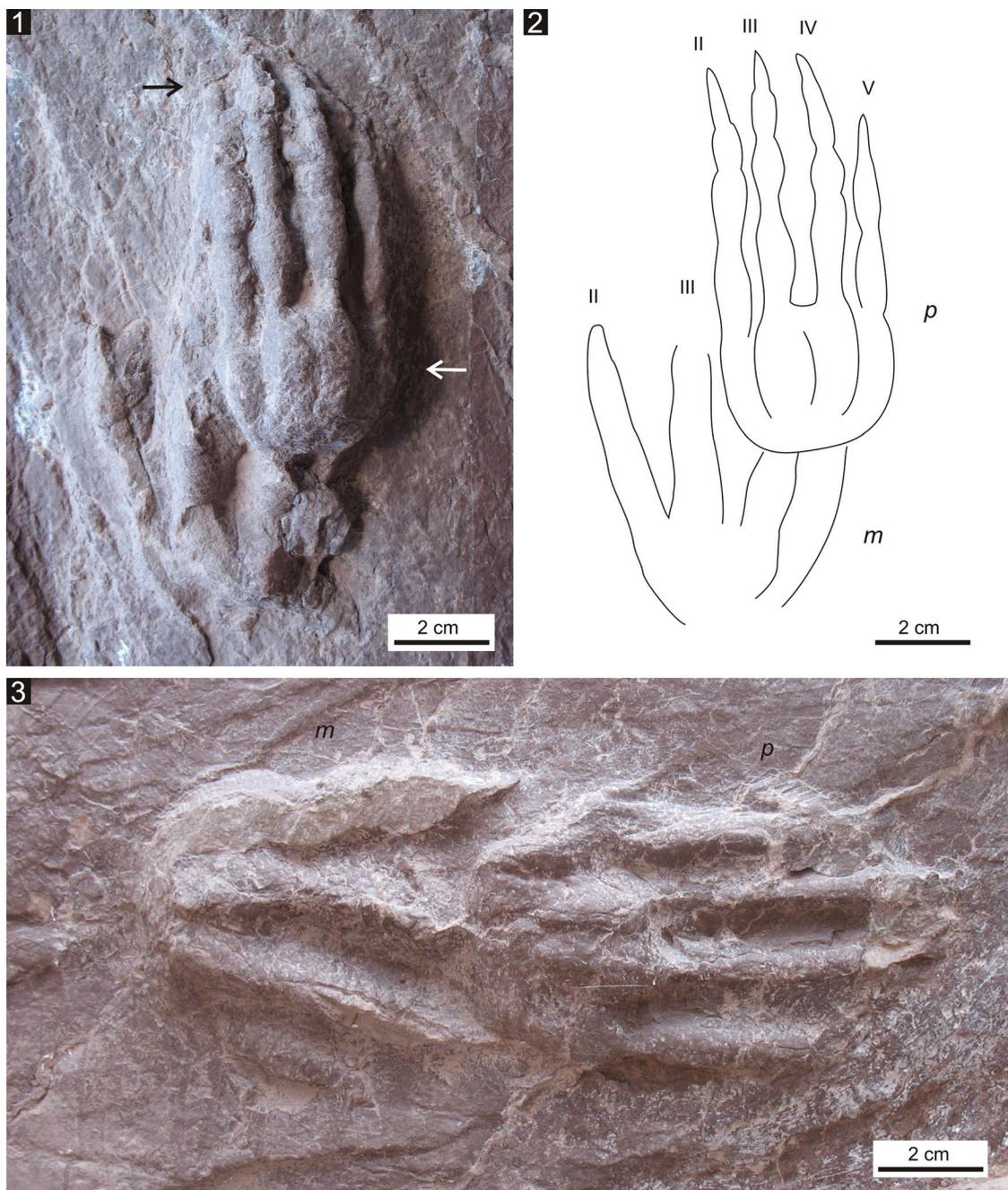


FIGURE 3. *Tacheria troyana* from the Vinchina Formation. Material preserved in the field. 1. Manus–pes set Tw1-1 (*m* and *p* respectively). 2. Outline drawing of Manus–pes set Tw1-1. 3. Manus–pes set F2. Note the strong elongated claws (black arrow) and the conspicuous phalangeal–metapodial pad impressions (white arrow).

claws (Figure 3). The digits III and IV are almost equal in length and longer than digits II and V, with the latter slightly shorter than digit II (Figure 3, Table 1). The hind foot impression (pes) generally overlaps the forefoot impression (manus) (Figures 3 and 4). Consequently, in some specimens it is difficult to observe all the characteristics of the forefoot impressions. When the hind foot and fore-

foot impressions are digitigrades, they are sub-equal in size (Table 1). Nevertheless, when the hind foot impression is plantigrade (Figure 4, Tw 2-1), it is markedly longer than the forefoot impression (Table 1). The average length of the hind foot impression is 111 mm, and the average width is 58 mm. The average length of the forefoot impression is 100 mm, and the average width is 72 mm. Con-

