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DAVID E. TINEO^{1,6}
LEANDRO M. PÉREZ^{2,6}
PAULA BONA^{3,6}
MARCOS A. COMERIO^{4,6}
JORGE I. NORIEGA^{5,6}
DANIEL G. POIRÉ^{1,6}

¹Centro de Investigaciones Geológicas, Universidad Nacional de La Plata (UNLP-CONICET). Calle Diagonal 113 y 64, B1900FWA La Plata, Argentina.

²División Paleoecología Invertebrados, Museo de La Plata (UNLP). Paseo del Bosque s/n, B1900FWA La Plata, Argentina.

³División Paleontología de Vertebrados, Museo de La Plata (UNLP). Paseo del Bosque s/n, B1900FWA La Plata, Argentina.

⁴Instituto de Estudios Andinos "Don Pablo Groeber", Universidad Nacional de Buenos Aires. Ciudad Universitaria, Pabellón II, C1428ZAA Buenos Aires, Argentina.

⁵CICYTTP-CONICET, Materi y España s/n, E3105BWA Diamante, Argentina.

⁶Consejo Nacional de Investigaciones Científicas y Técnicas. CONICET.

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DAVID E. TINEO^{1,6}, LEANDRO M. PÉREZ^{2,6}, PAULA BONA^{3,6}, MARCOS A. COMERIO^{4,6}, JORGE I. NORIEGA^{5,6}, AND DANIEL G. POIRÉ^{1,6}

¹Centro de Investigaciones Geológicas, Universidad Nacional de La Plata (UNLP-CONICET). Calle Diagonal 113 y 64, B1900FWA La Plata, Argentina.

tineo.d.e@gmail.com

²División Paleozoología Invertebrados, Museo de La Plata (UNLP). Paseo del Bosque s/n, B1900FWA La Plata, Argentina. pilosaperez@gmail.com

³División Paleontología de Vertebrados, Museo de La Plata (UNLP). Paseo del Bosque s/n, B1900FWA La Plata, Argentina. paulabona26@gmail.com

⁴Instituto de Estudios Andinos "Don Pablo Groeber", Universidad Nacional de Buenos Aires. Ciudad Universitaria, Pabellón II, C1428ZAA Buenos Aires, Argentina. comerio@gl.fcen.uba.ar

⁵CICYTTP-CONICET, Materi y España s/n, E3105BWA Diamante, Argentina. cidnoriega@infoaire.com.ar

⁶Consejo Nacional de Investigaciones Científicas y Técnicas. CONICET

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Palabras clave. Rheidae, icnología, Formación Guandacay, Provincia de Salta, Argentina.

THE Argentinean fossil record of vertebrate footprints is significant and has been extensively studied; however, sites with bird tracks are scarce and less known (Bonaparte, 1965; Aramayo, 1991, 2007; Galli *et al.*, 1992; Aramayo and Manera de Bianco, 1987, 1990, 1996; de Valais and Melchor, 2008; Genise *et al.*, 2009; Melchor, 2009; Alonso, 2012; Aramayo *et al.*, 2015). Although there are some studies of fossil footprints referred to Aves, there are no detailed descriptions or taxonomical assignations of such traces.

A bird trackway with three footprints was found in the lower levels of the Guandacay Formation (upper Miocene-Pliocene) (Ayaviri, 1967), Grupo Chaco (Stebinger, 1920; White, 1925), at the "Río Iruya" section, 62 Km NW of the city of San Ramón de la Nueva Orán (Salta Province, Argentina; Fig. 1.1). This unit is part of the fill of the Neogene foreland basin of Sierras Subandinas Australes. This Subandean terrain is a thin-skinned fold-thrust belt system which represents the easternmost expression of the deformation of the central Andes. Compressive tectonics created a foreland basin with clastic sequences of continental rocks of approximately 7500 m of thickness (Hernández *et al.*, 1996; Ramos, 1999).

The aim of this contribution is to report a new record of

Aramayoichnus rheae Aramayo *et al.*, 2015, from the Neogene of Northwestern Argentina, based on tridactyl footprints attributed to bird activity. This fossil evidence expands the paleogeographical and temporal distribution of this ichnospecies, showing the presence of rheids in the Late Miocene of the Subandean region.

The footprints were preserved as natural casts (convex hyporeliefes) in brownish-grey, fine to medium grain conglomerates; the base of the level is in contact with reddish-reddish brown mudstones and very fine sandstones (Fig. 1.2). The hypothesis that a rheiform bird could have registered this trackway is herein considered in association with the fossil record of the group in a stratigraphic and biogeographic context.

