

Application of neoichnological studies to behavioural and taphonomic interpretation of fossil bird-like tracks from lacustrine settings: The Late Triassic–Early Jurassic? Santo Domingo Formation, Argentina

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ABSTRACT

The purpose of this study is to apply neoichnological observations to the behavioural and taphonomic interpretation of a Late Triassic–Early Jurassic track surface from the Santo Domingo Formation (Argentina) containing hundreds of bird-like tracks and trackways. In addition, the factors affecting the formation and preservation of bird tracks in lacustrine settings are particularly addressed. The 5.5 m² fossil track surface contains different types of trace fossils: the avian ichnotaxa *Gruipedina dominguensis* (the most abundant), bird-like tracks with elongated hallux impressions, small epichnial rounded pits, and invertebrate traces (*Skolithos*, *Taenidium*). The modern environmental analogue chosen for the neoichnological studies was a coastal freshwater pond (the Bajo de los Huesos, Chubut, Argentina) seasonally occupied by sandpipers (*Calidris bairdii* and *Calidris fuscicollis*; Charadriiformes). The comparison between the fossil succession and the modern example suggests that they share lithology and sedimentary structures and that sedimentary processes and local palaeoenvironment were fairly similar and do not bias ichnological comparisons. Field observations allowed to distinguish twenty one behaviours that produced distinct traces and four modern footprint types (1 to 4) related to specific substrate conditions. In particular, the preferential formation of bird tracks parallel to the waterline, also confirmed by studies on droppings and invertebrate fauna of the pond, and other associated sedimentary features (ripple marks, wrinkle marks, mud drape thickness) and trace fossils were important for recognition of the shoreline in the fossil example. These observations also allowed us to distinguish the adjacent deeper and shallower parts of the fossil pond and can be applicable to other similar case studies. Contrasting sediment properties and footprint types, some relationships and constraints on the formation and preservation of modern footprints are proposed; although these are very complex processes that will require further studies. Five of the behaviours recognised in the modern pond were inferred from the sixteen trackways distinguished on the fossil track surface, including walking, walking with a zig-zag path, short runs, probing, and landing with legs directed forward (possible trace of flight). The recognition of traces of flight (*Volichnia*), probing marks, and tracks showing morphology similar to modern shorebirds (*G. dominguensis*), strongly suggest an avian affinity for the producers of the fossil tracks and, in consequence, the Santo Domingo track site would be younger than supposed.

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1. Introduction

Avian-like footprints pre-dating the oldest evidence of birds were recorded recently in the Late Triassic–Early Jurassic Santo Domingo Formation of Argentina (Melchor et al., 2002) and formerly in Late Triassic–Early Jurassic rocks of South Africa (Ellenberger, 1972). The

producers of these trace fossils remain unknown but, in any case, they show theropodian affinities suggested by bipedal trackways composed of tetradactyl footprints. The Santo Domingo track site contains one original track surface several square meters wide that reveals a footprint morphology and density very similar to those produced by modern birds feeding along ponds, which may be the result of either true avian behaviour or convergence. Hence, the general objective of this contribution is to analyze the palaeobiology of the theropodian producers of the Santo Domingo track site as reflected by their tracks and trackways, and particularly, of those reflecting possible avian

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behaviours. Among the track-producing behaviours, those ascribed to Volichnia or traces of flight (Müller, 1962) are the most critical ones, considering that their presence in the fossil track assemblage would demonstrate that the producers would have flight capacity, and consequently, bird affinities. On the contrary, its absence might indicate that the trace makers would have been theropods to some extent convergent with birds. Such convergence in behaviour and foot anatomy, probably reflecting an adaptation to walking in soft substrates (e.g. Barruel, 1973; Bang and Dahlström, 1975), would have been favoured by the exploitation of ephemeral ponds as food resource rich in invertebrate prey during the Late Triassic–Early Jurassic.

Traces of biological activity result from the interaction of particular behaviours, substrates, and other physical properties of the environment (e.g., salinity, oxygenation, temperature, current intensity and types, water turbidity). Neoichnological studies allow understanding of how the resulting traces originated by particular combinations of those components. Once this two-way relationship is established, trace fossils similar to modern ones can be utilized to extract behavioural, substrate, and palaeoenvironmental data. However, studies on the preservational and behavioural meaning of vertebrate tracks are scarce, although initiated in the beginnings of vertebrate ichnology by Reverend William Buckland (Sarjeant, 1974). Some studies focused on the process of fossil track formation and preservation, and identification of the producer, mainly through experimental devices and frequently using modern analogues (e.g., Padian and Olsen, 1984; Farlow, 1989; Gatesy et al., 1999; Manning, 2004 [and references therein]; Milàn, 2006; Milàn and Bromley, 2006). Other investigations employed detailed observations of track formation, track survivorship, areal distribution and sediment properties in saline lacustrine settings to evaluate the palaeobiological (including behavioural) information that can be extracted from fossil tracks and trackways (Cohen et al., 1991, 1993; Scott et al., 2007). A few studies applied modern observations to understand substrate and palaeoenvironmental signatures in a definite fossil example (Laporte and Behrensmeyer, 1980; Gatesy et al., 1999; Ashley and Liutkus, 2002).

In this study, several distinctive modern shorebird behaviours are distinguished using field observations and applied to the ethologic and taphonomic interpretation of the fossil track surface of the Santo Domingo Formation. Studies were carried out at Bajo de los Huesos locality (Chubut, Argentina), on modern analogues (i.e. Coombs,

1990): shorebirds, whose footprints and trackways are similar to the fossil tracks, and which inhabit ephemeral ponds also similar to that inferred for the Santo Domingo Formation (Melchor et al., 2002). The objectives of this work are: (1) To compare the Santo Domingo track site with a modern ephemeral pond visited by shorebirds (a) to refine the palaeoenvironmental interpretation of the former and (b) to analyse environmental and substrate influence on footprint type, formation, and preservation in order to distinguish between behavioural and non-behavioural characters of modern and fossil avian-like footprints and trackways, (2) To interpret the behaviour of trace makers of the Santo Domingo track site according to neoichnological observations on shorebirds, and (3) To document possible avian behaviours in the Santo Domingo track site, analysing their palaeobiological and evolutionary significance.

2. Materials and methods

The studied fossil track site is located in the Quebrada (gulch) de Santo Domingo situated in the Reserva Provincial Laguna Brava, in the precordillera of La Rioja Province, Argentina. The track surface belongs to the Santo Domingo Formation, which is considered of Late Triassic–Early Jurassic age. This age is based on characteristic fossil wood remains (Caminos et al., 1995), on a $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric age from interbedded basalt flows (Coughlin, 2001), and palaeomagnetic studies (Vizán et al., 2005). The formation reaches a minimum thickness of c. 1950 m and is in fault contact with Carboniferous igneous and sedimentary rocks (Caminos and Fauqué, 2001). The Santo Domingo Formation is a red bed succession that displays, from base to top, a transition from alluvial fan, fluvial braided (with calcretes), ephemeral fluvial and shallow lakes, and eolian environments (Vizán et al., 2005). The described track surface with bird-like footprints was recorded from a succession from the upper part of the Santo Domingo Formation, which had been interpreted as an ephemeral fluvial system. The main track surface is located at 1650 m from the base of the section, a second trampled surface with similar tracks has been recorded, although not studied to date.

The horizontal position and thin bedding of the hosting sedimentary succession facilitated the quarrying and complete removal of the slabs containing the main track surface. The whole track surface was composed of individual, fractured, slabs, which were labelled and

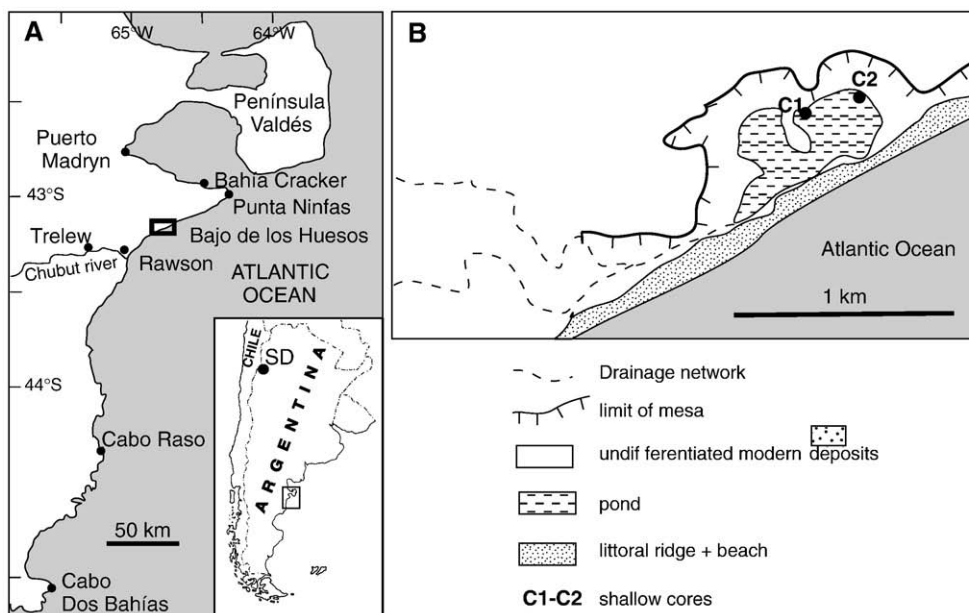


Fig. 1. Location map of the modern pond (Bajo de los Huesos) and fossil locality (SD, Santo Domingo). (A) Detail of the localities visited during the course of this study and mentioned in the text. The rectangle corresponds to (B). (B) Geomorphologic sketch of the Bajo de los Huesos area, indicating the position of shallow cores (C1–C2).

photographed in the field. The slabs containing the track surface were re-assembled in the laboratory for photographic documentation, moulding in plastic and casting. Fossil tracks and trackways were studied using the original rock slabs, the complete plastic cast of the track surface, and close up pictures of both, originals and casts. In order to identify a trackway, a minimum of three consecutive and alternate footprints were recognised. The different types of traces comparable with the modern ones were marked using chalk of different colour in the cast. The original track surface is housed at the Agencia de Cultura de La Rioja, Colección de Icnología, La Rioja, Argentina (LAR-IC 5) and a complete plastic cast is kept at the Museo Paleontológico 'Egidio Feruglio', Colección de Icnología, Chubut, Argentina (MPEF-IC 227).

The study on modern shorebirds and their traces started with a preliminary selection of possible study areas among ephemeral ponds that could show comparable tracks and located near our research centre at Trelew City, Chubut, Argentina, to facilitate protracted observations. The selected area is included in a xeromorphic shrubland region with sparse and low vegetation, and about 200 mm of annual precipitation. Such general semi-arid setting is also inferred for the studied Triassic succession (Melchor et al., 2002, 2006) reducing the possible influence of contrasting environmental settings in further comparisons. The selection of shorebirds as modern analogues was made, after preliminary field work and bibliographic research, based on the similarity of size, shape, and density of the selected modern tracks with the fossil example. Different localities (Península Valdés, Puerto Madryn, Bahía Cracker, Punta Ninfas, Bajo de los Huesos, Laguna Negra at Rawson city, Cabo Raso and Cabo dos Bahías; Fig. 1A) and bird species (*Actitis macularia*, *Calidris bairdii*, *Calidris fuscicollis*, *Charadrius falklandicus*, *Himantopus melanurus*, *Tringa flavipes*, and *Vanellus chilensis*) were observed preliminarily while searching for modern analogues. The selected modern environment and trace maker

analogues were a temporary pond located at Bajo de los Huesos (43°09'14" S; 64°46'13" W) about 45 km northeast of Trelew city (Chubut province, Argentina) and the shorebirds *C. bairdii* and *C. fuscicollis* (Charadriiformes). These migratory shorebirds visited the pond for a few weeks (about 6–8 weeks, depending on the year considered) during the spring season and their tracks were the most similar in shape, size and density to the fossil ones. Both species of *Calidris* are difficult to distinguish in the field particularly when large, mixed flocks are present. For this reason, therefore behavioural and ichnological observations correspond equally to both species. These species undertake great annual migrations, travelling from the northern hemisphere breeding areas to the southern hemisphere. Each migration involves the respective spring and summer seasons. Despite the large number of bird species observed at the Bajo de los Huesos, interactions with species of *Calidris* were very few and scarce footprints of birds other than *Calidris* species and *C. falklandicus* were observed. Bajo de los Huesos is part of a chain of small depressions located at the seaside that are seasonally filled with water. The depressions are separated from a steep gradient beach by a littoral gravely ridge about 5 m high and 80 m wide (Fig. 2A). This littoral ridge acts as a dam for rainwater draining a small continental area, thus filling the depression. The landward boundary is composed by low mesas (Fig. 1B). In addition, sea water can flood these depressions during exceptionally high tides or storms. The annual precipitation in the region is distributed throughout the year (average of 11 mm to 28 mm per month), with a slight increase during the end of the autumn and winter (May to August). These months also coincides with the maximum average relative humidity (62 to 69%) (Servicio Meteorológico Nacional, Argentina; for Trelew city, 1981–1990 period). During the coldest months (June to August) the hydrological balance is positive, because of the low temperatures (average temperature ranging from 6 to 8 °C during June to August, 2003)