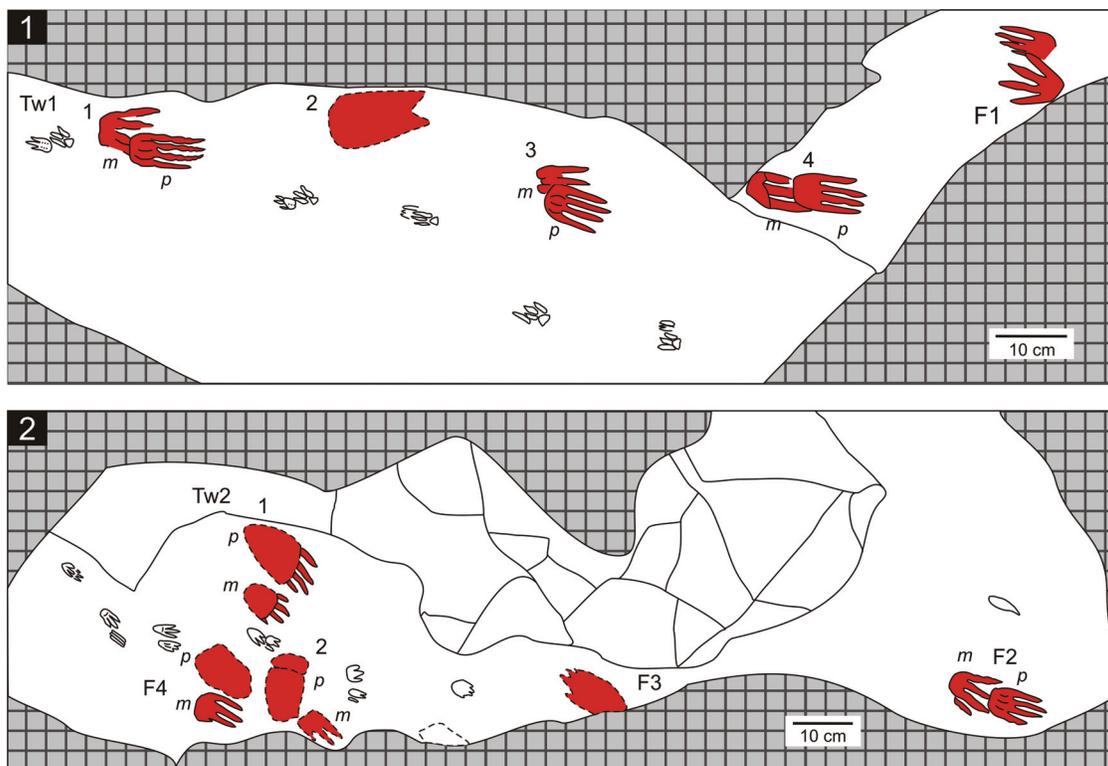


FIGURE 4. Drawing map of the tracking surface. 1. Upper area of the tracking surface. 2. Lower area of the tracking surface.

spicuous elongate phalangeal–metapodial (metacarpal and metatarsal) pads are present and specially developed behind digits III and IV. Together they represent the palm, which is slightly wider than long (Table 1). In trackways, hind foot imprints are frequently placed more lateral to the midline than the forefoot impression (Figure 4). Pace and stride are long (313 mm and 625 mm respectively, see Table 2) with footprint impres-

sions near to the midline producing a narrow trackway (external width of 190 mm).

DISCUSSION

Analysis of the Putative Trackmakers

The morphology and size range of the footprints and trackways analyzed herein strongly suggests that they were produced by a rodent or rodent-like mammal of medium to large size. Among all known South American taxa with tetradactyl manus and pes, the extinct rodent-like not-ungulates (i.e., hegetotheriids and mesotheriids) can be ruled out. Hegetotheriids as *Hegetotherium*, *Pachyrukhos* and *Hemihegetotherium* have digit III longer than digits II and IV, and digit V is greatly reduced (Sinclair 1909). In addition, *Pachyrukhos* has arrow-like hoofed ungual phalanges that do not correspond with the long, heavy, and pointed claws observed in the Vinchina specimens. And, mesotheriids as *Trachytherus* and *Mesotherium* have a pentadactyl manus with a reduced digit V and the remaining four digits subequal in size (Shockey et al. 2007). The ungual phalanges are moderately flattened with the distal ends fissured (Shockey et al. 2007).



FIGURE 5. Manus-pes set of the footprints preserved at Sierra de Mogna, San Juan province, Argentina. Modified from Leonardi (1994).

TABLE 1. Footprint measurements of *Tacheria troyana*. DN, digit number; TL, total length; TW, total width; L, digit length; PL, palm/sole length; PW, palm/sole width; SD, standard deviation; m, manus; p, pes; m-p, manus pes distance. Measurements are in mm.

