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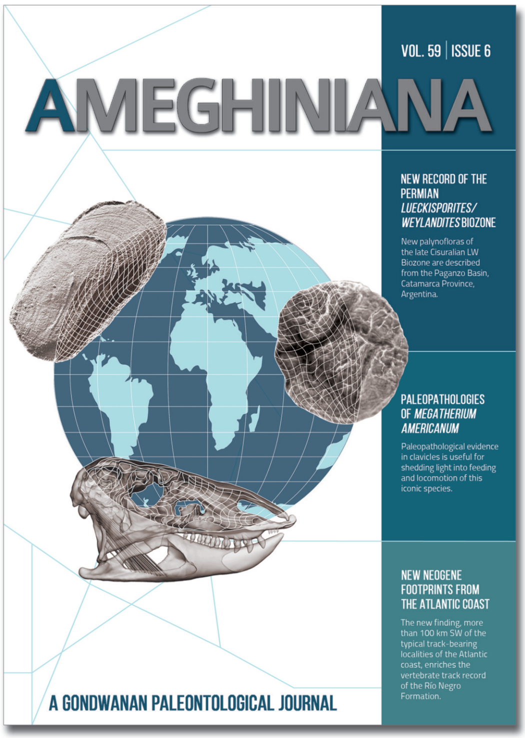

NEW VERTEBRATE TRACKS FROM THE NEOGENE RÍO NEGRO FORMATION (RÍO NEGRO PROVINCE, ARGENTINA)

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NEW VERTEBRATE TRACKS FROM THE NEOGENE RÍO NEGRO FORMATION (RÍO NEGRO PROVINCE, ARGENTINA)

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Abstract. New tetrapod footprints were recently found close to Pozo Salado, on the Atlantic shoreline west of Punta Mejillón area (Río Negro Province, Argentina). Footprints are preserved on the top-surface of a fine-grained sandstone included in a stratigraphic section belonging to the Neogene Río Negro Formation. The tracksite displays abundant footprints but a relatively low ichno-diversity. Both footprint morphologies and extra-morphologies suggest that the surface and subsurface remained compliant to producers of different size-classes during a relatively long time of exposure and trampling. Footprints sufficiently detailed to allow an ichnotaxonomic allocation were classified as *Gruipeda maxima*, *Gruipeda* cf. *maxima*, cf. *Porcellusignum* isp., and indeterminate Eutardigrada tracks, related to gruiform/ciconiiform birds, hydrochoerid rodents and ground sloths, respectively. The new finding, more than 100 km SW of the typical track-bearing localities of the Atlantic coast, enriches the vertebrate track record from the Río Negro Formation and adds a newly reported ichnospecies.

Key words. Vertebrate tracks. Río Negro Formation. Neogene. Atlantic shoreline. *Gruipeda*. *Porcellusignum*. Mammals. Birds.

Resumen. NUEVAS HUELLAS DE VERTEBRADOS DE LA FORMACIÓN RÍO NEGRO (PROVINCIA DE RÍO NEGRO, ARGENTINA). Nuevas huellas de tetrápodos han sido descubiertas cerca de Pozo Salado, en la costa atlántica al oeste del área de Punta Mejillón (provincia de Río Negro, Argentina). Las huellas están conservadas sobre la superficie de una arenisca de grano fino incluida en una sección estratigráfica perteneciente a la Formación Río Negro, de edad neógena. Las huellas son abundantes pero la icnodiversidad es relativamente baja. Tanto la morfología de las huellas como la extra-morfología asociada sugieren que la superficie y el espesor de sedimento involucrado fueron impresos por productores de diferentes clases de tamaño durante un tiempo relativamente largo de exposición. Las huellas suficientemente bien preservadas para permitir una asignación icnotaxonómica se clasificaron como *Gruipeda maxima*, *Gruipeda* cf. *maxima*, cf. *Porcellusignum* isp. y huellas indeterminadas asignadas a Eutardigrada. Las trazas se pueden relacionar con aves gruiformes/ciconiiformes, roedores hidroquéridos y perezosos terrestres, respectivamente. El nuevo hallazgo, a más de 100 km al SO de las típicas localidades portadoras de huellas de la costa atlántica, enriquece el registro de huellas de vertebrados de la Formación Río Negro y registra una icnoespecie adicional, no reportada hasta ahora.

Palabras clave. Huellas de vertebrados. Formación Río Negro. Neógeno. Costa Atlántica. *Gruipeda*. *Porcellusignum*. Mamíferos. Aves.

New vertebrate tracks from the Neogene Río Negro Formation, on the Atlantic shoreline of Río Negro Province, Argentina, are here reported and discussed. The vertebrate ichnofauna from the Río Negro Formation is mainly represented by mammal and avian footprints reported from different localities of the Atlantic coast and the Pampean region (see de Valais *et al*., 2020 for a summary of references). Among the vertebrate track record of the unit, footprints referred to mammals show the largest diversity in terms of both ichnotaxonomy and putative producers in comparison to tracks attributed to birds. Except for *Megatherichnium oportoi* Casamiquela, 1974, ichnotaxa related to mammal producers were erected by Casamiquela in Angulo and Casamiquela (1982), namely *Falsatorichnum* *calceocannabius*, *Macrauchenichnus rector*, *Caballichnus impersonalis* and *Porcellusignum conculcator*, attributed respectively to ground sloth, macrauchenid, equid and hydrochoerid producers. In addition, Aramayo (2007) reported undetermined tracks assigned to proterotherid and carnivore marsupials, as well as tracks referred to cf. *Mylodontidichnum* isp. With respect to avian footprints, Casamiquela described some tracks from Ingeniero Jacobacci town (Río Negro Province, Argentina) that were related to an avian origin (Casamiquela, 1969: 301, 1974: 265, 1987: 449, 1996: 89; see also Leonardi, 1994: 35; Melchor, 2009: 209) even though part of the materials still need a careful revision, in our opinion.