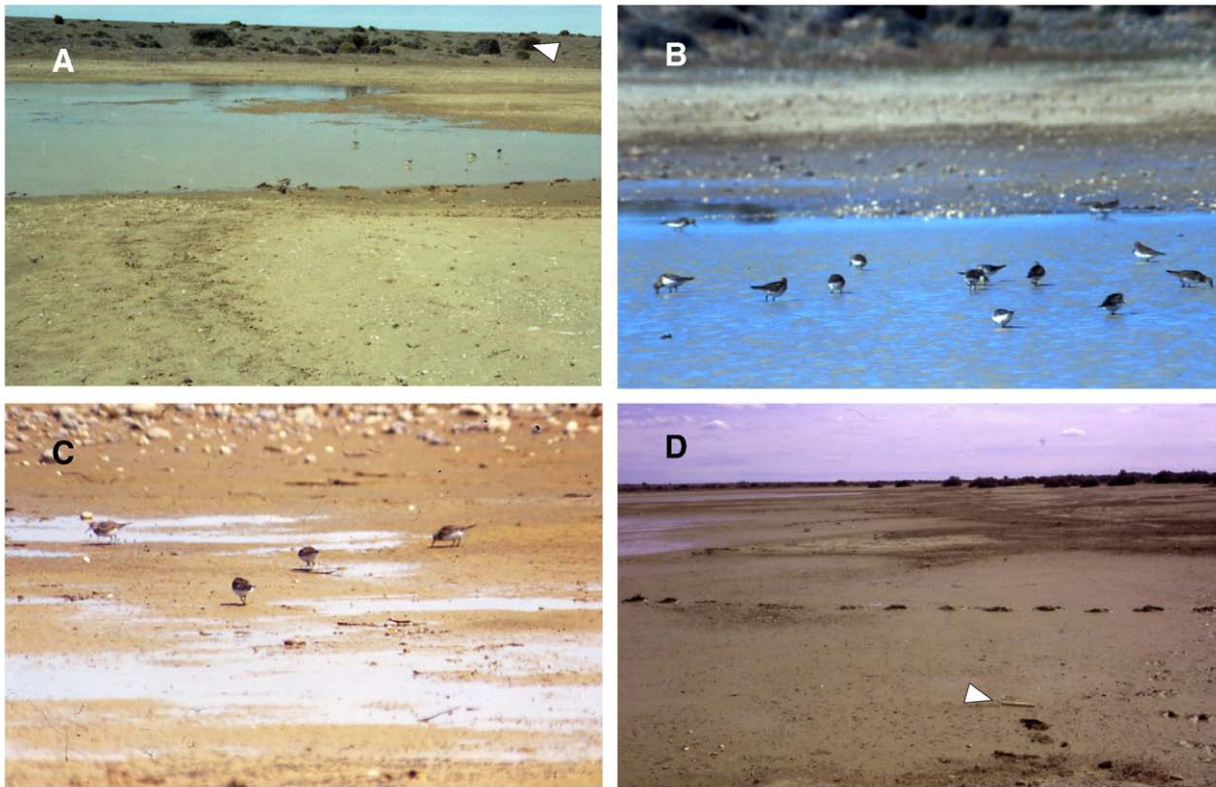


Fig. 2. The Bajo de los Huesos pond. (A) A few *Calidris bairdii* individuals foraging in water (October 10, 2003). The background is the gravelly littoral ridge (arrow). (B) A small flock of *C. bairdii* in shallow water. (C) Four *C. bairdii* feeding in wet exposed playas, although always close to the water. (D) Extensive wet playas during the last days of 2003 season (October 29). The birds are about 0.15 m tall. The ruler in foreground in (D) is 0.2 m long (arrowed).

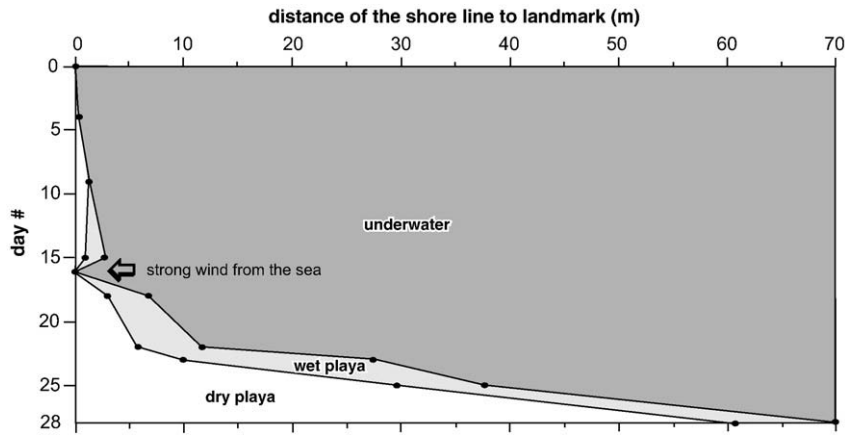


Fig. 3. Change in shoreline position related to a landmark during part of the 2003 season (October–November). Note exponential growth of area covered by exposed playa surfaces and the flooding of playas by strong wind on day # 16.

and low rate of evaporation. The depression commonly contains freshwater from August to November.

Bird behaviour was observed and described *in situ* and recorded in video for further analysis and to construct the drawings to illustrate different patterns. Photographs and videos were taken of footprints related to definite observed behaviours. Series of daily photographs documented the weathering of footprints. Samples of surface sediment were taken from spots on which the shorebirds were seen walking and producing footprints of different morphology or otherwise where footprints were not imprinted. The maximum depth of sampled material was approximately 25 mm. This depth was selected considering that the elastic deformation of an unconsolidated sediment is negligible below the depth of about one indenter (foot) diameter (Allen, 1997) and that foot size of the *Calidris* species ranges between 20 and 30 mm. These samples were studied in the laboratory to determine the water content using standard procedures for sediment grain size analyses (McManus, 1988). Organic matter content of selected samples was obtained by the Walkley–Black method (Jackson, 1964). Grain size analyses of selected sediment samples were conducted using a Mastersizer 2000® particle size analyzer (Malvern Instruments) at the University of La Pampa, Argentina. Previous to grain size analysis the samples were attacked with acetic acid (6%) and hydrogen peroxide (100 vol); dispersed with sodium hexametaphosphate (1%) and ultrasonic bath (30 s). Short cores (<0.40 m) were obtained using 50 mm in diameter PVC pipes at two selected locations, in order to document the types of sediments and to reconstruct the environmental history of the pond. Preliminary identification of the algae present in sediments was also conducted in a selected sample.

Diet composition was determined by faecal analysis. Droppings were collected and kept individually at -20°C . Each dropping was analyzed under a zoom binocular microscope (5–20× magnification) and the key components of food remains were identified as, for example, fragments of crustaceans or insects. In this way, the proportional occurrence of each prey species in the droppings was estimated. Aquatic invertebrates were collected using a D-frame entomological net. Additional riparian insects were collected with an aerial entomological net and also by washing the substrate in white pans with water. Specimens were stored in 75% alcohol, and carried to the laboratory for identification.

3. Results

3.1. The Bajo de los Huesos pond

These studies were conducted exclusively during the freshwater phase of the Bajo de los Huesos pond in the spring of 2002 and 2003, when the migratory shorebirds stayed at the pond (Fig. 2A–D). During

some days in March 2003 the depression was filled with sea water, but no birds or trackways were observed. The Bajo de los Huesos depression was completely dry from early November 2002 to late March 2003, at which time an exceptional high tide filled it partly for some days with sea water. On September 2003, the fresh water

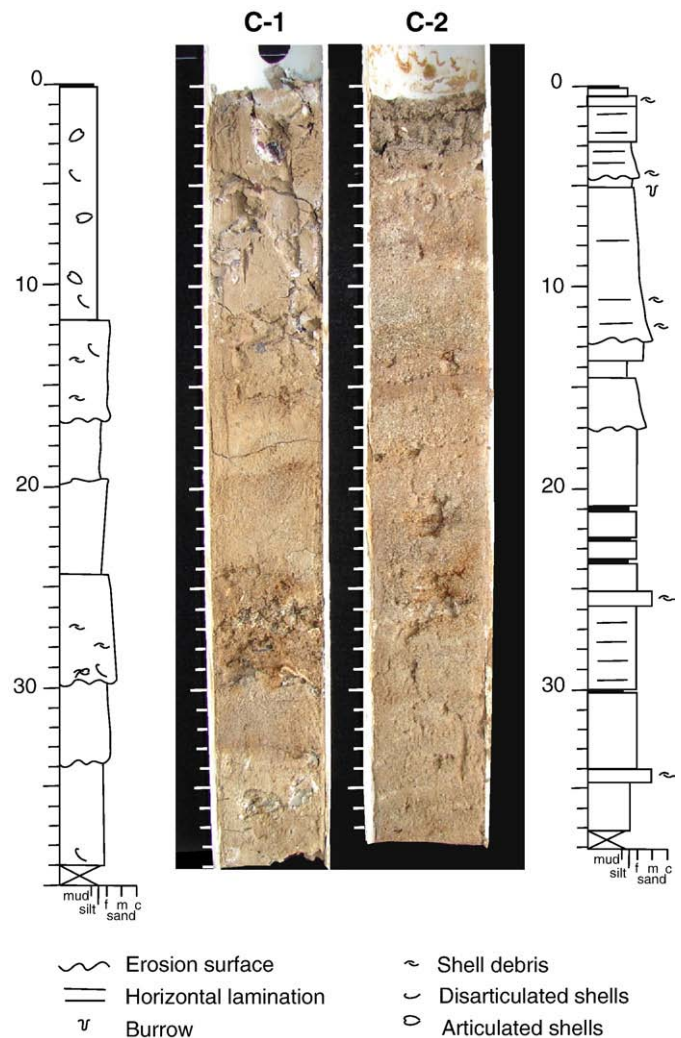


Fig. 4. Sedimentologic logs and photography of shallow cores taken at the Bajo de los Huesos pond (location in Fig. 1B).

occupied an area approximately 100 m wide and 600 m long parallel to the coast, whereas the maximum depth was about 0.50 m. The whole depression is about 1000 m long and 500 wide and is surrounded and partially divided by fine-grained sand of aeolian origin (Fig. 1B). The extension of the playas around the water body, where the footprints are imprinted, increased exponentially from October to November. However, changes in the direction and speed of wind could introduce significant variations in the exposed/submerged condition of different sectors of the playa. Completely dry, meter-scale zones of the playa showing desiccation cracks and footprints could be covered with water in few minutes because of a strong wind blowing from the sea. During the day, the exact outline of the water body might change several times because of the changing wind direction. In addition, some of the pond water flowing over old desiccation cracks was lost by infiltration.

With a constant rate of water loss by evaporation the growth of playas was exponential throughout the season. On October 6, 2003, a landmark was put in place on the pond shoreline opposite to the littoral ridge to check its displacement during the next 28 days. Fig. 3 displays the variation in the position of the shoreline and the progressive increase in the area covered by dry playa sediments. On day # 16 a strong wind pushed the water back up to the original

landmark, flooding an area that previously was subaerially exposed. During the last days of observation, the rate of change of the position of shoreline and the width of the wet playa increased markedly (Fig. 2D).

The surface of the playa at Bajo de los Huesos is commonly covered by a mud drape. The sediments of the depression are mostly sand and mud with contrasting features in the two obtained cores (Fig. 4), which were separated about 500 m (Fig. 1B). Core C-1 is characterized by a dominance of massive silts with shell debris and articulated shells of marine bivalves and subordinate fine-grained massive sands with highly fragmented shell debris. Core C-2 contains coarser-grained sediments and shows a dominance of fine- to medium-grained sands, commonly with horizontal lamination, and sparse fragmented shell debris (associated to the coarser sediments). Many sand beds in core C-2 display a basal erosive surface, shell debris, a fining-upward tendency and (in one case) invertebrate burrows in the top. Mud partings are common between sand beds.