| Track Number | DN | | TL | | TW | | LII | | LIII | | LIV | | LV | | PL | | PW | | m-p |
|-----------------|----|----|-----|-----|----|------|-----|----|------|----|-----|----|----|----|----|----|----|-----|-----|
| | p | m | p | m | p | m | p | m | p | m | p | m | p | m | p | m | p | m | |
| Tw1-1 r | 4 | 4? | 105 | 100 | 45 | 70 | 65 | 52 | 68 | - | 63 | - | 52 | - | 40 | 35 | 44 | 54 | 60 |
| Tw 1-2 l | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Tw 1-3 r | 4 | 4? | 103 | - | 58 | ≈ 70 | 59 | 40 | 62 | - | 60 | - | 52 | - | 30 | 40 | 55 | 55 | 40 |
| Tw 1-4 l | 4 | - | 103 | - | 51 | - | 58 | - | 70 | - | 70 | - | 65 | 70 | 42 | 38 | 50 | 57 | 70 |
| Tw 2-1 r | 4 | 4 | 160 | 103 | 75 | 75 | 45 | 60 | 60 | 58 | 58 | 42 | 42 | 37 | 37 | 40 | 50 | 100 | |
| Tw 2-2 l | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| F1 | 4 | 4 | 102 | 110 | 54 | 80 | 45 | 46 | 55 | 60 | 53 | 62 | 40 | 60 | 30 | 32 | 45 | 35 | 40 |
| F2 | 4 | 4 | 102 | 90 | 60 | 74 | 60 | 52 | 65 | - | 60 | 55 | 45 | 40 | 40 | 35 | 50 | 50 | 100 |
| F3 | 4 | - | 100 | - | 65 | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| F4 | 4 | - | 95 | 95 | 60 | 60 | - | - | - | - | - | - | - | - | 40 | 40 | 55 | 90 | |
| average | - | - | 111 | 100 | 58 | 72 | 57 | 47 | 64 | 60 | 61 | 58 | 51 | 53 | 36 | 37 | 49 | 51 | 71 |
| SD | - | - | 22 | 8 | 10 | 7 | 7 | 5 | 6 | 0 | 6 | 4 | 9 | 14 | 6 | 3 | 4 | 7 | 26 |

The South American Hystricognathi rodents (caviomorphs) of medium to large size and known apendicular skeleton as agoutis (Dasyproctidae), capybaras (Hydrochoeridae), pacas (Agoutidae) (Figure 6.1), maras (Caviidae: Dolichotinae) and *Erethizon* (within Erethizontidae) have tetradactyl manus and pentadactyl or tridactyl pes (Ellerman 1940; Candela and Picasso 2008), differing from the Vinchina footprints. The chinchillas and vizcachas (Chinchillidae) have four digits in both manus and pes. In the hind foot digit V is reduced and placed high on the foot, and does not reach the ground resulting in a functionally tridactyl foot (Ellerman 1940). It is completely reduced in the plains vizcacha (Ellerman 1940). In the same vein, the coypo (Myocastoridae) have five digits on the hind foot with webbing between digits I-IV and five digits on the forefoot with usually four digits imprints (Figure 6.2) (Ellerman 1940). The tetradactyl homopod *Coendou* differs from the Vinchina trackmaker in the wider plantar pads, equal digit length and pointed but thinner claws (Figure 6.3) (Candela and Picasso 2008). Within caviomorph

TABLE 2. Trackway measurements of *Tacheria troyana*. P, pace; S, stride; P α , pace angulations. Measurements are in mm and degrees.

| | N | P | S | P α |
|---------|-----|-----|-----|------------|
| Tw1 1-2 | 330 | - | - | - |
| Tw1 2-3 | 310 | 640 | 138 | |
| Tw1 3-4 | 300 | 610 | 147 | |
| Tw2 1-2 | 260 | - | - | |
| Av | 313 | 625 | 143 | |
| SD | 15 | 21 | 6 | |

rodents with known distal apendicular skeleton, *Tacheria troyana* is strongly comparable with those footprints that could be produced by the tetradactyl manus and pes of dinomyids (Figure 7).

The only living species of Dinomyidae, *Dinomys branickii*, have lost external signs of the first digit in the forefoot and hind foot, being functionally tetradactyl (Figure 7) (Peters 1873; Grand and Eisenberg 1982). The remaining skeletal elements of the pollex and hallux are found within a well-developed pad (Grand and Eisenberg 1982). Moreover, in *Dinomys* the third and fourth digits are almost equal in length and longer than the second and fifth (Figure 7) (Grand and Eisenberg 1982), as in *Tacheria troyana* (Figure 3). A similar pattern is present in the Miocene extinct dinomyids of La Venta, Colombia as *Olenopsis aequatorialis* (sensu Fields 1957, p. 337). *Olenopsis*, with longer and more robust digits than *Dinomys*, also would have functional tetradactyl manus and pes. It has five digits, but the first digit is represented by strongly reduced metacarpal, metatarsal I and proximal phalanges (Fields 1957, p. 341). Both *Dinomys* (Figure 7 and 8) and *Olenopsis* have hind foot lengths of twice the length of the forefoot and bulbous terminal metapods and phalanges (Peters 1873; Fields 1957). The forefoot and hind foot of *Dinomys*, in plantar view, have quite long pads marked by deep creases that run across the metacarpal and metatarsal phalangeal junctions (Figure 7). The skin extends halfway to the tips of the strong and recurved claws (Grand and Eisenberg 1982). Both features are clearly observed in *Tacheria troyana* (Figure 3).