In addition, Aramayo (2007) described two types of avian tracks relating them to terror birds and flamingos. Melchor (2009) reported the ichnospecies *Gruipeda dominguensis* de Valais & Melchor, 2008 from 'La Hermita' sanctuary (La Pampa Province, Argentina). Melchor *et al.* (2013) also described undetermined avian tracks and mentioned the occurrence of the ichnogenus *Phoenicopterichnum* Aramayo & Manera de Bianco, 1987, erected from upper Pleistocene deposits of Pehuen-Có (Buenos Aires Province, Argentina). Finally, footprints attributed to mammals and birds but not formally assigned to any ichnotaxa were also reported from the Río Negro Formation by Carmona *et al.* (2012) and de Valais *et al.* (2020).

New tetrapod tracks from Pozo Salado have been recently discovered. The track-bearing surface crops out on the shoreline, close to the Pozo Salado locality, about 100 km SW from Viedma, Río Negro Province, and preserves footprints of avian and mammal producers. Footprints attributable to birds are the most abundantly represented on the surface; generally, the tracks display a wide range of variability in terms of morphological details and hence an ichnotaxonomic assignment for all the material is not possible. Footprints allowing an ichnotaxonomic treatment were assigned to *Gruipeda maxima* Panin & Avram, 1962, cf. *Porcellusignum* isp. and Eutardigrada indet., that were related in literature to gruiform and/or ciconiiform birds, hydrochoerid rodents and ground sloths, respectively.

MATERIAL AND METHODS

The studied track-bearing surface (41° 00′ 52.3″ S; 064° 10′ 0.46″ W) is exposed near the protected natural area of Pozo Salado, along a NW-SE tract of the Atlantic shoreline (Río Negro Province, Argentina; Fig. 1). The track-bearing surface is exposed daily to wind and marine aerosol, and it is affected by wide-ranged tides, up to nine meters in span, twice a day, throughout the year. Intertidal exposed surfaces are subject to extreme and variable physical conditions in terms of temperature and desiccation (Bertness *et al.*, 2006; Archuby & Roche, 2019). About 20 footprints were observed, considered as weathered tracks due to recent modification (*sensu* Marty *et al.*, 2016). The studied surface reveals abundant footprints but low ichnodiversity; avian tracks are the most represented, although mammal tracks have been also identified. Footprints range in length from 5 to 20 cm and vary in appearance from faint to clearly preserved impressions, most likely due to multiphase trampling.

High-resolution digital photogrammetry was adopted with the aim of digitally preserving the record that, due to its geographical position (*i.e.*, exposure to strong winds, high energy water and high temperatures), is prone to rapid weathering. This technique was performed on those footprints that were deemed sufficiently detailed for ichnotaxonomic assignment. Images used for photogrammetric process were acquired using a reflex digital camera with 50 mm focal length and 6000 x 4000 pixel resolution. Three-dimensional meshes were obtained through the software Agisoft Metashape Professional (version 1.5.6, Educational License), scaled and converted into a colour topographic profile using the software Paraview (version 5.4.1). Footprint parameters were measured following Leonardi (1987); some measures were checked on three-dimensional meshes. In the case of digit imprint length, free digit has been considered.

GEOLOGICAL SETTING

The Río Negro Formation was established by Andreis (1965) to indicate epiclastic and volcaniclastic deposits exposed along the sea-cliffs and alluvial plains of the Río Negro and Buenos Aires provinces (Aramayo, 2007). This lithostratigraphic unit has been also recognized in inner areas of the La Pampa (Melchor, 2009) and Río Negro provinces (Escosteguy *et al.*, 2011), as well as in the Andes Range (Casamiquela, 1969; González Díaz & Nullo, 1980; Bilmes *et al.*, 2013). K-Ar absolute datings of vitreous concentrates, obtained from a tuff in the marine portion of the unit, indicated an average age of 9.4 Ma (Tortonian, Miocene;

Zinsmeister *et al.*, 1981). Fossil mammal remains were reported from the unit suggesting a late Miocene-early Pliocene age interval (*e.g.*, Aramayo, 1987; Alberdi *et al.*, 1997).

The Río Negro Formation was subdivided into three members by Zavala and Freije (2001). According to these authors, the lower member is represented by aeolian sandstones and reddish pelites sedimented in large dune and dry-wet interdune settings; the middle member is characterized by bioclastic sandstones and dark grey mudstones deposited in a shallow-marine paleoenviron-

