

Lithofacies distribution of invertebrate and vertebrate trace-fossil assemblages in an Early Mesozoic ephemeral fluvio-lacustrine system from Argentina: Implications for the Scoyenia ichnofacies

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Abstract

This paper discusses the lithofacies distribution and ichnotaxonomic assignment of invertebrate, vertebrate and plant trace fossils in an Early Mesozoic ephemeral fluvio-lacustrine system from northwest Argentina. The overall palaeoenvironment is envisaged as a distal, low-gradient fluvio-lacustrine setting under semi-arid climate, similar to a terminal fan. Depositional lobes (facies association A) are composed of distributary ribbon channels (facies A1), and associated pond and sheetflood deposits (facies A2). Lowlands between depositional lobes (facies association B) contained poorly drained floodplain zones similar to wetlands (facies B1) and shallow closed lakes (facies B2). Depositional lobes were fringed by playa-lake settings (facies association C), including mudflats (facies C1) that are partially eroded by ephemeral fluvial channels (facies C2). The ichnofauna of the Santo Domingo Formation displays high ichnodiversity (30 trace fossil types) and includes 5 trace fossil assemblages that are linked to sedimentary facies. These trace fossil assemblages are highly distinctive as half of the recognised trace fossil types are assigned to different assemblages. The ephemeral fluvial channel assemblage (facies A1 and C2) displays the lower ichnodiversity ($n=6$) and includes *Skolithos linearis*, *Diplichnites* sp., *Palaeophycus tubularis*, *Taenidium barretti*, *Dicynodontipus* sp. and footprints in cross-section. The floodplain pond assemblage (facies A2) shows the higher ichnodiversity ($n=15$) and is composed of *Diplichnites* sp., *Helminthoidichnites tenuis*, *P. tubularis*, *Rusophycus carbonarius*, *S. linearis*, *Spongeliomorpha carlsbergi*, *T. barretti*, appendage marks, burrows with brush-like features, epichnial bilobed traces, hypichnial bilobed ridges, bird-like footprint type A, tridactyl footprints, footprints preserved in cross-section, and small epichnial rounded pits. The poorly drained floodplain assemblage (facies B1) is of moderate ichnodiversity ($n=10$) and consists of *H. tenuis*, *S. carlsbergi*, *?Spongeliomorpha* sp., imbricated backfilled burrow fillings, root trace type A, *Tetrasauropus* sp., bird-like footprint type A, large pentadactyl footprints, tridactyl footprints, and footprints preserved in cross-section. The high ichnodiversity ($n=13$) nearshore lacustrine assemblage (facies B2) is the only assemblage that lacks vertebrate traces, and is composed of *Cochlichnus anguineus*, *Cruziana problematica*, *H. tenuis*, *Palaeophycus heberti*, *P. striatus*, *P. tubularis*, *Scoyenia gracilis*, *S. carlsbergi*, *T. barretti*, epichnial bilobed traces, hypichnial bilobed ridges, root trace type B, and scratch marks. The intermediate ichnodiversity ($n=9$) mudflat assemblage (facies C1) is typified by the largest ichnodiversity of vertebrate tracks and includes *H. tenuis*, *P. tubularis*, *S. carlsbergi*, *Dicynodontipus* sp., *Tetrasauropus* sp., bird-like footprints of types B and C, large pentadactyl footprints, and tridactyl footprints.

The trace fossil assemblages from Santo Domingo Formation are typical representatives of the Scoyenia ichnofacies. The distinctiveness of the studied trace fossil assemblages suggests that a future division of the Scoyenia ichnofacies would be possible, provided that occurrences of invertebrate, vertebrate and plant trace fossils in definite sedimentary facies are considered. The