3.2. Type, formation, and preservation of footprints

3.2.1. Type of footprints

Four types of footprints from *Calidris* species were recognized, according to their aspect shortly after production (Fig. 5). The first type

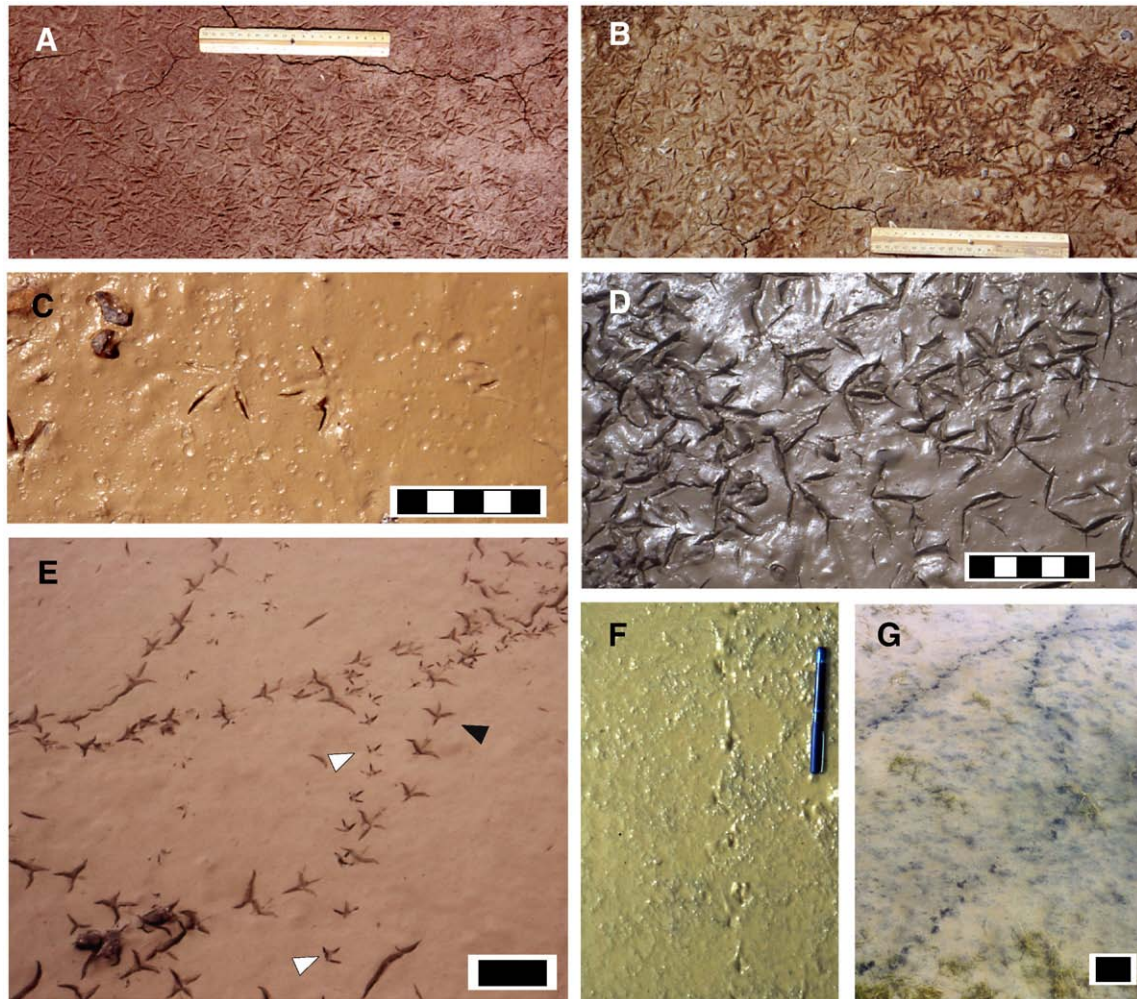


Fig. 5. Four morphological footprint types distinguished in this study. (A), (B) Type 1 footprints (thin impressions, high overprinting). Note colour enhancement in (B). (C) Type 2 footprint showing thin digits and pad impressions. Note also rain drop imprints. (D), (E). Type 3 footprints. Note widening of digit impressions and incipient growth of shrinkage cracks in (D). Most of the tracks in (E) are psi-shaped footprints resulting from widening of digit impressions and crack growth (black arrow). The white arrows indicate a trackway formed later with footprints that did not experienced marked desiccation. (F), (G) Type 4 footprints conforming trackways inferred by the alternate arrangement of marks. (F) Displays roughly rhomboidal marks and (G) shows irregular dark marks produced by disruption of underlying organic mud. All figures are from Bajo de los Huesos, except (F), which was taken at Cabo Raso. Ruler is 20 cm long, scale is 5 cm long and pen is 14 cm long.

of footprints is characterized by thin and poorly defined digit impressions. These footprints are produced underwater and are the rule in densely trampled areas produced by large flocks (Fig. 5A). A preservational variant of this type is due to contrast enhancement by changes in colour of sediments after subaerial exposure, probably due to greater loss of water of the sediment outside of the footprints (Fig. 5B). The second type is characterized also by thin digit impressions, but in this case their outlines are very well-defined and can have pad impressions (Fig. 5C). Probably these footprints are the best-suited for studying anatomical features of producers. They appear in sites with few trackways or in track patches with low density produced in wet, subaerially exposed sediments and can survive flooding induced by wind stress under a film of water. The third type occurs when type 2 footprints are exposed subaerially for some time. The shrinking of moist sediments during desiccation first produces an enhancement of the footprint visibility and enlargement of size, whose digits appear wider, best defined, and deeper impressed (Fig. 5D). These footprints, even when very useful to infer behaviour and when they look as the best preserved ones, do not reliably reflect the anatomy of the producer. This type corresponds to incipient psi-shaped cracks (Fig. 5E), which act as nucleation sites for desiccation cracks (e.g. Master, 1991; Martin, 2005). When the process of desiccation continues the footprints become increasingly distorted by crack growth and finally are difficult to recognize. The fourth type is composed by tracks produced under water in a very soupy substrate (ghost or blurred footprints), in which the digit impressions cannot be distinguished. These footprints result in indistinct marks arranged with an alternate pattern typical of trackways (Fig. 5F). At Cabo Raso, trackways of *Actitis macularia* looked like dark coloured marks arranged with an alternate pattern, because of the removal and exposure of an underlying layer of a dark, organic-rich mud (Fig. 5G).

3.2.2. Formation of footprints

The four types of footprints record those cases in which the contact of the feet with the sediment produced a recognizable mark. However, in many cases, walking shorebirds left no trace at all, even when they walked very close to others that left traces and even when, to the naked eye, sediments looked moist and plastic enough to produce traces. Without further analyses it was not possible to distinguish differences between sediments that produced and failed to form footprints. Slightly elevated and depressed patches in the plays showed different potential for producing footprints. Field observations on texture, moisture, subaerial or subaqueous nature of footprints, and presence of algal mats were recorded in order to explain differences in the production of footprints. When the desiccation of the pond progressed, dense track sites showing poorly defined tracks formed previously underwater were replaced by sites with single or few well-formed trackways.

A sampling of productive and non-productive sediments, for further analysis in laboratory, showed some differences for the parameters measured (Table 1). The grain size of sediments is fairly uniform, irrespective of the footprint type and, in most cases, of the formation or absence of footprints. The analysed samples can be classified as silty sands and sandy silts (Shepard, 1954). The samples for type 1 footprints (samples 13, 14, 15) display a relatively narrow range of moisture content (18–22%) and organic matter content (0.2–0.5%); a single analysed sample is classified as a silty sand (Table 1). Type 2 footprints (samples 1, 8, 16, 17, 18) reflect more variable water saturation (19–50%) and organic matter content (0.25–1.0%), including silty sands and sandy silts (Table 1). The sample with lowest water content (sample 18) also shows the lowest organic matter content, and those with higher water content (samples 1 and 8) also show the greater organic matter content. A sample where type 4 footprints were produced (sample 7) has a higher water saturation (85%) and organic matter content (1.8%). The substrate where type 3 footprints were seen was not sampled because it represents a mud with lower

Table 1

Summary of water saturation, organic matter content, median grain size and classification for selected sediment samples from the Bajo de los Huesos pond. Samples are organised after footprint types defined in this study

Sample #	Description/comments	Water saturation (%)	Organic matter (%)	Median grain size (µm)	Classification (1)
<i>Type 1 footprints</i>					
13	Subaqueous footprints (film of water)	21.6	0.48	nd	
14	Subaqueous footprints (film of water)	21.8	0.22	79.3	Silty sand
15	Subaqueous footprints (film of water)	18.5	0.29	nd	
<i>Type 2 footprints</i>					
1	Subaqueous footprints	49.6	1.01	29.2	Sandy silt
8	Subaerial footprints	34.2	0.89	78.7	Silty sand
16	Subaerial footprints	24.4	nd	nd	
17	Subaerial footprints	25.5	nd	nd	
18	Subaerial footprints	19.3	0.25	25.3	Sandy silt
<i>Type 4 footprints</i>					
7	Subaerial footprints in soupy substrate (*)	84.9	1.81	nd	
<i>Substrate where footprints are not produced</i>					
2	Subaerial mud (under water two days ago)	44.2	nd	nd	
3	Flooded desiccated mud	27.8	nd	93.1	Silty sand
4	Sandy substrate	9.3	0.32	nd	(fine-grained) sand
<i>Other cases</i>					
5	Poorly defined (collapsed) underwater footprints in soupy mud	47.8	1.4	24.8	Sandy silt
6	Well-defined subaqueous footprints – algal mat (*)	44.3	nd	nd	

(*) producer not seen; (1) after Shepard (1954); nd: no data.

water content than typical for formation of type 2 footprints. Footprints were not produced in a range of substrate conditions, including subaerially exposed mud with 44% of water (sample 2), flooded desiccated mud with 28% of water (sample 3) and a fine-grained sand with 9% water and 0.3% organic matter content (sample 4). The footprints associated with sample 5 are morphologically akin to those of type 4 (although the gross footprint outline is still recognizable) and the sediment also displays a high water (48%) and organic matter content (1.4%). The presence of algal mats was recognised in the field (sample 6), associated with well-defined footprints. However, other sediment samples also contain remains of cyanobacteria (*Anabaena* sp., *Calothrix* sp., *Microcoleus* sp., *Nostoc* sp., *Oscillatoria* sp., *Phormidium* sp.), diatoms (*Cymbella* sp., *Fragilaria* sp.) and freshwater chlorophycean algae (*Scenedesmus armatus*, *S. quadricauda*, *Schroederia setigera*) (S. Álvarez and G. Bazán, pers. comm., 2004).

3.2.3. Preservation of footprints

Immediately after their production, the footprints suffer different taphonomic processes. If not covered by a new layer of sediment, footprints were weathered by different agents, mainly desiccation, to become unrecognizable and finally disappear within 2 to 6 days. Different field observations in selected groups of footprints were carried out to follow the early taphonomic processes (Fig. 6). After 24 h, a sample of Type 2 footprints produced under a film of water (Fig. 6A) showed wet freshly exposed sediments and the footprints were still without any apparent morphologic changes (Fig. 6B). After 70 h the enhancement process by desiccation took place, and the footprints, still in wet sediment, appeared as better impressed, showing wider and deeper digit marks. Some of the digits showed cracks inside or arising

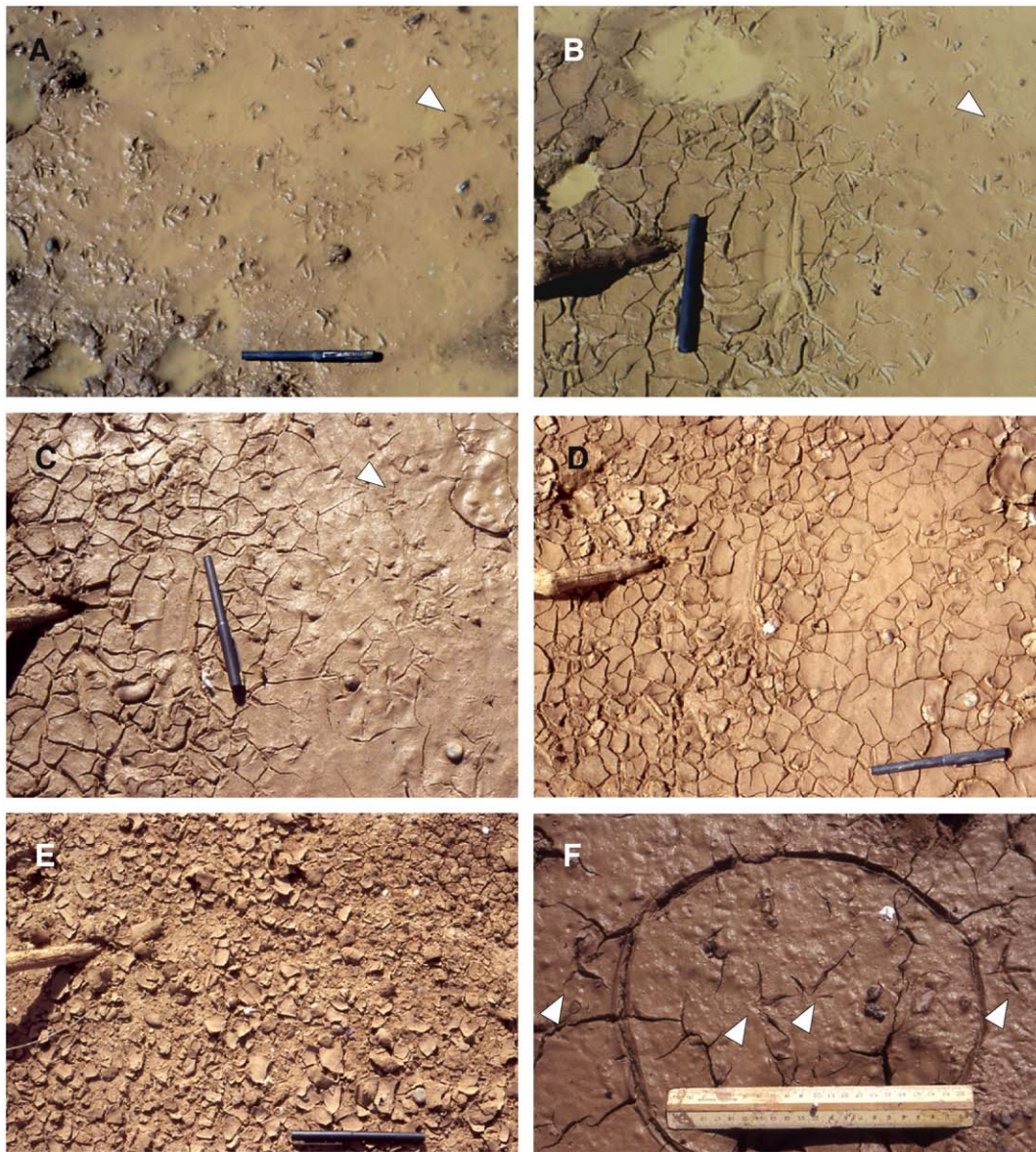


Fig. 6. The effect of desiccation on the preservation of modern footprints. (A)–(E) Sequence of photographs showing progressive desiccation of a playa surface with *Calidris* footprints. (A) Recently formed underwater footprints (the better defined footprints are arrowed). (B) Twenty four hours later. Note crack formation on the left and well-formed footprints on the right (arrows). (C) Seventy four hours after formation, the only recognizable footprints remain on the right side. (D) Seventy four hours after original impression. Intense crack propagation and mud curling. (E) Ninety four hours after formation. Complete destruction of the original playa surface due to curling of the surface mud drape and possible wind action. Arrows in B to C indicate the position of the same footprint. In addition, the stick on the left of figures B to E was kept in the same position. (F) Crack propagation in other footprints (arrows), 24 h after formation. Pen is 14 cm long. Ruler is 20 cm long.