MATERIALS AND METHODS

The material is located at the zone 20k (336425.59 m E, 7466327.56 m S UTM) (Fig. 1.1). Footprints were made by the animal on fine grain sediments (mudstones) and later preserved as a natural cast on the base of the overlying sandstone bed. The sedimentary report is based on direct field observations of details of the sedimentary sequence represented in a stratigraphic section.

Footprints were also measured *in situ*. The trackway was analyzed using standard parameters; e.g., stride length, pace length and pace angle were taken following Lockley (1993) and Leonard (1994), (Fig. 2), and are detailed in Table 1. Footprints of extant *Rhea americana* (Linnaeus, 1758), from the Jardín Zoológico de La Plata (Buenos Aires, Argentina), were used for establishing comparisons.

Acronyms and anatomical abbreviations. Museo de Ciencias Naturales "Carlos Darwin - Yacimiento paleoicnológico" (MD-YPI), Punta Alta, Argentina, and "Instituto Miguel Lillo", Paleozoología de Vertebrados (PVL), Tucumán, Argentina. Footprint (Fp); digit (D); left footprint (LFp); right footprint (RFp).

SYSTEMATIC ICHNOLOGY

Ichnogenus *Aramayoichnus* Aramayo *et al.*, 2015

Type ichnospecies. *Aramayoichnus rheae* Aramayo *et al.*, 2015 (by monotype) from Pehuen-Co – Monte Hermoso, Buenos Aires (Late Pleistocene).

Aramayoichnus rheae Aramayo *et al.*, 2015

Figure 2

Geographic occurrence. The footprints came from the Iruya River in the Province of Salta (GPS: 20k—336381.00 m E,

7466357.00 m S; UTM) (Fig. 1.1). The holotype MD-YPI-15-2 (a trackway of 10 footprints; Aramayo *et al.* 2015) came from "Reserva Geológica Paleontológica y Arqueológica Provincial Pehuen-Co – Monte Hermoso" (Late Pleistocene-AMS "Accelerator Mass Spectrometry" 12,000 B.P. ± 100; Aramayo and Manera de Bianco, 1996), in the southeast of the Buenos Aires Province. Additional material consists of another trackway of 5 footprints, and traces identified with this ichnotaxon are MD-93-6, a slab which contains isolated footprints (Aramayo and Manera de Bianco, 1996).

Stratigraphic occurrence. Lower levels of the Guandacay Formation (Upper Miocene–Pliocene) (Ayaviri, 1967), Grupo Chaco (Stebinger, 1920; White, 1925) (Fig. 1.2).

Description. The bipedal trackway is composed of three complete mesaxonic tridactyl footprints preserved in sequence, together with other incomplete footprints probably belonging to the same ichnotaxon (Fig. 2). The general shape of the footprints is rhomboidal with thick digits. Footprint length/width ratio is 1.4. The impression of the *pulvinus metatarsalis* (metatarsal–phalangeal pad) is oval and located at the postero-medial end of the footprint (Fig. 3). The angle between digits II and IV is of about 59° (a feature diagnostic of the genus, Aramayo *et al.*, 2015) and the mean angles between II–III and III–IV are 26° and 33°, respectively (Fig. 3). The impression of II is elongated with no mark of a claw and the proximal part of the pad is separated from the