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subdivision of the *Scoyenia* ichnofacies into recurrent groups of trace fossils (ichnosubfacies) with a palaeoecological and palaeoenvironmental meaning can be based on two approaches: distinction of associations of vertebrate tracks and recognition of ichnocoenoses related to substrates with different degrees of water saturation and firmness. The first approach can be based on an evaluation of the recurrent vertebrate ichnocoenoses used to recognise vertebrate ichnofacies. In this way, some of the candidate vertebrate ichnofacies are proposed as subdivisions of the *Scoyenia* ichnofacies. The second approach is based on the identification of crosscutting relationships between trace fossils and between trace fossils and sedimentary structures within some trace fossil assemblages. Using this methodology, it is possible to define distinct assemblages of trace fossils: a “pre-desiccation suite” with structures lacking ornamentation and developed in a soft substrate and a “desiccation suite” typified by striated traces that crosscut the former. These trace-fossil assemblages help to characterise the changes in organism–sediment interaction during progressive desiccation of a water-lain substrate. Additional neoichnological studies are necessary to assess the exact meaning of different trace fossil features in terms of substrate consistency.

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1. Introduction

Most trace fossil studies in continental settings are devoted to the description and interpretation of either invertebrate (and plant) or vertebrate trace fossils. Papers dealing with invertebrate traces commonly disregard associated vertebrate tracks or only mention them (e.g. Metz, 1993b; Goldring and Pollard, 1995; Rodríguez-Aranda and Calvo, 1998; Kim et al., 2005). Conversely, papers devoted to the description of vertebrate tracks may cite the presence of bioturbation or invertebrate traces, but no further descriptions and/or illustrations are provided (e.g. Covacevich and Lamperein, 1970; Johnson, 1986; Scrivner and Bottjer, 1986; Williamson and Lucas, 1996; Lockley et al., 2003). In addition, the host sedimentary rocks are not always described in detail (e.g. Bolliger, 1999; Braddy and Briggs, 2002; Hasiotis, 2004; Uchman et al., 2004). The lack of an integrated sedimentological/ichnological approach restricts the potential for a holistic analysis of the distribution of invertebrate, plant, and vertebrate trace fossils in relation to sedimentary facies. Another complicating factor is that the criteria employed for naming and describing invertebrate ichnofossils and tetrapod tracks are different (e.g. Keighley and Pickerill, 1998; Melchor and Genise, 2004). The taxonomy of tetrapod tracks has been largely based on anatomical features and identification of the supposed producer. In contrast, the main parameters used for classification of invertebrate trace fossils are morphologic features that reflect behaviour, irrespective of the producer. These differences have some implications in the recognition and erection of conceptual models about the distribution of trace fossils (archetypal or Seila-

cherian ichnofacies; Seilacher, 1967; Bromley, 1990). Continental ichnofacies are largely based on invertebrate trace fossils, with the exception of the *Scoyenia* ichnofacies, which only considers the presence of tetrapod tracks *sensu lato*. Since the original definition of the *Scoyenia* ichnofacies, there have been different proposals for restriction of its definition and/or subdivision (e.g. Frey et al., 1984; Pickerill, 1992; Donovan, 1994; Buatois and Mángano, 1995, 1998; Keighley and Pickerill, 2003) and even abandonment (Bromley and Asgaard, 1991; Hasiotis, 2004). Bromley and Asgaard (1991) and Bromley (1996) suggested that the *Scoyenia* ichnofacies represents freshwater firmground trace fossil associations and it is the continental equivalent of the marine *Glossifungites* ichnofacies because both share the presence of striated burrows. However, Buatois and Mángano (1995, 1998) considered that the *Scoyenia* ichnofacies represents a range of continental environments periodically exposed and inundated by meteoric water. In consequence, the *Scoyenia* ichnofacies includes a variety of substrate consistencies from soup-soft-ground to firmground. It has been argued that the *Scoyenia* ichnofacies is broadly defined and poorly constrained (Hasiotis, 2004). This statement ignores the advances produced in the definition of the *Scoyenia* ichnofacies since the influential work by Frey et al. (1984), and the subsequent distinction of other non-marine ichnofacies, as the *Mermia* and *Coprinisphaera* ichnofacies (Buatois and Mángano, 1995, 1998; Genise et al., 2000). A restriction on the definition of the *Scoyenia* and *Mermia* ichnofacies after Buatois and Mángano (1995, 1998) on the basis of the occurrence of morphological groupings of trace fossils has been recently proposed (Keighley and

Pickerill, 2003). On the basis of this restriction, Keighley and Pickerill (2003) found that some ichnocoenosis they studied are best considered as representatives of composite ichnofacies. This approach may be considered conceptually correct, however, the distinction of composite ichnofacies in the examples presented by Keighley and Pickerill (2003) is only made on the basis of presence of individual component trace fossils, instead of suites of trace fossils, and crosscutting relationships between trace fossil suites were not observed.