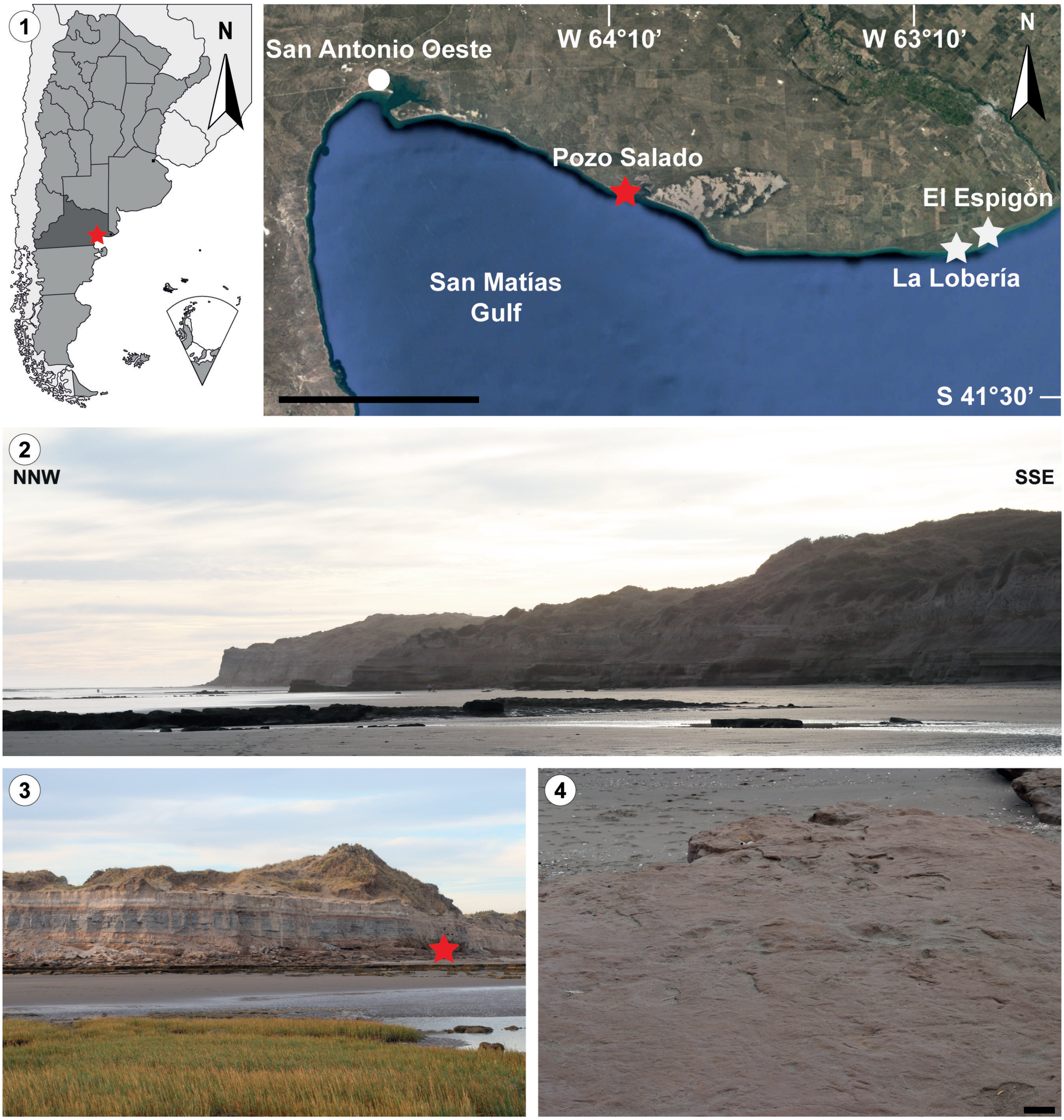

Figure 1. 1, location map of the new track-bearing surface in the Atlantic shoreline of the Río Negro Province (dark grey, left map) and close-up of the area (right map). The red star indicates the location of Pozo Salado locality. White stars indicate two historical localities, namely La Lobería and El Espigón tracksites. **2,** panoramic view of the cliffs of the Atlantic shoreline, where the Río Negro Formation is extensively exposed. **3,** stratigraphic section at Pozo Salado; red star indicates the area where the track-bearing surface crops out. **4,** discrete portion of the track bearing surface. Scale bars equal 50 km in **1** and 10 cm in **4**. Satellite image from Landsat/Copernicus 2018; Google Earth, accessed June, 2021).

ment (Zavala & Freije, 2001); finally, the upper member is represented by aeolian sandstones, mostly developed at the base, and paleosoils and tuffs prevailing at the top (Carmona *et al.*, 2012). Tetrapod tracks were reported from all members of the unit (Casamiquela, 1969; Aramayo, 2007; Carmona *et al.*, 2012; Melchor *et al.*, 2013).

In the area of Pozo Salado, the Río Negro Formation is exposed along the sea cliff through a mainly undisturbed, stratified succession gently dipping towards NNE (Fig. 2). The base of the stratigraphic section that was measured (total thickness less than six meters) is constituted by about 60 cm of reddish, fine- to medium-grained sandstones. The footprint-bearing horizon lies above, at the top-surface of a tabular, 25 cm-thick layer of reddish, fine-grained sandstones. As far as we were able to observe, clear clues indicating bacterial activity promoting track preservation by early lithification of trampled sediments are lacking, even if it cannot be completely discarded for some footprints associated to surface corrugation. The track-bearing level is mostly eroded, crops out discontinuously and can be partially covered by recent sediments of the Atlantic shoreline. Less than 5 cm of muddy, fine-grained purplish sandstones lie above the track-bearing surface. The section continues upward with a one-meter thick pelitic portion constituted by brownish mudstones composing centimetre-thick layers intercalated with fine-grained sandstones. Above lie about 2 m of well-sorted, medium-grained, light bluish sandstones of meter-scale, cross-bedded stratification and parallel lamination, followed by 40 cm thick, massive, reddish mudstones with tabular geometry. The measured section ends with 1.5 m of light bluish sandstones with large-scale, cross-bedded stratification and parallel lamination.