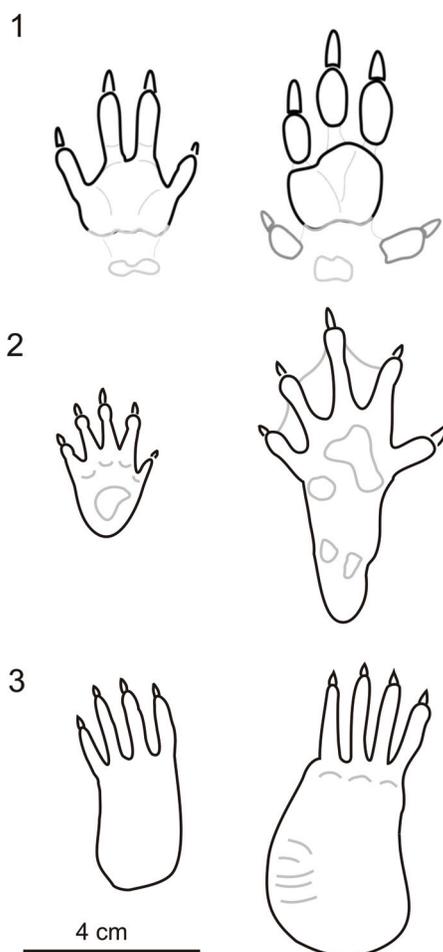


FIGURE 6. Footprints of extant caviomorph rodents. 1. Paca (*Cuniculus paca*) footprints, right forefoot (left) and hind foot (right) impression. 2. Coypu (*Myocastor coypus*) footprints, right forefoot (left) and hind foot (right) impression. 3. *Coendou* footprints, right forefoot (left) and hind foot (right) impression. Modified from De Angelo et al. (2008).

Grand and Eisenberg (1982) suggested that *Dinomys* has a long and narrow foot with a slightly mobile preaxial pad related with its predominately cursorial habit; opposite to the arboreal *Coendou* that has a short and broad foot with a more flexible, opposable pad for powerful grasping. The trackways of *Tracheria troyana* represent a digitigrade cursorial gait to occasionally plantigrade, as occurs in *Dinomys* (see Peters 1873, p. 233, pl. 3). The footprints represent the impression on the substrate of the digits and the metapodial-phalangeal junctions (Figure 7). That portion of the feet represents in *Dinomys* the half of the total length of the forefoot and a third of the total length of the hind foot (Figure 8). Based on the autopodial measurements provided by Peters (1873, pp. 233-234)

(manus 80 mm long and 30 mm wide, pes 125 mm long and 32 mm wide), *Dinomys* would produce forefoot and hind foot footprints of similar length (approximately 4 cm long), although the hind foot is 36% longer. The same reasoning could be used to explain the sub-equal size (see Table 1) of the Vinchina forefoot and hind foot impressions.

The Vinchina footprints are bigger than those produced by *Dinomys*, actually twice the size, denoting that its trackmaker was bigger than *Dinomys*. Indeed, the inferred gleno-acetabular distance of the trackmaker obtained through trackway analysis (sensu Thulborn 1990) is approximately 60 cm long. The body size of Oligocene and Middle Miocene dinomyids is fairly similar to *Dinomys*, although several species reach giant sizes during the Late Miocene and Pliocene (Rinderknecht and Blanco 2008; Nasif 2010). Another family of caviomorph rodents that include large-sized specimens is Neopiblemidae. Both families (Dinomyidae and Neopiblemidae) include fossils that belong to species of almost 10 times the size of the largest living rodent *Hydrochoerus* (Horovitz et al. 2006; Nasif 2010). Horovitz et al. (2006) proposed a phylogenetic hypothesis in which the pakarana *Dinomys branickii* appears as the closest extant relative of neopiblemids. The suggested hypothesis lead us to consider that the Vinchina trackmaker could also belong to a representative of Neopiblemidae. Unfortunately no morphological data support this hypothesis because no specimen of the group has preserved the distal appendicular skeleton, and the family lacks recent representatives. Moreover, the phylogenetic position of Dinomyidae within the caviomorphs is, at present, discussed. And, a recent phylogenetic hypothesis does not support the Chinchilloid superfamily and link Dinomyidae with Erethizontidae into Erethizontoids (Nasif 2009, 2010).

Carrano and Wilson (2001) established that when analyzing footprint producers, it is preferable to establish osteological synapomorphies that could be identified in the fossil footprints. Unfortunately, until now, phylogenetic studies of caviomorph rodents (including dinomyids) do not include characters of the distal autopodium in their analyses (e.g., Adkins et al. 2001; Huchon and Douzery 2001; Spotorno et al. 2004; Horovitz et al. 2006; Nasif 2010). In that context, we analyzed putative trackmakers based on anatomical features of the postcranial skeleton that are transcribed to the footprint morphology and trackway pattern. Until new osteological evidence is provided by the finding of new specimens of caviomorph rodents

The Dinomyid Bone-Teeth Record in South America

The dinomyids are a monophyletic group of hystricognathe rodents exclusive to South America diverse and widely distributed within the Miocene-Pliocene (Nasif 2010). They are represented by a single extant species, still poorly known, *Dinomys branickii*, dwelling in forested areas of the eastern Andes of Brazil, Perú, Ecuador, Bolivia, Venezuela and Colombia (White and Alberico 1992) (Figure 9). Until the recent revision of the Dinomyidae family by Nasif (2010), the systematic and evolutionary history of extinct dinomyids was still poorly understood despite its important South American Neogene record. Many extinct taxa are only known by their teeth, and most studies are restricted to cranial and dental anatomy.

