

ICHNOTAXONOMY OF BIRD-LIKE FOOTPRINTS: AN EXAMPLE FROM THE LATE TRIASSIC-EARLY JURASSIC OF NORTHWEST ARGENTINA

SILVINA DE VALAIS^{*1} and RICARDO N. MELCHOR²

¹CONICET, Museo Paleontológico 'Egidio Feruglio', Fontana 140, Trelew (9100), Chubut, Argentina, sdevalais@yahoo.com.ar;

²CONICET, Universidad Nacional de La Pampa, Av. Uruguay 151, L6300CLB Santa Rosa, La Pampa, Argentina, rmelchor@exactas.unlpam.edu.ar

ABSTRACT—The ichnotaxobases previously used to classify avian-like footprints, at the ichnogenetic, ichnospecific, and ichnofamily level, are varied and contrasting. Consequently, an agreement on the most adequate taxobases to use for classifying these vertebrate trace fossils is necessary. The authors follow an ichnotaxonomy treatment independent to the age, locality provenance, and possible tracemaker of the trace fossils. The ichnotaxobases used to classify tracks with avian affinities at ichnogenetic and ichnospecific levels are evaluated and a proposal is made for useful and appropriate ichnotaxonomic criteria, considering those currently in use. Previous criteria used to distinguish avian footprints from non-avian theropod or ornithischian tracks are discussed. These concepts are applied to the avian footprints from the upper part of the Late Triassic-Early Jurassic Santo Domingo Formation from La Rioja province, northwest Argentina, which has yielded a diverse assemblage of trace fossils. The most conspicuous avian footprint is *Gruipeda dominguensis* isp. nov. The ichnogenus *Gruipeda* Panin and Avram, 1962 is revised and an emendation of its diagnosis is suggested. *Trisauropodiscus* Ellenberger, 1972, from South Africa and *Antarctichnus* Covacevich and Lamperein, 1970 from Antarctica are considered as junior synonyms of *Gruipeda*. Three other morphotypes of avian footprints are left under open nomenclature: one is assigned as cf. *Alaripeda* isp., other as bird-like footprints type C, and the third bird-like footprint with elongated drag marks. These specimens could be related to avian origin, but the possibility of a case of convergence with birds is not discarded. The presence of tracks with a wide total divarication produced in ephemeral fluvial systems with shallow ponds and mudflats suggest that it is likely the attainment of a convergent avian-form feet to improve controlled movements.

INTRODUCTION

The ichnotaxobases used by different authors to classify avian-like footprints, both at ichnogenetic and ichnospecific levels, as well as to ichnofamilies, are varied and contrasting (e.g., Ellenberger, 1972, 1974; Currie, 1981; Lockley et al., 1992; Sarjeant and Langston, 1994; Fuentes Vidarte, 1996; Doyle et al., 2000; McCrea and Sarjeant, 2001). Most authors use the age of the track-bearing layers, the provenance locality, and the possible trackmaker for the systematic analysis. This method, however, is considered incorrect because the ultimate objective of ichnotaxonomy is not identification of the producer but a morphological classification of trace fossils (Melchor and Genise, 2004b). Consequently, we propose here a set of standard taxobases that reflect the intent of the previous authors and are considered useful for the morphologic and behavioral discrimination of avian-like footprints.

Many different criteria were used to distinguish avian and avian-like footprints from other vertebrate tracks, mainly from the small bipedal dinosaurs, such as the non-avian theropod and ornithischian footprints (e.g., Lockley et al., 1992; Fuentes Vidarte, 1996; Doyle et al., 2000; McCrea and Sarjeant, 2001). The record of avian and avian-like tracks starts in the Mesozoic Era, although pre-Cretaceous occurrences are rare and sparse, with a dramatic increase in the number of records of avian ichnotaxa in Early Cretaceous and younger rocks (e.g., Lockley et al., 1992; Sarjeant and Langston, 1994; Abbassi and Lockley, 2005).

Among the early Mesozoic records, there are a number of ichnogenera of purported bird tracks from the Late Triassic and Early Jurassic (e.g., Hitchcock, 1858; Ellenberger, 1970, 1972, 1974, 1975), but most of these tracks were later interpreted as dinosaur tracks, and even as indeterminate or non-determined bipedal tracks (Haubold, 1971, 1984; Olsen and Galton, 1984; Rainforth, 2005).

The Late Triassic-Early Jurassic Santo Domingo Formation from La Rioja province, northwest Argentina, has yielded three different kinds of small avian-like footprints (Melchor et al., 2002; Melchor et al., 2006). These bird-like footprints represent one of the few examples of pre-Cretaceous avian-like tracks.

The aims of this paper are: (1) to revise and discuss the ichnotaxobases used for the classification of avian footprints, independent of their age, and suggest those most appropriate for this kind of footprints, and (2) to apply these criteria in an ichnotaxonomic analysis of the Santo Domingo avian-like footprints and compare them with similar avian and avian-like ichnotaxa.

GEOLOGIC SETTING

The bird-like footprints in this study were recovered from the upper part of the Santo Domingo Formation, northwest La Rioja province, Argentina (Fig. 1). In particular, the studied material was collected at the Quebrada de Santo Domingo (28° 31' 48" S, 68° 44' 33" W). The unit is part of the filling of an isolated half-graben linked to the Triassic Ischigualasto-Villa Unión Basin. The formation reaches a minimum thickness of c. 1950 m (Fig. 2A) and is in fault contact, mostly by thrust faults, with Carboniferous igneous and sedimentary rocks (Fig. 1) (Caminos

*Corresponding author.

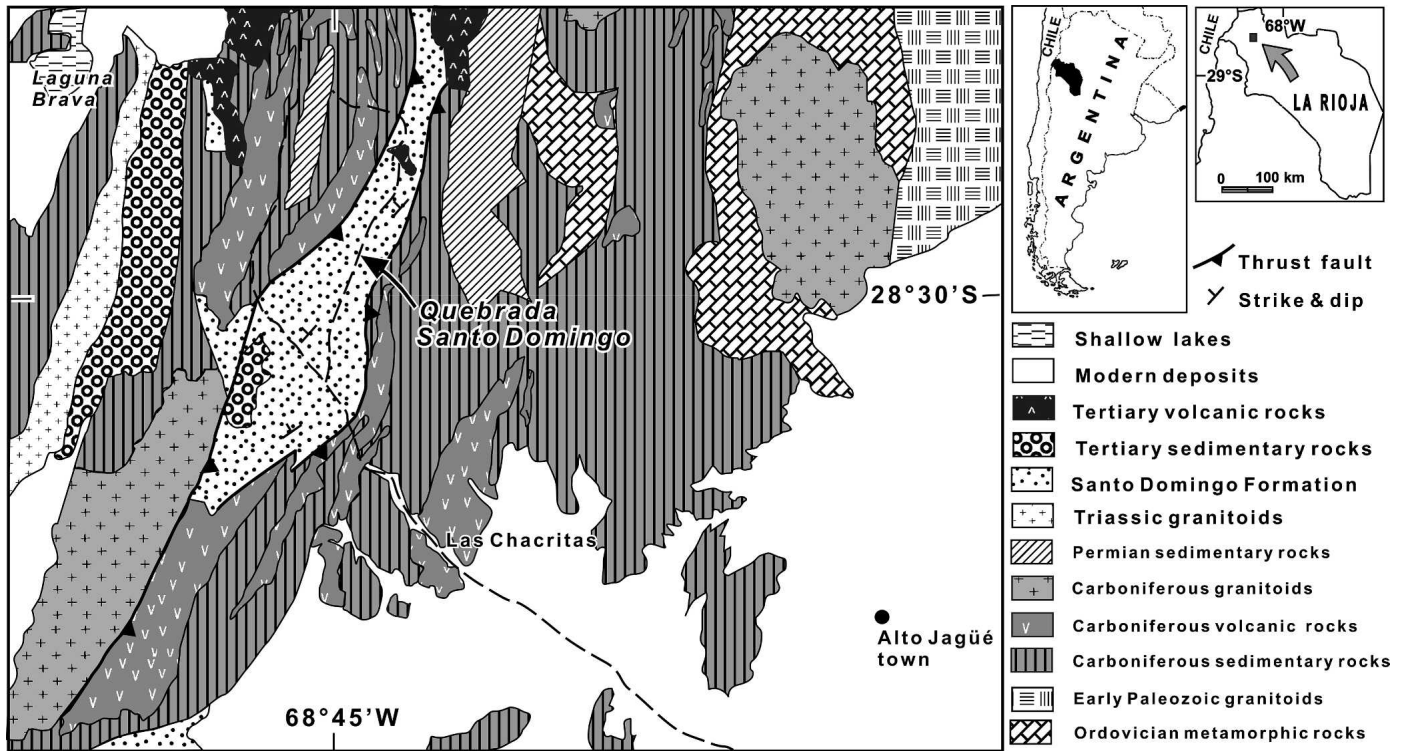


FIGURE 1. Simplified geologic map of the study area. Modified from Caminos and Fauqué (2001) and Melchor et al. (2006).

and Fauqué, 2001). The Santo Domingo Formation is a red bed succession that displays a thinning-upward trend in the lower 1650 m. The formation can be divided in four sections after the dominant lithofacies (Fig. 2A; Vizán et al., 2005): a basal conglomerate section (alluvial fans); a lower sandstone-dominated section with intercalated basalt flows (braided rivers and calcretes); a siltstone-dominated section that contains the described footprints, other vertebrate tracks and invertebrate traces (ephemeral rivers and shallow lakes); and an upper sandstone-dominated section (eolian deposits). The sedimentology and trace fossil assemblages of the siltstone dominated section (Fig. 2B) was analysed by Melchor et al. (2006). The overall palaeoenvironment is envisaged as a distal, low-gradient fluvio-lacustrine setting under semi-arid climate, similar to a terminal fan (Melchor et al., 2006). The Santo Domingo Formation is interpreted as Late Triassic-Early Jurassic, as suggested by the presence of the Middle-Late Triassic Gondwana wood morphogenus *Rhexoxylon* (Caminos et al., 1995), $^{40}\text{Ar}/^{39}\text{Ar}$ step-heating analysis on albite separate of interbedded basalt flows, which yielded a plateau age of 212.5 ± 7.0 Ma (Coughlin, 2001), and palaeomagnetic data (Vizán et al., 2005).

MATERIAL AND METHODS

The studied footprints were collected from six different stratigraphic levels, both as molds or molds and casts in siltstone slabs (Fig. 2B). This material is housed at the Agencia de Cultura de La Rioja, Colección de Icnología, La Rioja province, Argentina, under the abbreviation LAR-Ic. Casts of selected specimens

