

## Ichnos

An International Journal for Plant and Animal Traces

ISSN: 1042-0940 (Print) 1563-5236 (Online) Journal homepage: <http://www.tandfonline.com/loi/gich20>

# An Updated Review of the Avian Footprint Record from the Yacoraite Formation (Maastrichtian-Danian), Northwestern Argentina

Silvina de Valais & Carlos Cónsole-Gonella

To cite this article: Silvina de Valais & Carlos Cónsole-Gonella (2018): An Updated Review of the Avian Footprint Record from the Yacoraite Formation (Maastrichtian-Danian), Northwestern Argentina, Ichnos, DOI: [10.1080/10420940.2018.1538982](https://doi.org/10.1080/10420940.2018.1538982)

To link to this article: <https://doi.org/10.1080/10420940.2018.1538982>



Published online: 28 Dec 2018.



Submit your article to this journal [↗](#)



View Crossmark data [↗](#)

# An Updated Review of the Avian Footprint Record from the Yacoraite Formation (Maastrichtian-Danian), Northwestern Argentina

Silvina de Valais<sup>a</sup>  and Carlos Cónsole-Gonella<sup>b</sup> 

<sup>a</sup>CONICET – Instituto de Investigación en Paleobiología y Geología – Universidad Nacional de Río Negro-CONICET, Av. Roca 1424, General Roca (8332), Río Negro, Argentina; <sup>b</sup>CONICET – Instituto Superior de Correlación Geológica (INSUGEO) – Universidad Nacional de Tucumán-CONICET, Miguel Lillo 205 (4000), Tucumán, Argentina

## ABSTRACT

The Yacoraite Formation (Maastrichtian–Danian; Balbuena Subgroup; Salta Group), from Northwestern Argentina, represents a shallow epeiric unit which is the result of transgressions in the Andean basin of South America. Herein, we study the avian footprints from the Maimará locality, Jujuy province, and Quebrada del Tapón ichnosite, Salta province. The avian footprints from the Maimará locality is less diverse, made up: cf. *Alaripeda* isp., *Avipeda* isp., cf. *Gruipeda filiportatis*, and cf. *Gruipeda* isp. The avian track record from the Quebrada del Tapón ichnosite is composed of: cf. *Alaripeda* isp., *Ardeipeda* cf. *egretta*, *Gruipeda filiportatis* (= *Yacoraitichnus avis*) and others *Gruipeda* or compared to this ichnogenus, cf. *Uhangrichnus* isp., and several indetermined avian footprints. Both ichnological assemblages have tracks assigned to shorebirds or Charadriiformes. The facies distribution of trace fossils reinforces the overall model of a shorebird tracks dominance in moderate to low energy settings. This distribution can be divided into three sub-environments: (1) a moderate to high energy shoreline under wave action, (2) a supratidal body of ephemeral ponds, far away from direct wave influence and (3) a landward position, beyond the ephemeral ponds system. We have included all the ichnoassemblages within the shorebird ichnofacies as a subset of the *Scoyenia* Ichnofacies.

## KEYWORDS

Avian footprints; Yacoraite Formation; Cretaceous; Gondwana

## Introduction

The outcrops from the Yacoraite Formation (Maastrichtian-Danian), Northwestern Argentina, have provided interesting paleontological records. Particularly, the record from Salta is widely known since many decades ago, both from the skeletal remains as well as ichnological fossils (e.g., Bonarelli 1927; Benedetto and Sánchez 1971, 1972; Alonso 1978, 1980; Gasparini and Buffetaut 1980; Alonso and Marquillas 1986; Arratia and Cione 1996).

The ichnological record is composed of dinosaur and avian footprints and invertebrate trace fossils (e.g., Alonso 1978, 1980, 1989; Alonso and Marquillas 1986; Cónsole-Gonella et al. 2012b). Several years after these first trace fossil studies of the Yacoraite Formation in Salta, there has been renewed focus on the unit in the Jujuy province, Tres Cruces sub-basin (Figs. 1 and 2; Cónsole-Gonella, Griffin, and Aceñolaza 2009; Cónsole-Gonella and Aceñolaza 2009, 2010; Cónsole-Gonella et al. 2012a, 2012b, 2013, 2017;

Díaz-Martínez, de Valais, and Cónsole-Gonella 2016). In this sub-basin of Jujuy, Díaz-Martínez, de Valais, and Cónsole-Gonella (2016) and Cónsole-Gonella et al. (2017) described dinosaur tracks (*Hadrosauropodus* isp., titanosaurian, ornithischian and theropod tracks) and avian footprints (cf. *Alaripeda* isp.; *Avipeda* isp., cf. *Gruipeda* isp., cf. *Yacoraitichnus avis*) from the Maimará tracksite.

The Yacoraite Formation is homologous, both in age and facies, with other geological units from the Central Andes (see Marquillas et al. 2011). This situation is similar to the ichnological record of the Late Cretaceous Bolivian and Peruvian deposits (Cónsole-Gonella et al. 2017), where diverse dinosaur tracks have also been described (Leonardi 1981, 1984; Meyer, Hippler, and Lockley 2001; Lockley et al. 2002, among others). These deposits are part of epicontinental seas and very extensive lakes, in mixed carbonate-type clastic sequences (see Marquillas, del Papa, and Sabino 2005, and references therein). However, and beyond these similarities, one relevant difference

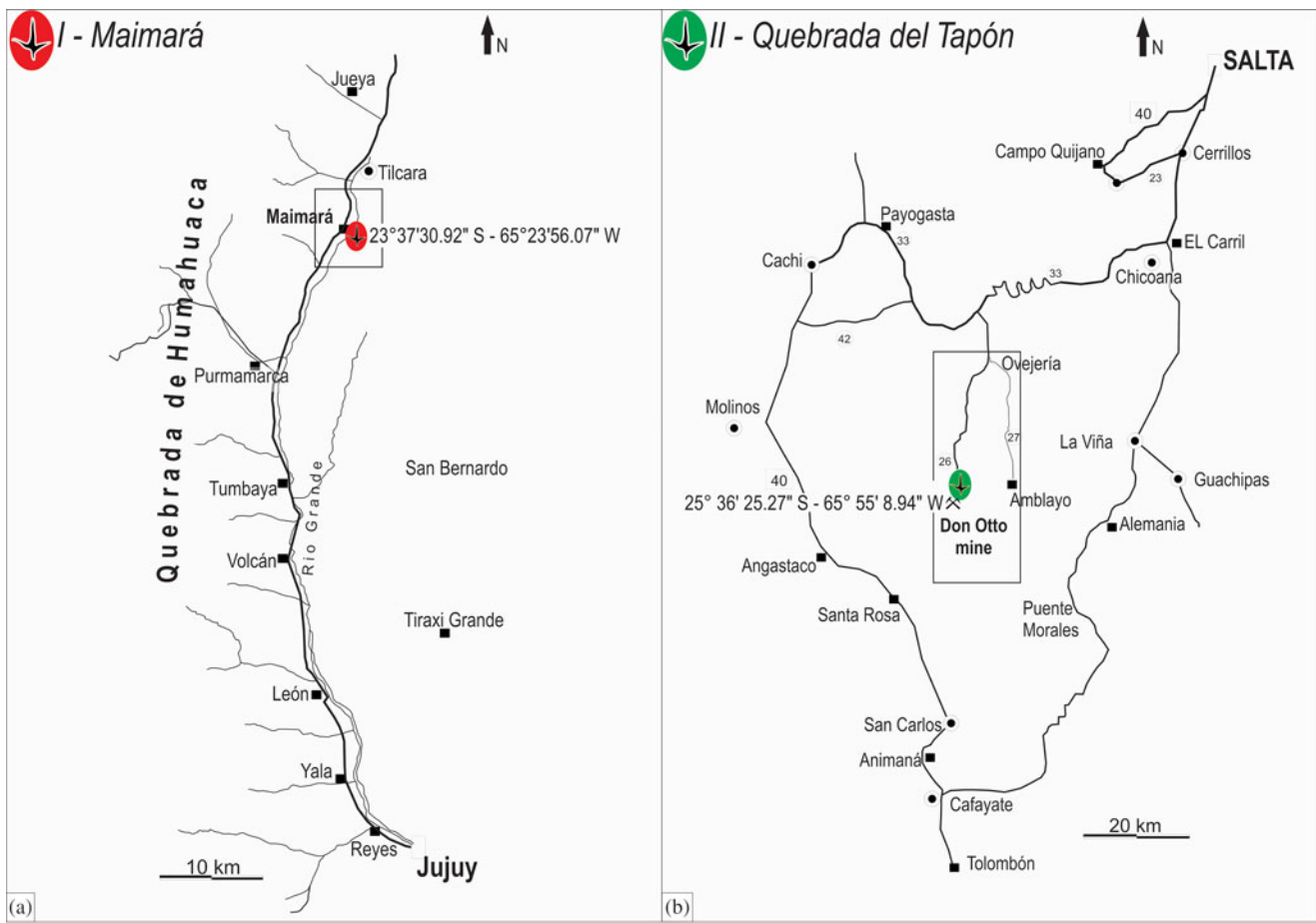


Figure 1. Location maps of the localities: (A) I – Maimará. (B) II - Quebrada del Tapón.