An additional problem with the ichnofacies approach in non-marine settings is that the principles utilised for recognition of potential vertebrate ichnofacies are not the same to those applied to erection of invertebrate ichnofacies. Lockley et al. (1994) recognised a number of vertebrate ichnocoenoses as candidates for vertebrate ichnofacies, although their definition was uneven and the number of case studies utilised in support of the proposal was commonly limited (McIlroy, 2004). Proposed vertebrate ichnofacies (e.g. Lockley et al., 1994) differs from archetypal or Seilacherian ichnofacies in that the recurrence in time is limited and, in many cases, also display restricted geographic distribution (e.g. Bromley, 1996; Keighley and Pickerill, 2003). Bromley (1996) considered that vertebrate ichnofacies have no sedimentological connotation and should be retained as ichnocoenoses or associations. The necessity of integrating vertebrate and invertebrate trace fossils in a single conceptual model has been advanced (e.g. Courel et al., 1979; Frey and Pemberton, 1987; Lockley et al., 1994; Buatois and Mángano, 1995), but no definite proposal has been made to date. This is in part, a reflection of the fact that the number of case studies that encompass invertebrate and vertebrate trace fossils is too few. In contrast, experiments on track formation have led Manning (2004) to reject the usefulness of any recurrent vertebrate ichnocoenosis to diagnose specific facies relationships.

This study aims to document the distribution of invertebrate, vertebrate and plant trace fossils in an ephemeral fluvio-lacustrine system, paying similar attention to all types of trace fossils and the sedimentological context. The distribution of trace fossils in each sedimentary facies is particularly emphasised and its palaeoenvironmental and palaeoecological meaning is analysed. Finally, the trace-fossil assemblages are compared with case studies from other similar lithofacies and palaeoenvironmental settings in the literature and the implications for continental ichnofacies are discussed. The primary objective of this work is to provide a detailed case study that may be utilised in the

future to analyse the distribution of invertebrate, vertebrate and plant trace fossils in continental settings.

Collected specimens are housed at the CRILAR (La Rioja province, Argentina), under the acronym LAR-Ic. Casts of additional uncollected material are kept at the Museo Paleontológico ‘Egidio Feruglio’, Colección de Icnología, Chubut, Argentina (MPEF-IC).

1.1. Ichnological information on ephemeral fluvio-lacustrine systems

The literature on ichnology of fluvio-lacustrine depositional systems has been recently reviewed by Buatois and Mángano (1996, 2004) with special emphasis on invertebrate trace fossils. The subenvironments distinguished by Buatois and Mángano (2004) found in ephemeral fluvio-lacustrine systems are inactive channels, desiccated overbank settings, and closed lakes. Abandoned or inactive channel deposits are characterised by low-diversity trace-fossil assemblages dominated by meniscate traces and tetrapod tracks, as well as subordinated vertical, inclined or horizontal burrows (e.g. Demathieu and Wycisk, 1990; Dalla Vecchia and Rustioni, 1996; Williamson and Lucas, 1996; Lockley et al., 2003; Buatois and Mángano, 2004, and references cited herein). Trace-fossil assemblages from inactive channels have been assigned to the Scoyenia ichnofacies (e.g. Woolfe, 1990; Sarkar and Chaudurri, 1992), although Keighley and Pickerill (2003) considered some occurrences to be a composite of the Scoyenia and Skolithos ichnofacies (see also Kim et al., 2005). The trace-fossil assemblages from desiccated overbank deposits include abundant arthropod trackways, tetrapod tracks, backfilled meniscate traces, ornamented burrows, and bilobate traces with striations (Buatois and Mángano, 2004). These assemblages are usually considered to represent the Scoyenia ichnofacies (e.g. Bromley and Asgaard, 1979; Gierlowski-Kordesch, 1991). As advanced by Smith et al. (1993) and latter elaborated by Buatois et al. (1996) and Buatois and Mángano (2002, 2004), desiccated overbank trace-fossil assemblages can be divided in a “pre-desiccation suite” with structures lacking ornamentation and developed in a soft substrate and a “desiccation suite” typified by striated traces that crosscut the former. The resulting palimpsest assemblages record the progressive desiccation of the substrate (Buatois and Mángano, 2004) and are considered by some authors as representative of Scoyenia–Skolithos or Mermia–Scoyenia–Skolithos composite or mixed ichnofacies (Keighley and Pickerill, 2003; Kim et al., 2005). Closed lake ichnofaunas are