Fine-grained sandstones, including those bearing vertebrate footprints, muddy sandstones, and mudstones intercalated between sandstones were referred to tidal

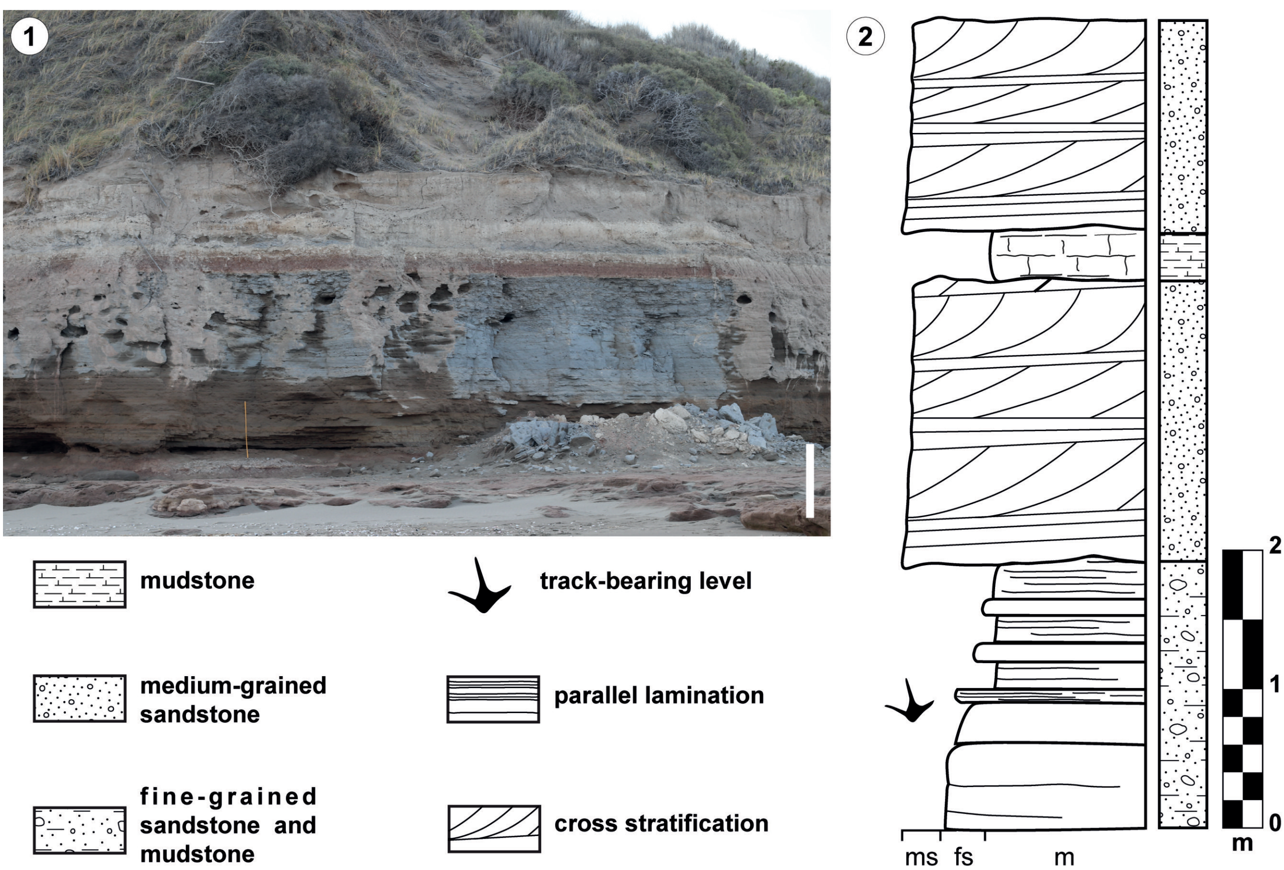

Figure 2. 1, stratigraphic section in the proximity of the track-bearing surface. **2,** schematic drawing of the measured stratigraphic section. Scale bar equals 2 m.

facies by Carmona *et al.* (2012) and Melchor *et al.* (2013), while overlying cross-bedded sandstones and reddish mudstones would correspond to aeolian and wet interdune facies, respectively (Zavala & Freije, 2001; Carmona *et al.*, 2012). We consider the deposits of Pozo Salado bearing tetrapod tracks to be very similar to those included by Carmona *et al.* (2012) in the sedimentary facies F3. It represents tidal flat deposits that, according to the authors, dominate the middle member of the unit. Moreover, if the stratigraphic position and trend of repetition of this sedimentary facies is considered (see Carmona *et al.*, 2012, fig. 2), then the short stratigraphic section we describe could belong to the upper portion of the middle member of the Río Negro Formation and it probably contains the boundary with the upper, aeolian-dominated, member of the unit.

SYSTEMATIC ICHNOLOGY

Gruipeda Panin & Avram, 1962
emend. de Valais & Cónsole-Gonella (2019)

Type species. *Gruipeda maxima* Panin & Avram, 1962, from the Miocene of Romania.

Emended diagnosis. Footprints showing four-digit imprints, three of which (II to IV) are directed forward and larger, the fourth (I), directed backward, spur-like and short. The interdigital angles between digits II and III and between digits III and IV are commonly less than 70°. The hallux imprint is posteromedially directed; the interdigital angle between digits I and II being smaller than that between digits I and IV. When present, digital pad traces displaying the relation I: 2, II: 2, III: 3, IV: 4. Webbing trace absent (from de Valais & Cónsole-Gonella, 2019: 232).