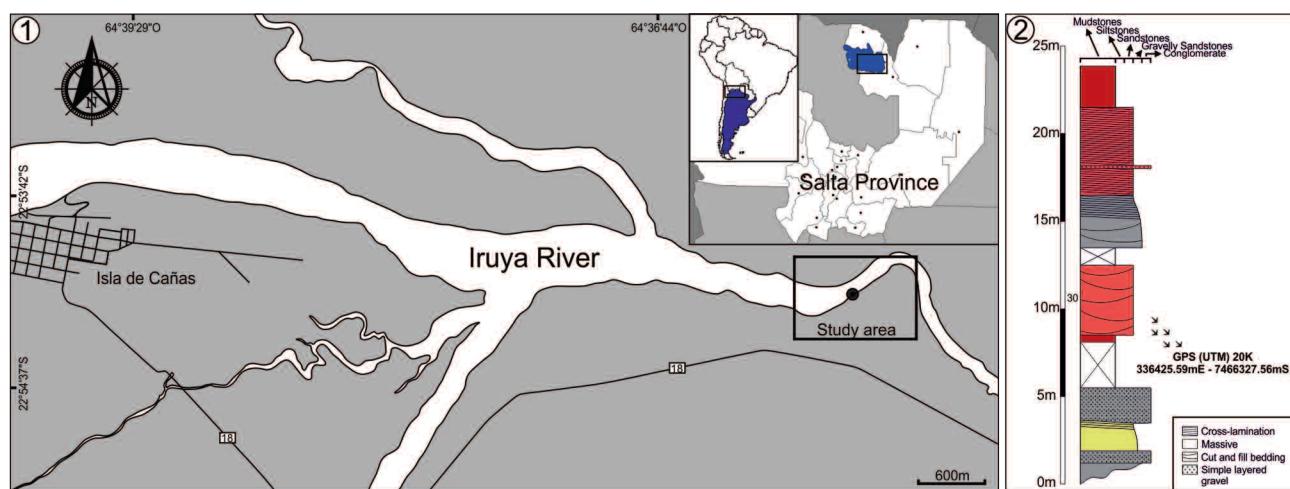


Figure 1.1, Location map of the study area in the Río Iruya section of the Guandacay Formation; 2, Sedimentary section.

TABLE 1 – Footprints standard parameters.

Footprints	Length	Width	Ratio L/W	DII		DIII		DIV		Pace angulation
				Length	Width	Length	Width	Length	Width	
LFp1	14.1	10.4	1.35	6.3	2.3	11.8	2.7	5.9	1.8	165°
RFp2	14.5	10.9	1.33	6.8	1.8	10.5	2.6	7.6	1.2	175°
LFp3	17.2	11.4	1.5	8.2	1.9	12.3	2.9	7.3	1.8	176°
Average	15.3	10.9	1.4	7.1	2.0	11.5	2.7	6.9	1.6	172°

meta-basipodium. The impression of III is the longest; it is fusiform with pronounced marks of pads. Its narrow proximal end is connected with the meta-basipodium trace; its distal end is laterally curved and triangular in shape, thus indicating a claw mark. The impression of IV is the shortest of all (see discussion). It is completely separate from the meta-basipodium and shows a thickening in its middle section, which probably represents the mark of its pad. It has rounded distal and proximal ends. Digit I, the hallux, is not present in the footprints; like an interdigital web trace.

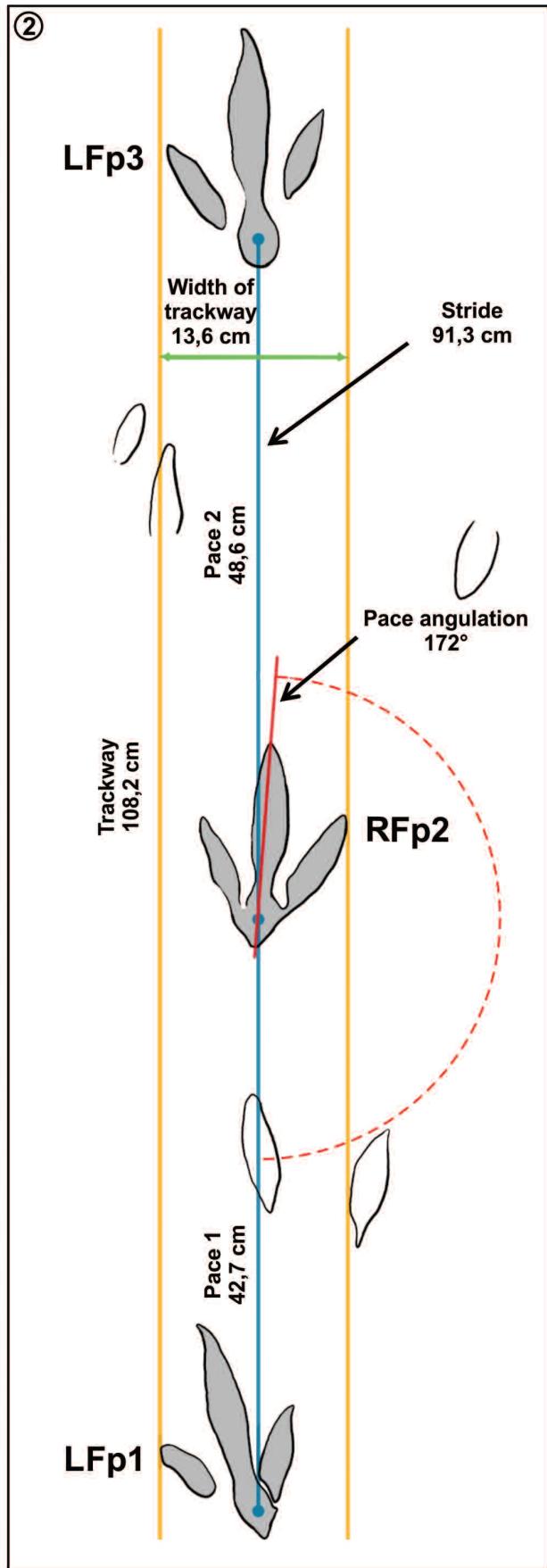
All the measurements of the footprints and their rotation angles with respect to the straight line of advance (pace angulation) are provided in Table 1. The measurements of the trackway are (Fig. 2.2): pace 1 length (LFp1–RFp2)= 42.7 cm; pace 2 length (RFp2–LFp3)= 48.6 cm; stride length= 91.3 cm; pace angulation average= 172°; trackway width= 13.6 cm; trackway length= 108.2 cm.