from them, which would correspond to an advanced Type 3 footprint (Fig. 6C). About 74 h after their formation the desiccation process advanced quickly developing cracks that completely obscured the footprints (Fig. 6D). After 94 h of continued desiccation and crack growth, the muddy upper lamina of sediment curled and became separated in individual pieces. At this stage, all evidence of previous footprints was lost (Fig. 6E). The complete weathering process of this footprint took 4 days. In other cases, type 3 footprints (enhanced footprints) gave rise to a system of larger and deeper desiccation cracks, which can be preserved for a longer period as recorded in the literature for saline mudflats (Master, 1991). Other observed footprint samples, revealed different rates of weathering. A footprint produced in moist sediment (type 1) showed the first signals of widening and cracking in toes (type 3 footprint) only after 20 min, and 24 h later the footprint was still recognizable with long cracks arising from toes (Fig. 6F). Another type 1 footprint produced near the latter and under similar conditions showed widened toes and an incipient crack in the extreme of two toes

after 1 h, and a well developed system of cracks 2 h later. After 24 h the footprint was hardly recognizable within the crack system.

Other weathering agents are represented by rain and the successive subaerial and subaqueous exposure driven by evaporation and flooding of playas by wind action that could erase or modify footprints within minutes after their production. This effect was already reported by Laporte and Behrensmeyer (1980), Cohen et al. (1991, 1993) and Scott et al. (2007).

3.3. Behaviour of species of *Calidris*

3.3.1. General behaviour and feeding behaviour

In the Bajo de los Huesos, during the spring of 2002 and 2003, *Calidris bairdii* was the last bird observed inhabiting the pond at the end of the season, and in 2003, it was also one of the first birds to arrive (Fig. 2A–C). In other examined localities, single or few individuals of this migratory species were seen during the spring along the Chubut

seacoast. The number of individuals in the Bajo de los Huesos ranged from a maximum of three hundred on October 24, 2003, to one the last day of the season (November 3, 2003). On various other days were recorded from 40 to 86 individuals, whereas most days the number of individuals ranged from about 10 to 20. In large flocks, vocalization and interactions between individuals were frequent, whereas in the smaller ones, no vocalizations or interactions were recorded. Commonly the water level was below the ankle joint, or in some cases above it, but never touching the bird's body (Fig. 2B). Individuals in large flocks had no preferential direction of movement on calm days, whereas in windy ones, they walked commonly facing the wind. The nearby flight or vocalization of birds of prey produced the immobilization of the flocks of *Calidris* or their sudden flight.

Large flocks, mostly composed of *Calidris bairdii* and *Calidris fuscicollis*, were observed feeding in the shallowest parts of the pond, sometimes divided in two or three groups. Usually, small flocks of few individuals detached from a large one, and flew to the waterline to feed (Fig. 2B and C). This preference for feeding in the waterline was also confirmed with the data from analysis of bird droppings and invertebrate fauna from the pond (see below). Those feeding at the waterline, commonly walked parallel to it. The latter behaviour was also observed in *Calidris falklandicus*. In a particularly cold and windy day (October 9, 2003), only three individuals were recorded at the pond, whereas a flock of about 15 were feeding on ground in the nearby vegetated dunes. The overall decrease in water depth throughout the spring resulted in more extended playas (Fig. 2D);

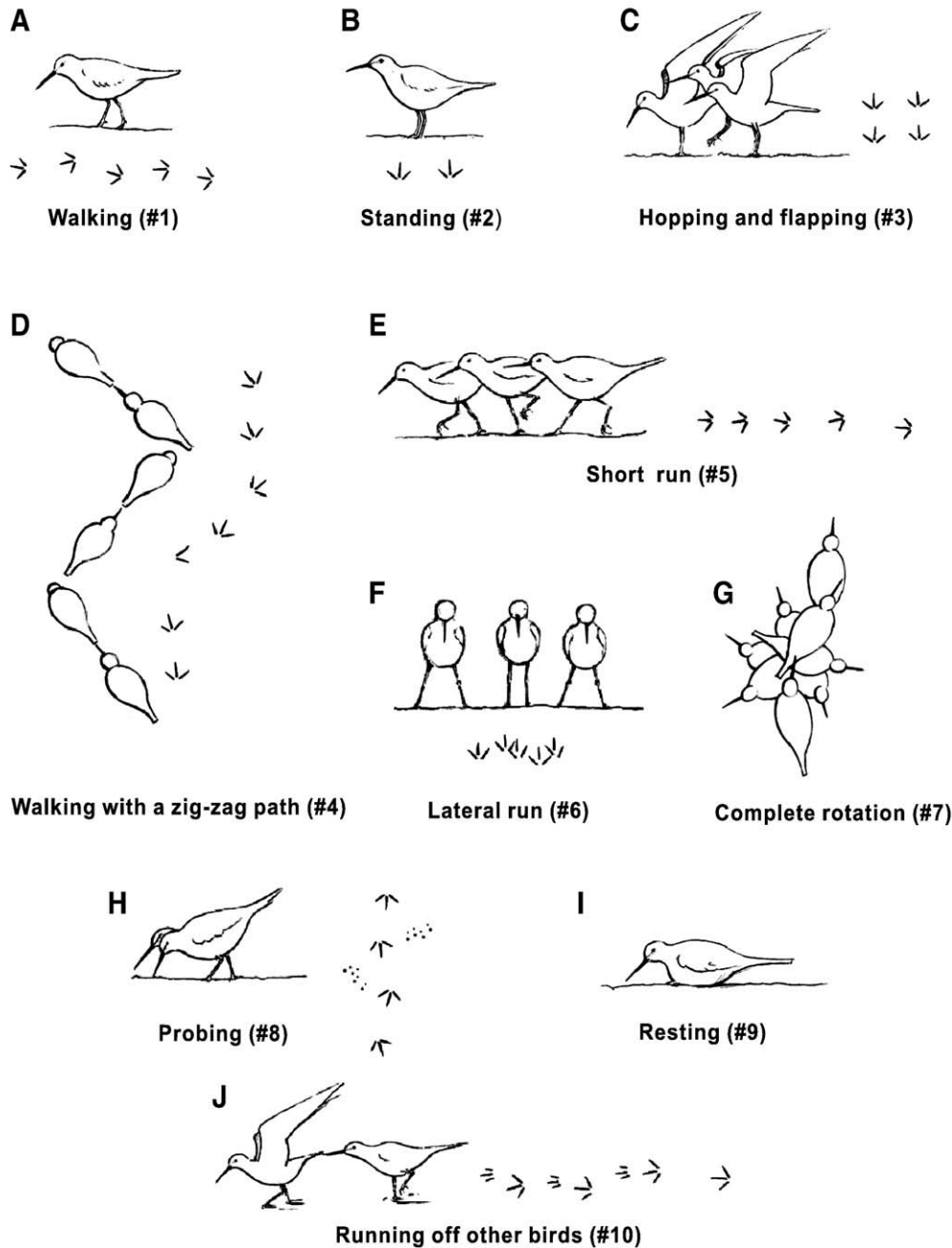


Fig. 7. Diagrams showing the 21 behaviours with ichnological meaning identified in *Calidris* and the resulting trackway. The traces produced by complete rotation and resting (G and I) were not observed. (A) Walking. (B) Standing. (C) Hopping and flapping. (D) Walking with a zig-zag path. (E) Short run. (F) Lateral run. (G) Complete rotation. (H) Probing. (I) Resting. (J) Running off at other birds. (K) Driving away by facing off. (L) Run and "U" turn. (M) High angle landing. (N) Landing with a run. (O) Lateral landing. (P) Landing with hopping. (Q) Landing with legs directed forward. (R) Simple take-off. (S) Take-off and flapping. (T) Run and flapping. (U) Take-off with hopping.

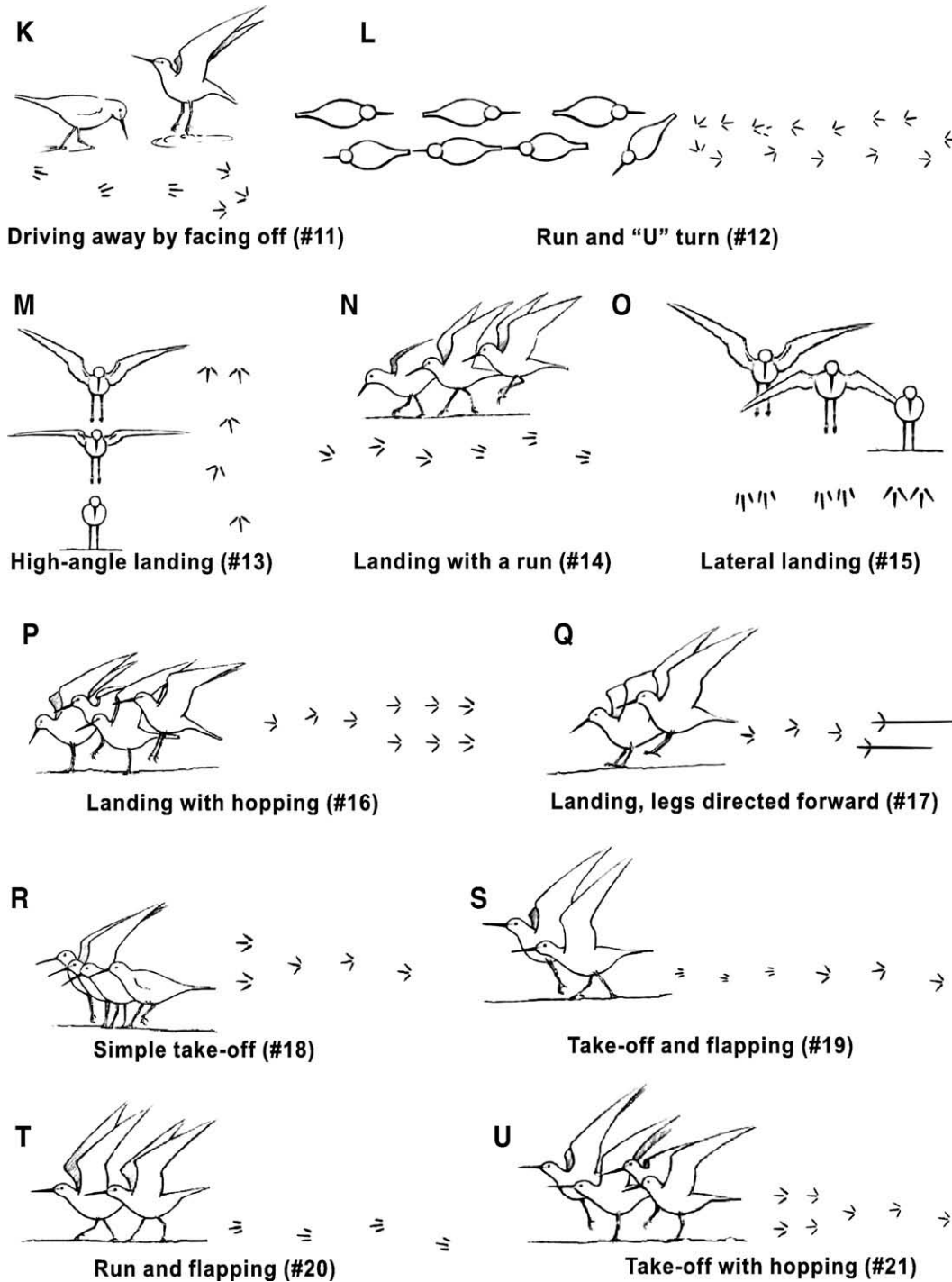


Fig. 7 (continued).

shorebirds spending more time feeding on exposed playas than in the water; and an abrupt decrease in number of shorebirds during the last days before complete desiccation of the pond. When water in the pond was scarce, during the last days of the season, small flocks were observed feeding on dry and wet sectors of the playa, searching for prey particularly along the desiccation cracks. The search for prey was mostly done visually, only in rare occasions some individuals were observed searching prey by tactile probing in moist sediment along the waterline.