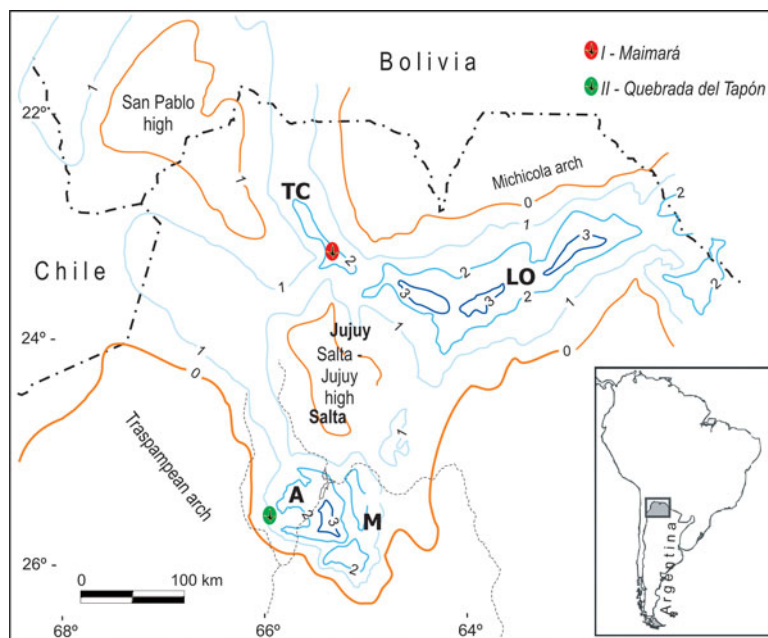
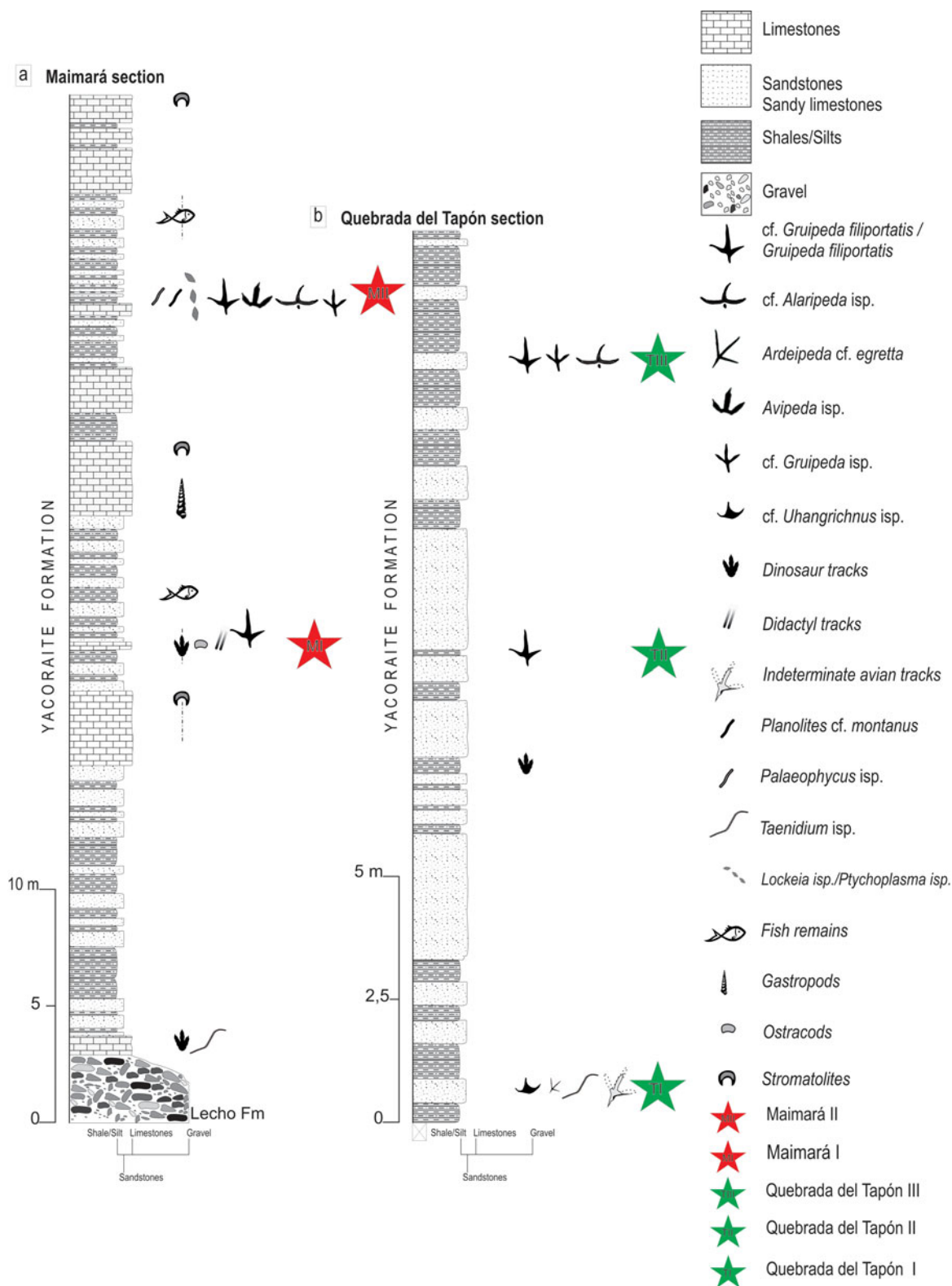


Figure 2. Isopach map of the Yacoraite Formation. Main sub-basins: TC, Tres Cruces; LO, Lomas de Olmedo; A, Alemania; M, Metán. Thickness in hundreds of meters (after Marquillas, del Papa, and Sabino 2005). The green and red ovals indicate the ichnofossiliferous localities.



**Figure 3.** Integrated logged section and track-bearing strata: (A) in the Maimará section, Tres Cruces sub-basin. (B) in the Quebrada del Tapón section, Alemania sub-basin.

between the Yacoraite Formation and the rest of Upper Cretaceous units of the Andean Basin is the avian footprint record, which remains unknown from Bolivian and Peruvian units.

Thus, the main goal of this contribution is to present, describe, and analyse the avian footprint record from two ichnological localities: the Maimará tracksite in the Jujuy province, and the Quebrada del Tapón

**Table 1.** Summary of measurements of the tracks from Maimará site, at the Quebrada de Humahuaca region, Jujuy province, and Quebrada del Tapón site, at the southern Valle del Tonco, Salta province, both in Argentina, with information on the localities of provenance and the current location of the material.

Ichnotaxa	TL	L	W	II–IV	II–III	III–IV	I–III	Locality provenance	Current location	References
<i>cf. Alaripeda</i> isp.	–	56.8	86.0	142	–	–	–	Maimará	<i>In situ</i> (Fig. 4A)	Cónsole-Gonella et al. (2017:338); de Valais, Cónsole-Gonella, and Díaz-Martínez (2016: 15)
	–	37.7	46.4	125	–	–	–			
	–	47.0	82.0	140	65	75	160			
	113.4*	68.0	90.7	145	73	62	167	Quebrada del Tapón	<i>In situ</i> (Figs. 4B,C), same surface than <i>cf. Gruipeda filiportatis</i>	
	74	46.7	70.8	140	84	56	170			
	69.7	–	74.9	158	98	61	161			
	–	46.2	72.8	151	–	–	–			
	–	–	–	–	–	–	161			
	<b>71.85</b>	<b>50.4</b>	<b>74.8</b>	<b>143</b>	<b>80</b>	<b>63</b>	<b>164</b>			
<i>Ardeipeda cf. egretta</i>	43.5	28.5	37.2	98	–	–	–	Quebrada del Tapón	<i>In situ</i> (Fig. 4F)	This work
<i>Avipeda</i> isp.	–	41.1	48.5	64	–	–	–	Maimará	<i>In situ</i> (Fig. 4I)	Cónsole-Gonella et al. (2017: 338); de Valais, Cónsole-Gonella, and Díaz-Martínez (2016: 15)
<i>Gruipeda filiportatis</i>		58.0	65.0	123	73	50	–	Quebrada del Tapón	<i>In situ</i> (Fig. 4N–O)	Alonso and Marquillas (1986:39); Cónsole-Gonella et al. (2017: 338); de Valais et al. (2016: 15)
		80.0	102.0	133	104	33	–			
		62.0	71.0	128	93	37	–			
	<b>98.4</b>	<b>65.6</b>	<b>71.5</b>	<b>134</b>	<b>96</b>	<b>38</b>	<b>180</b>		Lost holotype of " <i>Yacoraitichnus avis</i> " (Fig. 4M)	
<i>cf. Gruipeda filiportatis</i>	98.4	66.4	77.4	130	92	40	180	Maimará	<i>In situ</i> (Figs. 4G,J)	Cónsole-Gonella et al. (2017: 338); de Valais, Cónsole-Gonella, and Díaz-Martínez (2016: 15)
	158.4*	113.6*	83.0	123	72	48	170			
	–	79.2	–	–	–	36	–	Quebrada del Tapón	<i>In situ</i> (Figs. 4B,C)	
	–	54.1	58.7	111	70	56	–			
<i>cf. Gruipeda</i> isp.		<b>66.6</b>	<b>70.8</b>	<b>117</b>	<b>71</b>	<b>47</b>	<b>170</b>			
	–	64.5	–	125	–	–	–	Maimará	<i>In situ</i> (Figs. 4K,L)	Cónsole-Gonella et al. (2017: 338); de Valais, Cónsole-Gonella, and Díaz-Martínez (2016: 15)
	–	–	72.7	132	–	–	–			
	115.2	50.4	71.4	136	–	–	170			
	88.4	54.7	–	–	58	–	144			
	42.0*	32.7*	–	–	–	–	–			
–	24.4*	–	–	–	–	–				
	<b>101.8</b>	<b>56.5</b>	<b>72.1</b>	<b>131</b>	<b>58</b>	–	<b>157</b>			
<i>cf. Uhangrichnus</i> isp.	–	–	40.3	65	35	27	–	Quebrada del Tapón	<i>In situ</i> (Figs. D,E)	This work
	–	40.2	39.2	78	38	37	–			
	–	–	–	–	–	38	–			
	40.2	39.7	71	36	34	–				
Indeterminate avian tracks				104				Quebrada del Tapón	<i>In situ</i> (Fig. 4H)	This work
				119						

TL, total track length, taking into account the hallux imprint; L, track length; W, track width; II–IV, angle formed by the axis of the imprints of digits II and IV; II–III, angle formed by the axis of imprints of digits II and III; III–IV, angle formed by the axis of imprints of digits III and IV; I–III, angle formed by the axis of imprints of digits I and III. Linear measurements in millimeters and angles in degrees; the averages in bold; the values that were not incorporated into the averages are indicated with an asterisk.

tracksite in the Salta province, with emphasis on an updated ichnotaxonomical interpretation, and environmental and ichnofacies implications.

## Geological setting

The Yacoraite Formation (Maastrichtian–Danian) represents a shallow epeiric unit, which is the result of the marine transgressions in the Andean basin of South America, caused by the high global sea level of the Late Cretaceous (Hay et al. 1999; Marquillas, del Papa, and Sabino 2005; Marquillas et al. 2011; Scotese 1997). It is composed mainly of carbonates with varied depositional textures that are largely dolomitic; in

some of the proximal sections, conglomerates, calcareous sandstones and pelites. This formation is part of the Balbuena Subgroup (Upper Cretaceous–Lower Palaeocene), which is the early postrift deposit of the Salta Group (Lower Cretaceous–Eocene), an intra-continental rift-type basin (e.g., Salfity and Marquillas 1994; Viramonte et al. 1999; Marquillas, del Papa, and Sabino 2005). The Salta Group is widely distributed in northwestern Argentina and neighboring region (Fig. 2), and it is accumulated in seven sub-basins: Tres Cruces, Lomas de Olmedo, Metán, Alemania (Reyes 1972; Salfity 1982), El Rey (Salfity 1980), Sey (Schwab 1984) and Brealito (Sabino 2002).



**Table 2.** Ichnoassemblages distribution, ichnological content and palaeoenvironments from Maimará site, at the Quebrada de Humahuaca region, Jujuy province, and Quebrada del Tapón site, at the Southern Valle del Tonco, Salta province, both in Argentina.

Ichnoassemblage	Locality procedance	Trace fossils		Palaeoenvironmental Setting	References
		Vertebrate	Invertebrate		
M I	Maimará	cf. <i>Gruipeda filiportatis</i> didactyl tracks		Shoreline	Cónsole-Gonella et al. (2017); this work
MII	Maimará	cf. <i>Alaripeda</i> isp. <i>Avipeda</i> isp. cf. <i>Gruipeda</i> isp. cf. <i>Gruipeda filiportatis</i>	<i>Palaeophycus tubularis</i> <i>Planolites</i> cf. <i>montanus</i> <i>Lockeia</i> isp. <i>Ptychoplasma</i> isp.	Ephemeral ponds	Cónsole-Gonella et al. (2017); this work
TI	Quebrada del Tapón	<i>Ardeipeda</i> cf. <i>egretta</i> cf. <i>Uhangrichnus</i> isp. Indeterminate avian tracks	<i>Taenidium</i> isp.	Landward	This work
TII	Quebrada del Tapón	<i>Gruipeda filiportatis</i>	cf. <i>Palaeophycus</i> isp.	Ephemeral ponds	This work
TIII	Quebrada del Tapón	cf. <i>Alaripeda</i> isp. cf. <i>Gruipeda filiportatis</i> cf. <i>Gruipeda</i> isp.		Landward	This work

The Yacoraite Formation is Maastrichtian–Danian in age thus the Cretaceous–Paleogene boundary occurred during its accumulation (Marquillas 1985), and U–Pb dating indicates a Maastrichtian age for the Metán sub–basin (Salta province, Fig. 2; Marquillas et al. 2011).