Comparison and discussion

The new footprints herein described were preserved together with wood, desiccation cracks and molds of big clasts. This bipedal trackway fits with that which was recently described by Aramayo *et al.* (2015) and preserves a combination of characters that enables its referral to *Aramayoichnus rheae*, from the Pleistocene of the Southeast

coast of the Province of Buenos Aires. These characters included: the presence of metatarsal-phalangial pad impressions and the divarication of digits II – IV, commonly smaller than 80°, among others; it also differs from *Anchisauripus* in presenting a lower footprint length/width ratio and a greater digit divarication (Aramayo *et al.*, 2015). *Aramayoichnus rheae* is also a mesaxonic tridactyl footprint with claw marks, especially that which is externally curved in digit III. This characteristic enables the identification of the right/left footprint and, thus, the digit number. The footprints herein described have a digit IV that is shorter than the digit II, a feature that is consistent with the *Aramayoichnus rheae* footprint figured by Aramayo *et al.* (2015) in figure 14E. Nevertheless, it differs from the description given by Aramayo *et al.* (2015, p. 158), “digit IV impression longer than that of digit II”, and figured in their figure 14B. In our opinion, the footprint showed in that figure, interpreted by these authors as a right footprint, corresponds to a left one, and the ichnospecies has a characteristic digit IV that is shorter than its digit II.

Comparing the Miocene footprints and *Aramayoichnus rheae* (MD-YPI-15-2 and MD-93-6) with extant footprints of *Rhea americana* (Linnaeus, 1758), these footprints are similar in their general outline and size, and in their angle between II and IV, their lack of the impression of DI, their



longest DIII with pronounced marks of pads and the fact that their claw mark is laterally curved (Figs. 4.1 and 4.2). These similarities suggest not only that the Miocene footprints may be assigned to a rheid but also that the paleogeographic distribution of this group of birds dates back to the Oligocene–Miocene from the Vinchina Formation in low latitudes in North-Western Argentina (see Ramos, 1970). The feet are oriented with a slight outward rotation at a low angle toward the mid line of progression of the trackway of *Aramayoichnus rheae*, therefore suggesting that the prints were generated by a cursorial bird.

Bonaparte (1965) assigned three “Mio-Pliocene” (Turner, 1960) trackways from Quebrada del Yeso (La Rioja Province) to rheiform activity (PLV 2690 – 2692). Nevertheless, those footprints show several important morphological differences with *Aramayoichnus rheae* and extant rheid footmarks. In the PLV 2690 specimen, which consists of six tridactyl footprints, each track has straight digits without pads that connect with the meta-basipodium, and III lacks a claw mark while there is a larger angle between DII and DIV ($\sim 95^\circ$) (Bonaparte, 1965; see fig. 2). Specimen PLV 2691 reveals eight footprints with three narrow, elongated digits connecting digit III with the meta-basipodium and with a curved digit IV. The footprint the best preserved of this trackway shows an impression of an interdigital membrane (Fig. 4.3) and an angle between DII and DIV of nearly 83° . Finally, PLV 2692 presents only one footprint, which is similar to that of PLV 2691 but for the more elongate knuckles of its DIII and the fact that its angle between DII and DIV is of $\sim 85^\circ$. The angle between their digits, their absence of a claw mark at the shortest DIII, the fact that their DII and DIV are curved, and their bearing of an interdigital membrane trace, are clear differences that suggest that PLV 2690–2692 were not produced by rheids. Rather, the aforementioned morphological characteristics, web traces, narrow digits and curvature of digits II and IV, suggest that the trackmakers were probably ducks or geese (Anseriformes).