The diet of species of *Calidris* was studied by means of the analysis of their droppings and by the study of the invertebrate fauna of the pond, because it was impossible to observe directly the small prey or

the bird's success in hunting them. The invertebrate fauna collected during October 2003 was composed of crustaceans and insects. The crustaceans were Anostraca (*Branchinecta* sp.), Notostraca (*Lepidurus* sp.), Cladocera (Anomopoda), Copepoda (Calanoida) and undetermined Ostracoda. The insects were Coleoptera such as *Tropisternus setiger* (Hydrophilidae), *Rhantus signatus*, *Lancetes angusticollis* and *Lancetes waterhousei* (Dytiscidae); Diptera, such as larvae of Tipulidae and Chironomidae, and adults of Ephydriidae and Bibionidae; and Collembola. The distribution of these taxa in relation to the waterline of the pond showed significant differences. The Notostraca, were found only in the deepest part of the pond, at about 100 m from the coast. The Anostraca, Cladocera, Copepoda and *L. waterhousei* were

found from the centre of the pond to the waterline, whereas the Ostracoda and the remaining Coleoptera were absent at the centre of the pond. The Diptera and Collembola were typical inhabitants of the waterline, inhabiting the playa up to 1.5 m of the waterline in all cases and up to 0.20 m under water in the case of Chironomidae larvae and Collembola. All the crustaceans lay eggs capable of resisting the dry phase of the pond, whereas the coleopterans may arrive at the pond

by dispersal flights, and are able to develop rather quickly in ephemeral ponds. The life cycle of Diptera for this pond is unknown. The collected material shows that some invertebrates inhabit the whole pond (Anostraca, some Cladocera, Copepoda and the Coleoptera *L. waterhousei*), others avoid the deepest part of it (Ostracoda and most Coleoptera), whereas others basically inhabit the waterline and up to 1.50 m from the shore (Diptera and Collembola).

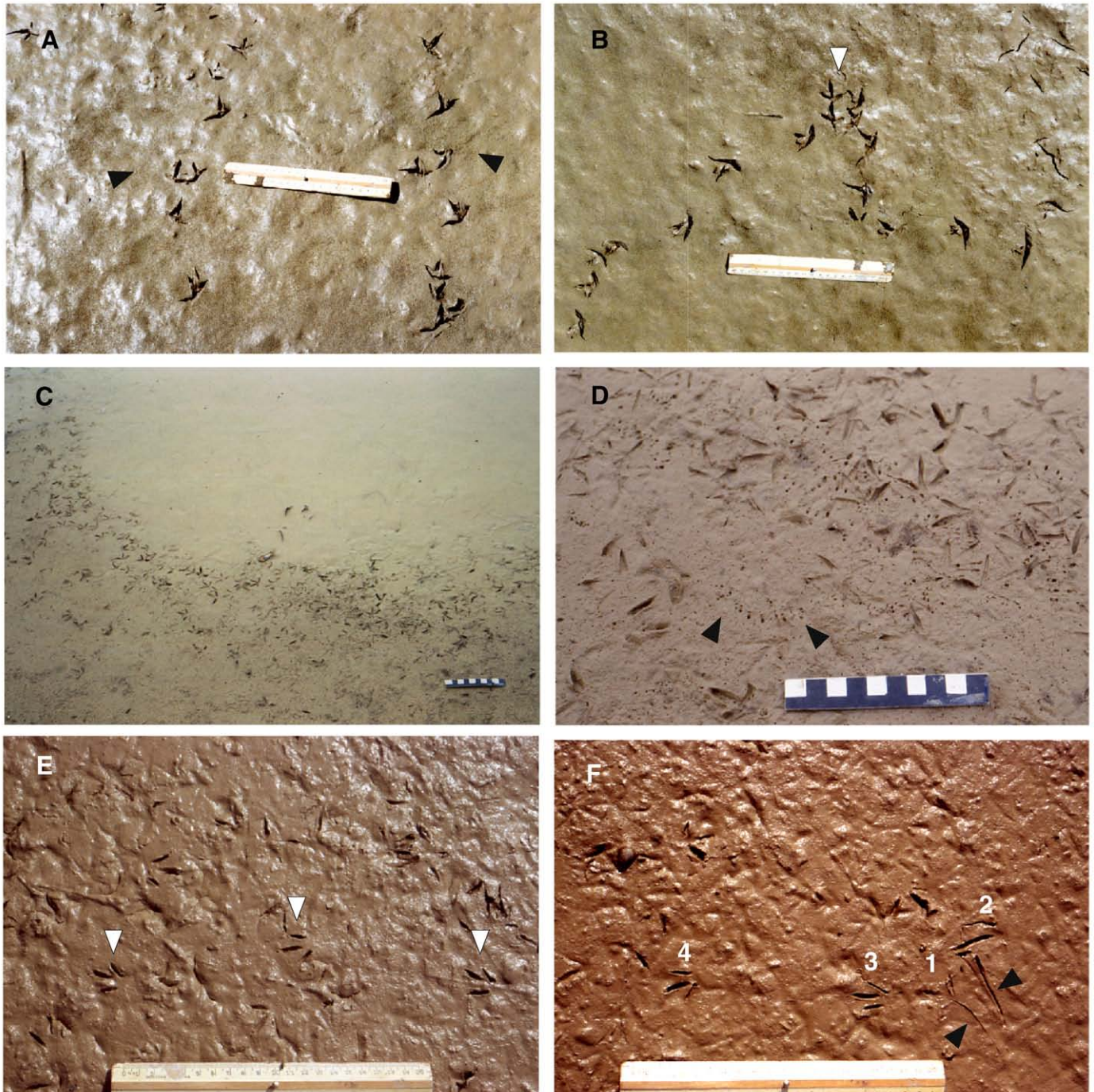


Fig. 8. Selected examples of *Calidris* behaviour that produced tracks. (A) Two nearly parallel walking trackways (# 1) with a couple or paired footprint resulting from a standing position indicated by arrows (# 2). (B) Walking trackway with a zig-zag pattern (# 4) with two pairs of footprints resulting from hopping. (C) Margin of the pond showing abundant walking trackways roughly parallel to the waterline. The centre and upper right of the image is covered by water. (D) Tracks and double probing marks (# 8), showing a dominant random pattern and also occasional arrangement in an arc (arrows). (E) Three consecutive footprints showing low divarication and lack of sole marks (arrowed). This trackway was produced by landing with a run (# 14). (F) Trace left by landing with legs directed forward (# 17). From right to left the two first components are slightly distorted tracks (1 and 2) associated with long hallux drag marks (arrows) followed by two consecutive footprints lacking sole mark (3 and 4). Ruler is 20 cm long, pen is 14 cm long, and scale divisions in (D) represent 1 cm.

The diet of *Calidris bairdii* and *Calidris fuscicollis* was analyzed by studying the contents of 30 droppings of individuals of these species. The most important item was *Daphnia* sp. (Cladocera), which was present in 93% of the droppings, each one containing 1 to 11 individuals. The second item were adults of Ephydriidae (Diptera), which appear in 33% of the droppings, each containing 1 to 4 individuals. Other dipterans, despite their abundance in the pond, were not recorded in faeces. The third item was probably a terrestrial coleopteran, which was not recorded during the field work. It was present in 17% of the droppings. The fourth and fifth items, an undetermined coleopteran and a copepod respectively, were only present in three droppings.

The most abundant remains found in the faeces were Cladocera and Ephydriidae, the latter only present near the waterline, showing that at least one third of the birds feed near the waterline at some time, and confirming the data obtained by direct observations.

3.3.2. Particular behaviours of *Calidris* producing traces

During fieldwork, 21 trace-producing behaviours with ichnological significance were identified. In most cases the traces were found after examination of the place in which the particular behaviour was displayed, in other cases, the traces were found without seeing the behaviour that produced them. In still other cases, mostly for behaviours observed in large flocks feeding in water, the resulting traces could be inferred, because of the low potential of forming and preserving traces under water, and the impossibility of identifying individual traces at dense track sites. In the following paragraphs, the observed behaviours and recorded and inferred tracks and trackways are described and illustrated (Figs. 7 and 8); distinguishing between common behaviours of individuals, behaviour in flocks, and behaviours associated with flight. Video records of part of the described behaviours are available as Supplementary online material (Appendix A). The observed *Calidris* tracks commonly range in length from 22 to 38 mm (allowing for the imprint of the hallux) and are slightly wider than long.

3.3.2.1. Usual behaviours independent of flock density.

- 1) Walking. This behaviour results in a straight or slightly curved trackway (Figs. 7A and 8A and C). The pace angulation commonly ranges from 160° to 180°, the stride length ranges from 120 to 280 mm, the tracks display a 0° to - 28° (inward) rotation with relation to the midline, and the average divarication between digits II–IV is 125°.
- 2) Standing. It results in paired footprints, commonly showing a small inward rotation (Figs. 7B and 8A).
- 3) Hopping aided by flapping. Occasionally, the birds hop with the two legs aided by flapping leaving a series of paired footprints (Figs. 7C and 8B).
- 4) Walking with a zig-zag path. While walking, the bird directs the body to one side and to the other alternatively looking for prey. It results in a trackway with more than two changes in direction (Fig. 7D).
- 5) Short run. In most cases the runs are short and finish in probing in the same direction of the run. In *Calidris falklandicus* it was common to observe successive, more or less long, runs parallel to the waterline finishing in probing with the body oriented toward the waterline. It results in a straight trackway showing a marked increase or decrease of stride length (depending upon the preserved trackway portion); up to 2.75 larger than the smaller stride length in a particular trackway (Fig. 7E).
- 6) Lateral run. Probably disturbed by strong wind, some individuals perform short lateral runs. It results in a lateral row of footprints (Fig. 7F).
- 7) Complete rotation. The bird turns 360° in a small circle, sometimes pecking. It would result in a trackway describing a small circle (Fig. 7G).
- 8) Probing. In most cases, the observed species peck in water after detecting prey visually. However, in a single day traces of probing were observed in moist sediments close to the waterline. Rows of holes are arranged in a line or an arc 50 to 60 mm long near the

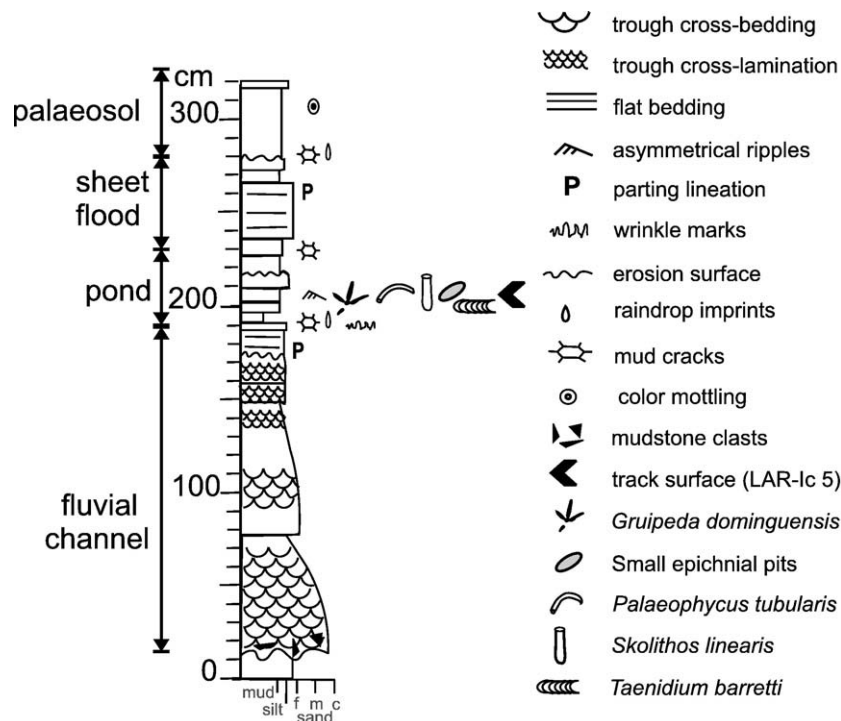


Fig. 9. Detailed sedimentary log of the succession of the Santo Domingo Formation containing the fossil track surface with abundant *Gruipeda dominguensis* tracks (LAR-Ic 5). Modified from Melchor et al. (2006).

trackways (Figs. 7H and 8D). In some cases double holes of different size indicate that they were made with the beak open.

- 9) Resting. Laid down with the body touching the ground and the legs directed forward (Fig. 7I).

3.3.2.2. Behaviours in large flocks.

- 10) Running off other individual from behind. Sometimes, in large flocks, one individual drives away another with a short run from behind, which results in a short run by both birds. In some cases the run is aided by flapping and in others there is a short flight. The trace of this agonistic behaviour was not observed but it would result in two consecutive short trackways with a progressive increase in stride length (Fig. 7J).
- 11) Driving away by face off behaviour. In large flocks, one individual runs at another, the latter turns back facing the former, and after that takes two steps laterally and walks or runs backwards (Fig. 7K). The trace of this agonistic behaviour was not observed.
- 12) Run and U-turn. A long run is finished in a U-turn and a slow walking and pecking along the line of the previous run. It was observed in individuals within large flocks, feeding in water.