### Studied sections

The avian tracks analysed here come from two localities, the Maimará locality (Jujuy province) and Quebrada del Tapón (Salta province).

**Maimará section.** The Maimará section pertains to the Tres Cruces sub-basin, at the northwestern area of the Salta Group, in the Quebrada de Humahuaca region, Jujuy province (23°37'30.92"S and 65°23'56.07"W; Figs. 1, 2). The section of the Yacoraite Formation in Maimará (Fig. 3) is composed of limestones of different textures, formed by oolitic and intraclastic grainstones, oo-intraclastic packstones, wackestones, fine calcareous sandstones, limestones and mudstones and stromatolitic levels (Cónsole-Gonella et al. 2017).

**Quebrada del Tapón section.** The Quebrada del Tapón section pertains to the Alemania sub-basin, at the southwestern area of the Salta Group, belonging to the Parque Nacional Los Cardones, in the Salta province (25°36'25.27"S and 65°55'8.94"W; Figs. 1, 2). The studied section of the Yacoraite Formation in the Quebrada del Tapón (Fig. 3) is composed of fine calcareous sandstones, limestones and mudstones.

### Materials and methods

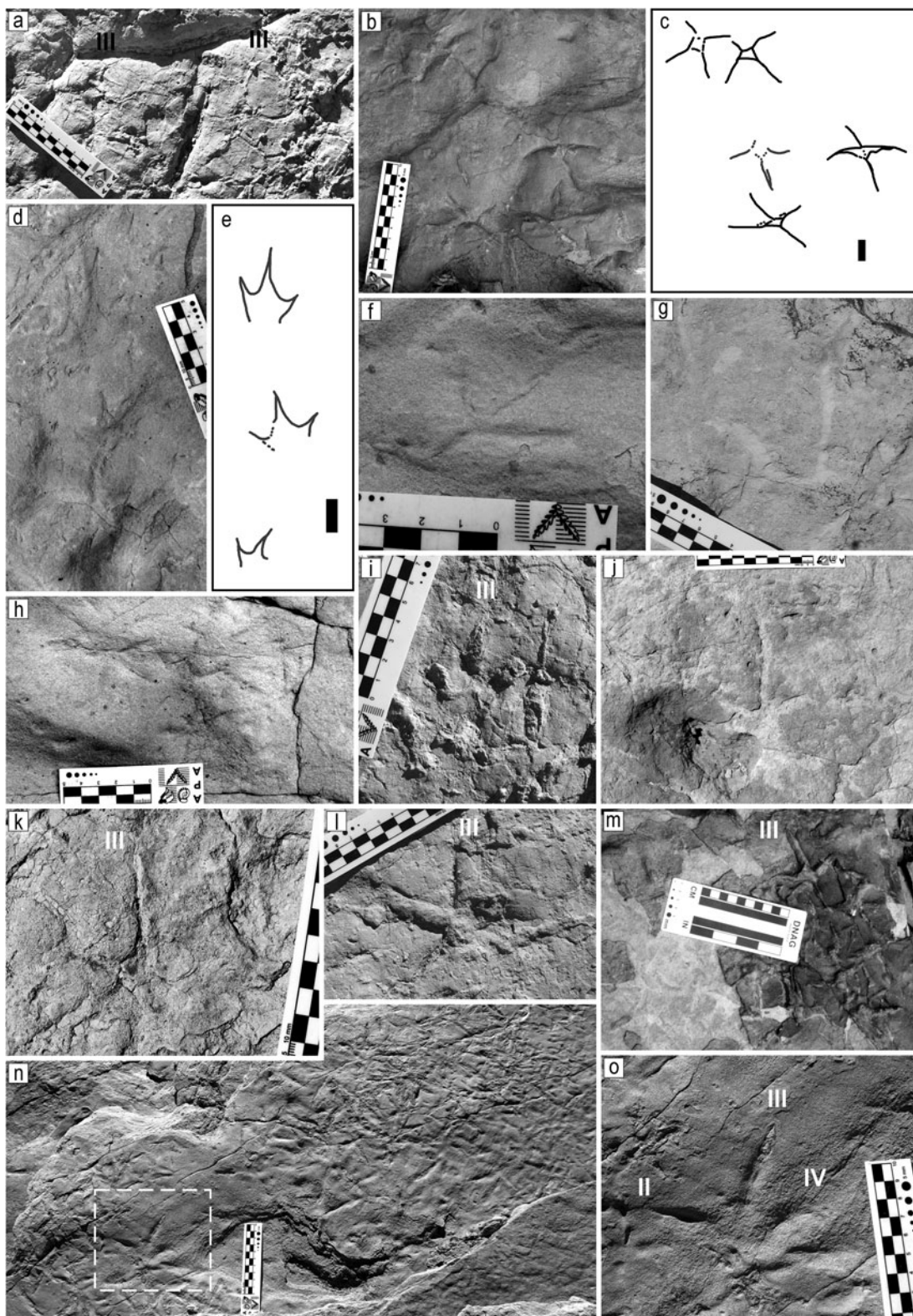
The specimens, all but one still *in situ*, come from two different localities: (1) the Maimará ichnosite:

many of these tracks have been previously mentioned (Cónsole-Gonella and Aceñolaza 2010; Cónsole-Gonella et al. 2012a, 2013, 2017), and some of them are still unpublished, and (2) Quebrada del Tapón locality, into the Valle del Tonco ichnosite: some footprints have been mentioned and described several decades ago (Alonso and Marquillas 1986) and some have been found during recent fieldtrips and briefly mentioned (de Valais, Cónsole-Gonella, and Díaz-Martínez 2016). A summary of the measurements, ichnoassemblages distribution, and other data of the tracks, is provided in Tables 1 and 2.

There is only one collected track-bearing slab from the Quebrada del Tapón locality, mentioned in the literature as the holotype of *Yacoraitichnus avis* (herein as junior synonym of *Gruipeda filiportatis*), housed in the collection of the paleontological department of the Facultad de Ciencias Naturales of the Universidad Nacional de Salta, Salta province, with no specimen number. Currently, this material could not be found at the assigned repository.

The general ichnological descriptions and interpretations follow the criteria by Bertling et al. (2006). Ichnotaxonomic assignment of the avian specimens follows the conventions by de Valais and Melchor (2008) and Lockley and Harris (2010). The measurements on the tracks follow the methodology by de Valais and Melchor (2008: see fig. 3).

The ichnofacial features have been analysed based on the concepts by Buatois and Mángano (2011), MacEachern et al. (2012) and Cónsole-Gonella et al. (2017). The archetypical ichnofacies are spelled capitalized and italicised *sensu* MacEachern et al. (2012).



**Figure 4.** Photographs of the avian footprints. (A) pair of tracks of *cf. Alaripeda* isp. (B) Surface with *cf. Alaripeda* isp. and *cf. Gruipeda filiportatis*. (C) Drawing of the tracks in b; *cf. Gruipeda filiportatis* in grey in the center on the picture. (D) Trackway of *cf. Uhangrichnus* isp. (E) Drawing of the tracks in (D). (F) *Ardeipeda cf. egretta*. (G, J) *cf. Gruipeda filiportatis*. (K, L) *cf. Gruipeda* isp. (M) original slab—currently lost—of *Gruipeda filiportatis* (= “*Yacoraitichnus avis*”). (N) Surface with *Gruipeda filiportatis*. (O) Detail of (N). A, G, I, J, K and L from Maimará locality. B, D, F, H, M, N and O from Valle del Tonco locality. III indicates the impression of digit III. Scale bar divisions is in cm.

## Avian track record

### *Alaripeda Sarjeant and Reynolds 2001*

**Type ichnospecies.** *Alaripeda logfreni* Sarjeant and Reynolds 2001, from the Late Miocene of California (not precisely located; *sensu* Sarjeant and Reynolds 2001), USA.

**Diagnosis.** Footprints showing three or, often, four digit impressions. The central digit (III) is directed forward, but may curve quite sharply; digit I is short, less than half the length of digit III, often oriented reverse of the axis of digit III but sometimes deviating up to 20°. The other digits (II and IV) are directed proximally. Length of digit III comparable to (or less than 25% greater than) that of digits II and IV. Webbing lacking; no indication of a metatarsal pad (from Sarjeant and Reynolds 2001: 29).

**Remarks.** This monotypic ichnogenus was created to include a slab with at least five complete well-preserved tetradactyl footprints with slender curved inward digit impressions and wide divarication (Sarjeant and Reynolds 2001).

Some other footprints assigned to *Alaripeda* have been mentioned in the literature (Johnson 1986; Scrivner and Bottjer 1986; Sarjeant and Reynolds 2001; de Valais and Melchor 2008; García Raguel et al. 2009; Mansilla et al. 2012; Reynolds 2012). Tracks from the Neogene Carpathian Romanian (Vialov 1965: pl. 7, slab 3) are comparable to *Alaripeda*. Also the tracks mentioned as *Ignotornis mcconnelli* from Double Mountain, Alaska, by Fiorillo et al. (2011), are similar to this ichnotaxon.

*Gruipeda* Panin and Avram 1962, originally described from the Miocene of Romania, differs from *Alaripeda* by having straight impressions of digits II to IV and a lower divarication of digits II–IV (an average of 140°). On the contrary, there are opposite opinions. Lockley and Harris (2010) claimed that *Alaripeda* is a *nomen dubium* seeing that it is not a different ichnotaxon but it is different preservation of the trackmaker foot morphology. Herein, we considered that *Alaripeda* reflects accurate foot morphology and displays enough different ichnotaxobases to deserve a separate ichnotaxonomical nomination.

### *cf. Alaripeda isp (Fig. 4A–C)*

**Referred material.** Eight tracks preserved as negative epichnia: two isolated and two arranged side by side –right and left– tracks from the Maimará locality, and four isolated from the Quebrada del Tapón locality

(in Cónsole-Gonella et al. 2017: 338; de Valais, Cónsole-Gonella, and Díaz-Martínez 2016: 15).

**Description.** The specimens are eight tridactyl and tetradactyl footprints, poorly preserved; those from Maimará display slight evidence of artificial digital elongation by desiccation. Two of them are apparently arranged side by side by stopping the right foot at side of the left one, resembling a stopping or hopping posture, while the others are isolated specimens. The digit imprints are slender and curved.

The length of the tracks including the hallux ranges from 37.7 to 68.0 mm, averaging 50.4 mm; one of the footprint displays an elongated, posteriorly directed hallux imprint: 113.4 mm total length (not included in average). Footprint width ranges from 46.4 to 90.7 mm (average 74.8 mm) and the length:width ratio is 0.67. The footprints have very slender digit imprints, up to 4 mm wide; the outer digit imprints (II and IV) are curved inward, while the digit imprints III are straight. The impression of digit III displays an average length of 35.44 mm, digits II and IV are subequal in length, while the hallux imprint is 50.4 mm long. The digit imprints display acute distal tips, similar to claw traces, but probably due to an artifact preservational. The average digit divarication measured along the axis taken from the proximal digit tip is 143° (II–IV), the angles between II–III and III–IV are 80° and 63°, respectively, and the average of I–III is 164°. The digit imprints converge in a small, sometime nearly rhomboid sole. No webbing trace was observed. The tracks side by side are separated by 66.4 mm.