The oldest record of the family corresponds to *Branisamys luribayensis* Hoffstetter and Lavocat 1970, from the Late Oligocene of Bolivia (Hoffstetter and Lavocat 1970; Patterson and Wood 1982; Mones 1986; Vucetich 1986; Nasif 2010). During the Neogene, a few species are represented in various countries of South America though there is a wide record of dinomyids in Argentina. In Ecuador, dinomyids are preserved in sediments of possible Miocene age at the Nabon area (Fields 1957; Patterson and Wood 1982). Also, they are preserved in La Venta (Middle Miocene), Colombia (Fields 1957; Walton 1997); the Urumaco Formation, (Laventanense South American Land Mammal Age), Venezuela (Linares 2004); Rio Acre (Late Miocene) and Minas Gerais (Pliocene-Pleistocene), Brazil (Paula Couto 1951; Frailey 1986); and the Camacho (Late Miocene) and Raigón formations (Pliocene-Pleistocene), Uruguay (Mones and Castiglioni 1979; Rinderknecht and Blanco 2008). In Argentina there is a wide record of dinomyids, and they are known

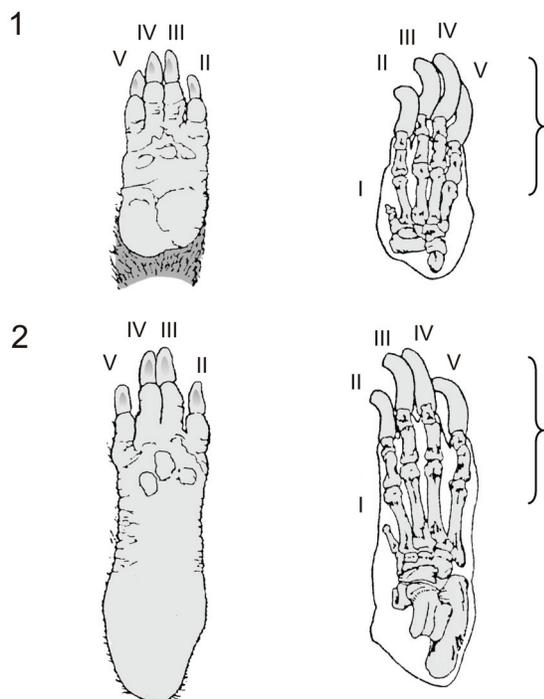


FIGURE 7. Foot structure of *Dinomys branickii*. 1. Fore-foot structure, to the left on plantar view, to the right on dorsal view. 2. Hind foot structure, to the left on plantar view, to the right on dorsal view. Note the printed area of the foot (the digits and the metapodial-phalangeal junctions) on the substrate. Modified from Grand and Eisenberg (1982).

with distal autopodium preserved, the most parsimonious hypothesis is that the footprints of Vinchina were produced by dinomyids or a close relative with a similar appendicular skeleton.

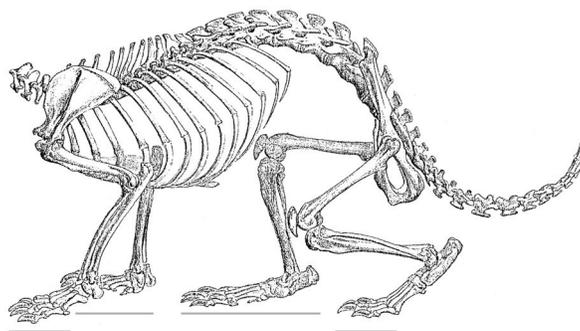


FIGURE 8. Postcranial skeleton of *Dinomys branickii*. Note the feet facing the ground in a digitigrade (black line) and plantigrade (grey line) position. Modified from Peters (1873).



FIGURE 9. Distribution of Dinomyidae in South America. 1, Bolivia; 2, Ecuador; 3, Colombia; 4, Venezuela; 5 - 7, Brazil; 8 y 9, Uruguay; 10 - 22, Argentina; blue area, Recent, Bolivia, Peru, Ecuador, Brazil, Colombia y Venezuela; 23, location of *Tacheria troyana*. Modified from Nasif (2010).

since the Middle Miocene by isolated teeth from the Laguna Blanca and Río Frías formations of Patagonia (Ameghino 1904). The highest diversity occurs during the Late Miocene and Pliocene in Central North Argentina. In the northeastern area they occur particularly in deposits known as the “conglomerado osífero” (McKenna and Bell 1997; Nasif et al. 2004; Candela 2005; Candela and Nasif 2006), in northwestern Argentina are recorded at the Chiquimil and Andalhuala formations (Herbst et al. 2000; Nasif 2006, 2010). And, in central Argentina they are recorded at the Salicas Formation, La Rioja province; the Ullum Formation, San Juan province and the Epecuén, Arroyo Chasicó, and other formations from Buenos Aires province (e.g., Bondesio et al. 1980; Contreras 1985; Candela 2005; Tauber 2005; Nasif 2010) (Figure 9). The occurrence of *Tacheria troyana* in Late Oligocene deposits of the Vinchina Formation could represent the oldest record of Dinomyidae in Argentina, suggesting the extension of its temporal and geographical distribution. It also would indicate

that dinomyids were widely distributed in South America since the Late Oligocene.