usually of moderate to low-diversity, confined to definite beds and are more abundant in lake-margin facies, where the assemblage includes abundant tetrapod tracks, arthropod trackways, meniscate traces and ornamented burrows (e.g. Covacevich and Lamperein, 1970; Bromley and Asgaard, 1979; Kim et al., 2002; Gillette et al., 2003; Buatois and Mángano, 2004; Kim et al., 2005). These assemblages have mostly been assigned to the Scoyenia ichnofacies (e.g. Bromley and Asgaard, 1979; Gierlowski-Kordesch, 1991; Keighley and Pickerill, 2003; Buatois and Mángano, 2004).

2. Stratigraphy

The studied trace-fossil assemblages were recovered from the upper part of the Santo Domingo Formation, northwest La Rioja province, Argentina (Fig. 1). The formation is provisionally considered the filling of an isolated half-graben that was genetically linked to the Triassic Ischigualasto-Villa Unión Basin. At the study locality, the formation reaches a minimum thickness of ~1950 m (Fig. 2) and is in fault contact, mostly by thrust faults (Fig. 1), with Carboniferous igneous and sedimentary rocks (Caminos and Fauqué, 2001). The general strike of the succession is N35°–45°E and dips 10–45° toward the northwest. The exposures are affected by numerous folds and thrust faults. The Santo Domingo Formation is a red bed unit that displays

a thinning-upward trend in the lower 1650 m. According to the dominant lithofacies, the formation can be divided in four sections (Fig. 2; 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 trace fossils (ephemeral rivers and shallow lakes), and an upper sandstone-dominated section (aeolian deposits). The Santo Domingo Formation is considered to be of Late Triassic age, as suggested by the presence of the Middle-Late Triassic Gondwana wood morphogenus *Rhexoxylon* (Caminos et al., 1995) and by an $^{40}\text{Ar}/^{39}\text{Ar}$ step-heating analysis of albite separate of the interbedded basalt flows, which yielded a plateau age of 212.5 ± 7.0 Ma (Coughlin, 2001). Recent palaeomagnetic work on the formation suggests that the age of the unit could be even earliest Early Jurassic (Vizán et al., 2005).

3. Facies associations and palaeoenvironments

A generalised palaeoenvironmental interpretation for the Santo Domingo Formation has been proposed by Limarino et al. (1990), although these authors did not recognised the repetition of certain stratigraphic intervals by thrust faulting (cf. Coughlin, 2001). In this paper, we describe the lithofacies and facies associations of the ~200-m-thick interval with trace fossils from the