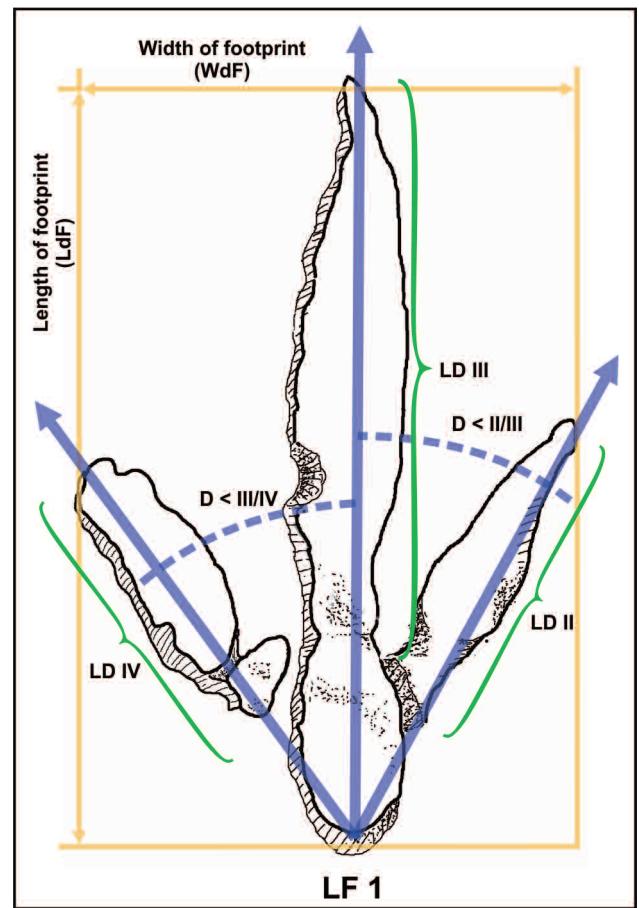


Figure 3. *Aramayoichnus rheae*: first left footprint of the complete trackway (LFp1); Drawing of the holotype showing the respective measurements. Abbreviations: D, digit; LD, digit length; LF, footprint length; LFp, left footprint; DII to DIV, impressions of digits II to IV; WF, width of the footprint.

Figure 2. 1, Complete trackway of *Aramayoichnus rheae*; 2, Drawing of the complete trackway with relevant measurements. Abbreviations: LFp, left footprint; RFp, right footprint.

As stated above, the occurrence of *Aramayoichnus rheae* in the Late Miocene of Northwestern Argentina extends the temporal and geographic distribution of the ichnological record of rheids. Rheidae are big South American running birds (ratites), which are currently represented by two living species, *Rhea americana* (Linnaeus, 1758), or “*Nandú*”, and *Pterocnemia pennata* (d’Orbigny, 1834), or