Remarks. Tetradactyly, digital proportions and pattern of interdigital angles of footprints in Figures 3.1, 3.3, and 4.1–4.4 fall into *Gruipeda*, an ichnotaxon originally based on a producer deemed a member of the Gruidae family. The ichnogenus *Gruipeda* has been revised by Sarjeant and Langston (1994) and de Valais and Melchor (2008). Subsequently, its diagnosis has been emended by de Valais and Cónsole-Gonella (2019), mainly with regard to the correspondence of digit axes I and III and measurement of interdigital angles. The ichnogenus *Gruipeda* is identified worldwide both in Mesozoic and Cenozoic rocks and contains more than ten ichnospecies (*e.g.*, Sarjeant & Langston, 1994; Ataabadi & Khazaee, 2004; McDonald *et al.*, 2007; de Valais & Cónsole-Gonella, 2019; Melchor *et al.*, 2020). *Gruipeda* differs from *Alaripeda* Sarjeant & Reynolds (2001) in having more straight digit impressions and lower interdigital angles; the latter ichnogenus has been considered a *nomen dubium* by Lockley and Harris (2010). The ichnogenus *Ardeipeda* Panin & Avram, 1962 is excluded for having impression of digit I as long as other digit impressions and lower interdigital angles if compared to *Gruipeda* (see also Lockley & Harris, 2010; de Valais & Cónsole-Gonella, 2019). Moreover, *Ardeipeda* traditionally includes footprints in which the axes of digit I and III lie in the same direction and interdigital angles between digit I and digit II and between digit I and digit IV are equal or sub-equal (see de Valais & Cónsole-Gonella, 2019). The ichnogenus *Avipeda* Vialov, 1965 is excluded for dactyly (*i.e.*, it includes tridactyl footprints), digit impressions sub-equal in length and thicker than in *Gruipeda*, also bearing claw marks and showing lower interdigital angles.

Gruipeda maxima Panin & Avram, 1962
Figure 3.1

Referred material. An isolated track, *in situ*.

Description. The specimen is a tetradactyl footprint with three digit imprints anteriorly directed and one posteriorly (Fig. 3.1). It is 174 mm long and 199 mm wide. Digit III imprint measures 104 mm in length, digit II imprint is 87.7 mm and digit IV is 87.5 mm. The hallux impression, backwardly directed and in contact with the proximal margin of the sole, measures 35.4 mm in length (Fig. 3.1). Interdigital angle between digits I and III impressions equals 132°; the same parameter for digits I-II, II-III and III-IV is 79°, 53° and 61° respectively. Interdigital angle between digits IV and I is 166°. Digit impressions II-IV are pointed, while the faint impression of digit I shows a spur-like morphology. No claw marks were observed. Finally, the footprint displays a slight curvature between digit impressions, more evident between digits II and III (white arrows in Figure 3.1). Although such a structure may indicate an interdigital web, it is not possible to conclude that the producer had webbed feet, since webbed morphology can result from sediment failure (Falkingham *et al.*, 2009).