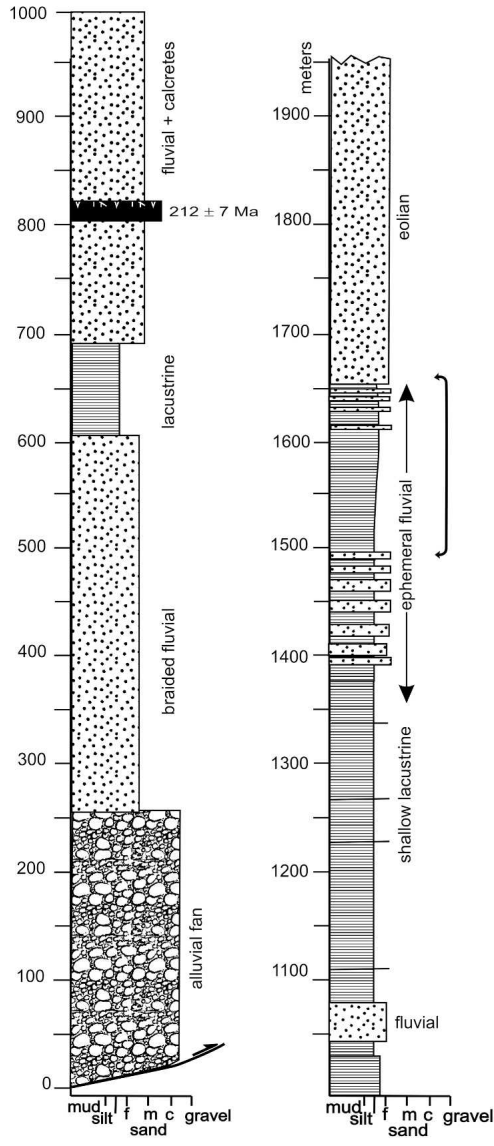
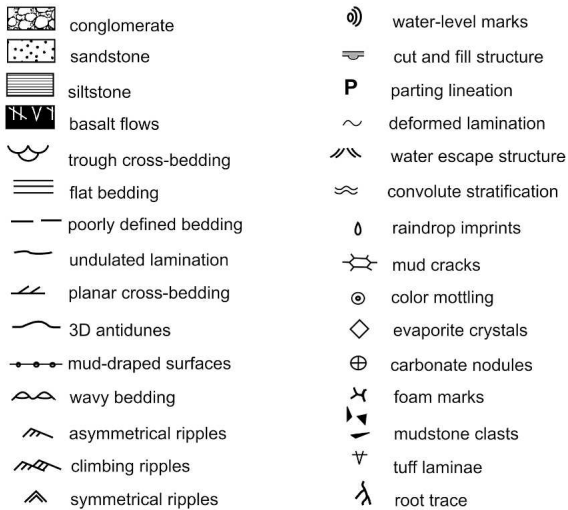
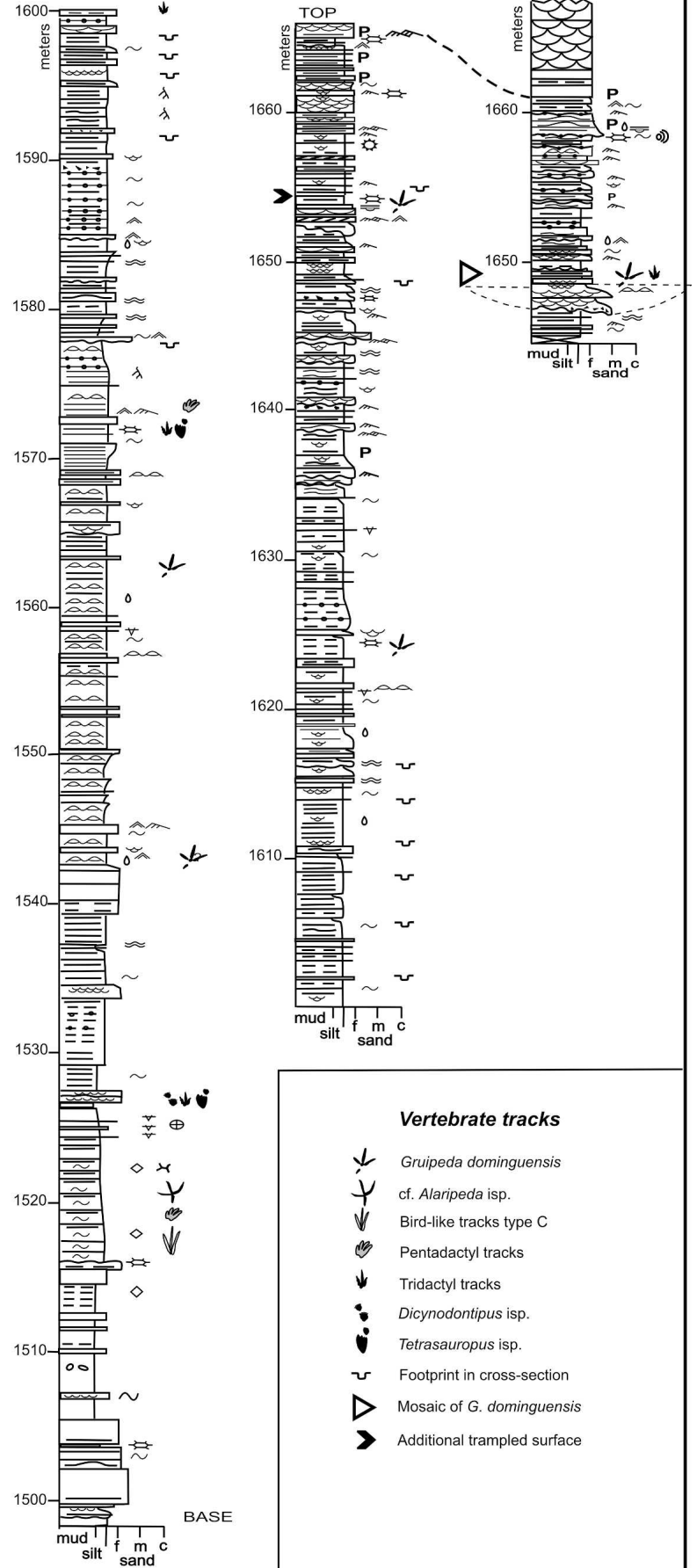
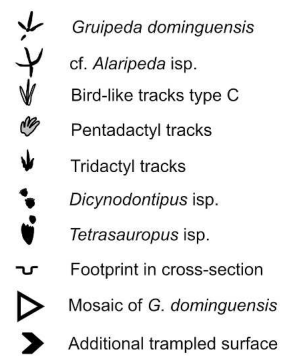
are also housed at the Museo Paleontológico Egidio Feruglio, Chubut province, Argentina, under the acronym MPEF-Ic.

The studied material was photographed with a digital camera. All measurements on these tracks follow the conventions and methodology by Leonardi (1987) and Thulborn (1990) (Figs. 3A–D), and are summarized in Table 1. In footprints with slightly curved digits (as is the case with specimen LAR-Ic-74), the digit length was measured parallel to the mean digit axis, and two values of angles between digit imprints were taken. One angle measures the axis parallel to the distal part of the digit, whereas the other is of the axis parallel to the proximal part of the digit (Fig. 3D).

Most of the footprints are preserved in several slabs composing a mosaic about 5.5 square meters, showing variable density and quality of preservation. This mosaic of slabs, named LAR-Ic 5 (Figs. 4, 5), includes both natural moulds and casts of footprints preserved in siltstone slabs covered by a submillimeter-thick clay drape. In some areas, the track density is fairly high (up to 520 footprints per square meter) with footprints moderately to poorly preserved because of high overprinting. In the rest of the mosaic, however, the preservation quality is moderate to good, including sparse sharp, and well-preserved footprints with distinct pad and claw impressions. The bird-like footprints in the mosaic are associated with an isolated, partially preserved and larger tridactyl track (Fig. 5A), as well as different invertebrate traces (de Valais et al., 2002; Melchor et al., 2006).

The remaining bird-like footprints from the Santo Domingo Formation occur in five additional stratigraphic horizons (Fig. 2A) and are mostly composed of single slabs, each bearing a few

FIGURE 2. Stratigraphy of the Santo Domingo Formation. **A**, Generalized lithologic log and paleoenvironmental interpretation of the Santo Domingo Formation (modified from Vizán et al., 2005), showing the footprint bearing interval detailed in Fig. 2B; **B**, Detailed sedimentologic log of the trace-fossil bearing section of the Santo Domingo Formation. Each footprint-bearing level is indicated (modified from Melchor et al., 2006).

a**Lithology and sedimentary structures****b****Vertebrate tracks**

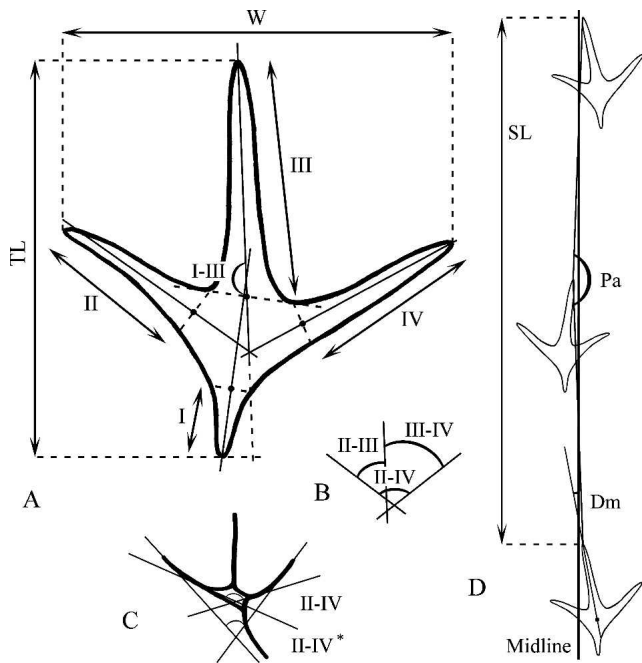


FIGURE 3. Diagram with the conventions of footprint and trackway measurements used in this paper. **A**, parameters corresponding to isolated tracks; **B**, detail of the measured angles among the impression of the digits II, III, and IV; **C**, detail of the measured angles in tracks with recurved digit impressions; **D**, parameters corresponding to trackways. For abbreviations, see Table 1.

footprints or one trackway (LAR Ic-6, 7, 8, 10 and 74) (Figs. 5, 6). All trackway measurements were taken from straight trackways.

ICHNOTAXONOMY OF BIRD-LIKE FOOTPRINTS

The ichnotaxonomy of vertebrate trace fossils was traditionally different from that of invertebrate trace fossils (e.g., Haubold, 1971; Bromley, 1990). The former is commonly based on the age and geographic provenance of the tracks, correlating them with the skeletal remains (e.g., Haubold, 1971, 1984, 1996; Lockley and Hunt, 1995), whereas the extramorphologic features (sensu Peabody, 1948) are ignored, and the identification of the trackmaker is usually the main objective (e.g., Scrivner and Bottjer, 1986; Doyle et al., 2000; Melchor and Genise, 2004a, b; Hunt and Lucas, 2005; Lucas, 2005). The main parameters used in the invertebrate ichnotaxonomy are the morphologic features that reveal behavior, without considering the age and geographic provenance of the trace fossil (Melchor and Genise, 2004a, b). In this paper, the ichnotaxonomic treatment is based on morphologic features of footprints, including those with anatomical and behavioral meaning. Examples of morphologic parameters that should be used are footprint shape, footprint and trackway parameters, and 'extramorphologic' features (e.g., Peabody, 1948, 1955; Haubold et al., 1995; Haubold, 1996) or "pressure-release features" (Brown, 1999), which are best referred to as not reflecting anatomy or 'extra-anatomic' (Melchor and Genise, 2004a,b). In accordance, the age of the footprint-bearing succession, the locality of provenance and the possible trackmarker are not considered of ichnotaxonomic importance (Melchor and Genise, 2004a,b).

A survey of the literature on ichnotaxonomy of avian footprints suggests that the chosen ichnotaxobases, at ichnofamilial, ichnogenetic and ichnospecific levels, and the hierarchy given to them by different authors is far from uniform.

TABLE 1. Summary of measured track and trackway parameters.

Ichnotaxa	<i>Gruipedes dominguensis</i>				cf. <i>Alaripeda isp</i>		Bird-like type C	
	Specimens LAR Ic-5, 6 to 8				LAR Ic-74	LAR Ic-10		
	Mean	Min.	Max.	n	Mean	n	Mean	n
L	26.42	17	33.5	132	10.3	6	15.7	1
TL	34.1	27	46	68	17.7	5	19.3	1
W	33.32	20.5	42.7	143	16	5	16.8	2
I	5.94	1	11.4	61	7.8	7	3.5?	1
II	13.7	8.8	19.2	124	7.3	5	11	1
III	19.44	12	31.7	131	7.9	6	14	2
IV	16.36	10.9	22.9	121	7.3	5	12	1
II-IV	115.4	87	137	131	150.5	6	43	2
II-IV*	—	—	—	—	94.2	5	—	—
II-III	59.8	36	78	125	74	5	25	2
II-III*	—	—	—	—	44	5	—	—
III-IV	56.2	28	77	124	78.6	5	26	2
III-IV*	—	—	—	—	50	5	—	—
I-III	158.7	107	198	63	153	5	144	1
Pa	170.17	150	182	18	110	3	—	—
Sl	170	99	230	17	31.5	3	—	—
Dm	11.4	0	29	38	15.6	5	—	—
L/W	0.8	0.58	1.17	—	0.64	—	1.02	—
III/I	3.27	1.38	7.75	—	1.01	—	0.4	—
III/II	1.42	1.02	2.22	—	1.08	—	1.27	—
III/IV	1.19	0.76	2.03	—	1.09	—	1.17	—

Linear measurements in millimeters and angles in degrees (see also Fig. 3).