Probably the run stirs the sediment in the bottom of the pond with potential prey, which can be caught while the walking. The trace was not observed, but can be inferred as distinctive due to the U-turn (Fig. 7L).

3.3.2.3. Behaviours associated with flight (Volichnia).

- 13) High angle landing. In the simplest case, the bird approaches nearly vertically the ground and both feet touch the substrate at the same time softly aided by hovering. The wings are completely separated from the body. The resultant trackway begins with a pair of footprints and continues with a walking pattern, probably exhibiting a larger pace length than usual for walking (Fig. 7M).
- 14) Landing with a run. The bird approaches the ground at an acute angle. The landing results in a short run in which the anterior digits touch the substrate first. The corresponding trace shows a trackway whose first footprint is composed of the marks of three toes, shorter and with a lower divarication angle than usual. The sole is not marked. Such a footprint indicates that the weight of body is partially supported by wings and it can be distinguished from other similar tracks produced by substrate differences

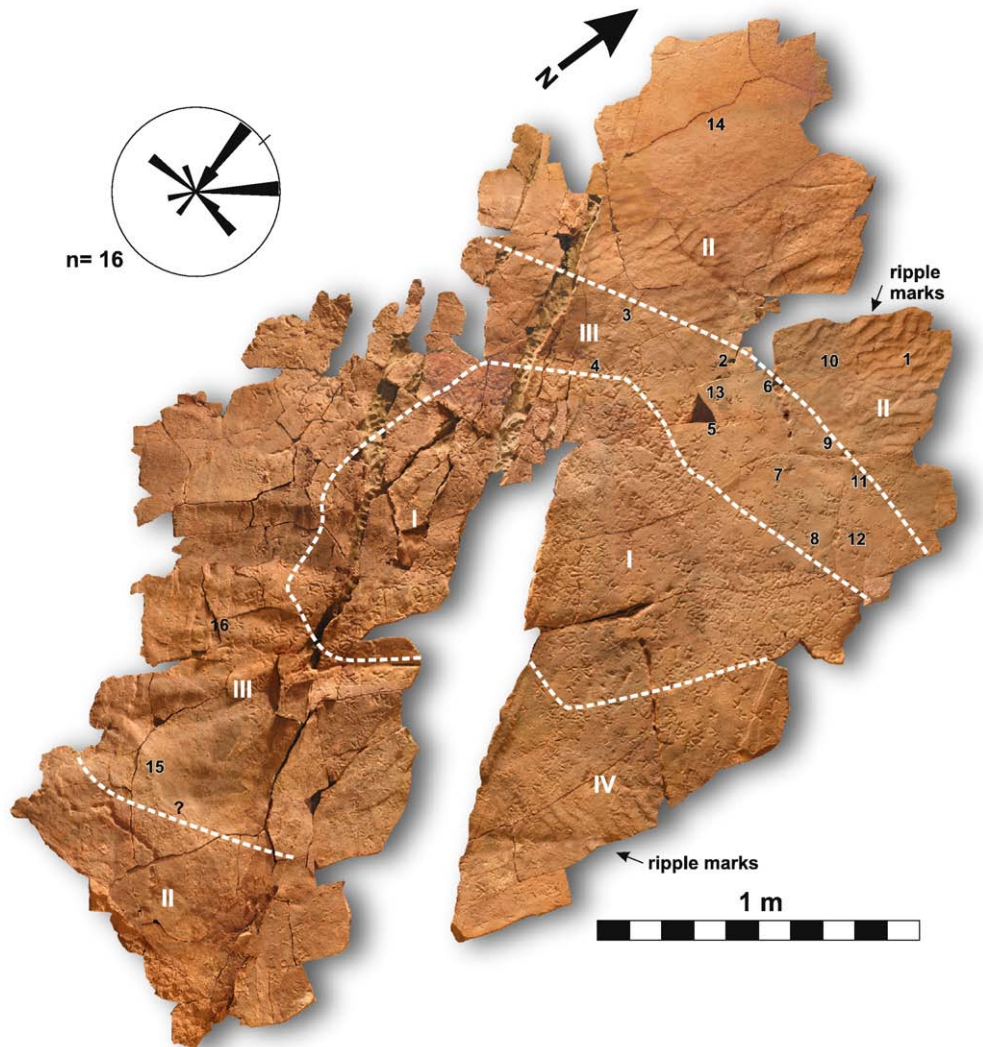


Fig. 10. Original mosaic of slabs quarried from the Santo Domingo Formation (LAR-Ic 5). The figure shows the start of each identified trackway, and a rose diagram with their orientation (arranged according with their original position in the field). Areas I to IV (defined on the basis of the type of footprints and associated sedimentary structures) are also shown. The central missing area corresponds with an intensely deformed sector that could not be recovered. Undulations on the left also are due to tectonism. Note that the north is toward the upper right corner.

because of the lower angle of digit divarication, which indicates that the foot is not completely pressed against the substrate (Figs. 7N and 8E).

- 15) Lateral landing. The approach to the ground is vertical. The landing results in a short lateral run. The trace would result in a lateral row of footprints followed by a common walking trackway (Fig. 7O). This trackway can be difficult to distinguish from those of a lateral run (# 6).
- 16) Landing with hopping. The landing result in a series of two or three jumps with both legs together. This would result in a series of two or three paired footprints followed by a common walking trackway (Fig. 7P).
- 17) Landing with legs directed forward. The bird approaches the ground at a low angle and the hallux touches the substrate first. Landing is carried out at an acute angle with both legs directed forward (Figs. 7Q and 8F). The corresponding trace observed in moist sediments is composed of two parallel grooves, thin and shallow in one extreme and wide and deep in the other, sometimes accompanied by partial or full footprint, which are followed by a normal walking trackway. The placement of the tracks with drag marks is not always side by side in a line perpendicular to the midline. In some cases, the wider tip of the grooves is associated with the beginning of a trackway. Similar grooves with trackways were observed after the landing of *Anas* sp., in which the grooves were produced by the hallux.
- 18) Simple take-off. Take-off may occur with both feet together placed as in a standing position immediately after a walk. The trace is a trackway abruptly ending with two footprints side by side (Fig. 7R). The footprints at the end of the sequence show well marked soles and crescent marks, and are commonly deeper than the previous tracks. Sometimes traces of landing and taking off may be present in the same trackway.
- 19) Taking off with flapping. Similar to landing traces, taking off traces may be indicated by a trackway composed of footprints with three toes and low angle of digit divarication (Fig. 7S). They can be distinguished from landing traces by a progressive reduction in the proportion of impressed digits and the absence of a normal trackway in the direction of progression. The feet are not completely pressed against the substrate because the body weight is partly supported by the incipient flight.
- 20) Run aided by flapping. A short run aided by flapping. The weight of the body is not translated to the feet, so even though they touch the substrate, they are not pressed against it. It results in trackways composed of tridactyl footprints, with low angle of digit divarication (i.e. in the range 60–70°) and lacking the sole mark (Fig. 7T).
- 21) Take-off with hopping. The take-off is preceded by two or three hops. This results in a walking trackway that finishes with two or three consecutive pairs of footprints (Fig. 7U).

3.4. The fossil track surface

The stratigraphic section containing the track surface is a 50 m thick interval dominated by fine-grained sandstones and siltstones (facies association A of Melchor et al., 2006). This interval includes ribbon channel sandstones of limited lateral extent with multistorey infill (fining-upward, fine-grained trough cross-bedded sandstone) and the associated finer-grained floodplain deposits (Fig. 9). The latter comprises laminated siltstones with mud drapes, desiccation cracks, ripples, and wrinkle marks; fine-grained sandstone beds with parallel lamination and parting lineation that pass laterally to climbing or current ripples; and massive mottled siltstones (Fig. 9).

The track surface is represented by a mosaic of slabs measuring about 5.5 m², showing variable density and quality of preservation of footprints (Fig. 10). This mosaic includes both natural moulds and casts (i.e. part and counterpart when available) of footprints preserved

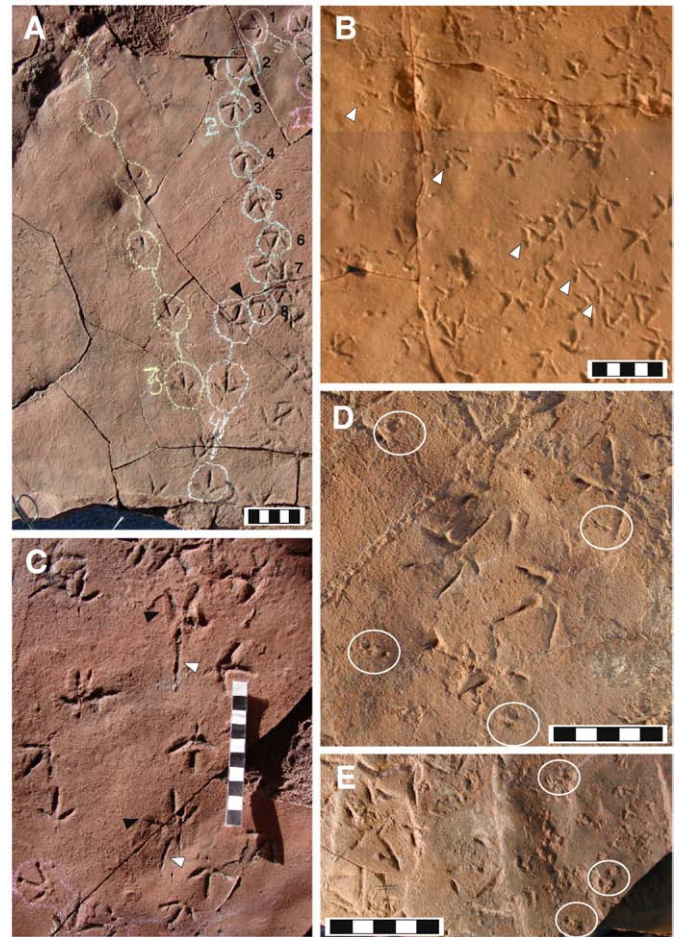


Fig. 11. Representative trace fossils from the track surface and inferred behaviours. (A) Part of the mosaic with *Gruipeda dominguensis* showing trackway # 2 (footprints 1 to 8) with a zig-zag path. Trackways # 3 and 4 display a walking behaviour with a straight course. The black arrow indicates the point of encounter between trackways # 2 and 4. (B) Part of trackway # 1 of *G. dominguensis* (white arrows) showing a progressive decrease in stride length. Interpreted as reflecting a short run. (C) Bird-like footprints with elongated hallux imprint (black arrow) associated to abundant *G. dominguensis* tracks. The white arrow indicates the drag mark of the hallux. These traces are consecutive and suggest landing with legs directed forward. (D), (E) Sparse *G. dominguensis* tracks and small epichnial rounded pits (circled), which are interpreted as probing marks. Note rippled surface in (E). (B), (D) and (E) are photos from the mosaic LAR-1c 5; (A) and (C) belong to the resin replica of that mosaic MPEF-1C 227. Scale divisions are 1 cm.

in siltstone slabs commonly covered by a thin clay drape. The thickness of the siltstone lamina composing the mosaic ranges from 30 mm in the centre to 4 mm in the marginal area of the mosaic. This change in thickness is accompanied by a different thickness of the clay drape on the top of the laminae, which is thicker (2 mm) in the centre of the mosaic and decreases in thickness to zero in the marginal area. Most of the traces recognised in the mosaic are bird-like footprints assigned to a single ichnospecies, *Gruipeda dominguensis* de Valais and Melchor (2008) (Fig. 11A and B). The associated trace fossils are “bird-like footprints with elongated hallux impressions” (Fig. 11C), small epichnial rounded pits (Fig. 11D and E), *Palaeophycus tubularis*, *Skolithos linearis* and *Taenidium barretti* (Melchor et al., 2006; de Valais and Melchor, 2008). *Gruipeda dominguensis* includes tridactyl or tetradactyl footprints with three digits directed forward and larger (II to IV) and the fourth or hallux (I), directed backward and short. The tracks (that average 34 mm long and 33 mm wide) are arranged in bipedal trackways commonly displaying a positive rotation in relation to the midline, a pace angulation of about 170°, and an average stride length of 170 mm. Webbing was not observed (de Valais and Melchor,

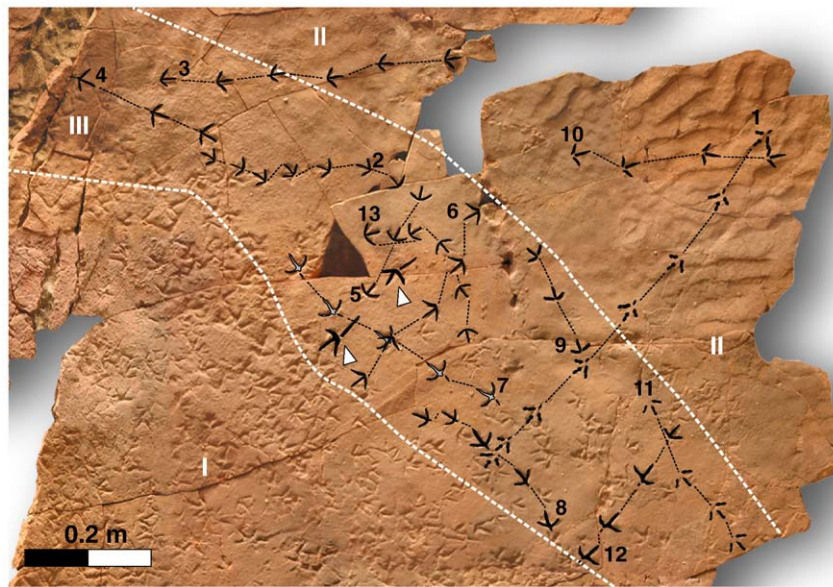


Fig. 12. Drawing on part of the mosaic of Fig. 10 highlighting the footprints that compose the trackways identified in areas II and III. Bird-like tracks with elongated hallux imprints are arrowed.