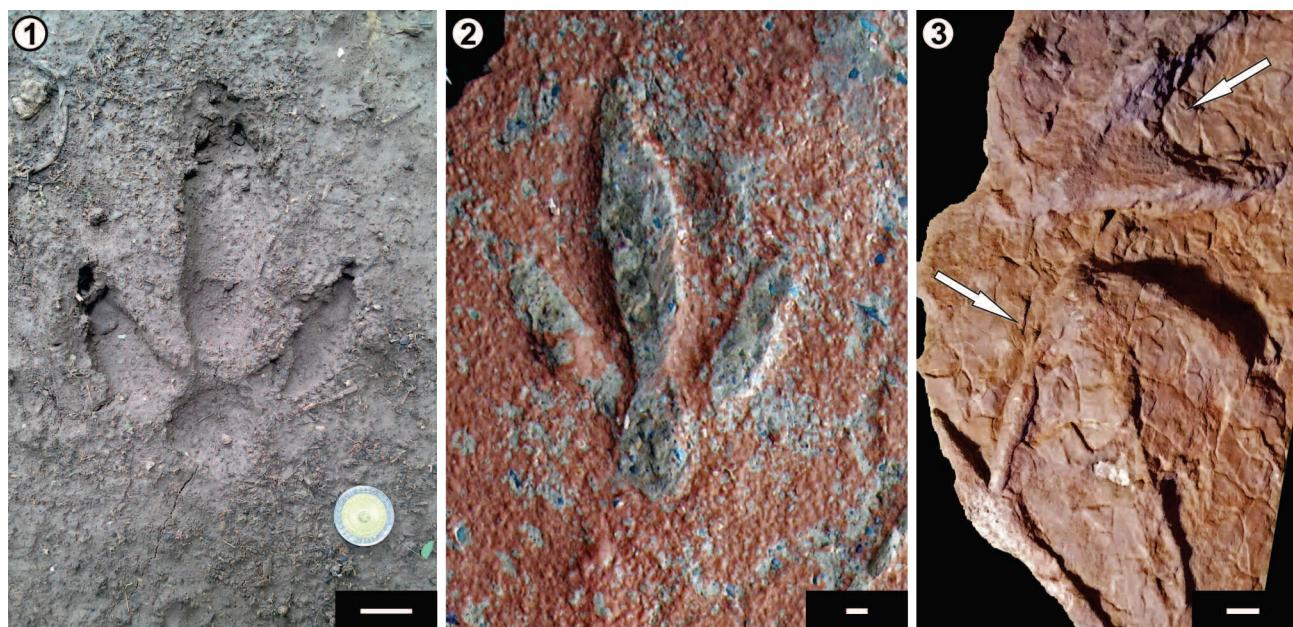


Figure 4. 1, Footprint of *Rhea americana* from the Zoológico de La Plata; 2, *Aramayoichnus rheae*; 3, Detail of the footprint PLV 2691. Scale bar= 1 cm.

"Choique". *Rhea americana* is the biggest species and lives in the South East of this continent, from the Southern region of Pampa Húmeda and reaching Sierras Centrales of the Punilla Sierras system. *Pterocnemia pennata* lives in the Patagonian scrub and steppes and at high altitudes in semi-deserts of the Andean plateau or in the Monte of Northwest Argentina. It is the smallest species (0.90 m to 1.2 m of maximum height) and its height matches the size of ~0.61 m estimated for *Aramayoichnus rheae* (estimation made following Lockley, 1993, p. 86). The pace of extant *Pterocnemia pennata* also coincides with that of *Aramayoichnus rheae*.

Fossil rheids referred to *Pterocnemia* sp. were recently reported from the late Miocene of La Pampa Province (Cenizo et al., 2011) and a new species of *Pterocnemia*, *P. mesopotamica* Agnolin and Noriega 2012, was described from different middle?–late and late Miocene geologic units at the Mendoza and the Entre Ríos provinces, respectively (Agnolin and Noriega, 2012). *Heterorhea dabbenei* Rovereto, 1914 and *Hinasuri nehuensis* Tambussi, 1995 are also known on the basis of fragmentary materials (Tambussi, 1995) from the early Pliocene of the province of Buenos Aires. The most abundant early Miocene Patago-

nian rheid is *Opisthodactylus patagonicus* Ameghino, 1891 (Degrange et al., 2012; Buffetaut, 2014). Recently, *Opisthodactylus horacioperezi* Agnolin and Chafrat (2015) was described from the early Miocene Chichinales Formation (Río Negro Province, Patagonia). A probable new species of *Opisthodactylus*, from Northwestern Argentina, was reported from late Miocene–early Pliocene rocks cropping out in the Santa María valley in the Tucumán Province (Noriega and Vezzosi, 2011). Finally, the occurrence of *Aramayoichnus rheae* in Salta is included within the geographic range of living *P. pennata* and is located not very far from the Neogene sites in which records of extinct rheids were found in Tucumán (*Opisthodactylus* sp.) and Mendoza (*P. cf. mesopotamica*).

CONCLUSION

A new record of *Aramayoichnus rheae* Aramayo et al., 2015 from the Neogene of Northwestern Argentina is herein reported and attributed to Rheidae activity. This record supports the presence of Rheidae, at least from the Miocene–Pliocene to the present, in the Subandean region of Northwest Argentina (already mentioned, with doubt, by Ramos, 1970 for the Vinchina Formation of Northwestern

Argentina; Middle Miocene, 15.6 ± 0.4 Ma sensu Ciccioli *et al.*, 2014). This fossil evidence expands the paleogeographical and temporal distribution of this ichnospecies and is consistent with the fossil record and the extant geographic distribution of the Rheidae in South America.

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