Abbreviations: **L**, footprint length, distance between the distal tip of digit III, including the claw impression, and the more proximal boundary of the sole; **TL**, total footprint length, distance between the distal tips of digit III and the point of intersection between the projection of the hallux to the prolongation of digit III axis; **W**, footprint width, distance between the distal tip of digits II and IV measured perpendicular to the footprint axis; **I**, length of digit I; **II**, length of digit II; **III**, length of digit III; **IV**, length of digit IV; **II-IV**, angle formed by the axis of digits II and IV. In curved digits, angle formed considering the axis taken from the proximal part of the digits, II and IV; **II-IV***, angle formed considering the axis taken from the distal part of the digits II and IV; **II-III**, angle formed by the axis of digits II and III. In curved digit, angle formed considering the axis taken from the proximal part of the digits, II and III; **II-III***, angle formed considering the axis taken from the distal part of the digits II and III; **III-IV**, angle formed by the axis of digits III and IV. In curved digit, angle formed considering the axis taken from the proximal part of the digit, III and IV; **III-IV***, angle formed considering the axis taken from the distal part of the digits III and IV; **I-III**, angle formed by the axis of digits I and III clockwise; **Pa**, pace angulation, angle formed by the segments joining corresponding points of three consecutive footprints; **Sl**, stride length, distance between the same point of two consecutive footprints on the same side of the trackway; **Dm**, divarication of the footprint from the midline, angle formed by the longitudinal footprint axis with the midline; **L/W**, proportion between the footprint length without the hallux and width (see above); **III/I**, ratio between the length of digit III and I; **III/II**, ratio between the length of digit III and II; **III/IV**, ratio between the length of digit III and IV; **FA**, footprint longitudinal axis, line parallel to digit III.

The ICZN (1999, Art. 10.3) explicitly allows the use of ichnofamilies and it is considered that they can be useful to recognize groups of tracks that share key morphological features. The use of ichnofamilies to classify avian footprints is uncommon, however, and the first attempts can be traced to Lockley et al. (1992), who defined two ichnofamilies (Ignotornidae and Trisauropedidae). Subsequently, Sarjeant and Langston (1994) and Sarjeant and Reynolds (2001) erected five morphofamilies for avian tracks (Gruipedidae, Charadriipedidae, Avipedidae, Anatipedidae, and Culcitapedidae), a proposal followed by McCrea and Sarjeant (2001) and Mustoe (2002). Apparently, morphofamilies are equivalent to ichnofamilies (cf. Kim et al., 2006), which is the term preferred herein, although it is not explicitly defined by Sarjeant and Langston (1994). Recently, the family Ignotornidae was emended (Kim et al., 2006) and a new family (Koreanor-

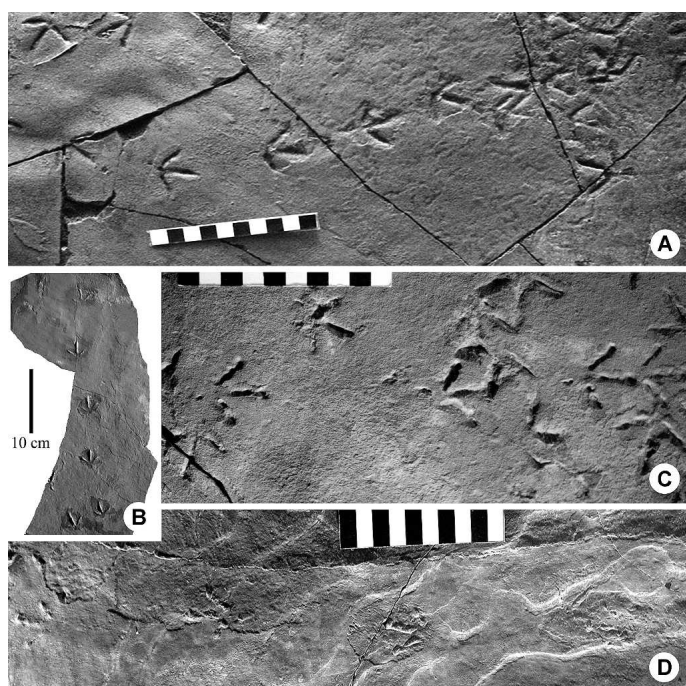


FIGURE 4. Photographs of trackways of *Gruipeda dominguensis* (LARC 5), collected from the Santo Domingo Formation. **A**, trackway number 10, holotype of the ichnospecies; **B–D**, trackways number 13, 2, 7, respectively, examples of the paratypes of the ichnospecies represented in the same slab. **A, B** are illuminated from the upper right corner, and **C–D** from the left corner. Scale bar equals 10 cm.

nipodidae) was added (Lockley et al., 2006). A revision of the definition of ichnofamilies for avian footprints suggests that there are two main approaches: a) Lockley and co-workers employ a large number of features and detailed descriptions (including number, morphology, and orientation of digits; footprint symmetry and size, presence and number of pad impressions and claw marks, presence and morphology of webbing, rotation of footprint, and stride length), and b) the approach of Sarjeant and co-workers that distinguishes ichnofamilies on the basis of a few key features (the number, relative position and proportionate length of digits; and the presence or absence of webbing impressions). A possible guide to the erection of ichnofamilies can be based on the main tracks types of modern birds (e.g., Elbroch and Marks, 2001). Under this approach, a minimum number of five types of bird tracks are recognised: anisodactyl footprints with relatively large hallux print, anisodactyl footprints with a reduced or absent hallux print (possibly including semipalmate tracks), anisodactyl webbed or palmate tracks, totipalmate tracks, and zygodactyls tracks. Following this approach, it is suggested that the number, relative position and proportionate length of digits, as well as the presence or absence of webbing impressions are useful taxobases to define ichnofamilies of bird-like footprints (as proposed by Sarjeant and Langston, 1994).

At ichnogenetic and ichnospecific levels, some features were used as ichnotaxobases more frequently than others (Table 2). For instance, the number, morphology, relative length, and orientation of the impressions of the digits or the total divarication are considered as ichnogenetic taxobases in most cases. Certain features are regarded as ichnogenetic taxobases by some authors, such as the footprint length:width ratio (Currie, 1981; Lockley et al., 1992), divarication between the impressions of the digits II-III and III-IV (Sarjeant and Langston, 1994), presence or absence of the impression of sole (Fuentes Vidarte, 1996),

heel (Sarjeant and Langston, 1994; Doyle et al., 2000; McCrea and Sarjeant, 2001), and webbing (Sarjeant and Langston, 1994; Doyle et al., 2000; McCrea and Sarjeant, 2001), and the correspondence of the axis of the impression of the digit I with that of the III (Sarjeant and Langston, 1994; Doyle et al., 2000).

Other characters were used indistinctly to name ichnogenera or ichnospecies by different authors, including: (1) presence of claw marks (considered as an ichnogenetic taxobase after Hitchcock, 1858; Currie, 1981; Lockley et al., 1992; Fuentes Vidarte, 1996; and McCrea and Sarjeant, 2001; and ichnospecific after Doyle et al., 2000); (2) number of phalangeal pads (as ichnogenetic after Hitchcock, 1858; Lockley et al., 1992; Doyle et al., 2000; McCrea and Sarjeant, 2001; and ichnospecific after Ellenberger, 1972, 1974); and (3) size of the footprint (as ichnogenetic after Hitchcock, 1858; Ellenberger, 1972, 1974; Fuentes Vidarte, 1996; and McCrea and Sarjeant, 2001; and ichnospecific after Currie, 1981; Lockley et al., 1992; and McCrea and Sarjeant, 2001). In the same way, the trackway parameters (e.g., pace length, stride length, trackway width, pace angulation, and divarication of the footprints from the midline) are considered useful to name ichnogenera (Lockley et al., 1992; Doyle et al., 2000), or ichnospecies (Ellenberger, 1972, 1974; Sarjeant and Langston, 1994; McCrea and Sarjeant, 2001). Hitchcock (1858) considered the stride length and the pace angulation of greater hierarchy than the trackway width and the divarication of the footprint.

Most authors consider the details of the morphology, contour, and range and absolute length of the digit impressions, especially of the hallux, as ichnospecific taxobases. Other features often regarded in an ichnospecific level are: (1) the morphology of the impressions of claws (Hitchcock, 1858; Lockley et al., 1992; Doyle et al., 2000; McCrea and Sarjeant, 2001), phalangeal pads (Hitchcock, 1858; Ellenberger, 1972, 1974; Lockley et al., 1992), sole (Ellenberger, 1972, 1974), and heels (Doyle et al., 2000); (2) range of the divarication between the impressions of the digits II-III, III-IV (Sarjeant and Langston, 1994; McCrea and Sarjeant, 2001), and II-IV (Hitchcock, 1858; Ellenberger, 1972, 1974; Currie, 1981; Doyle et al., 2000); and (3) distance between the tips of the middle and the inner and outer digit imprints and projection of the impression of the III beyond the external digit imprints (Hitchcock, 1858).

After examination of the ichnotaxobases proposed in the literature and considering a hierarchy of morphological attributes for ichnogenera and ichnospecies, a set of ichnotaxobases is suggested. Under this rationale, it is proposed that the ichnogenetic taxobases most useful to distinguish avian-like footprints are: the number, morphology, relative length, and orientation of the digit imprints, particularly that of digit I, length:width ratio of footprints, number of phalangeal pad marks, divarication between the impressions of the digits II-III, III-IV, and II-IV, and presence or absence of webbing.

The ichnospecific taxobases proposed in this study are: range of length:width ratio of footprints, footprint size range, proportion of digit length I:II:III:IV, range of the angles among the impressions of the digits, morphology of the sole, rotation of the footprint in relation to the midline, pace angulation, and stride length. The trackway parameters are considered as useful ichnotaxobases for the erection of ichnospecies under the rationale that similar tracks may be arranged in different and repetitive trackway patterns. These trackway patterns can deserve separate ichnospecific names, provided that they represent a specific behavior. The clue for the interpretation of the behavioural meaning of these trackway patterns must be obtained from neoichnological observations.

The proposed ichnofamilial, ichnogenetic and ichnospecific taxobases compose a set of characters that may be used fully or partially depending on the critical assessment of the material under study, to define ichnotaxa. Erection of new ichnotaxa