**Remarks.** These footprints are characterised by having curved inward, slender digit imprints II and IV and comparatively large hallux impression. However, the scarce available material and its poor quality of preservation preclude any definite ichnotaxonomic assignment, so we will leave it in open nomenclature.

### *Ardeipeda Panin and Avram, 1962*

**Type ichnospecies.** *Ardeipeda egretta* Panin and Avram, 1962, from the Middle Miocene, Putna locality, Vrancea area, Romania.

**Emended diagnosis.** Avian footprints showing four digits, three (II to IV) directed forward and large, the fourth (digit I) backward and somewhat smaller. The interdigital angles between digits II and III and between III and IV are less than 70°. The axis of digit



I corresponds, or almost corresponds, with that of digit III, the interdigital angle between digits I and II being almost equal to that between digits I and IV. Webbing absent (Sarjeant and Langston 1994: 10, modified from Panin and Avram 1962: 463).

**Remarks.** Based on the possible trackmaker (the Ardeidae family, *sensu* Panin and Avram, 1962, or taxa producing heron-like tracks, *sensu* Mustoe, 2002), it was erected the ichnogenus *Ardeipeda* Panin and Avram, 1962. Later, Sarjeant and Langston (1994: 10) have revised these ichnotaxa to distinguish tracks with a large, posteriorly directed, hallux imprint, with both lateral and medial divarications (i.e., II–III and III–IV) measuring up to 70°. Herein, we followed this ichnotaxonomical proposal.

### **Ardeipeda cf. egretta (Fig. 4F)**

**Referred material.** One footprint, as positive epichnia, from the Quebrada del Tapón locality.

**Description.** The specimen is an isolated, purportedly left track, with a length of 28.5 mm, a total length including the hallux impression of 43.5 mm, and a width of 37.2 mm. The impressions of the digits are straight, slender, with a maximum width of 3.7 mm, lacking distinguishable digital pad traces. The hallux impression measures 15 mm. The angles formed by the digit imprints are of 38° and 56° between both lateral digits and the III, while the total divarication angle is 102°. The angle between I and III digit imprint is of 175°. The digit imprints converge in a very small, nearly rhomboid sole. No webbing or claw traces were observed.

**Remarks.** *Ardeipeda gigantea* Panin and Avram, 1962, and *A. incerta* Panin and Avram, 1962, are both from the same locality as the type ichnospecies. *A. gigantea* is quite similar to *A. egretta* but differs mainly by the larger size of their tracks, so its validity should be considered. *A. incerta* displays impression of interdigital webbing.

The features of the tracks allow assigning it to the ichnogenus *Ardeipeda* with confidence, but as there is only an only isolated and poorly preserved specimen, the ichnospecific identification is uncertain.

### **Avipeda Vialov, 1965**

**Type ichnospecies.** *Avipeda phoenix* Vialov, 1965, from the Early-Middle Miocene Stebnyk Formation, of Ukraine.

**Emended diagnosis.** Avian footprints of small to large size, showing three short, thick digits, with distinct claws. Length of central digit (III) less than 25% greater than that of the lateral digits. Total interdigital span 95° or less. Digits closely convergent or united proximally; webbing lacking or limited to the most proximal part of the interdigital angles (Sarjeant and Langston 1994: 12, modified from Vialov 1965: 112).

**Remarks.** *Avipeda* Vialov, 1965 was created as an ichnotaxon to include all the fossil avian footprints (e.g., Sarjeant and Langston 1994; Pali 2013). Subsequently, Sarjeant and Langston (1994) redefined and emended *Avipeda*'s diagnosis to embrace tridactyl tracks with thick digit impressions and without webbing traces. Herein, we follow their emendation.

### **Avipeda isp. (Fig. 4I)**

**Referred material.** One partial *in situ* footprint, as positive epichnia, from the Maimará locality (*in* Cónsole-Gonella et al. 2017: 338; de Valais, Cónsole-Gonella, and Díaz-Martínez 2016: 15).

**Description.** The specimen is a partial track, lacking the more proximal sector of the sole, with a length and width of 41.1 mm (partial) and 48.5 mm, respectively. It is not possible to know whether it is a left or right track. No sole trace is preserved and the proximal ends of the impression of the digits are not in contact. The impressions of the digits are thick, with a maximum width of 7.8 mm, lacking distinguishable digital pad traces, and only digit III imprint displays an acuminate claw trace. The angles formed by the digit imprints are 30° and 38° between both lateral digits and the III, while the total divarication angle is 65°.

**Remarks.** The general aspect of this specimen resembles the ichnogenus *Avipeda*, although the absence of certain specific features, such as the claw traces in digit II and IV imprints, is probably due to a preservational bias, which precludes an ichnospecific assignment with confidence.

### **Gruipeda Panin and Avram, 1962 emend. de Valais and Cónsole-Gonella, nov.**

**Type Ichnospecies.** *Gruipeda maxima* Panin and 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 (modified from de Valais and Melchor 2008: 152, Sarjeant and Langston 1994: 8, and Panin and Avram 1962: 465).

**Remarks.** The ichnogenus *Gruipeda* was created by Panin and Avram (1962) based on the possible track-maker (the Gruidae family), but subsequently Sarjeant and Langston (1994: 8) and de Valais and Melchor (2008) have revised the ichnotaxa. Herein, we have emended the diagnosis, mainly, because the correspondence between the axes of the digit I and III imprints is not always easily understood nor it is found in the specimens included in the ichnogenus. For the rest of the characteristics, we followed the ichnotaxonomical proposal by Sarjeant and Langston (1994) and de Valais and Melchor (2008).

#### **Gruipeda filiportatis (Vialov, 1965) (Fig. 4M–O)**

- 1918 Impression de pieds d'oiseaux Grozescu:  
p. 142, pl. 12.  
1965 *Avipeda filiportatis* Vialov: p. 112, pl. 15.  
1966 *Avipeda filiportatis* Vialov: p. 124, pls. 32–34.  
1986 *Yacoraitichnus avis* Alonso and Marquillas:  
p. 39, pl. 2, fig. 4.  
1994 *Gruipeda filiportatis* Sarjeant and Langston:  
pp. 8–9.  
2010 *Ardeipeda filiportalis* Lockley and Harris:  
p. 25 (*lapsus calami*).  
2017 *Yacoraitichnus avis* Cónsole-Gonella et al.:  
p. 338, fig. 10f.

**Type material.** Three tracks on a trackslab (see Vialov 1965: pl. 15; Vialov 1966: pls. 33, 34: fig. 1), housed in the Institute of Geology and Geochemistry of Combustible Minerals (IGGCM) of National Academy of Sciences of Ukrainian.

**Additional material.** Three track-bearing slabs, accounting two footprints belonging to a partial trackway (Vialov 1966: pl. 32), two isolated tracks in two individual slabs (Vialov 1966: pls. 34: Fig. 2 [same

slab in Grozescu 1918: pl. 12], 35), housed in the IGGCM, Ukrainian.

**Referred material.** At least three *in situ* tracks, as negative epichnia, and one track-bearing slab, as positive hypichnia (mentioned in Materials and Methods sections as “the holotype of *Yacoraitichnus avis*”), all of them from Quebrada del Tapón, Valle del Tonco locality (*in* Alonso and Marquillas 1986: 39; Cónsole-Gonella et al. 2017: 338; de Valais, Cónsole-Gonella, and Díaz-Martínez 2016: 15).

**Emended Ichnospecific Diagnosis.** *Gruipeda* preserved usually as tetradactyl, in some cases as tridactyl, asymmetrical laterally footprints, with an average of length:width ratio of 0.8. Footprint length (considering hallux impression) and width averages about 60 and 80 mm, respectively. Large divarication of digits II–IV, around of 140°. The angle between digits II–III is more than double than those between digits III and IV. Relative digit length is I < II < IV < III. When present, the hallux impression is very short and displays a posterior position. The impression of digit III has a distinctive, acuminate claw trace; the digit IV imprint is curved while digit III and II imprints are straight.

**Description.** Among the specimens there are three tridactyl footprints, asymmetrical laterally, poorly preserved as negative epichnia. The tracks are isolated, *in situ*, preserved on the same surface with a very high track density, so others individual specimens are difficult to be recognised. Besides, there is the slab with the track originally described by Alonso and Marquillas (1986, fig. 4M).

The length and width of the tracks average 66.4 and 77.4 mm, respectively. The footprints have straight III and IV digit imprints, while the IV is S-shaped. All of them are rather slender, less than 6 mm maximum wide, and display long and sharp claw traces. The III digit impression has five clear digital pad traces. The average total angle divarication (II–IV digit imprint) is high, of 130°, while the averages between II–III and III–IV are quite unequal, 92° and 40°, respectively. The angle between I and III imprints is 180°. The digit imprints converge in a nearly rhomboid sole. No webbing traces were observed.

**Remarks.** Alonso and Marquillas (1986) have erected “*Yacoraitichnus avis*” based on a single slab as holotype, which displays a unique complete track and several isolated digit imprints. The impressions are poorly preserved in a mudstone covered by a

submillimeter-thick clay drape. Regrettably, currently the holotype could not be found at the repository mentioned at the bibliography; for that reason, we have used for comparison the original description and illustrations by Alonso and Marquillas (1986) and shared photographs of the slab by Alonso (see Fig. 4M). The ichnospecific diagnosis of “*Yacoraitichnus avis*” was: tridactyl footprint, with well-marked digits displaying claw traces, digit III much greater than II and IV; II and IV display variable angle with III; digit III with lateral pronounced enlargement (translated from the original in Spanish by Alonso and Marquillas 1986: 39). However, the “holotype” also displays a hallux imprint, so the tracks are actually tetradactyl. These data allow for the synonymising of these tracks with *Gruipeda filiportatis* (Vialov 1965).

Several tracks from the Laziale-Abruzzese-Campano domain, within the Apennine chain, in central Italy, have been mentioned as comparable with these footprints from the Yacoraite Formation (*sensu* Nicosia et al. 2007), but the authors claimed that the Italian tracks are larger than the Argentinian ones. Unfortunately, there are not published photographs of these tracks, just shape-illustrations (Nicosia et al. 2007: fig.14).

*Jindongornipes kimi* Lockley et al., 1992, was created based on two slabs bearing several tracks each one—KPE 50006 mentioned as holotype and KPE 5004 as paratype—from the Jindong Formation, in the Gyeongsangnam province, South Korea. One of the footprints in the holotype of *J. kimi* is quite similar to *Gruipeda filiportatis* (see Lockley et al. 2006: fig. 8.b; Kim and Huh 2018: fig. 3.3.b), but due to its poor preservational quality, it is complicated an ichnotaxonomical re-assignment.

Lockley and Harris (2010) suggested the combination of *Ardeipeda filiportatis* (*Ardeipeda filiportalis* as a *lapsus calami*), but in view that *Ardeipeda* is characterised by having a hallux imprint almost as long as the imprints of the other digits, we don't support this opinion.

#### **cf. *Gruipeda filiportatis* (Fig. 4B,C,G,J)**

**Referred material.** Three partial *in situ* tracks, two from the Maimará locality and one from the Quebrada del Tapón, Valle del Tonco, locality, both preserved as negative epichnia (*in* Cónsole-Gonella et al. 2017: 338; de Valais, Cónsole-Gonella, and Díaz-Martínez 2016: 15).