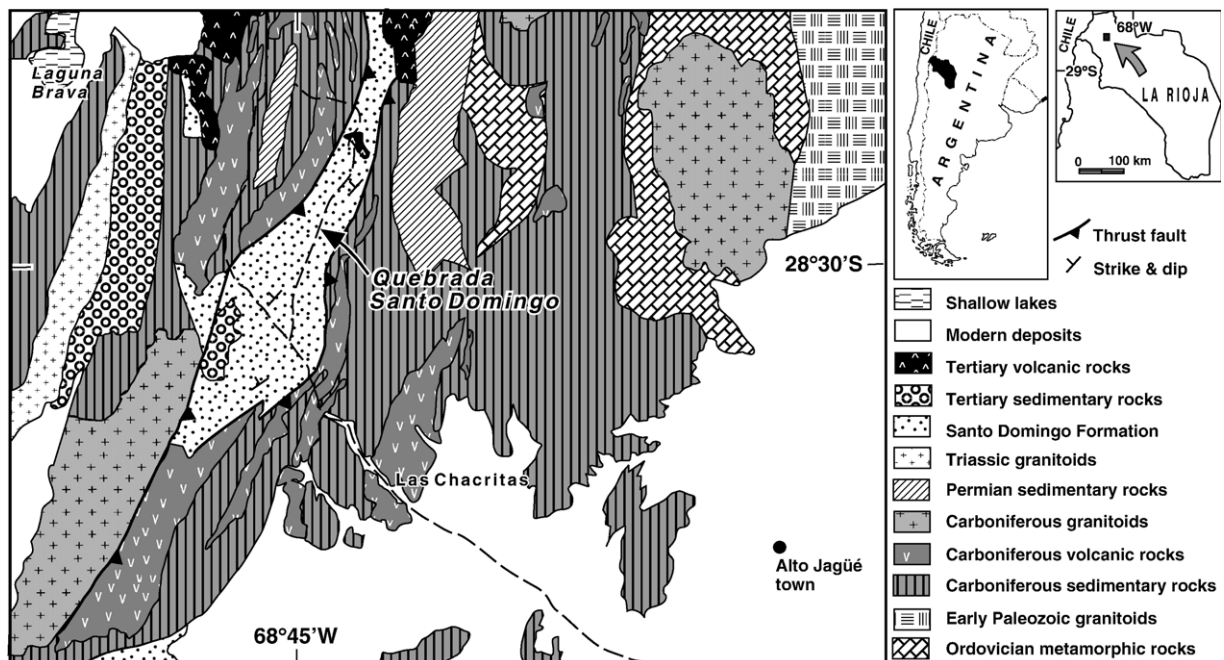
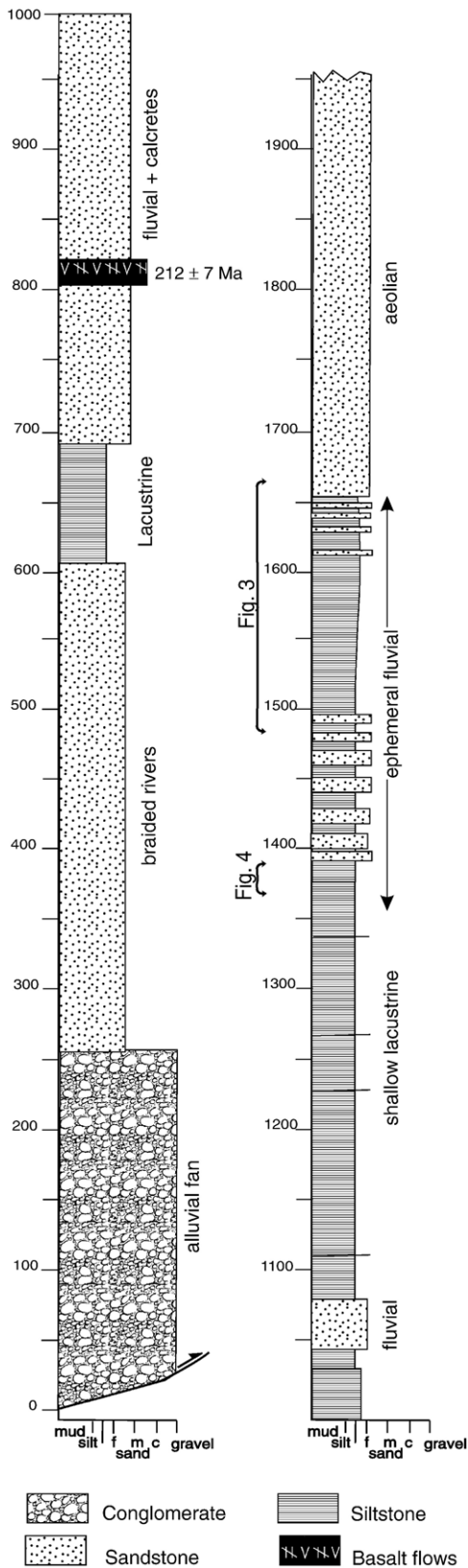