The Record of Caviomorph Rodent Footprints in South America

The large footprints of Vinchina *Tracheria troyana* are not comparable to any other footprint recorded in South America. Indeed, the record of South American Hystricognathi rodent footprints is scarce, and it is mostly restricted to cavioid (i.e., hydrochoerids and caviids) footprints, recorded in Argentina. Angulo and Casamiquela (1982) proposed a new ichnotaxon *Porcellusignum consulcator* for digitigrade footprints with tridactyl and occasionally tetradactyl impressions recorded in the Río Negro Formation, at Balneario El Cóndor, Río Negro province, Argentina. The material was assigned with doubt to Hydrochoeridae, unfortunately the photographs of the footprints are not clarifying. Besides the material recorded by Angulo and Casamiquela (1982), Aramayo (2007) described additional specimens assigned to cf. *Porcellusignum* isp. preserved in the Río Negro Formation (Late Miocene-Early Pliocene), between the Balneario El Cóndor and La Lobería, Río Negro province, Argentina. The footprints were interpreted as produced by hydrochoerids and the material consists of tetradactyl manus and tridactyl pes impressions. In addition, heteropod footprints (tetradactyl manus and tridactyl pes) assigned to dolichotine caviids were described by Aramayo and M. de Bianco (2009) from Pleistocene deposits of Pehuen-Có, Buenos Aires province, Argentina. More recently, Krapovickas et al. (2009b) described heteropod footprints (tetradactyl manus and tridactyl pes) preserved in Miocene deposits of the Toro Negro Formation at Vinchina, La Rioja province, Argentina. The footprints were suggested to be produced by two separate groups: hegetotheriid notoungulates and caviomorph rodents (most likely dolichotine caviids). All the previously mentioned footprints, with tetradactyl manus and tridactyl pes, differ strongly from *Tracheria troyana*, not only on its digit arrangement but also in the general morphology and larger size of the footprint. Furthermore, some mammal footprints, described and illustrated by Leonardi (1994), were assigned with doubt to rodents and are recorded in the Neogene of Argentina, all of them are markedly dissimilar to *Tracheria troyana*. One of the records is preserved at Salar del Rincón, Salta province, possibly in the Trinchera Formation. Another is preserved at Catua in the boundary between Salta and Jujuy provinces. Finally, small galloping mammal foot-

prints are recorded at the Quebrada del Jarillal Formation at Sierra de Mogna, San Juan province, Argentina.

CONCLUSIONS

The record of Cenozoic South American rodent and/or rodent-like footprints has recently gained more attention, although it is still uncommon. The detailed study of new findings of South American rodent footprints enhances the knowledge of its temporal and geographical distribution. The tetradactyl footprints of the Vinchina Formation provide valuable information about the possible early occurrence of dinomyids in South America. It could represent the oldest record of dinomyids in Argentina, extending the geographic distribution of the group to northwestern Argentina during the Late Oligocene.

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REFERENCES

- Adkins, R.M., Gelke, E.L., Rowe, D., and Honeycutt R.L. 2001. Molecular phylogeny and divergence time estimates for major rodent groups: evidence from multiple genes. *Molecular Biology and Evolution*, 18:777–791.
- Ameghino, F. 1904. Nuevas especies de mamíferos, Cretáceos y Terciarios de la República Argentina. *Anales de la Sociedad Científica Argentina, Córdoba*, LVII: 162–175, 327–341, LVIII: 35–41, 56–71, 182–192, 225–290.
- Angulo, R.J. and Casamiquela, R.M. 1982. Estudio estratigráfico de las unidades aflorantes en los acantilados de la costa norte del Golfo de San Matías (Río Negro y extremo austral de Buenos Aires) entre los meridianos 62° 30' y 64° 30' W. *Mundo Ameghino*, 2:20–86.
- Aramayo, S.A. 2007. Neogene vertebrate palaeoichnology of the North Atlantic coast of the Río Negro province, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro*, 65: 573–584.
- Aramayo, S.A. and Manera de Bianco, T. 2009. Late Quaternary palaeoichnological sites on the southern Atlantic coast of Buenos Aires province, Argentina: Mammal, bird and hominid evidence. *Ichnos*, 16:25–32.
- Bondesio, P., Laza, J., Scillato Yané, G., Tonni, E.P., and Vucetich, M.G. 1980. Estado actual del conocimiento de los vertebrados de la Formación Arroyo Chasicó (Plioceno temprano) de la provincia de Buenos Aires. *Actas II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso latinoamericano de Paleontología*, 3:101–127.
- Candela, A.M. 2005. Los roedores del “Mesopotamiense” (Mioceno tardío, Formación Ituzaingó) de la provincia de Entre Ríos (Argentina) p. 37–48. In Aceñolaza, F.G. (ed.), *Temas de la biodiversidad del Litoral fluvial argentino II*. INSUGEO, Miscelánea 14, Tucumán.
- Candela, A. and Nasif, N.L. 2006. Systematics and biogeographic significance of *Drytomomys typicus* (SCALABRINI m AMEGHINO, 1889) nov. comb., a Miocene Dinomyidae (Rodentia, Hystricognathi) from Northeast of Argentina. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 3:165–181.
- Candela, A. and Picasso, M. 2008. Functional anatomy of the limbs of Erethizontidae (Rodentia, Caviomorpha): indicators of locomotor behavior in Miocene porcupines. *Journal of Morphology*, 269:552–593.
- Carrano, M.T. and Wilson, J.A. 2001. Taxon distributions and the tetrapod track record. *Paleobiology*, 27:564–582.
- Ciccioli, P.L. 2008. *Evolución paleoambiental, estratigrafía y petrología sedimentaria de la Formación Toro Negro (Neógeno), Sierras Pampeanas Noroccidentales (provincia de La Rioja)*. Unpublished Ph.D.Thesis, Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Argentina.
- Ciccioli, P.L., Limarino, C.O., and Marensi, S.A. 2005. Nuevas edades radimétricas para la Formación Toro Negro en la Sierra de Los Colorados, Sierras Pampeanas Noroccidentales, provincia de La Rioja. *Revista de la Asociación Geológica Argentina*, 60:251–254.
- Ciccioli, P.L., Limarino, C.O., Marensi, S.A., Tedesco, A.M., and Tripaldi, A. 2008. Estratigrafía De La Cuenca De Vinchina, Sierras Pampeanas Noroccidentales, Noroeste De La provincia De La Rioja. *XVII Congreso Geológico Argentino, San Salvador de Jujuy, Abstract*, 1:343–344.
- Ciccioli, P.L., Limarino, C.O., Marensi, S.A., Tedesco, A.M., and Tripaldi, A. 2010. Estratigrafía de la Cuenca de Vinchina (Terciario), Sierras Pampeanas, provincia de La Rioja. *Revista de la Asociación Geológica Argentina*, 66:146–155.