**Description.** The footprints from the Maimará locality are preserved on two different surfaces. One specimen is a partial footprint (Fig. 4G), of 79.2 mm long, formed just by the III and IV digit impressions, both displaying accurate claw traces. The IV imprint displays an S-shaped and is about 69.3 mm long, while the III digit imprint has parallel straight edges and is 73.2 mm long. The angle between the digit prints is 43°. No phalangeal pad traces are distinguishable. The shape of the other track is quite distorted because of the erosion and/or weathering (Fig. 4J). It is 83 mm width and 113.6 mm long seeing that the impression of the digit III is extraordinarily elongate, besides it seems to display a hallux impression (about 30 mm long).

The track from the Quebrada del Tapón locality is poorly-preserved (Fig. 4B,C), lacking the sole trace and the digital ends of the impressions of the digits, so they are not in contact. It is at least of 54.1 mm long and 58.7 mm width, with the impression of digit III of 33.8 mm long. The angles between digit impressions are not measurable.

**Remarks.** Because these tracks are partially and/or poorly preserved, it is difficult to assign them with confidence to an ichnotaxon, however, the general morphology allows referring them to the ichnospecies but with doubts.

#### **cf. *Gruipeda isp.* (Fig. 4K,L)**

**Referred material.** At least seven *in situ* tracks, as negative epichnia from the Maimará locality (*in* Cónsole-Gonella et al. 2017: 338; de Valais, Cónsole-Gonella, and Díaz-Martínez 2016: 15).

**Description.** The specimens are tridactyl and tetradactyl footprints, mostly poorly preserved, with two pairs of tracks (i.e., four tracks altogether) apparently arranged side by side, with the right foot stopping beside the left; one of the pairs displays elongated hallux imprints.

The length of the footprints averages 101.8 mm with hallux imprint, ranging from 88.4 to 115.2 mm, and 56.5 mm without, ranging from 50.4 to 64.5 mm. The footprint width is approximately 72.1 mm, and it ranges from 71.4 to 72.7 mm. The footprints have straight, slender digit imprints, less than 4 mm wide. The impression of digit III is the longest, with an average length of 45.2 mm; digit II and IV imprints are subequal in length. The average hallux impression is 49.2 mm. The average total angle divarication

(II–IV digit imprint) is  $138^\circ$ , and the angle between I and III digit imprint is  $161^\circ$ . The digit imprints converge in a small, sometime nearly rhomboid sole. No webbing or claw traces were observed.

**Remarks.** While the general morphology of the footprints allows the assignment to the ichnogenus *Gruipeda*, it is not possible the assignment at ichno-specific level because of the poor quality of preservation and the lack of detailed features.

### **Uhangrichnus Yang et al., 1995**

**Type Ichnospecies.** *Uhangrichnus chuni* Yang et al., 1995, from the Late Cretaceous Uhangri Formation, from southwestern South Korea.

**Emended Diagnosis.** Tridactyl tracks showing clear evidence of webbing between digits II and IV. Hallux impressions absent. The tracks are wider than long. The divarication angles between digits II–IV are commonly about  $100^\circ$ . Digits II and IV are slightly curved inward rather than straight. The anterior margin of both web impressions between digits II and III, and III and IV is slightly concave anteriorly rather than straight or only slightly concave (Mansilla et al. 2012: 504, modified from Yang et al. 1995: 22).

**Remarks.** In general terms, this ichnotaxon was created to group tridactyl tracks wider than long, with basal web impressions between digits II–III and III–IV (Yang et al. 1995). Later, based on new material, this ichnotaxon was revised by other authors (e.g., Lockley and Harris 2010; Fiorillo et al. 2011; Lockley et al. 2012; Mansilla et al. 2012; Buckley, McCrea, and Lockley 2016). Lockley et al. (2012) have emended its diagnosis to include a new trackway from the same locality of the holotype, composed of tetradactyl tracks.

### **cf. Uhangrichnus isp. (Fig. 4D,E)**

**Referred material.** Three tracks, preserved as negative epichnia, composing probably a trackway, from the Quebrada del Tapón locality.

**Description.** The specimen is a trackway composed of three poorly preserved tridactyl tracks. The first track is so badly preserved that only the distal tip of the digit III imprint can be distinguishable, while the second and third ones are poorly preserved, making data collection difficult. The tracks are about 39.7 mm

wide and at least 40.2 mm long —the proximal border of the sole is not clear—. The angle between the impressions of digits II–IV is about  $100^\circ$ . The webbing imprint is limited to the proximal portion of digits, and the sole trace displays a rhomboid outline.

The trackway is relatively narrow respect to the footprint wide, with a high pace angulation of  $169^\circ$  and stride length 160 mm.

**Remarks.** In view of the fact that these footprints have poor preservation, it is not possible to delimit the complete general form of the track, so we tentatively assign these tracks to cf. *Uhangrichnus* isp.

### **Indeterminate avian tracks (Fig. 4H)**

**Referred material.** Several *in situ* tracks, as negative epichnia from the Quebrada del Tapón locality.

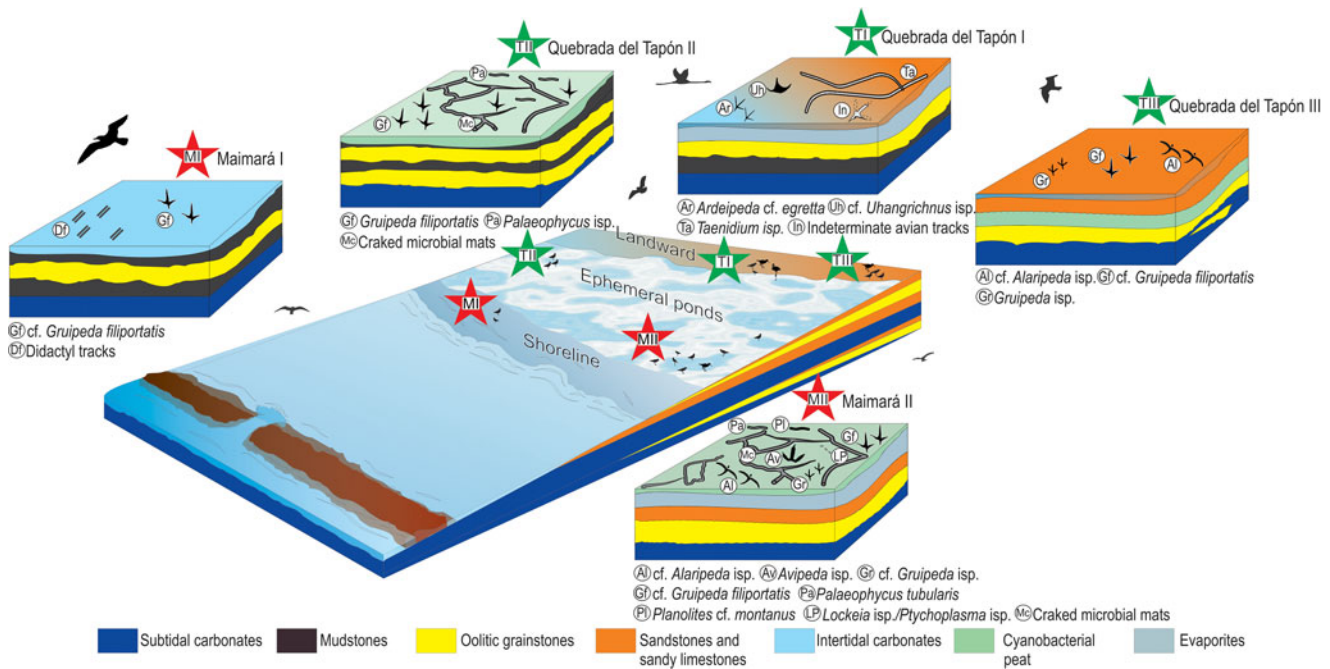
**Description and remarks.** The tracks display a general morphology with three slender, acuminate, digit imprints anteriorly directed, with relative spread disposition. In some areas of the footprint-bearing surfaces, the trampling is so high that it is almost impossible to distinguish each specimen. The footprints display no morphological detail and cannot be ichnotaxonomically assigned with confidence, although it is possible to distinguish the shape typically referred as avian morphology (see de Valais and Melchor 2008, for further explanations).

## **Discussion**

### **Ichnological record and paleobiological implications**

For many years, the record of avian tracks from the Yacoraite Formation has been represented by one ichnogenus, “*Yacoraitichnus avis*”, considered as junior synonym of *Gruipeda filiportatis* in this contribution, from the Quebrada del Tapón, in the Valle del Tonco (see Alonso and Marquillas 1986; Leonardi 1994). Subsequently, this avian track record has increased because of new finds, both from the Quebrada del Tapón and from the Maimará locality (e.g., Cónsole-Gonella et al. 2017; de Valais, Cónsole-Gonella, and Díaz-Martínez 2016). So, the avian track record from the Quebrada del Tapón ichnosite is composed of tracks assigned to different ichnotaxa, cf. *Alaripeda* isp., *Ardeipeda* cf. *egretta*, *Gruipeda filiportatis* (Vialov 1965) (= *Yacoraitichnus avis*) and others *Gruipeda* or compared to this ichnogenus, cf. *Uhangrichnus* isp., and several indeterminate avian tracks. The avian





**Figure 5.** Block diagram illustrating sedimentary facies and environmental distribution of ichnoassemblages in Maimará and Quebrada del Tapón localities. Not in scale.

ichnological record from the Maimará locality, less diverse than the record from the Quebrada del Tapón, is composed of tracks assigned to *cf. Alaripeda* isp., *Avipeda* isp., *cf. Gruipeda filiportatis* and *cf. Gruipeda* isp.

Both ichnological records are composed of tracks assigned to shorebirds. The term shorebird is used in ecology to describe those birds frequenting shorelines, mudflats or shallow waters. However, taxonomically speaking, shorebirds are usually considered as Charadriiformes, a very diverse group, considered as monophyletic for some authors (e.g., Livezey 2010; Mayr 2011), or with polyphyletic origin based on molecular evidence (van Tuinen, Waterhouse, and Dyke 2004; Colwell 2010). The tracks linked to shorebirds show a positive or inward rotation respect to the midline and a similar general size and morphology, probably because of convergence or plesiomorphism of the trackmakers (Lockley and Harris 2010). The ichnogenus *Uhangerichnus* is characterised by having webbing imprints between the digits II–III and III–IV. Similar tracks have been previously related to Anseriformes (see Mansilla et al. 2012), although groups within Charadriiformes (e.g., Laridae) display webbed feet which could imprint footprints similar to this ichnogenus. The trackmakers of the footprints assigned to the ichnogenera *Alaripeda*, *Ardeipeda*, *Avipeda* and *Gruipeda* have not been identified to date with confidence; however, present-day tracks of Charadriiformes (e.g., *Calidris*, *Charadrius*) are quite

similar to some ichnospecies of *Gruipeda* (see Genise et al. 2009; McCrea et al. 2015).

There are no trackways preserved from both Maimará and Valle del Tonco ichnosites, with just one exception (i.e., a short trackway of *cf. Uhangerichnus* isp.; Fig. 4D,E).