2008). Due to high degree of overprinting, the identification of individual trackways was aided by the anisodactyl character of the tracks. Even when the hallux imprint is missing, digit IV is longer than digit II and curved and the II–III angle is a few degrees larger than the III–IV angle (Fig. 11A). In “bird-like footprints with elongated hallux impressions” (de Valais and Melchor, 2008) the general morphology is similar to *G. dominguensis*; however, the impression of the hallux is up to four and a half times longer than the average length in *G. dominguensis* tracks. In these traces, a minor widening of the impressions of digits II and IV was also observed. One of the specimens includes a right-left pair with the typical arrangement in a trackway and separated 151 mm (Fig. 11C). There is also an isolated footprint of similar characteristics.

Small epichnial rounded pits (Melchor et al., 2006) are circular to oval holes, commonly paired, preserved as negative epichnia (Fig. 11D and E). In each pair of pits, one is smaller (1.6–4.4 mm) than the other (3–5 mm) and they are in contact or separated by up to 4.8 mm. Most paired pits display a raised margin that usually only cover one third of the perimeter. They appear on the bedding surface in large number (up to 2000 pits/m²).

Considering the distribution of trace fossils and sedimentary structures, it is possible to distinguish four areas with transitional boundaries in the mosaic (Fig. 10). A central area (area I) showing high track density (up to 520 footprints/m²) with *Gruipedes dominguensis* footprints moderately to poorly preserved. Digit impressions are wide (up to 7 mm) and the depth of footprints is the largest measured (about 2–3 mm deep). In this area, no single trackway was distinguished due to dense overprinting. Area II occupies a marginal position and contains shallow and well-defined *G. dominguensis* footprints showing distinct pad and claw impressions, and thin digit imprints, in addition to current ripples and wrinkle marks. The density of footprints is low (maximum value about 190 footprints/m²) and some tracks display inverted relief. Most of the *G. dominguensis* footprints in area II can be assigned to definite trackways with confidence. The orientation of ripple crests suggests transport toward N 115° (Fig. 10). Area III is located between the former ones and contains most of the identified trackways. It is characterized by well-defined *G. dominguensis* footprints, presence of bird-like footprints with elongated hallux impression and absence of sedimentary structures. The orientation of trackways is both parallel and perpendicular to the boundary with adjacent areas I and II (Fig. 12).

Area IV shows moderately-preserved footprints with density similar to that of area III, abundant small epichnial rounded pits, invertebrate traces (*Palaeophycus*, *Skolithos* and *Taenidium*) and current ripples. No clear spatial relation between *G. dominguensis* trackways and epichnial pits was recognised.

4. Discussion

4.1. Environmental and substrate comparisons

To extract behavioural inferences from trace fossils, it is necessary to distinguish as much as possible the influence of environment and substrate in their production and to differentiate preservation from true behavioural components. Accordingly, the comparison between tracks of the Triassic–Jurassic mosaic and the Bajo de los Huesos pond has a methodological objective: to evaluate the possible influence of environment and sediments on the type, formation, and preservation of the fossil footprints and morphology of trackways. In addition this comparison also has a palaeoenvironmental objective: to refine the environmental and substrate inferences on the Triassic–Jurassic pond at the time of footprint production.

The dominant lithology and sedimentary structures in both cores from the Bajo de los Huesos are laminated silt to fine-grained sand, which are similar to those of the interval containing the fossil footprints (Figs. 4 and 9). In particular, the grain size of core C-1 sediments is closer to those of the fossil example, whereas the presence of common mud drapes in core C-2 sediments is also shared with the Santo Domingo section. The lithological differences between both modern cores suggest that sedimentation in core C-2 was of higher energy, probably related to sheet flooding during rains or, more rarely, to washover by marine waters during storms. These high energy events were punctuated by periods of lower energy sedimentation in the pond, probably related to subaqueous settling of fine-grained sediments during the spring. The greater proportion of mud, absence of laminated sands and presence of articulated or unbroken bivalve shells, suggest sedimentation under lower energy conditions at the location of core C-1 (Fig. 4). This feature can be linked to its location in a small “embayment” protected from the fluvial currents coming from the west (Fig. 1B). The section containing the fossil footprints (Fig. 9) can be interpreted essentially as the deposits of shallow ponds that were frequently desiccated (laminated siltstones

with mud drapes, desiccation cracks, ripples, and wrinkle marks), crevasse-splay or proximal sheetflood deposits (fine-grained sandstone beds with parallel lamination and parting lineation that pass laterally to climbing or current ripples), and poorly developed palaeosols (massive mottled siltstones). The modern pond and the fossil section lack evaporite minerals, which suggest that both settings contained mostly freshwater, although in both cases the climate was semi-arid. In the modern and fossil example, there is evidence of formation of algal mats, as indicated by biofilms, cyanobacteria, chlorophycean algae, and diatoms in the modern example and wrinkle marks in the fossil one. In addition to similar sediments, the sedimentation processes inferred for both settings are dominated by sheetflows related to rains and local ponding of freshwater. The main difference is the major (palaeo)geographic setting: the fossil example was interpreted as representing a distal, low gradient fluvio-lacustrine environment (Melchor et al., 2006), whereas the Bajo de los Huesos pond is the result of the damming of an ephemeral drainage network by a littoral ridge. In consequence, it is concluded that the local environment and sediments of modern and fossil examples are fairly similar and that the minor differences recorded are not significant enough to bias behavioural and ichnological conclusions.

4.2. Type and distribution of modern footprints in relation to environmental and substrate conditions

During the wet phase, the Bajo de los Huesos showed a range of substrate conditions for formation and preservation of traces, which resulted in different types of trampled areas and footprints. The different footprint types were produced indistinctly in sediments that range from sandy silts to silty sands. In consequence, the subtle variation in grain size of the sediments analysed does not appear to produce consistent differences in terms of production and type of footprints. With the pond full of water, the exposed playa surfaces were reduced and mostly large flocks of *Calidris* feed in the water along raised areas of the bottom, producing dense patches of type 1 footprints. In addition, small flocks foraging along the waterline left trackways parallel to that boundary. The analyses of modern muds from Bajo de los Huesos where type 1 footprints were produced suggest a limited range in water content (18–22%) and relatively low organic matter content (0.2–0.5%). Although the organisms that compose algal mats were recognised in the sediment samples (cyanobacteria, diatoms, chlorophycean algae), a biofilm was not observed associated to this type of footprints during field work. In successive days after the maximum expansion of the Bajo de los Huesos pond, the emergent playa surface grew exponentially (Fig. 3), providing larger areas with wet exposed sediments or covered by a film of water as result of wind-induced flooding. Small flocks of *Calidris* continued foraging on these areas of the pond, which provided the best substrate for producing type 2 footprints. The increase in the number of well-formed footprints is related to the presence of thicker mud laminae on the playa surface, produced by settling from suspension when the playa was covered by water. This thicker drape of cohesive muds on the playa surface would improve the formation of footprints. The modern muds where type 2 footprints were produced exhibit a wider range of water (19–50%) and organic matter content (0.25–1.0%) than those previously discussed. Even when the number of samples is limited, there seems to be a direct relationship between these parameters. Well-defined footprints can be produced even underwater and with high water saturation (sample 1, Table 1) probably due to the presence of a significant amount of organic matter. Organic matter in sediments promotes temporary stabilization of the substrate by increasing the retention of pore water and grain cohesion (Forster and Nicolson, 1981; Scott et al., 2007). The presence of cyanobacteria in the sediments is significant because they are the most common biostabilization agents in modern substrates (Gerdes et al., 2000; Noffke et al., 2003a). The last stage of the modern pond

exhibited extended but dry playa surfaces where footprints are not formed, extended systems of desiccation cracks and few previously formed track sites and footprints in many cases showing enhancement by shrinkage (type 3 footprints). Type 4 footprints (ghost or blurred footprints) are more common in the first stages of the pond.

Some further inferences about substrate properties not adequate for footprint formation can be drawn from the analysis of the modern sediment samples from the Bajo de los Huesos pond. A sandy subaerial substrate with low water saturation (sample 4, Table 1) does not yield footprints. This represents a simple case commonly reported in the literature (e.g., Laporte and Behrensmeier, 1980). The local scenario suggests that this sand was probably transported by wind. A mud that was exposed to desiccation and renewed flooding (sample 3, Table 1) also does not yield footprints. Desiccated mud commonly displays an increased consolidation in part because of early carbonate or evaporite cementation especially in semi-arid settings (e.g., Eugster and Hardie, 1978; Renaut, 1990; Scott et al., 2007). In addition, microbial mats become hydrophobic and delay the water infiltration (de Winder et al., 1989; Scott et al., 2007).

4.3. Palaeoenvironmental and taphonomic interpretation of the fossil track surface

Sedimentologic analysis of the succession suggests that the track surface was deposited in a small and shallow (i.e. less than a few centimetres deep) pond of sheetflood origin emplaced in a low relief landscape (Melchor et al., 2006). Considering the distribution of biogenic and sedimentary features and comparing them with the modern track types and trackway patterns observed at the Bajo de los Huesos, it is possible to interpret the evolution of the pond. The density and morphology of footprints in area I of the mosaic (Fig. 10) make them comparable with modern type 1 footprints, which were produced with the pond full of water. It is argued that area I represents the deeper part of the pool, where water was ponded, allowing settling of fines from suspension, as also suggested by the greater thickness of the mud drape in this area. This area kept water for more time and the producers of *Gruipedina dominguensis* crossed the area repeatedly. The lower density and well-defined outline of *G. dominguensis* tracks in areas II, III and IV allow comparison with the type 2 footprints identified in the modern pond. The shallowest part of the fossil pond is represented by area II, there we can distinguish a sector of flat bedding, where the speed of water flow was greater during the sheetflood, and a slightly deeper sector where subaqueous current ripples migrated more slowly (Fig. 10). In area II the mud drape was thin or absent, which indicates that it became exposed subaerially shortly after the flooding event. The presence of wrinkle structures in area II is indicative of the development of algal mats, which are considered as produced by cyanobacteria (Noffke et al., 2002, 2003b). It is likely that the presence of algal mats in the fossil example contributed to the preservation of well-defined *G. dominguensis* footprints, as suggested by the common association of type 2 footprints with algal mats or the organisms responsible for their formation, in the Bajo de los Huesos. There are few studies addressing the role of microbial mats for footprint preservation in modern settings (Marty et al., 2007; Scott et al., 2007). Some authors consider that microbial mats are important in the preservation of traces, especially when related to early calcification of the sediments (Scott et al., 2007). However, recent studies suggest that continued growth of microbial mats can obliterate footprints (Marty et al., 2007).

The trackways identified in area III are dominantly parallel to its maximum elongation (Figs. 10 and 12). This preferential orientation is similar to the pattern parallel to the shoreline observed in modern trackways at the Bajo de los Huesos (Fig. 8C) and in other lake settings (e.g. Master, 1991; Cohen et al., 1993). According with the behavioural observations from Bajo de los Huesos locality, the diversity of invertebrate prey near the waterline is different from other parts of

the pond, resulting in the preference of shorebirds for this zone. In consequence, area III corresponds to the shoreline of the fossil pond. The absence of type 3 footprints (enhanced by shrinkage) and mudcracks in the track surface suggests burial before significant desiccation. Observations at Bajo de los Huesos suggest that type 3 footprints may appear between 20 min and 70 h after footprint formation, depending on whether they were formed subaerially or under water, respectively. Although shrinkage cracks are controlled by many additional factors (including clay mineralogy, grain size, and rate of water loss; Allen, 1982, p. 550), neoichnological observations suggest that the lifetime of the fossil pond did not exceeded a few days (probably no more than 3 days). This aspect was critical for the preservation of the fossil track surface because continued desiccation would have destroyed the surface in a few days, as indicated by observations at Bajo de los Huesos. Area IV seems to have a similar depth rank to area II (as indicated by the presence of current ripples) and is laterally equivalent to area III (Fig. 10), which may suggest that that area also represented the waterline for some time. However, the presence of small epichnial rounded pits and invertebrate trace fossils are distinctive and will be interpreted on the basis of behavioural observations in the Bajo de los Huesos in the next section.

Considering the comparison of the types of tracks preserved the most probable scenario for the fossil track surface is a pond that suffered hours to a few days of evaporation after the initial sheetflood event, supporting small groups of trace makers feeding therein.