- Contreras, V.H. 1985. Los Dinomyidae (Rodentia-caviomorpha) de la Formación Ullum (Mioceno superior), provincia de San Juan, Argentina. *Reunión de Comunicaciones paleontológicas de la APA delegación San Juan, Resúmenes*:1–2.
- Cuerda, A.J., Cingolani, C.A., Varela, R., and Schauer, O.C. 1984. *Descripción geológica de la Hoja 19d Mogna*. Servicio Geológico Nacional, Boletín 192, Buenos Aires.
- De Angelo, C., Paviolo, A., Di Blanco, Y., Di Bitetti, M., and Chiappe, A. 2008. *Guía de huellas de los mamíferos de Misiones y otras áreas del subtrópico de Argentina*. Ediciones del Subtrópico, Tucumán.
- Ellerman, J.R. 1940. *The Families and Genera of Living Rodents. Volume I. Rodents other than Muridae*. British Museum of Natural History, London.
- Fields, R.W. 1957. Hystricomorph rodents from the late Miocene of Colombia, South America. *University of California Publications in Geological Sciences*, 32:273–404.
- Frailey, C. 1986. Late Miocene and Holocene Mammals, exclusive of the Notoungulata, of the Río Acre Region, Western Amazonian. *Contributions in Science*, 374:1–46.
- Grand, T. and Eisenberg, J. 1982. On the affinities of the Dinomyidae. *Säugetierkundliche Mitteilungen*, 30:151–157.
- Herbst, R., Anzotegui, L., Esteban, G., Mautino, L., Morton, S., and Nasif, N. 2000. Síntesis paleontológica del Mioceno de los valles Calchaquíes, noroeste argentino, p. 263–287. In Aceñolaza, F. and Herbst, R. (eds.), *El Neógeno de Argentina*, Serie de Correlación Geológica, Tucumán.
- Hoffstetter, R. and Lavocat, R. 1970. Découverte dans le Déséadien de Bolivie de genres pentalophodontes appuyant les affinités africaines des rongeurs caviomorphes. *Comptes Rendus de L'Académie des Sciences*, 271:172–175.
- Horovitz, I., Sánchez-Villagra, M., Martín, T., and Aguilera, O. 2006. The fossil record of *Phoberomys pattersoni* Mones 1980 (Mammalia, Rodentia) from Urumaco (Late Miocene, Venezuela), with an analysis of its phylogenetic relationships. *Journal of Systematic Palaeontology*, 4:293–306.
- Huchon, D. and Douzery, E. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. *Molecular Phylogenetics and Evolution*, 20:238–251.
- Krapovickas, V., Mángano, M.G., and Marsicano, C.A. 2009a. Cenozoic tetrapod footprints from the Vinchina Basin, La Rioja, Argentina. *Ameghiniana*, 46:33.
- Krapovickas, V., Ciccioli, P.L., Mángano, M.G., Marsicano, C.A., and Limarino, C.O. 2009b. Paleobiology and paleoecology of an arid-semiarid Miocene South American ichnofauna in anastomosed fluvial deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 284:129–152.
- Leonardi, G. 1994. *Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene) with an Appendix on Mexico and Central Americas*. República Federativa do Brasil, Ministério de Minas e Energia, Secretaria de Minas e Metalurgia, Companhia de Pesquisa de Recursos Minerais. Brasília, Brazil.
- Linares, O. 2004. Bioestratigrafía de la fauna de mamíferos de las formaciones Socorro, Urumaco y Codore (Mioceno medio-Plioceno temprano) de la región de Urumaco, Falcon, Venezuela. *Paleobiología Neotropical*, 1:1–26.
- McKenna, M. and Bell, S. 1997. *Classification of Mammals. Above the species level*. Columbia University Press, New York.
- Melchor, R.N., Genise, J.F., and Visconti, G. 2007. Icnocenos de vertebrados e invertebrados en facies fluviales meandrosas: la Formación Vinchina (Mioceno), La Rioja Argentina. *Quinta Reunión Argentina de Icnología y Tercera Reunión de Icnología del MERCOSUR, Resúmenes*, Argentina, p. 54.
- Melchor, R.N., Genise, J.F., Farina, J.L., Sánchez, M.V., Sarzetti, L., and Visconti, G. 2010. Large striated burrows from fluvial deposits of the Neogene Vinchina Formation, La Rioja, Argentina: A crab origin suggested by neoichnology and sedimentology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 291:400–418.
- Mones, A. 1986. Palaeovertebrata Sudamericana. Catálogo Sistemático de los Vertebrados Fósiles de América del Sur. Parte I. Lista preliminar y bibliografía. *Courier Forschungsinstitut Senckenberg*, 82:1–625.
- Mones, A. and Castiglioni, L.R. 1979. Additions to the knowledge on fossil rodents of Uruguay (Mammalia: Rodentia). *Paläontologische Zeitschrift*, 53:77–87.
- Nasif, N. 2006. Primer registro de un Dinomyidae (Rodentia, Hystricognathi) protohipsodonte en el Mioceno tardío del Noroeste argentino. Implicaciones paleoambientales. *Ameghiniana*, 43(4): 47.
- Nasif, N. 2009. Phylogenetic position of *Dinomys branickii* Peters (Dinomyidae) in the context of Caviomorpha (Hystricognathi, Rodentia). *Cladistics*, 25:26.
- Nasif, N. 2010. *Los Dinomyidae (Rodentia, Caviomorpha) del Mioceno superior del noroeste argentino. Su anatomía cráneo-dentaria*. Ph.D. Thesis, Universidad Nacional de Tucumán, Argentina.
- Nasif, N.L., Aceñolaza, F., and Esteban, G. 2004. Nuevo material de xenartros y roedores para la Formación Ituzaingó (Mioceno superior), provincia de Entre Ríos, Argentina. *Ameghiniana*, 41(4):4.
- Patterson, B. and Wood, A. 1982. *Rodents from the Oligocene of Bolivia and the relationships of the Caviomorpha*. Bulletin of the Museum of Comparative Zoology, 149:371–543.
- Paula Couto, C. 1951. Uma especie do Genero *Tetrastylus* Ameghino 1886. Em Lagoa Santa. *Boletim do Museu Nacional, Nova Serie Geologia*, 15:1–16.