### Stratigraphy and facies of track-bearing surfaces

**Maimará section.** The overall facies arrangement is indicative of a lagoon shoreline with some tidal influence, where two ichnoassemblages are represented (Figs. 3, 5; Table 2). (1) The ichnoassemblage I (MI in Figs. 3, 5; Table 2) is composed of *cf. Gruipeda filiportatis* and indeterminate didactyl footprints. Below stratigraphically a few centimeters, in a different surface, some dinosaur footprints are preserved, assigned to titanosaurs and indeterminate biped dinosaurs (Cónsole-Gonella et al. 2017). Its sedimentary facies is made up of wackestones-packstones, microsparite and bioclasts are represented by broken ostracods. Although didactyl footprints were recognised in this facies by Cónsole-Gonella et al. (2017), this is the first description of the associated avian footprints. The interpretation of the palaeoenvironmental setting in the ichnoassemblage I is a moderate to high-energy shoreline (Fig. 5). (2) The ichnoassemblage II (MII in Figs. 3, 5; Table 2) is composed of *cf. Alaripeda* isp.; *Avipeda* isp., *cf. Gruipeda filiportatis* and *cf. Gruipeda* isp., and abundant, although not diverse, invertebrate

trace fossils (*Palaeophycus tubularis*, *Planolites* cf. *montanus*, *Lockeia* isp. and *Ptychoplasma* isp.). Its facies is dominated by mudstones, with some sparite and gypsum. The palaeoenvironmental setting of the ichnoassemblage II is inferred as a supratidal system of ephemeral bodies of water dominated by sedimentation (Cónsole-Gonella et al. 2017), with low energy, far away from direct wave action (Fig. 5). In this facies there are also frequent petee-type structures (Fig. 5) that reflects the establishment and later decay of microbial mats in the substrate (*sensu* Gavish et al. 1985).

*Quebrada del Tapón section.* This section is the track-bearing unit and belongs to the upper third of the Don Otto member of the Yacoraite Formation. The section is named "green section" (Gorustovich et al. 2013). In this section there are three ichnoassemblages (Figs. 3, 5; Table 2): (1) The ichnoassemblage I (TI in Figs. 3, 5; Table 2) is integrated by *Ardeipeda* cf. *egretta*, cf. *Uhangrichmus* isp. and indeterminate avian tracks, associated with invertebrate trace fossils (frequently *Taenidium* isp.). Facies of the ichnoassemblage I are composed of calcareous sandstones and some traces of gypsum, suggesting a landward position, beyond water direct influence (Fig. 5). (2) The ichnoassemblage II (TII in Figs. 3, 5; Table 2) is composed of *Gruipeda filiportatis* and some poorly preserved invertebrate trace fossils (cf. *Palaeophycus* isp.; Figs. 3 and 5; Table 2) in a surface with some jelly roll structures (*sensu* Gerdes 2007), which suggest microbial mats decayment after desiccation. Facies are made up of mudstones, which with the jelly roll structures, suggest a low energy setting, probably a supratidal pond (Fig. 5). (3) The ichnoassemblage III (TIII in Figs. 3, 5; Table 2) is composed of cf. *Alaripeda* isp., cf. *Gruipeda filiportatis*, and cf. *Gruipeda* isp. (Figs. 3, 5; Table 2). Facies here are resembling the ichnoassemblage TI, supporting the idea of a palaeoenvironment representing a landward position (Fig. 5).

### **Environmental and ichnofacies implications**

In general terms, the ichnological assemblages recovered from the avian track-bearing surfaces from the Maimará and the Quebrada del Tapón sites are represented mainly by shorebird footprints, with presence of invertebrate trace fossils in some ichnoassemblages (Fig. 5). Regarding the environmental distribution of the track-bearing surfaces, the sedimentary features suggest three differentiated positions (Fig. 5), which implies that the studied sections in both localities display a homologous distribution of facies and

ichnological content. These positions are: (A) a shoreline position under waves action, with subaerial exposure during low tide or more important, during stages of withdrawal of the water body by wind or evaporation (Maimará ichnoassemblage I, Fig. 5); (B) a playa-lake position, according to the criterion of Briere (2000), as a supratidal system of bodies of water, beyond waves impact, that are dominated by sedimentation with very low energy, as ephemeral ponds (Maimará ichnoassemblage II and Quebrada del Tapón ichnoassemblage II, Fig. 5); and (C) a landward position, beyond the ephemeral ponds system (Quebrada del Tapón ichnoassemblages I and III, Fig. 5).

The ichnoassemblage I from Maimará (Figs. 3, 5) may represent the shoreline of a well-established water column, with an inferred diachronism until the formation of avian footprints (e.g., in a context of birds feeding on the surface during low tide). The palaeodepositional setting of both ichnoassemblages II from Maimará and the Quebrada del Tapón localities (Fig. 5) are inferred as part of a playa lake system in the terms of Briere (2000), also referred to as a "flooded playa" (referred to as playa lake or PL zone in Cónsole-Gonella et al. 2017). Briere (2000: 3) stated that a playa-lake system is "an arid zone feature, transitional between playa and lake, neither dry more than 75% of the time nor wet more than 75% of the time" (Fig. 5). PL zone was flooded during periods of maximum lake growth. The PL zone is made up of ephemeral bodies of water, that were established in the supratidal zone, beyond the direct influence of waves, but suffering periodical flooding and withdrawal (Cónsole-Gonella et al. 2017).

Ichnoassemblages I and III of the Quebrada del Tapón suggest a landward position. This is also inferred by the facies arrangement and the trace fossils composition, dominated by *Taenidium* in the ichnoassemblage I (Fig. 5). *Taenidium* has been assigned to various tracemakers, such as insect larvae and adults, as well as earthworms (Melchor et al. 2006).

Although further research is needed to understand the whole environmental setting at the Quebrada del Tapón section, it is possible to assess the avian-trampled surface of ichnoassemblage II in the context of a mudflat in a peritidal setting (Fig. 5). This interpretation is reinforced regarding from the presence of dinosaur tracks stratigraphically below from the avian track-bearing surface (Fig. 3) which is indicative of a shoreline that is variable in energy, as has been noted by Alonso and Marquillas (1986). Structures suggesting cracked microbial mats of the ichnoassemblage II

in Maimará and Quebrada del Tapón are indicative of dry phases that produce mat decay in the mudflat area (Gehling 1999; Catuneanu 2006). The relevant role of microbial mats in track preservation of peritidal environments has been previously observed (e.g., Kvale et al. 2001; Marty, Strasser, and Meyer 2009; Carmona et al. 2011, 2012; Cuadrado, Carmona, and Bournod 2011, 2012; Fernández and Pazos 2013).

It is well known that tidal flats can bear ecosystems which allow shorebirds to develop several feeding strategies, and some of these strategies are in fact, important agents producing bioturbation (Cadee 1990).

Carmona et al. (2011) studied the taphonomy of bird footprints in a present-day mesotidal environment from Bahía Blanca, Buenos Aires province, Argentina. Interestingly, these authors noted that the avian footprints showed resistance both to tide and wind erosion and to the heavy rains and storms that affected the tidal flat. The footprints were even preserved after several months (Carmona et al. 2011), displaying resistance to long term seasonally weathering. Microbial mats provide early cementation to trampled surfaces, allowing footprint consolidation and lithification (e.g., Marty, Strasser, and Meyer 2009; Carmona et al. 2011).

In regard of the palaeobiological implications for both the Maimará and Quebrada del Tapón suites, they are suggesting an association among the avian trackmakers and the worm-like burrowers. This association seems to show recurrence in time since Mesozoic to modern times, as has been suggested by Lockley, Hunt, and Meyer (1994) and Doyle, Wood, and George (2000). Lockley et al. (1992) have reviewed the avian footprints record of Mesozoic birds, remarking that these mixed suites suggest a particular microhabitat. This hypothesis was built on, resulting in the ichnofacies model proposed by Lockley, Hunt, and Meyer (1994), which established the shorebird ichnofacies, displaying a partially overlap with the archetypical *Scoyenia* Ichnofacies. Lockley, Hunt, and Meyer (1994) claimed that the composition of the shorebird ichnofacies is dominated by these mixed suites of avian footprints with invertebrate burrows and trails that suggest feeding activities by shorebirds. These feeding strategies resemble those of the modern wading birds (Lockley, Hunt, and Meyer 1994). In fact, neoichnological studies reinforced that concept. Low energy stages in such environments allow, firstly, the establishment of microbial mats, and secondly its colonization by the invertebrates, probably food of the wading birds (e.g.,

Swennen and Van der Baan 1959; Cadee 1990). All these evidence are supporting a putative trophic network composing of at least three levels, namely: the producers, represented by the bacteria or the algae of the mats, the herbivores, represented by the invertebrates, and probably some birds, feeding on the microbial mats, and finally the consumers carnivores, others birds eating the invertebrates.

Although the shorebird ichnofacies has been placed within the *Grallator* ichnofacies by Hunt and Lucas (2005), we support Melchor et al. (2006), Díaz-Martínez et al. (2015) and Cónsole-Gonella et al. (2017) that observed that it is preferable to keep this association as an ichnosubfacies within the archetypical *Scoyenia* Ichnofacies. The shorebird ichnosubfacies is recording ichnocoenoses of shorebirds attributable to Charadriiformes (waders and gulls), Anseriiformes (ducks and geese) and Ciconiiformes (storks and herons), and has been interpreted as effectively a lacustrine ichnofacies, although potentially associated with playas, marine influenced lagoons or other lake types (after Doyle, Wood, and George 2000). Within the *Scoyenia* Ichnofacies, the shorebird ichnosubfacies is delimiting zones of moderate to low energy that allows wading birds to feed.

## Conclusions

The avian track record of the Yacoraite Formation from Salta was known since many years ago, but now it is possible to understand their diversity and to extend the geographical distribution to the Tres Cruces sub-basin in Jujuy. For many years, the only avian ichnotaxon was “*Yacoraitichnus avis*”, in synonymy with *Gruipeda filiportatis* in this contribution. Several other avian ichnotaxa and abundant tracks are recorded. The tracks described here as cf. *Uhangrichnus* isp. could be related to Anseriformes or any other similar, web-footed taxon. The producer to the tracks assigned to or vinculated with *Alaripeda*, *Ardeipeda*, *Avipeda* and *Gruipeda* have not been identified to date with confidence, but could be related to Charadriiformes (shorebirds) or taxa morphologically similar.

The facies distribution of trace fossils in the two studied sections for the Yacoraite Formation reinforces the model of a shorebird-dominant ichnofauna in a peritidal restricted palaeoenvironment. This distribution can be divided into three sub-environments: a moderate to high energy shoreline under wave action, a supratidal body of ephemeral ponds, far away from direct wave influence, and a landward position. In the



ephemeral ponds, microbial mats have played a main role in the stabilisation of substrate, enabling tracks preservation. As has been discussed in neoichnological studies, the stabilisation of the substrate by microbial activity allows long-term resistance of footprints, which has been reflected also in the ichnodiversity. The observed association among environmental constraints, microbial mats, avian footprints and invertebrate trace fossils is evidence of a trophic interaction of a particular paleoecosystem.

As we stated in the discussion, we support the validity of the shorebird ichnosubfacies, as a subset of the *Scoyenia* Ichnofacies. However, further works are necessary in order to elucidate this issue, providing global occurrences in space and time of this ichnosubfacies.

## Acknowledgements

We are grateful to colleagues P. Herrera, P. Machuca, D. Lizarraga and M. Griffin for their help in different stages of the fieldwork. We are also very grateful to the CNEA and the people working on Mina Don Otto for their invaluable help in the fieldwork, especially to S. Gorustovich and A. Zelaya, who have invited us to study the Valle del Tonco locality and provided valuable geological information and support. We wish to thank the editors M. Gingras and H. Klein for the accompaniment in the editorial paths of the journal, and the reviewers I. Díaz-Martínez and L. G. Buckley for their great job, which finally managed to improve our manuscript.