4.4. The behaviour of Santo Domingo trace makers

Five of the twenty one behaviours described from the Bajo de los Huesos can be identified with certainty in the fossil example. They include walking (# 1), walking with zig-zag path (# 4), short runs (# 5), probing (# 8) and landing with the legs directed forward (# 17) (Fig. 11). A total of 16 trackways were identified in the mosaic of slabs from the fossil track surface, they are referred to in the text according their distribution among the different behaviours of modern sandpipers from the Bajo de los Huesos.

Walking is the most common behaviour (as it is in the modern analysed example), which is represented by twelve trackways (3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 14, and 16). The resulting trackways display a slightly curved path, the pace length ranges from 75 to 95 mm and the pace angulation is in the range 160–180° (average 170°). Walking with a zig-zag path (# 4) can be inferred in trackways # 2 and 13 (Fig. 12). Trackway # 2 is composed of 7 footprints and displays four consecutive changes in direction in the range of 50°, describing a zig-zag pattern. A similar track pattern was illustrated by Elbroch and Marks (2001, p. 106) for a spotted sandpiper and a dunlin (p. 109). Trackway # 13 (five footprints) displays three different directions of movement. Two trackways represent a change in the stride length and, in consequence, are interpreted as variants of short runs (behaviour # 5). In particular, trackway # 1 (Fig. 12) exhibits a progressive decrease in stride length from 241 mm to 102 mm (8 footprints), although the pace angulation remains high and averages 176°. This trackway is interpreted as a short run followed by a stop. A similar trackway of a piping plover was illustrated by Elbroch and Marks (2001, p. 102). Trackway # 15 (8 footprints) display a progressive increase in stride length, from 161 to 192 mm in the first four tracks, followed by the remaining footprints with a pace length in the range 126–131 mm (Fig. 12). This trackway is interpreted as a short run followed by a return to a normal walking pattern. In consequence, both trackways suggest changes in stride length during runs between 1.5 and 2.3 times the walking stride, which is in agreement with the estimation of running strides in modern piping plovers up to 2.1 longer than those of walking strides (D. Boretos, in Elbroch and Marks, 2001, p. 103).

The probing behaviour (# 8) is represented by small epichnial rounded pits associated with *Gruipeda dominguensis* footprints, and

invertebrate traces in area IV (Figs. 10 and 11D and E). These paired pits were considered as possible pecking or probing marks (Melchor et al., 2006) due to the strong resemblance to modern and fossil bird pecking marks (e.g. Swennen and van der Baan, 1959; Erickson, 1967; Frey and Pemberton, 1986, 1987; Brown et al., 1987; Yang et al., 1995; Elbroch and Marks, 2001). It was not possible to associate the probing marks with a definite trackway, although there are numerous nearby footprints. In addition, the association with the only invertebrate trace fossils recorded in the fossil track surface, and the lateral equivalence with area III, contributes support to the idea that this area represents the shoreline. Records of modern probing tracks of plovers, sanderlings, and sandpipers from the literature suggest significant differences within the probe feeding pattern, which is related to the speed of progression of each bird species. In plovers, which are very fast, probe feeding is not concentrated but spread along a thin line. Sanderlings are slower and typically leave a regular pattern of double or single holes along a curved path. Sandpipers walk slowly and produce a higher density of probes per pace than the other mentioned bird species. Sandpiper holes are frequently double, both as result of a double probe strategy (Elbroch and Marks, 2001, p. 266–267) and of probing with the bill open, as those observed at Bajo de los Huesos pond. Each hole in the small epichnial rounded pits is of different size (Fig. 11D and E), as those commonly observed at Bajo de los Huesos pond (Fig. 8D). In consequence, it is likely that they were made with the bill open.

Other behaviour that can be inferred by comparison with observations of modern sandpipers presented herein is low angle landing with legs directed forward (# 17). In particular a pair of bird-like footprints with elongated hallux marks is fairly distinctive (Fig. 11C). A key feature in these fossil footprints is the marked elongation of the hallux mark and, also the enlargement of the impression of digits II and IV, as those observed at the modern pond (Fig. 8F). They are considered as possible drag marks produced by the rear of the feet when landing. In consequence, these traces can be ascribed to Volichnia, which is an ethological category originally created by Müller (1962, 1978) to include traces of landing, jumping and take-off in insects. This category has been mostly employed to designate arthropod traces by Walter (1978, 1983) and more recently by Mayoral (2001), Braddy and Briggs (2002); Lucas et al. (2005); and Minter et al. (2007). The description of fossil flight traces attributed to vertebrates, despite the use of Volichnia, has been sparse. Exceptions are the work by Abbassi (2005), who described Miocene bird take-off traces, and Billon-Bruyat et al. (2004), whom presented purported Jurassic pterosaur landing traces. Description of modern flying traces is rare (Bang and Dahlström, 1975; Elbroch and Marks, 2001). Bang and Dahlström (1975, p. 76) reported wing marks in snow when taking off. Elbroch and Marks (2001) illustrated and described the take-off in a killdeer's trackway in sand, as two final tracks, deeper and clearer from the rest (p. 103). The deeper final footprints of a trackway are a key feature which was also observed in the simple take-off behaviour (# 18) during this study. These authors also described (p. 150) a typical take-off pattern in modern plover trackways, which needs to run in order to lift from the ground. The progressive reduction in the proportion of impressed digits is characteristic of this mode of take-off and is similar to the take-off with flapping behaviour described herein (Fig. 7S, # 19).

Among the modern behaviours recognised in the fossil track surface, those corresponding to probing and landing with the legs directed forward are particularly significant because they would indicate a distinct avian affinity for the producer of *Gruipeda dominguensis* footprints. We are not aware of any record of Triassic to Middle Jurassic beaked theropods or indication of a pecking behaviour by theropods. Different Late Jurassic to Cretaceous theropod groups bear a beak (e.g. Xu et al., 1999, 2001; Clark et al., 2002) and were potentially capable of pecking. In consequence, we

cannot reject the possibility that the small epichnial rounded pits were produced by non-avian theropods.

4.5. Palaeobiological and evolutionary significance of the Santo Domingo track surface

The Late Triassic–Early Jurassic age for the Santo Domingo Formation based on fossil wood remains (Caminos et al., 1995), a radiometric age (Coughlin, 2001), and palaeomagnetic studies (Vizán et al., 2005), is difficult to reconcile with the avian-like footprints recovered from the unit (Melchor et al., 2002) according with the known body fossil record of birds, which would have started in the Late Jurassic (Ostrom, 1979). In order to complete this brief analysis, it is necessary to remark that other avian-like footprints were also recorded for Late Triassic–Early Jurassic rocks of South Africa (Ellenberger, 1972; Lockley et al., 1992). In consequence, the problem of Triassic–Jurassic avian-like footprints is not restricted to the case of the Santo Domingo Formation. Well-dated bird tracks have been recognised since the Early Cretaceous. In particular, the discoveries from East Asia are remarkable, including bird tracks from early Berriasian beds from China and a variety of bird footprint types from the Early Cretaceous of China and South Korea (Lockley et al., 1992; Lim et al., 2000; Kim et al., 2006; Zhang et al., 2006; Lockley et al., 2006, 2007). Berriasian bird tracks have also been reported from Spain (Fuentes Vidarte, 1996) and Canada (McCrea et al., 2001).

The purpose of the behavioural and ichnological analysis accomplished herein is to contribute to this scenario by dealing with the identity of possible trace makers and their behaviour. In a first approach to the interpretation of the Late Triassic–Early Jurassic track surface of the Santo Domingo Formation, it was suggested that the possible producers of these tracks were an unknown group of small theropods with some avian characters (Melchor et al., 2002). This possible convergence could be explained in terms of adaptation to foraging in temporary ponds with a diverse invertebrate fauna, as suggested by the associated invertebrate trace fossils (Melchor et al., 2006) and the known fossil record for the Triassic–Jurassic of Argentina. Freshwater invertebrates recorded for the Triassic–Jurassic of Argentina include crustaceans (Conchostraca and Ostracoda), insects (Trichoptera, Odonata, Plecoptera, Coleoptera, Diptera, and Hemiptera) and molluscs (Bivalvia) (e.g., Gallego and Martins Neto, 1999, 2001; Gallego, 2001). This fauna would be a potential source of food in temporary ponds such as those of the Santo Domingo Formation, even when for that unit there are no known records of invertebrate body fossils. This available feeding resource would have strongly favoured the presence of predators, such as small theropods. In particular, long toes are considered an adaptation to walk on unstable substrates (Barruel, 1973, p.17; Bang and Dahlström, 1975, p. 75) as those visited by the producers of *Gruipeda dominguensis*. In game birds, shorebirds and those with semi-palmate feet (Charadriiformes, Galliformes, and Gruiformes) the footprint usually lacks the mark of the hallux, which is absent, greatly reduced or raised above the level of the other toes (Elbroch and Marks, 2001 p. 25). The reduction or absence of a hallux is common in some birds that are adapted to walking (Elbroch and Marks, 2001, p. 31), although there are also birds that walk and have a prominent hallux. Both anatomical features are present in the fossil example. Specialized feeding on temporary ponds, require from modern birds a high migratory capacity aided by flight, to survive during dry periods. This fact would support the hypothesis of a producer with flight capacity for the Santo Domingo track site. However, alternative feeding strategies during the dry phase of the temporary ponds, such as feeding in low vegetated or bare dry soil, as done by the modern shorebirds studied herein, may be another possibility for putative Triassic–Jurassic non-avian theropods producers of the footprints.

The hypothesis of theropods with flight capacity (i.e. true birds) as producers of the Santo Domingo footprints is suggested by the new

neoichnological observations on shorebirds at the Bajo de los Huesos pond presented herein. In particular, the flight capacity of the Triassic–Jurassic producers is strongly suggested by the record of landing traces. The presence of probing marks is also indicative of typical bird behaviour and the morphology of *Gruipeda dominguensis* is identical to modern anisodactyl shorebird footprints. This ichnological evidence would indicate a younger age for the Santo Domingo Formation than currently accepted.

5. Conclusions

The following conclusions on the modern example were useful for interpreting the fossil material:

1. Twenty one behaviours potentially producing traces were recognized in the studied species of *Calidris*, including nine of them related to flight capacity and two more, such as probing or pecking, also typically related to birds. In addition, individuals usually fed by visual probing in shallow water along the shore, resulting in dense arrays of tracks roughly parallel to the shoreline. A preference for feeding near the waterline is also reflected in the common presence in *Calidris* faeces of those invertebrates (crustacean and insects) found preferentially near the shoreline.
2. Although footprint formation is a complex phenomenon, some relationships can be suggested between sediment properties and the resultant footprint types. The limited variation of grain size (sandy silts and silty sands) and no preferred occurrence of footprint types with a definite grain size, suggest that its influence is minimal in the studied examples. Type 1 footprints (dense arrays of thin and poorly defined digit impressions) seem to occur in sediments with low water (<20%) and organic matter content (<0.5%). Type 2 footprints (well-defined, lacking shrinkage features) probably require greater water (20–50%) and/or organic matter content (0.25–1.0%). Type 4 footprints (blurred footprints) are related to high water (>50%) and organic matter content (1.8%). Footprints are not produced in fine-grained sand with low water (9%) and organic content (0.3%) and in recently flooded desiccated mud.

In accordance with the previous conclusions based on the modern example, the following conclusions on the fossil track site could be obtained from the comparisons and analyses:

3. The distribution of trace fossils and sedimentary structures in the fossil surface allows us to distinguish four areas, which can be interpreted using the observations from the modern example. Area I displays high track density (type 1 footprints), a conspicuous mud drape and absence of ripples, which is interpreted as reflecting intense trampling in a subaqueous sector of the pond. Presence of well-defined tracks and definite trackways of *Gruipeda dominguensis* akin to type 2 footprints in areas II and III (located marginal to area I) suggest mostly subaerial exposure of wet sediments at the margins of the pond. The dominantly parallel orientation of trackways in area III is characteristic of the shoreline, as inferred from neoichnological observations. Absence of type 3 footprints and desiccation cracks is indicative of limited exposure and shrinkage of mud in the fossil pond. Neoichnological observations suggest that this time was no more than a few days (possibly about 3 days if the Bajo de los Huesos observations apply).
4. Five of the twenty one behaviours described for *Calidris* species can be identified with certainty among the 16 trackways distinguished in the fossil track surface. These behaviours include walking (the most common); short runs; probing, probably using the double peck technique (small epichnial rounded pits), and probable low angle landing (footprints with elongated hallux impressions). The most significant are those that indicate flight capacity and probing behaviour for the producers of *Gruipeda dominguensis* tracks.

5. The presence of flight trace fossils (Volichnia), i.e. footprints with elongated hallux impressions that are interpreted as representing low angle landing, associated with probing marks and a similar morphology of *Gruipeda dominguensis* with tracks of modern shorebirds, strongly suggest an avian affinity for the producers of the fossil tracks. This ichnological evidence is supported by detailed neoichnological observations at the Bajo de los Huesos pond, and cast doubts about the currently accepted Late Triassic–Early Jurassic age of the hosting Santo Domingo Formation, which would be probably younger if it has to match the known body fossil record of birds.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2008.08.014.

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