Fig. 1. Simplified geologic map of the study area. Modified from Caminos and Fauqué (2001).



upper part of the formation (Figs. 3 and 4). The following description and interpretation is limited to the intervals with trace fossils. A detailed palaeoenvironmental and stratigraphic study of the whole formation will be presented elsewhere.

Three facies associations were distinguished on the basis of the dominant lithology (sandstone/mudstone ratio) and sedimentary features. Each facies association is composed of two lithofacies, which are labelled with the corresponding capital letter and a number. A summary of the description and interpretation of the facies associations is presented in Table 1. Figs. 3 and 4 present the vertical distribution of lithofacies, and Fig. 5 shows some selected sedimentary features.

Facies association A represents a 50-m-thick interval showing the highest proportion of sand in the analysed section. It includes shallow, ribbon channels of limited lateral extent with multistory infill (facies A1) and the associated floodplain deposits (facies A2), that comprise shallow ponds frequently desiccated and associated crevasse-splay or proximal sheetflood deposits. Relatively thick sandstone beds with parallel lamination or three-dimensional antidunes (Rust and Gibling, 1990) and parting lineation indicates poorly channelled, shallow settings experiencing high energy flows (Limarino et al., 1990). The lateral transition from parallel-laminated sandstones or siltstones to climbing or current ripples with evidence for exposure (Fig. 5A) is interpreted as product of flow waning and is in agreement with typical sheetflood or crevasse-splay processes. Wrinkle marks (Fig. 5B) suggest the presence of microbial mats on the depositional surfaces of the ponds.

Facies association B is a siltstone-dominated interval characterised by well-laminated siltstones and tabular sandbodies. Facies B1 includes a 68-m-thick section of thinly laminated siltstones (Fig. 5C) interpreted as having been deposited in a shallow subaqueous and intermittently exposed body of water under wind-driven, oscillatory or combined flows. The common presence of mud drapes suggests low-energy and intermittent flows. A complete interpretation of this facies requires consideration of the trace fossil content. Incipient pedogenic modification, suggested by root marks, and the abundance of footprints disrupting the sedimentary laminae to different depths from the

Fig. 2. Generalised lithologic log and palaeoenvironmental interpretation of the Santo Domingo Formation (modified from Vizán et al., 2005). Also indicated are the positions of Figs. 3 and 4.