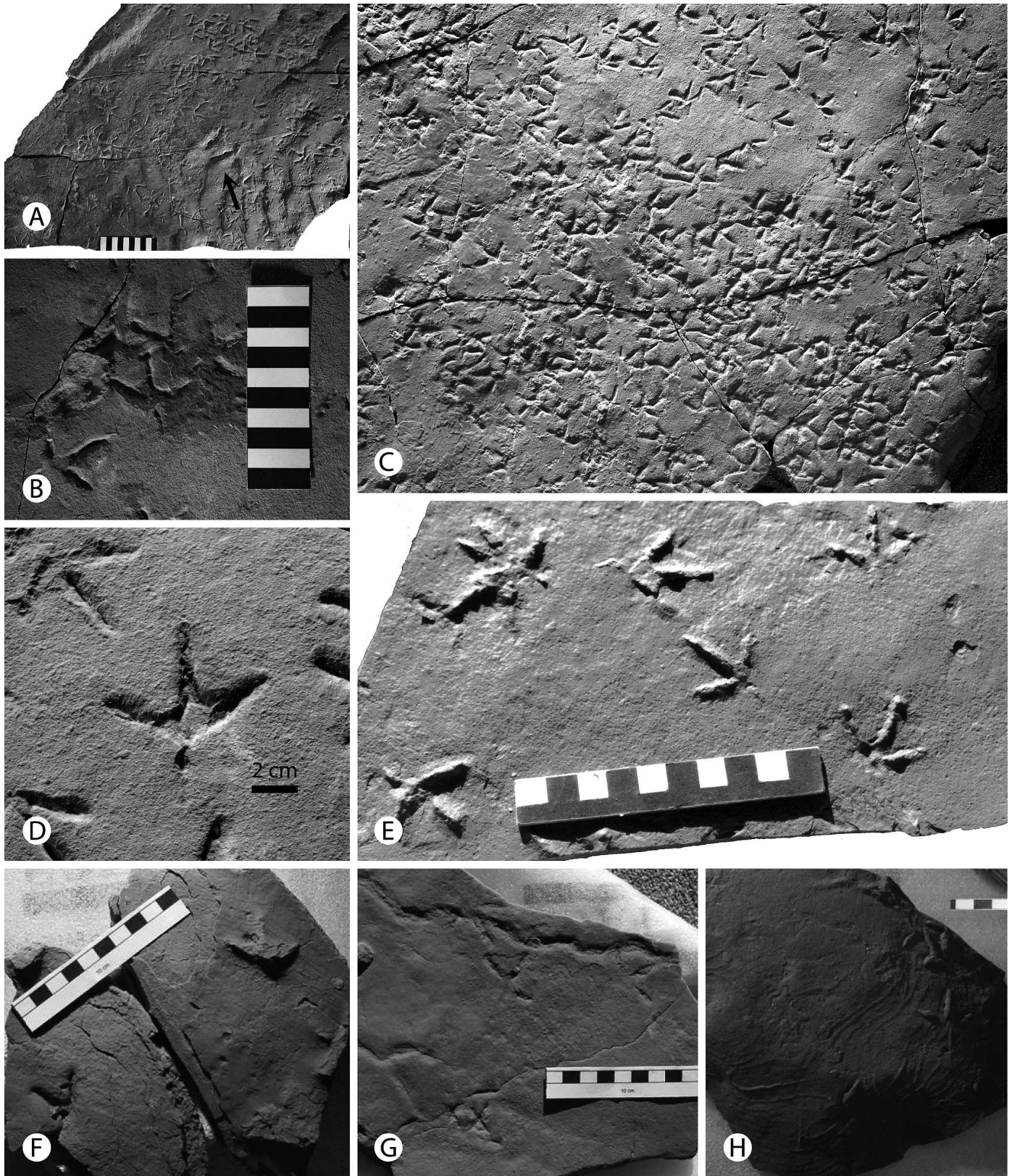


FIGURE 5. Photographs of isolated and group of footprints of *Gruipea dominguensis* (LAR-Ic 5 to 8), collected from the Santo Domingo Formation. **A–E**, LAR-Ic 5, from the stratigraphically highest avian-like track-bearing level; **F–H**, additional material of *Gruipea dominguensis* (LAR-Ic 6 to 8), from the other three bird track levels in the section. The arrow in **A** indicates a partial large tridactyl footprint (LAR-Ic 9). All the photographs are illuminated from the upper right corner, with the exception of **A** from the right side. Scale bar is 2 cm in **D**, **F**; 5 cm in **I**; in the rest of the photographs is 10 cm.

TABLE 2. Summary of ichnogenic and ichnospecific taxobases used by different authors in the ichnotaxonomy of bird-like footprints, by different authors (Hitchcock, 1858; Ellenberger, 1972, 1974; Currie, 1981; Lockley et al., 1992; Sarjeant and Langston, 1994; Fuentes Vidarte, 1996; Doyle et al., 2000; McCrea and Sarjeant, 2001).

Source	Ichnogenic taxobases	Ichnospecific taxobases
Hitchcock (1858)	<ul style="list-style-type: none"> - relative size of the footprint, including the concept of pachydactylous (thick-toes) vs leptodactylous (narrow-toes) tracks - number, position, morphology, size, curvature, and orientation of the digit imprints - presence and size of the heel impressions - integuments of the feet - presence of the claw marks - number and size of the phalangeal pad impressions - stride length - pace angulation 	<ul style="list-style-type: none"> - width and length of the footprints - range of total and between lateral digit imprints - divarication - distance between the tips of the middle and the inner and outer digit imprints - absolute and relative length and width of the digit imprints - length of the phalangeal pad impressions - description of the claw marks - distance of the center of the heel from the line of direction - projection of III beyond the lateral digit imprints - trackway width - divarication of the footprint from the midline - range of width and length of the footprints - morphology of the sole - length of the digit imprints - divarication between the impression of the digits II-IV - number and characteristics of the phalangeal pad impressions - pace length - stride length - pace angulation - divarication of the footprint from the midline
Ellenberger (1972, 1974)	<ul style="list-style-type: none"> - width and length of the footprints - number, morphology, and orientation of the digit imprints 	<ul style="list-style-type: none"> - size of the footprint - range of relative length of the digits - absolute divarication between the impression of the digits II-IV
Currie (1981)	<ul style="list-style-type: none"> - number, morphology, and relative length of the digit imprints - length:width of the footprint - divarication between the impression of the digits II-IV - presence of claw marks 	<ul style="list-style-type: none"> - size of the footprint - range of relative length of the digits - absolute divarication between the impression of the digits II-IV
Lockley et al. (1992)	<ul style="list-style-type: none"> - length:width of the footprint - divarication between the impression of the digits II-IV - number, morphology, relative length, and orientation of the digit imprints - presence and number of phalangeal pad impressions - presence of claw marks - pace length - divarication of the footprint from the midline - trackway width 	<ul style="list-style-type: none"> - size of the footprint - details of the hallux - contour and length of the digit imprints - range of divarication between the impression of the digits II-IV - number and morphology of the claw marks. - morphology of phalangeal pad impressions
Sarjeant and Lagston (1994)	<ul style="list-style-type: none"> - number, morphology, relative length, and orientation of the digit imprints - divarication between the impression of the digits II-III-IV, I-II, I-IV, and I-III - correspondence of axis of digits I with that of digit III - presence and size of the heel impressions - presence of webbing impressions 	<ul style="list-style-type: none"> - size of the footprint - range of divarication between the impression of the digits II-III-IV, and I-III - morphology and relative length of the digit imprints - trackway width - stride length
Fuentes Vidarte (1996)	<ul style="list-style-type: none"> - number, morphology, relative length, and orientation of the digit imprints - size of the footprint - presence of claw marks - divarication between the impression of the digits II-IV and III-I - presence and morphology of the sole 	<ul style="list-style-type: none"> - None used
Doyle et al. (2000)	<ul style="list-style-type: none"> - number, morphology, relative length, and orientation of the digit imprints - divarication between the impression of the digits II-IV - presence of webbing impression - the correspondence of the axis of digit imprints I and III - presence of the heel impressions - presence of phalangeal pad impressions - pace length - stride length - trackway width 	<ul style="list-style-type: none"> - size of the footprint - range of the length of the digit imprints - range of the divarication between the impression of the digits II-IV - presence and morphology of claw marks - morphology of the heel impressions
McCrea and Sarjeant (2001)	<ul style="list-style-type: none"> - size and contour of the footprint - number, morphology, relative length, and orientation of the digit imprints - divarication between the impression of the digits II-IV - presence of claw marks - presence of phalangeal pad impressions - presence of the heel impressions - presence of webbing impression 	<ul style="list-style-type: none"> - morphology, relative length, and curvature of the digit imprints - divarication between the impression of the digits II-IV, II-III, and III-IV - morphology of claw marks - divarication of the footprint from the midline - trackway width - pace length

should always be based on a large sample size and consider the full variability of the footprint population (e.g., to establish the range of the track size and angles among the digit impressions). If the only material available are a few specimens of footprints of potentially distinctive morphology that cannot be compared with a known ichnotaxa, it is considered desirable to leave these in open nomenclature, instead of creating a new ichnotaxa. Whenever possible, the type material for a new ichnotaxa should be a trackway instead of a single track (Sarjeant, 1989), thus conveying not only anatomical but also behavioral information. In invertebrate ichnology, the size of a trace fossil is commonly not regarded as a valid ichnotaxobase, although it may be used in some cases as an ichnospecific taxobase (e.g., Uchman, 1995; Bertling et al., 2006). Accordingly, it is recommended that the use of footprint size in vertebrate ichnotaxonomy be restricted to an ichnospecific level, but preferably in association with other attributes. It is envisaged that the proper use of size as ichnotaxobase should be based on an analysis of the footprint population and discrimination of distinct and separate modal values. Comparison with existing ichnotaxa must consider a set of features, not only the size of footprints. Regarding the size of footprints, it is recommended that the average size of type material with a range of variation be considered as included under the same ichnospecies. The selection of that range of variation is necessarily arbitrary and it is herein proposed that be considered as belonging to the same ichnospecies all the footprints that fall in the range of one standard deviation or 50% larger and smaller from the average size of the type series material.

SYSTEMATIC ICHNOLOGY

GRUIPEDA Panin and Avram, 1962
emend. de Valais and Melchor, nov.

Urmionis Lambrecht, 1938:243, pl. 19 (*partim*).
Gruipeda Panin and Avram, 1962:465, pl. 7, fig. 25.
Charadriipeda Panin and Avram, 1962:465, pl. 7, fig. 26 (*partim*).
Antarctichnus Covacevich and Lamperein, 1970:66, pl. 2–3, fig. 6–7.
Trisauropodiscus Ellenberger, 1972:81, fig. 47 A, B, C, D, E–48.
(*nov. syn.*) (*partim*).
Trisauropodiscus; Lockley, Yang, Matsukawa, Fleming, and Lim, 1992:125, figs. 8, 13–15 (*partim*).
Gruipeda; Sarjeant and Langston, 1994:8, figs. 6–7.
Antarctichnus; Jianjun and Shuonan, 1994:240, figs. 3–4.
Antarctichnus; Leonardi, 1994:75, pl. 15, fig. 2.
Antarctichnus; Doyle, Wood, and George, 2000:522, figs. 6–8.
Charadriipeda ichnosp. 1; Payros, Astibia, Cearreta, Pereda-Suberbiola, Murelaga, and Badiola, 2000:124, pl. 21, fig. 7.
Gruipeda; Sarjeant and Reynolds, 2001:28, pl. 8, fig. 10–11.
Bird-like footprints, Melchor, de Valais, and Genise, 2002:936, fig. 1.
cf. *Gruipeda*, de Valais, 2004:31.
Bird-like footprints, Melchor, Bedatou, and de Valais, 2004:56.
Gruipeda; Atabadi and Khazaei, 2004:369, fig. 5.
Bird-like footprints, Melchor and de Valais, 2006:16, fig. 8c.
Bird-like footprints type A: Melchor, Bedatou, de Valais, and Genise, 2006:18, fig. 9C.

Type Ichnospecies—*Gruipeda maxima* Panin and Avram, 1962:465, pl. 7, fig. 25.

Emended Ichnogenetic Diagnosis—Footprints showing four digits, 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 axis of digit I does not correspond with that of digit III, the interdigital angle between digits I and II being smaller than that between digits I and IV. When present, phalangeal pad marks displaying the relation I: 2,

II: 2, III: 3, IV: 4. Webbing absent. (modified from Sarjeant and Langston, 1994:8).

Remarks—Panin and Avram (1962) described several new avian ichnotaxa from the Miocene of Romania, using the possible tracemaker as the main basis for classification. Sarjeant and Langston (1994) have revised the systematic approach by Panin and Avram (1962) to make the ichnotaxa independent of definite avian groups, and have emended their original ichnogenetic diagnosis. Regarding *Gruipeda*, Sarjeant and Langston (1994:8) indicated in the diagnosis that the interdigital angle between digits I and II was greater than between digits I and IV, based on measurements from a linear drawing of the type material in Panin and Avram (1962:fig. 25, pl. 7). On the basis of our analysis of the same figure and accompanying text, it is inferred that those authors considered that the angle I-II was smaller than the angle between I-IV. This error is corrected in the new emended diagnosis. The reference to 'avian footprints' in the diagnosis by Sarjeant and Langston (1994) was removed because there is a wide range of avian footprints and because we prefer to separate the ichnotaxonomic treatment of the possible trackmarker.

The ichnogenus *Trisauropodiscus* Ellenberger, 1972 displays a marked morphologic similarity with *Gruipeda* Panin and Avram, 1962. The former ichnogenus was originally defined from the Late Triassic of South Africa, and was also recorded from the Early Jurassic North America (Lockley et al., 1992). The ichnospecies of *Trisauropodiscus* erected by Ellenberger (1972) included tracks of very different morphology, although some of them displayed a strong avian-like aspect (e.g., *T. aviforma*, the type ichnospecies). *T. aviforma* was originally comprised of five varieties, named A to E, which are quite similar among themselves, including tridactyl or tetradactyl slender-toed avian-like tracks, with a total digit divarication ranging from 90° to 120°, and trackways with positive (inward) rotation of the prints. In *T. aviforma*, the hallux imprint when preserved, show variable length and orientation although commonly is short and posteromedially directed. In consequence, by comparison with the type ichnospecies, *Trisauropodiscus* is herein considered as a junior synonym of *Gruipeda*. However, other ichnospecies originally included in *Trisauropodiscus* (e.g., *T. superaviforma*) show a contrasting morphology that warrant separation under a different ichnogenus (e.g., Lockley et al., 1992).