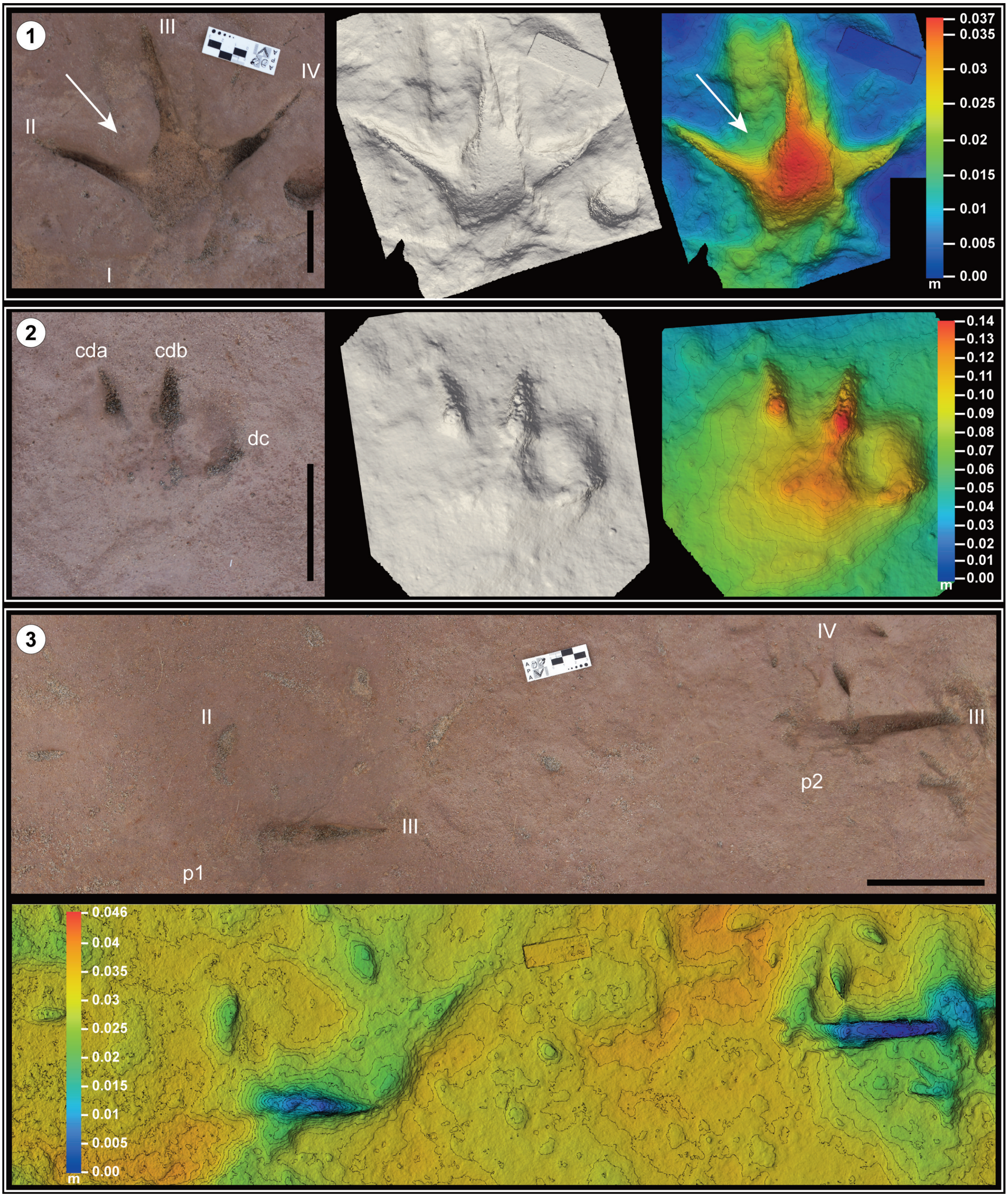

Figure 3. Best preserved tracks from Pozo Salado (Río Negro Province, Argentina). **1,** track referred to ***Gruipeda maxima*** and associated digital outputs representing track three-dimensional morphology (solid mesh in the center and digital elevation model to the right; both visualized as casts). Scale bar equals 5 cm. **2,** track referred to cf. ***Porcellusignum*** and associated digital outputs representing track three-dimensional morphology (solid mesh in the center and digital elevation model to the right; both visualized as casts); **cda**, central digit 'a'; **cdb**, central digit 'b'; **dc**, digit 'c'. This nomenclature is needed in order to differentiate digit impressions, obviating incompleteness of track that prevents digit count and identification. Scale bar equals 5 cm. **3,** partial avian trackway and related digital elevation model representing track three-dimensional morphology. Scale bar equals 10 cm. Roman numerals refer to digital count.

Remarks. On the basis of dactyly, digit proportions and orientations, interdigital angles II-III and III-IV less than 70°, interdigital angle I-II smaller than I-IV, and spur-like morphology of digit I, we assign the footprint to *Gruipeda maxima* (see Sarjeant & Langston, 1994; de Valais & Melchor, 2008; de Valais & Cónsole-Gonella 2019), an ichnotaxon that has been related to cariamid (*e.g.*, Aramayo, 2007), gruiform (*e.g.*, Lockley & Harris, 2010; de Valais & Cónsole-Gonella, 2019) and ciconiiform (*e.g.*, Díaz-Martínez *et al.*, 2012) producers.

Gruipeda cf. ***maxima*** Panin & Avram, 1962
Figures 3.3, 4.1–4.4

Referred material. Four footprints, two aligned (p1 and p2 in Fig. 3.3) and likely belonging to a same trackway, and two isolated (Fig. 4.3–4.4). All materials *in situ*.

Description. Footprint p1 (Figs. 3.3, 4.1), that is probably a right track based on digit trace identification, is characterized by the incomplete impression of digits II and III. Digit II measures 5.6 cm in length, digit III is 11 cm in length and more deeply impressed than digit II. Interdigital angle between digits II and III is 92°. Footprint p2 (Figs. 3.3, 4.2) is characterized by a digit III that is 10.2 cm in length and that results as deep as digit III in p1. Digit IV is 7.9 cm in length. Interdigital angle between digit III and IV is 85°. The two remaining footprints (Fig. 4.3–4.4) are characterized by only two slender digit impressions each one, digit III being the longest one, with interdigital angles equal to 74° and 58°, respectively. No webbing and/or claw traces were observed.

Remarks. We refer these footprints to *Gruipeda* cf. *maxima* on the basis of general morphology, appearance of digit impressions and available digit proportions. In the case of isolated footprints in Figure 4.3 and 4.4, values of interdigital angle also support the proposed ichnotaxonomic allocation.

Indeterminate avian tracks
Figure 4.5–4.7

Referred material. An isolated footprint and two isolated digit traces, *in situ*.

Description and remarks. Among indeterminate avian tracks we include an isolated, didactyl track with incompletely preserved digit impressions, separated by an interdigital angle smaller than 90° (Fig. 4.5), and several elongated, shallow impressions here interpreted as digit traces (Fig. 4.6–4.7).

Porcellusignum Casamiquela in Angulo and Casamiquela, 1982

Type species. *Porcellusignum conculcator* Casamiquela in Angulo and Casamiquela, 1982.

Diagnosis. Digitigrade impressions of a medium-sized mammal, functionally tridactyl but occasionally tetradactyl. Manus and pes sub-equal in dimensions; digital impressions acuminate and large, sometimes transversely or diagonally elongated, grouped in sets of three, with the central digit in a more advanced position and asymmetrically located. Footprints are randomly distributed, suggesting high mobility of the producer. Tail trace absent (translated from Casamiquela in Angulo & Casamiquela, 1982: 52–53).

Remarks. Casamiquela established the ichnotaxon *Porcellusignum conculcator* on the basis of dozens of footprints preserved on at least two boulders in the Balneario El Cóndor locality. A peculiar feature of the material is represented by the high digitigrady (*i.e.*, unguligrady?), that was related to not compliant substrate properties during track formation (Angulo & Casamiquela, 1982). Based on footprint dimensions, Casamiquela referred these tracks to a member within Hydrochoeridae (Angulo & Casamiquela, 1982).

cf. ***Porcellusignum*** isp.
Figure 3.2

Referred material. An isolated footprint, *in situ*.