## Funding

This research was supported by grants PICT 1665 (C. Cónsole-Gonella) and PICT 2057 (C. Cónsole-Gonella and S. de Valais) from the Agencia Nacional de Promoción Científica y Técnica, and PIUNRN 40-A-402 (S. de Valais) from Universidad Nacional de Río Negro.

## ORCID

Silvina de Valais  <http://orcid.org/0000-0002-2661-8015>  
 Carlos Cónsole-Gonella  <http://orcid.org/0000-0002-4457-1660>

## References

- Alonso, R. N. 1978. Icnitas de dinosaurio de la Formación Yacoraite (Cretácico superior). Su importancia paleozoogeográfica y cronoestratigráfica. Facultad de Ciencias Naturales, Universidad Nacional de Salta. Unpublished Bachelor of Science Thesis Profesional.
- Alonso, R. N. 1980. Icnitas de dinosaurios (Ornithopoda, Hadrosauridae) en el Cretácico superior de norte de Argentina. *Acta Geológica Lilloana* 15:55–63.
- Alonso, R. N. 1989. Late Cretaceous Dinosaur Trackways in Northern Argentina. In *Dinosaur tracks and traces*, D. Gillette and M. Lockley (eds.), 223–228. Cambridge University Press, Nueva York.
- Alonso, R. N., and R. A. Marquillas. 1986. Nueva localidad con huellas de dinosaurios y primer hallazgo de huellas de aves en la Formación Yacoraite (Maastrichtiano) del norte argentino. Abstracts 4th Congreso Argentino de Paleontología y Bioestratigrafía, 33–41.
- Arratia, G., and A. Cione. 1996. The record of fossil fishes of Southern South America. In *Contributions of Southern South America to Vertebrate Paleontology*, G. Arratia (ed.), vol. 30: 9–72 Munich: Verlag Dr. F. Pfeil.
- Benedetto, J. L., and T. Sánchez. 1971. El hallazgo de peces Pycnodontiformes (Holostei) en la Formación Yacoraite (Cretácico Superior) de la Provincia de Salta, Argentina, y su importancia paleobiológica. *Acta Geológica Lilloana* 11:151–176.
- Benedetto, J. L., and T. Sánchez. 1972. *Coelodus toncoensis* nov. sp. (pisces, Holostei, Pycnodontiformes) de la Formación Yacoraite (Cretácico Superior) de la Provincia de Salta. *Ameghiniana* 14:59–71.
- Bertling, M., S. Braddy, R. G. Bromley, G. R. Demathieu, J. Genise, R. Mikulas, J. K. Nielsen, K. S. S. Nielsen, A. K. Rindsberg, M. Schlirf, and A. Uchman. 2006. Names for trace fossils: a uniform approach. *Lethaia* 39(3): 265–86.
- Bonarelli, G. 1927. Fósiles de la formación petrolífera. *Boletín de la Academia Nacional de Ciencias de Córdoba* 30:55–115.
- Briere, P. R. 2000. Playa, playa lake, sabkha: Proposed definitions for old terms. *Journal of Arid Environments* 45(1): 1–7.
- Buatois, L. A., and M. G. Mángano. 2011. *Ichnology: Organism-Substrate interactions in space and time*. New York: Cambridge University Press.
- Buckley, L. G., R. T. McCrea, and M. G. Lockley. 2016. Analysing and resolving Cretaceous avian ichnotaxonomy using multivariate statistical analyses: approaches and results. In *Dinosaur tracks. The next steps*, P. L. Falkingham, D. Marty, and A. Richter (eds.), 258–310. Bloomington: Indiana University Press.
- Cadee, G. C. 1990. Feeding traces and bioturbation by birds on a tidal flat, Dutch Wadden Sea. *Ichnos* 1(1):23–30.
- Carmona, N. B., C. N. Bournod, J. J. Ponce, and D. G. Cuadrado. 2011. The role of microbial mats in the preservation of bird footprints: a case study from the mesotidal Bahía Blanca estuary (Argentina). In *Microbial mats in siliciclastic depositional systems through time*, N. Noffke and H. Chafetz (eds.), vol. 101, 37–45. SEPM Special Publication.
- Carmona, N. B., J. J. Ponce, A. Wetzel, C. N. Bournod, and D. G. Cuadrado. 2012. Microbially induced sedimentary structures in neogene tidal flats from Argentina: paleo-environmental, stratigraphic and taphonomic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 353-355:1–9.
- Catuneanu, O. 2006. *Principles of sequence stratigraphy*. Amsterdam: Elsevier.
- Colwell, M. A. 2010. *Shorebird ecology, conservation, and management*. Berkeley: University of California Press.
- Cónsole-Gonella, C. A., M. Griffin, and F. G. Aceñolaza. 2009. Gastropods associated with fossil traces from



- Yacoraite Formation (Maastrichtian-Danian), and its paleoenvironmental significance, Jujuy, Northwestern Argentina. *Acta Geologica Sinica* 83(1):860–867.
- Cónsole-Gonella, C. A., and F. G. Aceñolaza. 2009. Icnología de la Formación Yacoraite (Maastrichtiano-Daniano) al sur de la localidad de Maimará, Cordillera Oriental de Jujuy, Argentina. *Acta Geológica Lilloana* 21: 100–110.
- Cónsole-Gonella, C. A., and F. G. Aceñolaza. 2010. Tafofacies e icnofacies de los niveles maastrichtianos-danianos correspondientes a la Formación Yacoraite, Cordillera Oriental de la provincia de Jujuy, Argentina. *Boletín de la Sociedad Geológica Mexicana* 62:221–31.
- Cónsole-Gonella, C., S. de Valais, M. C. Sánchez, and R. Marquillas. 2012a. Nuevo registro de huellas de vertebrados en la Formación Yacoraite (Maastrichtiano-Daniano), Maimará, Cordillera Oriental argentina. *Ameghiniana* 49: R141.
- Cónsole-Gonella, C., M. Griffin, A. Cione, S. Gouiric-Cavalli, and F. G. Aceñolaza. 2012b. Paleontología de la Formación Yacoraite (Maastrichtiano-Daniano) en el ámbito de la Subcuenca de Tres Cruces, Cordillera Oriental de la provincia de Jujuy, Argentina. In *Aportes sedimentológicos a la geología del noroeste argentino*, ed. R. Marquillas, J. Salfity, and M.C. Sánchez, 45–56. Salta, Argentina: SC Publisher.
- Cónsole-Gonella, C., S. de Valais, M. C. Sánchez, R. A. Marquillas, and P. Herrera Oviedo. 2013. Icnocenosis de vertebrados e invertebrados en el subgrupo balbuena (Maastrichtiano-Daniano), Quebrada de Humahuaca, noroeste argentino. Abstracts 2nd Simposio Latinoamericano de Icnología. Santa Rosa. La Pampa, 34.
- Cónsole-Gonella, C., S. de Valais, R. A. Marquillas, and M. C. Sánchez. 2017. The Maastrichtian-Danian Maimará tracksite (Yacoraite Formation, Salta group), Quebrada de Humahuaca, Argentina: environments and ichnofacies implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 468:327–50.
- Cuadrado, D. G., N. B. Carmona, and C. N. Bournod. 2011. Biostabilization of sediments by microbial mats in a temperate siliciclastic tidal flat, Bahía Blanca estuary (Argentina). *Sedimentary Geology* 237(1-2):95–101.
- Cuadrado, D. G., N. B. Carmona, and C. N. Bournod. 2012. Mineral precipitation on modern siliciclastic tidal flats colonized by microbial mats. *Sedimentary Geology* 271-272:58–66.
- de Valais, S., and R. Melchor. 2008. Ichnotaxonomy of bird-like footprints: an example from the late Triassic-Early Jurassic of northwest Argentina. *Journal of Vertebrate Paleontology* 28(1):145–259.
- de Valais, S., C. Cónsole-Gonella, and I. Díaz-Martínez. 2016. Registro de huellas avianas en la Formación Yacoraite (Maastrichtiano-Daniano), NOA, Argentina. *Ameghiniana* 53(4):15.
- Díaz-Martínez, I., S. de Valais, and C. Cónsole-Gonella. 2016. First evidence of *Hadrosauropodus* in Gondwana (Yacoraite Formation, Maastrichtian-Danian), northwestern Argentina. *Journal of African Earth Sciences* 122: 79–87.
- Díaz-Martínez, I., O. Suárez-Hernando, B. Martínez-García, J. M. Hernández, S. García Fernández, F. Pérez-Lorente, and X. Murelaga. 2015. Early Miocene shorebird-like footprints from the Ebro Basin, La Rioja, Spain: palaeoecological and paleoenvironmental significance. *Palaios* 30:424–31.
- Doyle, P., J. L. Wood, and G. T. George. 2000. The shorebird ichnofacies: an example from the Miocene of Southern Spain. *Geological Magazine* 137(5):517–36.
- Fernández, D. E., and P. J. Pazos. 2013. Xiphosurid trackways in a Lower Cretaceous tidal flat in Patagonia: palaeoecological implications and the involvement of microbial mats in trace-fossil preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 375: 16–29.
- Fiorillo, A. R., S. T. Hasiotis, Y. Kobayashi, B. H. Breithaupt, and P. J. McCarthy. 2011. Bird tracks from the Upper Cretaceous Cantwell Formation of Denali National Park, Alaska, USA: a new perspective on ancient Northern polar vertebrate biodiversity. *Journal of Systematic Palaeontology* 9 (1):33–49.
- Gasparini, Z., and E. Buffetaut. 1980. *Dolichochampsia minima*, n.g. n.sp., a representative of a new family of Eusuchian crocodiles from the Late Cretaceous of northern Argentina. *Neues Jahrbuch Geologie und Paläontologie, Monatshefte* 5:257–271.
- García Raguél, M., I. Cuevas González, I. Díaz-Martínez, and F. Pérez-Lorente. 2009. Fragmentos de roca con huellas de aves en el terciario de alcanadre (La Rioja): descripción, estructuras y problemas de identificación. *Zubía* 27:81–158.
- Gavish, E., W. E. Krumbein, and J. Halevy. 1985. Geomorphology, mineralogy and groundwater geochemistry as factors of the hydrodynamic system of the Gavish Sabkha. In *Hypersaline Ecosystems. Ecological Studies (Analysis and Synthesis)*, ed. G.M. Friedman and W. E. Krumbein (eds.), 186–217. Berlin: Springer.
- Gehling, J. G. 1999. Microbial mats in terminal proterozoic siliciclastics: Ediacaran death masks. *Palaios* 14(1):40–57.
- Genise, J. F., R. N. Melchor, M. Archangelsky, L. O. Bala, R. Straneck, and S. de Valais. 2009. Application of neo-ichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: the late Triassic-Early Jurassic? Santo Domingo Formation, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 272(3-4):143–61.
- Gerdes, G. 2007. Structures left by modern microbial mats in their host sediments. Chapter 2. In *Atlas of microbial mat features preserved within the siliciclastic rock record*, J. Schieber, P. K. Bose, P. G. Eriksson, S. Banerjee, S. Sarkar, W. Altermann, and O. Catuneanu, 5–38. Amsterdam: Elsevier.
- Gorostovich, S., F. Guidi, N. Bárbaro, H. Nievas, and G. Tomellini. 2013. Observaciones geológicas y ambientales en la Quebrada Sunchales y el Río Tonco, Mina de Uranio Don Otto, Provincia de Salta. *Revista de la Asociación Geológica Argentina* 70(3):377–81.
- Grozescu, H. G. 1918. Geologie de la région subcarpatique de la partie septentrionale du district de Bacău. *Extrait de l'Annuaire de l'Institut Geologique de Roumanie* 8:213–58.
- Hay, W. W., R. M. DeConto, C. N. Wold, K. M. Wilson, S. Voigt, M. Schulz, A. R. Wold, W.-C. Dullo, A. B. Ronov, A. N. Balukhovskiy, and E. Soding. 1999. An alternative global Cretaceous paleogeography. In *Evolution of the Cretaceous Ocean-Climate System. Geological Society of*