Antarctichnus Covacevich and Lamperein, 1970 was recorded from Tertiary rocks of Antarctica, Europe and U.S.A. (e.g., Doyle et al., 2000, and references therein). This ichnogenus includes tridactyl or tetradactyl avian tracks showing the impression of digits II, III and IV of subequal shape and size, a short impression of digit I, and the axis of digit I posteriorly directed and not aligned with that of digit III. Herein, on the basis of its morphology, the ichnogenus *Antarctichnus* is considered as a junior synonym of *Gruipeda*.

The ichnogenus *Gruipeda* Panin and Avram, 1962 can be distinguished from other ichnotaxa with avian affinities. The ichnogenus *Plesiornis* Hitchcock, 1858, from the Triassic of U.S.A., was re-defined by Gierliński (1996a) as a monospecific ichnogenus, *P. pilulatus*, to include new tracks from Late Triassic-Early Jurassic of Poland. It differs from *Gruipeda* by having an U-shaped outline, thicker digit imprints, lower total divarication, and footprints directed forward. The ichnogenus *Kayentapus* Welles, 1971, from the Early Jurassic of U.S.A. includes tracks with slender digit imprints, and medium to large total divarication. It differs from *Gruipeda* by having forwardly directed footprints that are longer than wide, and a rarely imprinted hallux. *Archaeornithipus* Fuentes Vidarte, 1996, from the Late Jurassic-Early Cretaceous of Spain, is morphological similar to *Gruipeda*, but the impression of the hallux is proportionally shorter and the ratio length:width is larger than in *Gruipeda*. The ichnotaxa *Ignotornis* Mehl, 1931, from the Cretaceous of U.S.A., *Jindongornipes* Lockley et al., 1992 and *Koreanornis* Kim, 1969,

both from the Early Cretaceous of Korea, are very similar in general aspect; suggesting that a revision is needed to ascertain their ichnotaxonomic status. These ichnogenera differ from *Gruipeda* in having a higher number of pad impressions in the digits (as much as 4 in digit III and 5 in digit IV). *Aquatilavipes* Currie, 1981, was originally erected to name avian tracks from the Cretaceous of Canada, and was later recognized from many other localities in the world (i.e., the Cretaceous of U.S.A., Lockley et al., 1992; China, Li et al., 2002; Japan, Lockley et al., 1992; Azuma et al., 2002). This ichnotaxa groups tracks with a general morphology very similar to those of *Gruipeda*, although lacks a hallux impression. The ichnogenus *Yacoraitichnus* Alonso and Marquillas, 1986, from the Late Cretaceous of Argentina, represents avian-like footprints with a high digit divarication (II-IV) and clear claw impressions. However, the poor preservation of the type material and the lack of a proper description and illustration, make the comparisons with other avian footprints difficult. Other ichnogenus from the Late Cretaceous of Argentina is *Barrosopus* Coria et al., 2002, which is distinguished from *Gruipeda* because the impression of the digit II is not proximally in contact with the impressions of the III and IV, and lacks a hallux imprint.

Sarjeant and Langston (1994:11) redefined the ichnogenetic diagnosis of *Charadriipeda* Panin and Avram, 1962 to include tridactyl avian footprints having the impression of the digits II to IV directed forward and showing a total divarication up to 70°, as well as interdigital web impression almost reaching the digit tips.

Several tracks from the upper Eocene of the western Pyrenees, Europe, were separated in six morphotypes (1 to 6) (Payros et al., 2000). In particular, some specimens included in *Charadriipeda* ichnosp. 1 and ichnosp. 2 display tridactyl and tetradactyl footprints, with slender digit imprints and wide divarication. Considering the emended diagnosis of *Charadriipeda* by Sarjeant and Langston (1994) these specimens cannot be compared with that ichnogenus because of the presence of hallux impressions. On the base of the general morphology, their affinity with *Gruipeda* is considered.

The ichnogenus *Carpathipeda* László and Péter, 1990, from the Neogene of Romania, represent tridactyl footprints with slender digit impressions, which is distinguished from *Gruipeda* by lacking the impression of the hallux and by a greater asymmetry respect to the digit III axis.

Aviadactyla Kordos, 1985, from the Miocene of Hungary, displays slender digit impressions, occasional claw and pad marks, and a total divarication exceeding 95°. However, this ichnogenus lacks the hallux impression. *Tetraornithopedia* Kordos, 1985, also from the Miocene of Hungary, is a tetradactyl avian footprint that could be included under *Gruipeda*, although the published drawings do not permit to decide about its comparison. The ichnogenus *Ardeipeda* Panin and Avram, 1962, from the Miocene of Romania, is similar to *Gruipeda*, although the impression of digit I is longer and the angle between I-III is close to 180°. *Iranipeda* Vialov, 1989 was erected to embrace the ichnospecies *Urmiornis abeli* Lambrecht, 1938, from the Pliocene of Iran. Posteriorly, Sarjeant and Langston (1994) synonymized it under *Gruipeda*, a concept maintained by Ataabadi and Khazae (2004), but rejected by Doyle et al (2000). Herein, the position of Sarjeant and Langston (1994) is provisionally followed, although a revision of the original material is necessary. *Alaripeda* Sarjeant and Reynolds, 2001, from the Miocene of California (no locality is given), U.S.A., differs from *Gruipeda* by having curved impressions of digits II to IV and a large divarication of digits II-IV (180°).

GRUIPEDA DOMINGUENSIS, isp. nov.

(Figs. 4, 5)

Bird-like footprints, Melchor, de Valais, and Genise, 2002:936, fig. 1.

cf. *Gruipeda*, de Valais, 2004:31.

Bird-like footprints, Melchor, Bedatou, and de Valais, 2004:56.

Bird-like footprints, Melchor and de Valais, 2006:16, fig. 8c.

Bird-like footprints type A, Melchor, Bedatou, de Valais, and Genise, 2006:18, fig. 9C.

Etymology—Referring to the locality where the footprints were discovered.

Holotype—LAR-Ic 5, trackway number 10 (Fig. 4A).

Paratypes—LAR-Ic 5, trackways 1 to 9, 11 and 13 (Fig. 4B–D).

Additional Material—The remaining isolated footprints on the slabs of LAR-Ic 5, LAR-Ic 6 to 8, and MPEF-IC 227 (cast of LAR-Ic 5) (Figs. 5, 6).

Holotype Locality—Quebrada de Santo Domingo, La Rioja province, Argentina.

Stratigraphic Provenance—Santo Domingo Formation (Late Triassic-Early Jurassic)

Ichnospecific Diagnosis—*Gruipeda* preserved as tridactyl or tetradactyl footprints, commonly with a footprint length smaller than 50 mm, and a length:width ratio of 0.7–0.9. Bipedal trackways displaying a zero to inward rotation with relation to the midline, pace angulation ranging from 150° to 182°, and a stride length from 2.5 to 5 times the footprint length. Footprints slightly asymmetric, typically with the angle between digits II-III larger than those of digits III-IV, and a large divarication of digits II-IV in the range 90°–135°. Relative digit length is I < II < IV < III. Hallux impression present in almost half of the footprints with a posterior to posteromedial position. Occasional rhomboid to rounded sole.

Description—The specimens are represented by numerous tracks produced by a bipedal trackmaker. Table 1 summarizes the measurements from 145 imprints, including 13 trackways, the latter account for 55 of the measured footprints. The footprints range from 20.5 to 42.7 mm wide, and 27 mm to 46 mm long when the hallux is preserved, or 17 mm to 33.5 mm, when the impression of the hallux is absent. Digit impressions are slender, with a maximum width of 4 mm and may display a tapered or subparallel outline. The impressions of digits II and IV usually bear slim claw marks that depart laterally from the footprint axis, whereas the impression of digit III is straight or slightly curved inward. Digits II to IV radiate from a hypothetical point in the center of the sole, being the axis of digit I normally displaced medially from the axis of III. The sole, when preserved, has a rhomboid to rounded outline. The average length of the impression of the digits III, IV, II and I are, in decreasing order, 19.4 mm, 16.3 mm, 13.7 mm, and 5.9 mm.

The average divarication of the impression of digits II and IV is 115°. The angles formed by the digits II and III, and by the III and IV, have an average difference of about 4°, being about 60° and 56°, respectively. The hallux displays a wide angle with respect to digit III, from 107 to 198°, with an average of 159°.

Nearly half (49.3%) of the tracks are tetradactyl showing a small hallux impression ranging 2–8 mm behind the sole or proximal end of digit III. The remaining measured tracks are tridactyl, lacking the hallux impression. Tridactyl and tetradactyl tracks are found in the same trackway, suggesting a same producer under different conditions of preservation (Fig. 4A). The stride length ranges from 99 to 230 mm and changes in the direction of the trackway, pace length or pace angulation are common. Most footprints shows a positive (inward) rotation relative to the midline, which ranges from 0° to 29°, with a mean of 11°.

Remarks—*Gruipeda dominguensis* is different enough from the other ichnospecies of the ichnogenus to deserves a separate nomination. At present, there are eleven proposed *Gruipeda* ichnospecies, including: *Gruipeda abeli* (Lambrecht, 1938) Sarjeant and Langston, 1994, *G. maxima* Panin and Avram, 1962, *G. lambrechtii* Ataabadi and Khazae, 2004, *G. minima* (Panin, 1965) Sarjeant and Langston, 1994, *G. minima* (Panin and

Avram, 1962) Sarjeant and Langston, 1994, *G. calcarifera* Sarjeant and Langston, 1994, *G. diabloensis* Remeika, 1999, *G. disjuncta* (Panin and Avram, 1962) Sarjeant and Langston, 1994, *G. filiportatis* (Vialov, 1965) Sarjeant and Langston, 1994, *G. becassi* (Panin and Avram, 1962) Sarjeant and Langston, 1994, and *G. intermedia* Panin, 1965.

Gruipeda abeli, *G. maxima*, and *G. lambrechtii*, are larger than *G. dominguensis* (about five times larger the two first and more than twice larger the third). In *G. minor* the length of the impression of digit III in relation with those of digits II and IV is larger than in *G. dominguensis* and the tracks seem to have a partial webbing mark. *G. minima* is more asymmetrical and the hallux imprint is twice longer. *G. calcarifera*, has the digits III and IV proximally joined, digits I and II separate, and all of them show a biconvex outline. *G. diabloensis* is more asymmetric (angles between II-III is near 20° larger than III-IV) than *G. dominguensis*, with the impressions of the digit II and IV biconvex and slightly curved anteriorly. *G. disjuncta* is represented likely by undertracks, with no impressions of sole and hallux preserved, so it is not possible to reach any concise comparison with this ichnotaxon. It was not possible to examine the original description of *G. filiportatis*; although this ichnotaxon was interpreted as stork footprints (Sarjeant and Langston, 1994): consequently, it should be distinct from *G. dominguensis*.

The inclusion of *G. becassi* to this ichnogenus is herein questioned because the length of digit I is almost as long as those of the remaining digits. The ichnospecies *Gruipeda intermedia* Panin, 1965 was reassigned to the ichnogenus *Iranipeda* Vialov, 1989 (Doyle et al., 2000).

The ichnogenus *Kayentapus* Welles, 1971, is composed of three ichnospecies, two of them have a quite nonavian theropod-like morphology (*K. hopii* Welles, 1971 and *K. minor* (Lull, 1953) Weems, 1971). The remaining ichnospecies, *K. soltykovensis* (Gierliński, 1991) Gierliński, 1996b, displays slender digit impressions which give it an avian-like aspect. The latter ichnospecies differs from *G. dominguensis* because of the lower divarication angle (II-IV about 85°–90°) and the impression of the hallux is medially directed. *Yacoraitichnus avis* Alonso and Marquillas, 1986, from the Late Cretaceous of Argentina, the only component of the ichnogenus, represents avian-like specimens. Leonardi (1994:239) revealed a photograph of the material; it looks quite similar to *G. dominguensis*. Nevertheless, it is not possible to make valid comparisons between both ichnotaxa because of the low quality of conservation of *Y. avis* and the scarce available information (see above). *Alaripeda logfreni* Sarjeant and Reynolds, 2001, a monotypic ichnogenus from the Miocene of California, U.S.A., distinguishes from *G. dominguensis* by smaller size, lower length:width ratio, and markedly curved external digit impressions.