Description. The footprint is tridactyl, 65.4 mm longh and 53.6 mm wide. It appears to be not completely preserved and, as a consequence, the width value is not considered to be reliable; digit count and identification are prevented as well. Free-digit length of central digit 'a' (**cda** in Fig. 3.4) equals 4.2 cm, that of central digit 'b' (**cdb** in Fig. 3.4) is 4.5 cm, while that of digit 'c' (**dc** in Fig. 3.4) is 2.3 cm. Interdigital angle between central digit 'a' and central digit 'b' is 21°; that between central digit 'b' and digit 'c' is 58°. A fourth digit impression is weakly noticeable in the field and can be visualized through the digital elevation model in Figure 3.2.

Another faintly impressed feature of the track is an enlarged pad more deeply impressed in its central portion, anteriorly to digit cda and cdb.

Remarks. The footprint looks like the fore-footprints of some extant small-sized caviomorph rodent based on its general appearance and the sub-equal and almost parallel central digit impressions. Looking at the vertebrate ichnological record from the Río Negro Formation, a similar pattern and proportions of digit impressions are observed in footprints classified as cf. *Porcellusignum* isp. by Aramayo (2007). Nevertheless, both records seem quite different from the figured type series of *Porcellusignum*. For the time being we consider that the material presented here could represent a totally different preservational variant of *Porcellusignum* and we tentatively assign the track to cf. *Porcellusignum* isp. The most important difference between the material here presented and that of Casamiquela is the impression of the pad anterior to digit impressions, that would mirror the palm pad of the producer fore autopod, assuming that the footprint is a fore print.

Indeterminate Eutardigrada tracks
Figure 4.8–4.9

Referred material. Two footprints, *in situ*.

Description and remarks. Elongated, sub-elliptical impressions with no digital impressions or claw traces. This material resembles large tracks related to producers among Eutardigrada reported from the Río Negro Formation, but it does not retain diagnostic features (*e.g.*, sharp outline, clear digit impressions, trackway parameters) to allow an inclusion into one of the ichnotaxa erected from the area to date (*i.e.*, *Megatherichnum* Casamiquela, 1974, *Mylodontidichnum* Aramayo & Manera de Bianco, 1987 and *Falsatorichnum* Casamiquela in Angulo & Casamiquela, 1982).