- Peters, W. 1873. Ueber *Dinomys*, eine merkwürdige neue Gattung von Nagethieren aus Peru. *Festschrift zur Feier des Hundertjährigen Bestehens der Gesellschaft Naturforschender Freunde*, 1873:227–234.
- Ramos, V.A. 1970. Estratigrafía y estructura del Terciario en la Sierra de Los Colorados (provincia de La Rioja), República Argentina. *Revista de la Asociación Geológica Argentina*, 25:359–382.
- Rinderknecht, A. and Blanco R.E. 2008. The largest fossil rodent. *Proceedings of the Royal Society B*, 275:923–928.
- Shockey, B.J., Croft, D.A., and Anaya, F. 2007. Analysis of function in the absence of extant functional homologues: a case study using mesotheriid notoungulates (Mammalia). *Paleobiology*, 33:227–247.
- Sinclair, W.J. 1909. Mammalia of the Santa Cruz Beds. Volume VI, Paleontology. Part I, Tyotheria, pp. 1–110. In Scott, W.B. (ed.), *Reports of the Princeton University Expeditions to Patagonia*, 1896–1899. Princeton University, E. Schweizerbart'sche Verlagshandlung (E. Nägele), Stuttgart.
- Spotorno, A.E., Valladares, J.P., Marin, J.C., Palma, R.E., and Zuleta, C. 2004. Molecular divergence and phylogenetic relationships of chinchillids (Rodentia: Chinchillidae). *Journal of Mammalogy*, 85:384–388.
- Tabbutt, K.D., Naeser, Ch.W., Jordan, T.E., and Cerveny, P.F. 1989. New fission-track ages of Mio-Pliocene tuffs in the Sierras Pampeanas and Precordillera of Argentina. *Revista de la Asociación Geológica Argentina*, XLIV:408–419.
- Tauber, A. 2005. Mamíferos fósiles y edad de la Formación Salicas (Mioceno tardío) de la sierra de Velazco, La Rioja, Argentina. *Ameghiniana* 42:443–460.
- Tedesco, A.M. 2007. *Estratigrafía, evolución paleoambiental y tectosedimentaria de la cuenca de La Troya (Paleógeno y Neógeno, Precordillera de La Rioja)*. Ph.D. Thesis. Universidad de Buenos Aires.
- Thulborn, T. 1990. *Dinosaur Tracks*. Chapman and Hall, London.
- Tripaldi, A., Net, L., Limarino, C., Marensi, S., Ré, G., and Caselli, A. 2001. Paleoambientes sedimentarios y procedencia de la Formación Vinchina, Mioceno, noroeste de la provincia de La Rioja. *Revista de la Asociación Geológica Argentina*, 56:443–465.
- Turner, J.C.M. 1964. *Descripción geológica de la Hoja 15c, Vinchina, provincia de La Rioja, Boletín N° 100*. Dirección Nacional de Geología y Minería, Buenos Aires.
- Vucetich, M.G. 1986. Historia de los roedores y primates en Argentina: su aporte al conocimiento de los cambios ambientales durante el Cenozoico. *Actas IV Congreso Argentino de Paleontología y Bioestratigrafía*, 2:157–165.
- Walton, A. 1997. Rodents, pp. 292–409. In Kay, R., Madden, R., Cifelli R., and Flynn, J. (eds.), *Vertebrate Paleontology in the Neotropics, the Miocene Fauna of La Venta, Colombia*. Smithsonian Institution Press, Washington D.C.
- White, T. and Alberico, M. 1992. *Dinomys branickii*. Mammalian species. *American Society of Mammalogist* 410:1–5.