ALARIPEDA Sarjeant and Reynolds, 2001

Avipeda sp. D, Scrivner and Bottjer, 1986:295, fig. 3D.

Type 2 tracks, Johnson, 1986:1, fig. 2.A.

Alaripeda Sarjeant y Reynolds, 2001:29, figs. 12, 13, lám. 9.

Small lacertoid footprints, Melchor, Bedatou, and de Valais, 2004:56.

Bird-like footprints type B, Melchor, Bedatou, de Valais, and Genise, 2006:18, fig. 9D.

Type Ichnospecies—*Alaripeda logfreni* Sarjeant and Reynolds, 2001:29, pl. 9, figs. 12,13.

Ichnoenergetic 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—Sarjeant and Reynolds (2001) created this monotypic ichnogenus to include a slab with several tetradactyl footprints with slender curved digit impressions and wide divarication. Three tracks from the Miocene of California, U.S.A., originally named as *Avipeda* sp. D by Scrivner and Bottjer (1986), were later included under the ichnogenus *Alaripeda* (Sarjeant and Reynolds, 2001).

Two types of tracks with avian affinities are mentioned from the Paleocene of Wyoming, USA (Johnson, 1986), named as Type 1 and 2. Those belonging to the Type 2 tracks display a similar morphology to the ichnogenus *Alaripeda*, including curved imprints of digits II and IV, with a total divarication of about 150°–180°, absence of web mark, and posteromedially directed hallux impression.

The ichnogenus *Alaripeda* Sarjeant and Reynolds, 2001 is distinguished from other ichnotaxa with avian affinities. *Magnoavipes* Lee, 1997, from the Late Cretaceous of U.S.A., differs from *Alaripeda* in having a posteriorly directed small heel impression instead of the hallux impression, and a larger length:width ratio (0.84 against 0.48).

Three different forms of avian-like tracks, named as 'Morphotype I,' 'II,' and 'III,' were described from the middle Tertiary of the Fildes Peninsula, West Antarctica (Covacevich and Vickers-Rich, 1982). The footprints represented into the 'Morphotype III' display a general morphology very similar to *Alaripeda*, with curved external digit impressions, long hallux impression, and similar interdigital angles. However, they differ from the type material of the ichnogenus by the proximal widening of the impression of the digit II, III and IV, probably due to taphonomical bias, and by a more marked asymmetry.

cf. *ALARIPEDA* isp.

(Fig. 6A, B)

Small lacertoid footprints, Melchor, Bedatou, and de Valais, 2004:56.

Bird-like footprints type B, Melchor, Bedatou, de Valais, and Genise, 2006:18, fig. 9D.

Referred Material—LAR-Ic 74, slab with a trackway composed by seven footprints.

Locality—Quebrada de Santo Domingo, La Rioja province, Argentina.

Stratigraphic Provenance—Santo Domingo Formation (Late Triassic–Early Jurassic) (Fig. 2A).

Description—The specimen is represented by seven small, tetradactyl footprints arranged in a single bipedal trackway.

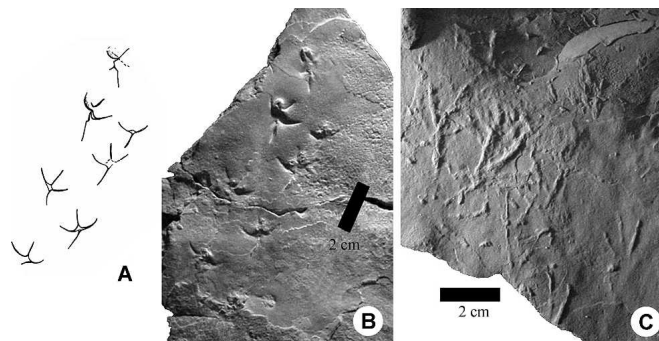


FIGURE 6. Photographs of the specimens belong to cf. *Alaripeda* isp. and bird-like type C (LAR-Ic 74 and LAR-Ic 10, respectively), collected from the Santo Domingo Formation. A, outline drawing of LAR-Ic 74; B, photo of LAR-Ic 74; C, photo of LAR-Ic 10. Scale bar is 2 cm.

Their measurements are summarized in the Table 1. Length of individual tracks including the hallux ranges from 15.6 mm to 19.3 mm (average of 17.7 mm), and without the hallux ranges from 9.8 to 10.8 mm (average 10.3 mm). Footprint width ranges from 15.5 mm to 17.1 mm (average 16 mm) and the length:width ratio is 0.64. The footprints have very slender digit imprints, less than 1 mm wide, the outer digits (II and IV) are curved inward whereas digits III and I are straight to slightly curved. The impression of digit III is the longest (average length of 7.9 mm), digits II and IV are subequal in length (about 7.3 mm), and the hallux imprint average 7.8 mm, some of them with elongated marks. Most digit imprints display acute claw marks. The footprints display an positive rotation with respect to the midline (between -8° to -20°), and some of them exhibit clear marginal ridges in the rear of the footprint. The pace angulation ranges from 102° to 114° , and the stride length between 31 mm to 32.4 mm. The average digit divarication measured along the axis taken from the proximal digit tip is 150° (II-IV), 74° (II-III), 79° (III-IV), and 153° (I-III), and the divarication measured along the axis taken from the distal digit tips is 94° (II-IV*), 44° (II-III*), and 50° (III-IV*) (Fig. 3D). The digit imprints converge in a small, sometime nearly rhomboid sole. No webbing mark was observed.

Remarks—These footprints are distinguished for their very small size, the low pace angulation, curvature of digit imprints II and IV, and comparatively large hallux impression. The seven tracks comprising the trackway suggest different modes of locomotion of the producer. The first four tracks exhibit a walking gait (sensu Leonardi, 1984), followed by two tracks arranged side by side by stopping the right foot at side of the left one, resembling a stopping posture. Finally, the trackmaker begins its displacement again by moving the left foot.

The scarce available material preclude any definite ichnotaxonomic assignment. Although display avian-like features, it is not possible to suggest the affinity of the producer with confidence.

Those specimens belonging to the Type 2 tracks from the Paleocene of Wyoming (Johnson, 1986), included herein in the ichnogenus, are larger than LAR-Ic 74.

BIRD-LIKE FOOTPRINTS TYPE C (Fig. 6C)

Bird-like footprints type C, Melchor, Bedatou, de Valais, and Genise, 2006:19, fig. 9E.

Referred Material—LAR-Ic 10, a slab showing, at least, two isolated footprints.

Locality—Quebrada de Santo Domingo, La Rioja province, Argentina.

Stratigraphic Provenance—Santo Domingo Formation (Late Triassic-Early Jurassic).

Description—The slab LAR-Ic 10 contains, at least, two moderately preserved tetradactyl footprints that does not seem to belong to a single trackway, associated with very faint digit imprints that does not conform any definite pattern. The measurements are restricted to the two distinct tracks. They are 15.7 mm and 18.7 mm long (the last one is a minimum value), without the hallux impression, and 19.3 mm with hallux impression, and 12.5 mm and 14.3 mm wide. Digit imprints are subequal in length, straight and very slender, about 1.5 mm wide, some of them exhibit probable phalangeal pads and claw marks.

One of the footprints display an unclear short hallux impression, directed medioposteriorly. No sole mark was observed and the proximal ends of the digit impressions are not in contact. The divarication of the digit imprints II-IV is small (42° and 44°), the angles between II-III and III-IV are subequal (25° and 26°).

Remarks—The moderate to poor preservation and the low relief of the tracks suggests the specimens are undertracks; al-

though its bird-like aspect is clear. The main differences with the other bird-like tracks described herein are small digit divarication, footprints considerably longer than wide, and medioposterior position of the hallux imprint. As with cf. *Alaripeda*, the affinity of the producer of these tracks is unknown. Some specimens of the morphotype 4 described by Payros et al. (2000) from the late Eocene of the western Pyrenees, display longer than wider tracks with slender digit imprints. However, they differ from bird-like footprint type C by having the hallux impressions posteriorly directed and by showing a larger divarication.

BIRD-LIKE FOOTPRINTS WITH ELONGATED HALLUX IMPRINTS

Associated with LAR-Ic 5, there are three bird-like footprints with elongated hallux impressions (Fig. 7A, B) and a minor widening of the impressions of digits II and IV. The impression of the hallux is 29.5 mm, 40 mm, and 27.4 mm long (up to four and a half of the average length in the associated *Gruipeda dominguensis* tracks), and a total track length of 63 mm, 74.2 mm, and 60.2 mm, respectively. The two first tracks display raised rims associated with digits II and IV and comprise a right-left pair separated by 147 mm (Fig. 7A).

The general morphology of these tracks shows clear affinities with *Gruipeda dominguensis*, although some salient morphological features are different. It is suggested that these footprints should be considered under a separate ichnotaxa for the following reasons: (1) the relative length of the hallux impression related to the remaining digits is proposed as an ichnogenetic taxobase; (2) the sharp contrast between the range of hallux length from a large population of *G. dominguensis* and the specimens referred herein; and (3) the different track morphology. The elongation of the hallux print is a distinctive extra-anatomic feature, which is related to the drag of digit I. This feature could reveal a particular behavior and, in consequence, is a meaningful ichnotaxonomic feature.

AVIAN NATURE OF FOOTPRINTS

Many authors have suggested different criteria to distinguish avian footprints from non-avian theropod or ornithischian tracks (Currie, 1981; Lockley et al., 1992; Fuentes Vidarte, 1996; Gierliński, 1996a; Doyle et al., 2000; McCrea and Sarjeant, 2001; Wright, 2004). The characters used in this paper to distinguish avian from non-avian footprints, are modified from those suggested by previous authors: (a) an overall similarity to modern anisodactyl bird tracks, mainly shorebird tracks; (b) slender digits, commonly lacking clear phalangeal pad impressions; (c) a hallux impression posterior or posteromedially directed, visible both in shallow and deep tracks; (d) footprints wider than long (without considering the hallux); (e) slender claw marks displaying distal curvature of lateral and medial claws away from the foot axis; (f) a defined 'heel' or metatarsal-phalangeal pad im-

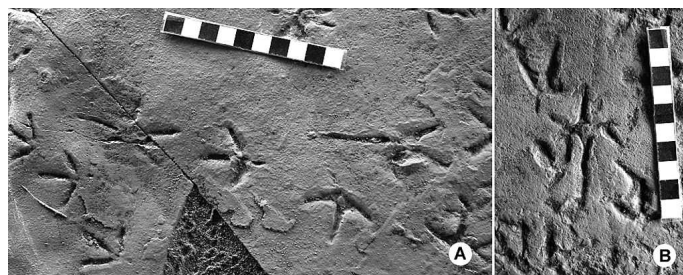


FIGURE 7. Photographs of the bird-like footprints with elongated hallux imprints. **A**, two footprints arranged in a single trackway, illuminated from the upper side; **B**, an isolated footprint, illuminated from the upper left corner. Scale bar equals 10 cm.

pression of digit III, visible in some footprints; (g) lack of impressions of the proximal metatarsal-phalangeal pads on the external digits; and (h) a centered sole or an area delimited by the proximal tips of the digit impressions where they converge.

Additional footprint features indicating an avian affinity are afforded by comparison with tracks of modern waterbirds and waders (Covacevich and Lamperein, 1970; Lockley et al., 1992; Lockley et al., 1994; Fuentes Vidarte, 1996; Doyle et al., 2000), such as: (i) high track density and absence of preferred orientation, suggesting a gregarious behaviour; (j) occurrence in a shallow lacustrine setting, an environment where bird tracks are preferentially preserved; and, (k) associated pecking traces.

When the tracks are abundant enough, it is feasible to incorporate additional parameters or features that may help to identify bird tracks, such as distinctive behaviour reflected in the trackways (i.e., zigzagging), or particular spatial distribution (i.e., movement parallel to the coast line).