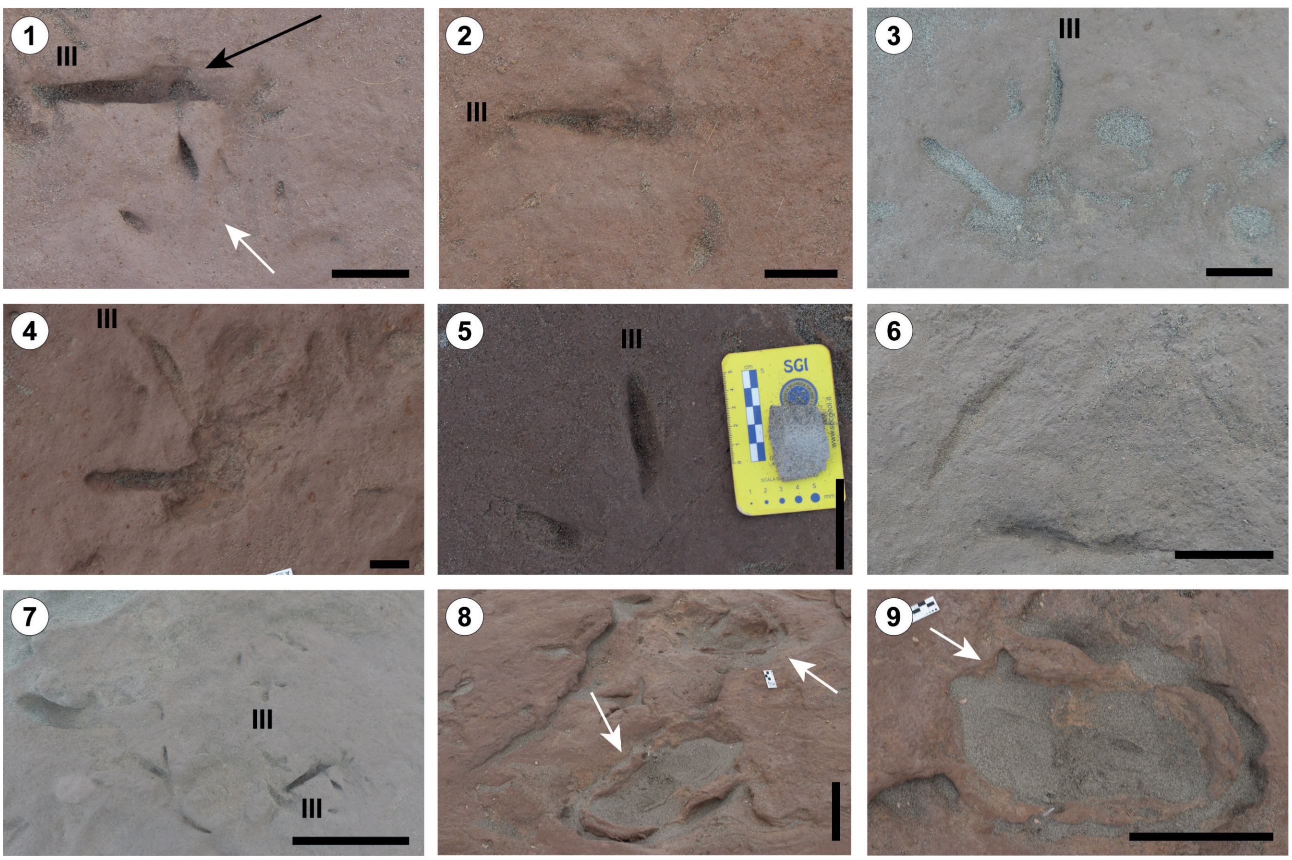

Figure 4. Additional material preserved on the studied track-bearing surface. **1–4,** footprints assigned to ***Gruipeda*** cf. ***maxima***. Black arrow indicates a track assigned to ***Gruipeda maxima***, white arrow indicates a track not classified. Scale bars equal 5 cm. **5–6,** indeterminate avian tracks. Scale bars equal 5 cm. **7,** partial view of avian footprints on the track-bearing surface. Scale bar equals 20 cm. **8–9,** ground sloth tracks. Scale bar equals 20 cm. Roman numeral indicates digit III impressions.

DISCUSSION AND CONCLUSIONS

Similarly to other ichnosites from the same unit, footprints from Pozo Salado occur in facies preserving more than one track type, namely tracks related to small (cf. *Porcellusignum* isp.) and large (indeterminate Eutardigrada tracks) mammals, and bird footprints, some of which fit the ichnogenus *Gruipeda*.

Despite a trackmaker identification based on recognition of phylogenetic characters mirrored in footprints morphology (see Carrano & Wilson, 2001; Romano *et al.*, 2016) is prevented by the poor detail recorded in our material, a brief comment about producers of footprints assigned to *Gruipeda* is noteworthy. Regardless the quality of footprint detail for trackmaker identification, difficulty and, in some cases, impossibility in recognizing with confidence taxonomic categories from bird tracks are most likely due to high convergence among producers' feet to plesiomorphic conditions of certain autopodial elements, as already highlighted by Sarjeant and Langstone (1994) and Lockley and Harris (2010) among others. Based on these inherent limitations, the ichnogenus *Gruipeda*, as well as other ichnotaxa such as *Alaripeda* and *Avipeda*, have been traditionally assigned to shorebirds even if, to date, more exclusive attributions have not been proposed. In the case of shorebirds, both the ichnological and osteological record suggest that extant foot morphology and behaviors were already established in several clades since the latest Cretaceous (Lockley & Harris, 2010). This obviously favors recognition and interpretation of possible behaviors from a neoichnological standpoint, but definitely complicates the identification of the producer in taxonomical terms. According to de Valais and Cónsole-Gonella (2019, and references therein), the term shorebirds is used in ecology to describe birds attending shorelines, shallow waters and mudflats, while from a taxonomic standpoint it would indicate the diverse clade of Charadriiformes. This group includes birds both with non-webbed (*e.g.,* Haematopodidae) and webbed feet (*e.g.,* Laridae). Based on neoichnological observations, footprints presently left by members within Scolopacidae and Charadriidae (Charadriiformes) strongly resemble in morphology fossil footprints assigned to different ichnospecies within *Gruipeda* (see Genise *et al.*, 2009; McCrea *et al.*, 2015). As mentioned before, also cariamids, gruiformes and ciconiiformes have been previously considered as putative producers.

Shorebird tracks and traces are the most abundant among the medium- to small-sized avian track fossil record (Greben & Lockley, 1993) and occur in depositional settings associated to fluvial, floodplain, lakeshore and marine shoreline paleoenvironments, which strongly promote their formation and inclusion into the record (Lockley & Harris, 2010; Lockley *et al.*, 2021). The recurrence of ichnoassociations of bird tracks and traces related to feeding activities of shorebirds has been used to establish, in the context of terrestrial vertebrate ichnofacies, the shorebird ichnofacies, originally in lacustrine paleoenvironments (Lockley *et al.*, 1994; Lockley, 2007; see Santi & Nicosia, 2008 for criticisms) but potentially associated with other settings (Doyle *et al.*, 2000). On the contrary, the same recurrent ichnoassociation has been included in the original ichnofacies concept of Seilacher (1964) to identify the shorebird ichnosubfacies as a subset of the *Scoyenia* ichnofacies of Seilacher (1967) (*sensu* Melchor *et al.*, 2006; de Gibert & Saez, 2009; see Díaz-Martínez *et al.*, 2015, 2016; Astibia *et al.*, 2017; Cónsole-Gonella *et al.*, 2017), indicating zones of moderate to low energy that allow birds to feed (de Valais & Cónsole-Gonella, 2019). Regrettably, footprints from Pozo Salado cannot be considered indicative of any ichnofacies for the time being, because associated, diagnostic invertebrate traces were not observed on the bearing surface.

To date, the vertebrate ichnological record from the Río Negro Formation has been mainly restricted to an area of about 30 km on the Atlantic shoreline of Argentina, between El Faro and La Lobería localities. The new material from Pozo Salado, found 100 km west of these localities, extends the area with track-bearing localities. With respect to ichnofaunal composition, the ichnospecies *Gruipeda maxima* is here reported for the first time, enriching the vertebrate track record from the unit. Taking into account that footprints comparable to *Gruipeda maxima* have been documented from already known localities, further findings and studies may confirm the occurrence of this ichnotaxon in the Río Negro Formation.

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