- America, *Special Paper 332*, E. Barrera, and C. C. Johnson (eds.), 1–47. Colorado: GSA (Geological Society of America).
- Hunt, A. P., and S. G. Lucas. 2005. Tetrapod ichnofacies and their utility in the Paleozoic. In *Pennsylvanian footprints in the Black Warrior Basin of Alabama*, ed. R.J. Buta, A.K. Rindsberg, and D.C. Kopaska-Merkel, vol. 1, 113–119. Birmingham: Alabama Paleontological Society Monograph.
- Johnson, K. R. 1986. Paleocene bird and amphibian tracks from the Fort Union Formation, Bighorn Basin, Wyoming. *Contributions to Geology* 24:1–10.
- Kim, J. Y., and M. Huh. 2018. *Dinosaurs, birds, and pterosaurs of Korea. A paradise of Mesozoic vertebrates*. Singapore: Springer.
- Kvale, E. P., A. D. Johnson, D. L. Mickelson, K. Keller, L. C. Furer, and A. W. Archer. 2001. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksites, Bighorn Basin, Wyoming, U.S.A. *Palaios* 16(3):233–54.
- Leonardi, G. 1981. As localidades com rastros fósseis de Tetrápodes na América Latina. *Abstract 2nd Congreso Latinoamericano de Paleontología* 2:929–40.
- Leonardi, G. 1984. Le impronte fossili di dinosauri. In Bonaparte, J.F., Colbert, E.H., Currie, P.J., de Ricqlès, A., Kielan-Jaworowska, Z., Leonardi, G., Morello, N., and Taquet, P. (eds.). *Sulle orme dei dinosaur*, 165–186. Venice: Erizzo Editrice.
- Leonardi, G. 1994. *Annotated atlas of South America tetrapod footprints (Devonian to Holocene)*. Rio de Janeiro, Brasil: Companhia de Pesquisa de Recursos Minerais.
- Livezey, B. C. 2010. Phylogenetics of modern shorebirds (Charadriiformes) based on phenotypic evidence: analysis and discussion. *Zoological Journal of the Linnean Society* 160(3):567–618.
- Lockley, M. G., and J. Harris. 2010. On the trail of early birds: a review of the fossil footprint records of avian morphological and behavioral evolution. In *Trends in ornithology research*, P.K. Ulrich and J.H. Willett (eds.), 1–63. Hauppauge NY: Nova Publishers.
- Lockley, M. G., K. Houck, S.-Y. Yang, M. Matsukawa, and S.-K. Lim. 2006. Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang National Park area, Goseong county, South Korea: evidence and implications. *Cretaceous Research* 27(1):70–101.
- Lockley, M. G., A. Hunt, and C. Meyer. 1994. Vertebrate tracks and the ichnofacies concept: implications for palaeoecology and palichnostratigraphy. In *The paleobiology of trace fossils*, S.K. Donovan (ed.), 241–268, Chichester: Wiley.
- Lockley, M. G., J.-D. Lim, J. Y. Kim, K. S. Kim, M. Huh, and K.-G. Hwang. 2012. Tracking Korea's Early Birds: A review of cretaceous avian ichnology and its implications for evolution and behavior. *Ichnos* 19:1–2.
- Lockley, M., A. S. Schulp, C. A. Meyer, G. Leonardi, and D. K. Mamani. 2002. Titanosaurid trackways from the upper Cretaceous of Bolivia: evidence for large Manus, wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23(3):383–400.
- Lockley, M. G., S.-Y. Yang, M. Matsukawa, F. Fleming, and S.-K. Lim. 1992. The track record of Mesozoic birds: evidence and implications. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 336(1277):113–34.
- MacEachern, J. A., K. L. Bann, M. K. Gingras, J. K. Zonneveld, S. E. Dashtgard, and S. G. Pemberton. 2012. The Ichnofacies Paradigm. In *Developments in sedimentology, 64, trace fossils as indicators of sedimentary environments*, D. Knaust and R. Bromley (eds.), 103–138. Amsterdam: Elsevier.
- Mansilla, H., S. de Valais, W. Stinnesbeck, N. Varela, and M. Leppe. 2012. New avian tracks from the upper paleocene to lower Eocene at Fossil Hill, King George Island, Antarctica. *Antarctic Science* 24(05):500–506.
- Marquillas, R. A. 1985. Estratigrafía, sedimentología y paleoambientes de la Formación Yacoraite (Cretácico Superior) en el tramo austral de la cuenca, norte argentino. Doctoral Thesis, Universidad Nacional de Salta.
- Marquillas, R. A., C. E. del Papa, and I. Sabino. 2005. Sedimentary aspects and paleoenvironmental evolution of a rift basin: Salta group (Cretaceous-Paleogene), north-western Argentina. *International Journal of Earth Sciences* 94(1):94–113.
- Marquillas, R. A., J. A. Salfity, S. J. Matthews, M. Matteini, and E. Dantas. 2011. U-Pb zircon age of the Yacoraite Formation and its significance to the Cretaceous-Tertiary boundary in the Salta basin, Argentina. In *Cenozoic geology of the Central Andes of Argentina*, ed. J.A. Salfity and R.A. Marquillas, 227–246. Salta, SCS Publisher.
- Marty, D., A. Strasser, and C. A. Meyer. 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos* 16(1-2):127–42.
- Mayr, G. 2011. The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the conflict between morphology and molecules. *Zoological Journal of the Linnean Society* 161(4):916–34.
- McCrea, R. T., L. G. Buckley, A. Guy Plint, M. G. Lockley, N. A. Matthews, T. A. Noble, L. Xing, and J. R. Krawetz. 2015. Vertebrate ichnites from the Boulder Creek Formation (Lower Cretaceous: middle to upper Albian) of northeastern British Columbia, with a description of a new avian ichnotaxon, *Paxavipes babcockensis* ichnogen. et isp. nov. *Cretaceous Research* 55:1–18.
- Melchor, R. N., E. Bedatou, S. de Valais, and J. F. Genise. 2006. Lithofacies distribution of invertebrate and vertebrate trace fossil assemblages in an early Mesozoic ephemeral fluvial system: implications for the *Scoyenia* ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 239(3-4):253–85.
- Meyer, C. A., D. Hippler, and M. G. Lockley. 2001. The Late Cretaceous vertebrate ichnofacies of Bolivia—facts and implications. *Asociación Paleontológica Argentina, Publicación Especial, 7. VII International Symposium on Mesozoic Terrestrial Ecosystems*, Buenos Aires: 133–138.
- Mustoe, G. E. 2002. Eocene bird, reptile, and mammal tracks from the Chuckanut Formation, Northwest Washington. *Palaios* 17(4):403–13.
- Nicosia, U., F. M. Petti, G. Perugini, S. D’Orazi Porchetti, E. Sacchi, M. A. Conti, N. Mariotti, and A. Zarattini. 2007. Dinosaur tracks as paleogeographic constraints: new scenarios for the Cretaceous geography of the peri-adriatic region. *Ichnos* 14(1-2):69–90.

- Palii, V. M. 2013. The contribution of O.S. Vialov to the development of ichnological classification and nomenclature. *Stratigraphy and Geological Correlation* 21(3): 249–51.
- Panin, N., and E. Avram. 1962. Noe urme de vertebrate in Miocenul Subcarpaților rominești. *Studii și Cercetări de Geologie* 7:455–84.
- Reyes, F. C. 1972. Correlaciones en el Cretácico de la cuenca andina de Bolivia, Perú y Chile. *Revista Técnica de Y.P.F. Bolivianos* 1:101–104.
- Reynolds, R. E. 2012. Ichnites in the Bouse Formation, Amboy, San Bernardino County, California. In *Searching for the Pliocene: field trip guide to the southern exposures*, ed. R.E. Reynolds 136–139. Fullerton: California State University.
- Sabino, I. F. 2002. Geología del Subgrupo Pirgua (Cretácico) del noroeste argentino. Doctoral Thesis, Universidad Nacional de Salta.
- Salfity, J. A. 1980. Estratigrafía de la Formación Lecho (Cretácico) en la Cuenca Andina del Norte Argentino. Special Publication, Doctoral Thesis 1. Universidad Nacional de Salta, Salta, 91 pp.
- Salfity, J. A. 1982. Evolución paleogeográfica del Grupo Salta (Cretácico-Eogénico), Argentina. Abstract 5th Congreso Latinoamericano de Geología 1, 11–25.
- Salfity, J. A., and R. A. Marquillas. 1994. Tectonic and sedimentary evolution of the Cretaceous-Eocene Salta Group basin, Argentina. In *Cretaceous tectonics of the Andes*. J.A. Salfity (ed.), 266–315. Braunschweig/Weisbaden: Friedr Vieweg and Sohn. Earth Evolution Sciences Monograph Series.
- Sarjeant, W. A. S., and W. Langston, Jr. 1994. *Vertebrate footprints and invertebrate traces from the Chadronian (Late Eocene) of Trans-Pecos*. Texas: Texas Memorial Museum Bulletin 36.
- Sarjeant, W. A. S., and R. E. Reynolds. 2001. Bird footprint from the Miocene of California. In *The changing face of the East Mojave Desert: Abstracts from the 2001 Desert Symposium*, Reynolds R.E. (ed.), 21–40. California.
- Scotese, C. R. 1997. *Continental Drift*, 7th Edition, 79 pp. PALEOMAP Project, Arlington.
- Schwab, K. 1984. Contribución al conocimiento del sector occidental de la cuenca sedimentaria del grupo Salta (Cretácico-Eogénico) en el noroeste argentino. Abstracts 9th Congreso Geológico Argentino 1:586–604.
- Scrivner, P. J., and D. J. Bottjer. 1986. Neogene avian and mammalian tracks from Death Valley National Monument, California: their context, classification and preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 57(2-4):285–331.
- Swennen, C., and G. Van der Baan 1959. Tracking birds on tidal flats and beaches. *British Birds* 12:15–8.
- van Tuinen, M., D. Waterhouse, and G. J. Dyke. 2004. Avian molecular systematics on the rebound: a fresh look at modern shorebird phylogenetic relationships. *Journal of Avian Biology* 35(3):191–4.
- Vialov, O. S. 1965. *Stratigrafiya neogenovykh molass Predkarpatskogo progiba*. Kiev: Naukova Dumka. [In Russian.]
- Vialov, O. S. 1966. *Sledy zhiznedeiatel'nosti organizmow i ikh paleontogicheskoe znachenie*. Kiev: Naukova Dumka. Academy of Sciences, Ukrainian.
- Viramonte, J. G., S. M. Kay, R. Becchio, M. Escayola, and I. Novitski. 1999. Cretaceous rift related magmatism in Central-Western South America. *Journal of South American Earth Science* 12(2):109–21.
- Yang, S. Y., M. G. Lockley, R. Greben, B. R. Erickson, and S. K. Lim. 1995. Flamingo and duck-like bird tracks from the Late Cretaceous and Early Tertiary: evidence and implication. *Ichnos* 4(1):21–34.