A large angle between the impressions of the digits II and IV (total divarication), about 110° – 120° or more, was mentioned as an avian feature (e.g., Lockley et al., 1992), caused by the single, fused elements formed by the tarsometatarsus, as in all birds, with some exceptions, such as in specimens of *Archaeopteryx* and *Rahona* (Forster et al., 1998; Mayr et al., 2005). Lim et al. (2000) have suggested that this feature could be useful to distinguish unwebbed bird footprints from those of dinosaurs. Fuentes Vidarte (1996) claims that this feature is used to enlarge the sole area, which allow a bipedal animal to control the movements in wet or soft substrate, as well to improve landing after flight (Brown et al., 1989). Therefore, this character is not always useful for distinction of avian from non-avian footprints, because it might be influenced by the consistency and moisture content of the substrate and not only on the anatomy and the behavior of the trackmaker (e.g., Covacevich and Vickers Rich, 1982; Fuentes Vidarte, 1996; Sarjeant and Reynolds, 2001). However, if a large number of tracks showing large total divarication are preserved in different substrate conditions, as is the case of *Gruipeda dominguensis*, the track morphology is likely to reflect the anatomy of the foot. In our case study, the presence of a total divarication higher than 110° in most of the tracks, is suggestive of a trackmaker with highly spread digits.

The absence of conspicuous phalangeal pad impressions in some avian footprints (Lockley et al., 1992) contrasts with the presence of well-marked phalangeal pad impressions in *Grallator*-like theropod or similar tracks. In some cases, the avian tracks bear the phalangeal pad impressions clearly preserved, both in fossil (e.g., *Anatipeda* Panin and Avram, 1962) as well as in extant specimens (e.g., Anatidae footprints). However, the phalangeal pads impressions are different in size and number to those of the non-avian theropods. Likewise, it is considered that the quality of the preservation of the phalangeal pad imprints is normally not only related to foot anatomy but to substrate condition. The sole of non-avian theropods is not centered and normally located on a side behind the impression of the phalangeal pads of digit IV (Leonardi, 1984; fide Fuentes Vidarte, 1996).

Another purported avian feature is trackways with a high pace angulation (Fuentes Vidarte, 1996). Nevertheless, this character is not considered useful to separate between avian and non-avian theropod tracks, because it is commonly recorded in both groups of tracks (e.g., Aguirrezalba et al., 1985; Casanovas et al., 1991; Lee, 1997).

DISCUSSION

Some authors disagree with the validity of the criteria to distinguish avian from non-avian footprints mentioned above. Thulborn (1990, p. 224) claimed that it is unlikely that the footprints of Mesozoic birds could ever be distinguished with certainty from those of small theropods, which shared an almost identical

pattern of foot structure. Padian and Chiappe (1998) have argued that the criteria for recognising avian footprints are vague, and what have been demonstrated as 'avian features' exclusive of bird tracks could correspond by convergence to other taxa.

The avian characters and additional features mentioned above can be found isolated in non-avian footprints, such as the presence of slender digits in non-avian dinosaur footprints the wide pace angulation and total divarication (e.g., Thulborn, 1998). However, the occurrence of several of the diagnostic features for avian footprints in a track assemblage is distinctive and exclusive of birds (e.g., Currie, 1981; Thulborn, 1990; Fuentes Vidarte, 1996; McCrea and Sarjeant, 2001). A feature that is not in agreement with an avian origin for *Gruipeda dominguensis* is the absence of a 'heel' formed by the metatarsal-phalangeal pad impression of digit III, being the sole composed by a surface where all digit imprints converge.

The known record of *Gruipeda* has been considered as ranging from different outcrops sparse in the word, from Eocene to Pliocene age (Panin, 1965; Panin and Avram, 1962; Vialov, 1965, 1989; Sarjeant and Langston, 1994; Sarjeant and Reynolds, 2001; Ataabadi and Khazae, 2004), herein extending back its record to the Late Triassic-Early Jurassic.

The tracks of *Gruipeda dominguensis* have a strong resemblance to those of plovers, which are migratory shorebirds belong to the Charadriidae (e.g., *Calidris*, *Charadrius*, *Pluvialis*, *Phalaropus*), whose tracks are similar in shape and size to the fossil ones (e.g., Brown et al., 1987). Neoichnological studies on a shallow pond in a locality named Bajo de los Huesos, Chubut, Patagonia, Argentina, have confirmed not only a close morphological similarity between the fossil tracks and those of extant plovers, but also similar track distribution, density, and behavioural patterns (Genise et al., in review).

The bird-like footprints with elongated hallux imprints described above are strikingly comparable with modern bird landing traces (pers. observ.). These tracks are similar to skipping traces, although differ from them by a pronounced hallux drag mark, which is absent in modern bird skipping traces (e.g., Elbroch and Marks, 2001). This purported landing traces summed to the presence of small rounded to oval paired pits preserved in the same slab, LAR-Ic 5 (Melchor et al., 2006), which resemble bird pecking traces may suggest an avian affinity for the producer of *Gruipeda dominguensis* and associated trace fossils. The pecking traces could have been produced by non-avian dinosaurs, though no evidence is currently known. Although the possibility of a behavioural convergence cannot be discarded, the later inferences cast doubts about the age assignment of the Santo Domingo Formation.

CONCLUSIONS

Agreements on common and simple ichnotaxonomic criteria are needed to facilitate communication between researchers and highlight the utility of trace fossils in paleoenvironmental, paleoecological, behavioural, and census studies. These conventions are especially important for vertebrate ichnology, a field where tracks have been traditionally classified using the age of footprint bearing rocks, supposed producer, and provincial names as main ichnotaxobases.

After an analysis of the ichnotaxobases used to classify avian-like footprints, it is proposed that the ichnotaxobases to be used at the ichnofamily level are: the number, relative position and proportionate length of digits; and the presence or absence of webbing impressions. Suggested taxobases for the ichnogenetic level are: the number, morphology, relative length, and orientation of the digit imprints, specially that of digit I, length: width ratio of footprints, number of phalangeal pad marks, divarication between the impressions of the digits II-III, III-IV, and II-IV, presence or absence of webbing, rotation of the foot-

print in relation to the midline, the pace angulation, and the stride length. The proposed ichnospecific taxobases are: range of length:width ratio of footprints, proportion of digit length I:II:III:IV, range of the angles among the impressions of the digits, morphology of the sole, and range of pace angulation and stride length. The application of these ichnotaxobases to the Late Triassic-Early Jurassic Santo Domingo avian-like ichnofauna resulted in the recognition of four distinct morphotypes of tracks. The most abundant tracks are assigned to a new ichnospecies of *Gruipeda* Panin and Avram, 1962, *G. dominguenis*. At the same time, the ichnogenus *Gruipeda* is revised and an emendation to its diagnosis and comparisons with other ichnotaxa are suggested. Three other morphotypes are represented by scarce material: cf. *Alaripeda* isp., bird-like footprints type C, and bird-like footprint with elongated hallux imprints.

The avian characters and additional features indicating an avian affinity found in the whole Santo Domingo bird-like track assemblage are: the hallux impression posterior or posteromedially directed, small footprints wider than long with a general similarity to modern shorebird tracks, slender digits, slender and curved lateral and medial claws, large angle between digits II and IV, and some footprints marking the sole where digits converge.

The specimens from Santo Domingo could be related to an avian origin, but the possibility of an extraordinary case of convergence with birds is not discarded. In those tracks with a wide total divarication, if the environment had shallow ponds associated with ephemeral fluvial systems, the muddy plains would be abundant, favouring the attainment of a convergent avian-form feet to improve the control of movements in that slippery substrate. Associated purported landing (bird-like track with elongated hallux impressions) and pecking (small rounded to oval paired pits) traces are strongly suggestive of an avian affinity and may even challenge the certainty of the age currently assigned to the Santo Domingo Formation.

ACKNOWLEDGMENTS

We thank J. F. Genise for suggestions on early drafts and help in the preparation of the systematic section, and the technical staff of the Museo Paleontológico Egidio Feruglio for the preparation and moulding of the specimens. This research was funded by grant PICT6156 from the Agencia Nacional de Promoción Científica y Técnica. The Agencia Cultural of La Rioja and Dirección de Medio Ambiente de La Rioja are thanked for permission to study these tracks. Emma Rainforth shared photographs of the Ellenberger collection of tracks (Montpellier) from South Africa. The suggestions by Anthony Martin and an anonymous reviewer considerably helped to improve the original manuscript.

LITERATURE CITED

- Abbassi, N., and M. G. Lockley. 2005. Eocene bird and mammal tracks from the Karaj Formation, Tarom Mountains, Northwestern Iran. *Ichnos* 11:349–356.
- Aguirrezalba, L. M., J. A. Torres, and L. I. Viera. 1985. El Weald de Igea (Camerós-La Rioja). *Sedimentología, Bioestratigrafía y Paleocnología de grandes reptiles (Dinosaurios)*. *Minube* 37:111–138.
- 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. 4th Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Argentina. Abstract Volume:33–41.
- Atabadi, M. M., and A. R. Khazae. 2004. New Eocene mammal and bird footprints from Birjand Area, Eastern Iran. *Ichnos* 11:363–370.
- Azuma, Y., Y. Arakawa, Y. Tomida, and P. J. Currie. 2002. Early Cretaceous bird tracks from the Tetori Group, Fukui Prefecture, Japan. *Memoir of the Fukui Prefectural Dinosaur Museum* 1:1–6.
- Bertling, M., S. Braddy, R. G. Bromley, G. R. Demathieu, J. Genise, R. Mikuláš, J. K. Nielsen, K. S. S. Nielsen, A. K. Rindsberg, M. Schirf, and A. Uchman. 2006. Names for trace fossils: a uniform approach. *Lethaia* 39:265–286.
- Bromley, R. G. 1990. *Trace fossils: Biology and Taphonomy*. Special Topics in Paleontology 3, Unwin Hyman, London.
- Brown, T. Jr. 1999. *The science and art of tracking*. Berkley Books, New York, 213 pp.
- Brown, R., J. Ferguson, M. Lawrence, and D. Lees. 1987. *Tracks & signs of the birds of Britain and Europe*. Christopher Helm Ltd., Kent, 328 pp.
- Brown, R., J. Ferguson, M. Lawrence, and D. Lees. 1989. *Reconnaissance feathers, traces and indices of the oiseaux*. Ed. Bordes, Paris:25–59.
- Caminos, R., and L. Fauqué. 2001. Geologic sheet 2969-II Tinogasta (1:250,000). Servicio Geológico de Minería Argentina.
- Caminos, R., A. B. Zamuner, O. C. Limarino, and L. Fauqué. 1995. Triásico Superior fosilífero en la Precordillera riojana. *Revista de la Asociación Geológica Argentina* 50:262–265.
- Casanovas-Cladella, M. L., F. Pérez-Lorente, M. Ruiz de Azcárate, J. Santafé, and F. Torcida Fernández. 1991. Terópodos carnosauros en la Virgen del Campo II, Enciso (La Rioja, España). *Zubia* 9: 113–126.
- Chiappe, L. M. 1995. The first 85 million years of avian evolution. *Nature* 378:349–355.
- Coria, R. A., L. M. Chiappe, and L. Dingus. 2002. Bird footprints from the Anacleto Formation (Late Cretaceous), Neuquén, Argentina. *Ameghiniana* 39:453–463.
- Coughlin, T. J. 2001. *Linked orogen-oblique fault zones in the Central Argentine Andes: the basics of a New Model for Andean orogenesis and metallogenesis*. Ph.D. dissertation, Queensland University, Queensland, Brisbane, 157 pp.
- Covarevich, V., and C. Lamperein. 1970. Hallazgo de icnitas en Península Fildes, Isla Rey Jorge, Archipiélago Shetland del Sur, Antártica. *Serie Científica del Instituto Antártico Chileno* 1:55–74.
- Covacevich, V., and P. Vickers Rich. 1982. New bird ichnites from Fildes Peninsula, King George Island, West Antarctica. 3rd Symposium of Geology and Geofisic of Antartica, Madison, U.S.A. Abstract Volum: 245–254.
- Currie, P. 1981. Bird footprints from the Gething Formation (Aptian, Lower Cretaceous) of northeastern British Columbia, Canada. *Journal of Vertebrates Paleontology* 1:257–264.
- De Valais, S. 2004. *Ichnotaxonomy of avian-like footprints from the Santo Domingo Formation (Late Triassic)*. Northwest Argentina. 1st International Congress on Ichnology, Trelew, Argentina. Abstracts Volum: 31.
- De Valais, S., R. N. Melchor, and J. F. Genise. 2002. Instantánea de una icnofauna desconocida dominada por huellas de dinosaurios con rasgos avianos del Triásico Superior de La Rioja (Argentina). 8th Congreso Argentino de Paleontología y Bioestratigrafía, Corrientes, Argentina. Abstract Volume:31–32.
- Doyle, P., J. L. Wood, and G. T. George. 2000. The shorebird ichnofacies: an example from the Miocene of southern Spain. *Geological Magazine* 137:517–536.
- Elbroch, M., and E. Marks. 2001. *Bird tracks & sign—A guide to North American species*. Stackpole Books, Mechanicsburg, USA, 456 pp.
- Ellenberger, P. 1972. Contribution à la classification des pistes de vertébrés du Trias: les types du Stomberg d'Afrique du Sud (I). *Palaeo-vertebrata, Memoire Extraordinaire, Montpellier*, 134 pp.
- Ellenberger, P. 1974. Contribution à la classification des pistes de vertébrés du Trias: les types du Stomberg d'Afrique du Sud (II). *Palaeo-vertebrata, Memoire Extraordinaire, Montpellier*, 142 pp.
- Forster, C. A., S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science* 279:1915–1919.
- Fuentes Vidarte, C. 1996. Primeras huellas de aves en el Weald de Soria (España). Nuevo icnogénero, *Archeornithipus* y nueva icnoespecie *A. meijiidei*. *Estudios Geológicos* 52:63–75.
- Gatesy, S. M., K. M. Middleton, F. A. Jenkins, and N. H. Shubin. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature* 339:141–144.
- Gierliński, G. 1991. New dinosaur ichnotaxa from the Early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85:137–148.
- Gierliński, G. 1996a. Avialian theropod tracks from the Early Jurassic strata of Poland. *Zubia* 14:79–87.
- Gierliński, G. 1996b. Dinosaurian ichnotaxa from the Lower Jurassic of Hungary. *Geological Quarterly* 40:119–128.

- Haubold, H. 1971. *Ichnia amphibiorum et reptiliorum fossilium*; pp. 1–124 in O. Kuhn (ed.), *Handbuch der Paläoherpetologie*, Stuttgart, Fischer.
- Haubold, H. 1984. *Saurierfährten* 2nd ed. Wittenberg Lutherstadt, Ziemsen, 231 pp.
- Haubold, H. 1996. Ichnotaxonomie und Klassifikation von Tetrapodenfährten aus dem Perm. *Hallesches Jahrbuch für Geowissenschaften*, B 18: 23–88.
- Haubold, H., A. Hunt, S. Lucas, and M. Lockley. 1995. Wolfcampian (Early Permian) vertebrate tracks from Arizona and New Mexico. In Lucas, S. G. and Heckert, A. B. (eds.), *Early Permian Footprint facies*. *Bulletin New Mexico Museum of Natural History and Science* 6: 135–165.
- Hunt, A. P. and S. G. Lucas. 2005. Tetrapod ichnofacies and their utility in the Paleozoic; pp. 113–119 in: R. J. Buta, A. K. Rindsberg, and D. C. Kopaska-Merkel, (eds.), *Pennsylvanian Footprints in the Black Warrior Basin of Alabama*. *Alabama Paleontological Society Monograph* no. 1.
- Hitchcock, E. 1858. A report on the sandstone of the Connecticut Valley especially its fossil footmarks. *Natural Sciences in America*, Arno Press, New York, 220 pp.
- Jianjun, L. and Z. Shuonan. 1994. [New materials of bird ichnites from Fildes Peninsula, King George Island of Antarctica and their biogeographic significance]; pp. 239–245 in Sh. Yanbin (ed.), *Stratigraphy and Palaeontology of Fildes Peninsula, King George Island, Antarctica*. *Monograph* 3, Science Press. [Chinese 239–245, 249–250; English 246–248].
- Johnson, K. R. 1986. Paleocene bird and amphibian tracks from the Fort Union Formation, Bighorn Basin, Wyoming. *Contributions to Geology* 24:1–10.
- Kim, B. K. 1969. A study of several sole marks in the Haman Formation. *Journal of Geological Society of Korea* 5:243–258.
- Kim, J. Y., S. H. Kim, K. S. Kim and M. Lockley. 2006. The oldest record of webbed bird and pterosaur tracks from South Korea (Cretaceous Haman Formation, Changseon and Sinsu Islands): More evidence of high avian diversity in East Asia. *Cretaceous Research* 27:56–69.
- Kordos, L. 1985. Lábnymok az ipolytarnóci alsó-miocén korú homokköben. *Geologica Hungarica, serie Palaeontologica* 46:259–415.
- Lambrecht, K. 1938. *Urniformis abeli* n. sp., eine Pliozene Vogelfährte aus persien. *Paleobiologica* 6:242–245.
- Leonardi, G. 1987. Glossary and manual of tetrapod footprint palaeoichnology. *Departamento Nacional da Produção Mineral, Brasília, Brasil*, 115 pp.
- Leonardi, G. 1994. Annotated atlas of South America tetrapods footprints (Devonian to Holocene). *Companhia de Pesquisa de Recursos Minerais, Rio de Janeiro, Brasil*, 247 pp.
- Lee, Y.-N. 1997. Bird and dinosaur footprints in the Woodbine formation (Cenomanian), Texas. *Cretaceous Research* 18:819–864.
- Li, D., Y. Azuma, and Y. Arakawa. 2002. A new Mesozoic bird track site from Gansu province, China. *Memoir of the Fukui Prefectural Dinosaur Museum* 1:92–95.
- Lim, J.-D., Z. Zhou, L. D. Martin, K. S. Baek, and S. Y. Yang. 2000. The oldest known tracks of web-footed birds from the Lower Cretaceous of South Korea. *Naturwissenschaften* 87:256–259.
- Lockley, M. G., and A. P. Hunt. 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. Columbia University Press, New York, 338 pp.
- Lockley, M., Hunt, A., and Meyer, C. 1994. Vertebrate tracks and the ichnofacies concept: Implications for palaeoecology and palichnography; pp. 241–268, in S.K. Donovan (ed.), *The Paleobiology of trace fossils*, John Wiley and Sons, Chichester.
- 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 B* 336: 113–134.
- Lockley, M., M. Matsukawa, H. Ohira, J. Li, J. Wright, D. White, and P. Chen. 2006. Bird tracks from Liaoning Province, China: New insights into avian evolution during the Jurassic-Cretaceous transition. *Cretaceous Research* 27:33–43.
- Lucas, S. G. 2005. Tetrapod ichnofacies and ichnotaxonomy: Quo vadis? *Ichnos* 12:157–162.
- Mayr, G., B. Pohl, and S. Peters. 2005. A well-preserved *Archaeopteryx* specimen with theropod features. *Science* 310:1483–1489.
- McCrea, R. T., and W. A. S. Sarjeant. 2001. New ichnotaxa of bird and mammal footprints from the Lower Cretaceous (Albian) Gates Formation of Alberta; pp. 453–478 in D. H. Tanke, and K. Carpenter, (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington and Indianapolis.
- Mehl, M. G. 1931. Additions to the vertebrate record of the Dakota Sandstone. *American Journal of Science* 11:441–452.
- Melchor, R. N., and S. de Valais. 2006. A review of Triassic tetrapod track assemblages from Argentina: a reassessment. *Palaeontology* 49:355–379.
- Melchor, R. N., and J. F. Genise. 2004a. Invertebrate vs. vertebrate ichnology... or one ichnology? 1st International Congress on Ichnology, Trelew, Argentina. *Abstracts Volume*:55–56.
- Melchor, R. N., and J. F. Genise. 2004b. Critical appraisal of vertebrate ichnotaxonomy. 32nd International Geology Congress, Florence, Italy. *Abstracts Volume*, pt. 1:597.
- Melchor, R. N., E. Bedatou, and S. de Valais. 2004. Ichnology of ephemeral fluvial systems: example from the Late Triassic Santo Domingo Formation, Northwest Argentina. 1st International Congress on Ichnology, Trelew, Argentina. *Abstracts Volume*:56.
- Melchor, R. N., S. de Valais, and J. F. Genise. 2002. The oldest bird-like fossil footprints. *Nature* 417:936–938.
- 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 fluvio-lacustrine system: implications for the Scoyenia ichnofacies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 239:253–285.
- Olsen, P. E., and P. M. Galton. 1984. A review of the reptile and amphibian assemblage from the Stormberg of Southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontology African* 25:87–110.
- Padian, K., and L. M. Chiappe. 1998. The origin and early evolution of birds. *Biological Review* 73:1–42.
- Panin, N. 1965. Coexistence de traces de pas de vertébrés et de mécano-glyphes dans le Molasse Miocène des Carpatés orientales. *Revue Roumaine de Géologie, Géophysique et Géographie. Série de Géologie* 9:141–163.
- Panin, N., and E. Avram. 1962. Noe urme de vertebrate in Miocenul Subcarpaților românești. *Studii și Cercetări de Geologie* 7:455–484.
- Payros, A., H. Astibia, A. Cearreta, X. Pereda-Suberbiola, X. Murelaga, and A. Badiola. 2000. The Upper Eocene South Pyrenean Coastal Deposits (Liedena Sandstone, Navarre): sedimentary facies, benthic foraminifera and avian ichnology. *Facies* 42:107–132.
- Peabody, F. E. 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. *California University, Bulletin Department of Geological Sciences* 27:295–468.
- Peabody, F. E. 1955. Taxonomy and the footprints of tetrapods. *Journal of Paleontology* 29:915–924.
- Rainforth, E. C. 2005. Ichnotaxonomy of the fossil footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts). Ph.D. dissertation, Columbia University, Department of earth and Environmental Sciences, Manhattan, New York, 1302 pp.
- Remeika, P. 1999. Identification, stratigraphy, and age of Neogene vertebrate footprints from the Vallecito-Fish Creek Basin, Anza-Borrego Desert State Park, California. *San Bernardino County Museum Association Quarterly* 46:37–45.
- Sarjeant, W. A. S. 1989. 'Ten paleoichnological commandments': A standardized procedure for the description of fossil vertebrate footprints; pp. 369–370, in D. D. Gillette and M. G. Lockley (eds.), *Dinosaur tracks and traces*, Cambridge University Press, Cambridge.
- 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, 86 pp.
- Sarjeant, W. A. S., and R. E. Reynolds. 2001. Bird footprint from the Miocene of California In: R. E. Reynolds (ed.), *The changing face of the East Mojave Desert: Abstracts from the 2001 Desert Symposium, Californis*, April 2001:21–40.
- 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* 57:285–331.
- Swennen, C., and G. van der Baan. 1959. Tracking birds on tidal flats and beaches. *British Birds* 12:15–18.
- Thulborn, R. A. 1990. *Dinosaur Tracks*. Chapman & Hall, London, 410 pp.
- Thulborn, R. A. 1998. Australia's earliest theropods: footprint evidence

- in the Ipswich Coal measures (Upper Triassic) of Queensland. *Gaia* 15:301–311.
- Uchman, A. 1995. Taxonomy and paleoecology of flysch trace fossils: The Marmoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria* 15:1–115.
- Vialov, O. S. 1965. Stratigrafiya neogenovix molass Predcarpatskogo progiba: Naukova Dumka (Kiev), Part K, 191 pp.
- Vialov, O. S. 1966. Sledy zhiznedeiatelnosti organizmow i ikh paleontogicheskoe znachenie. Kiev: Naukova Dumka. Academy of Sciences, Ukrainian, 219 pp.
- Vialov, O. S. 1989. Pliocene bird tracks from Iran assigned to the genus *Urmiornis*. *Palaeontological Journal* 23:119–121.
- Vizán, H. S. Geuna, R. N. Melchor, E. S. Bellosi, and J. F. Genise. 2005. Preliminary paleomagnetic data from the Santo Domingo Formation (La Rioja, NW Argentina): Geochronologic and tectonic implications. 16th Congreso Geológico Argentino, Abstracts Volume: 223–226.
- Welles, S. P. 1971. Dinosaur footprints from the Kayenta Formation of Northern Arizona. *Plateau* 44:27–38.
- Wright, J. L. 2004. Bird-like features of dinosaurs footprints; pp. 176–184 in P. J. Currie, E. B. Koppelhus, M. A. Shugar, and J. L. Wright (eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds (Life of the Past)*. Indiana University Press.

Submitted August 4, 2006; accepted June 6, 2007.