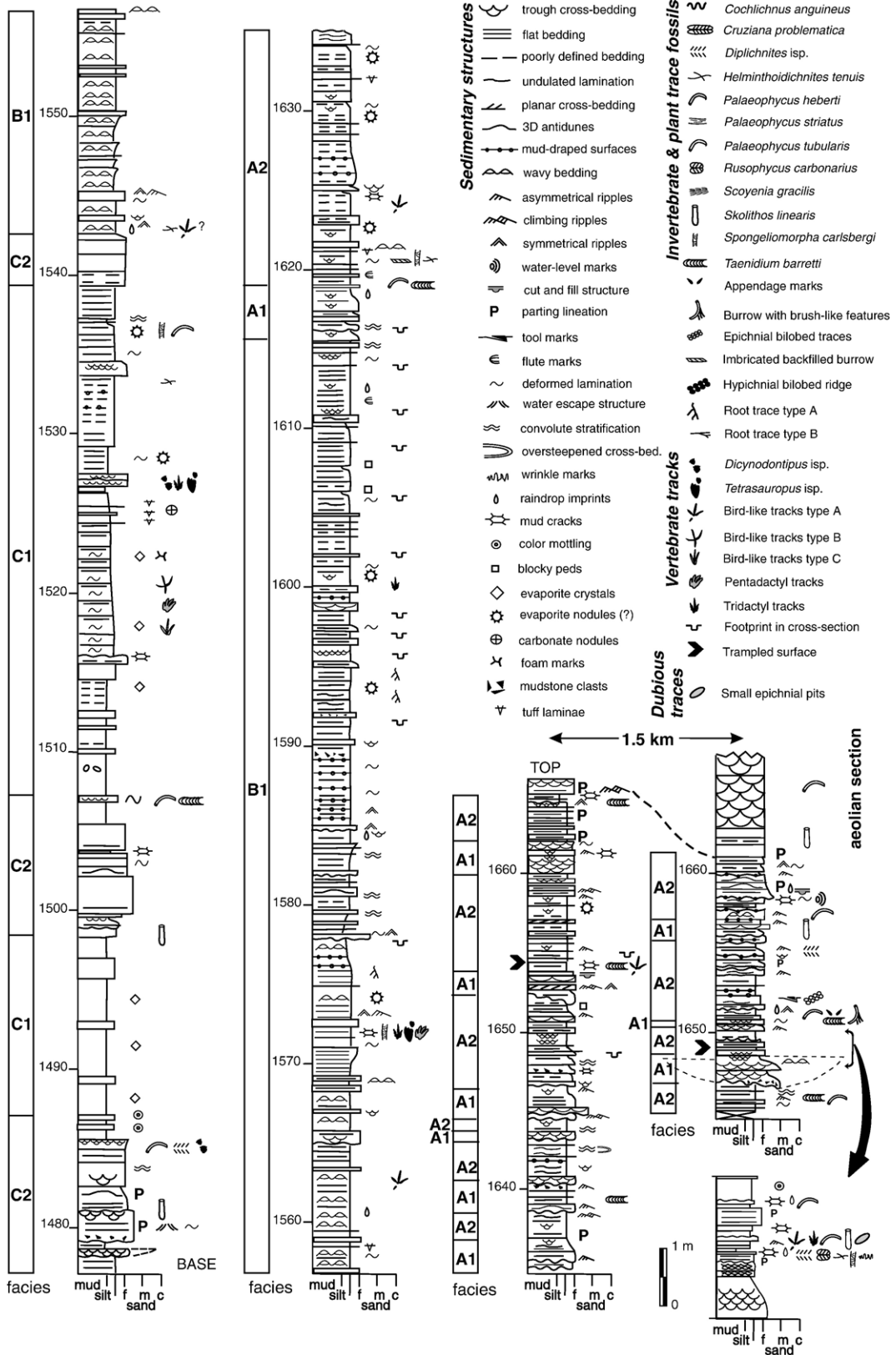


Fig. 3. Detailed sedimentologic log of the upper trace fossil-bearing section (see Fig. 2) including sedimentary lithofacies and ichnofossils. Note that the upper part of the log shows a correlative section located 1.5 km apart.

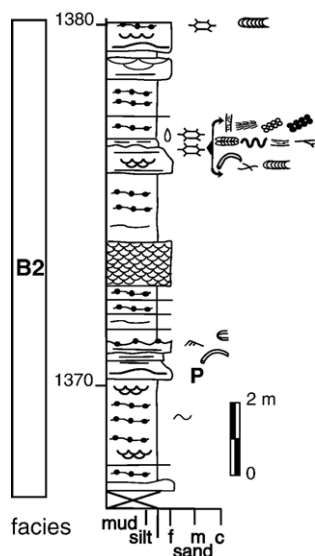


Fig. 4. Detailed sedimentologic log of the lower trace fossil-bearing section (see Fig. 2) that correspond to shallow freshwater lakes (facies B2). See references in Fig. 3.

depositional surface, yields information on the moisture content of the floodplain sediments. The deformation produced by the footprints and its depth of penetration indicates that the sediments contained an appreciable water-saturation (e.g. Lockley, 1986; Nadon, 2001). In consequence, a poorly drained floodplain setting is envisaged, although not permanently waterlogged, possibly including a wetland-like environment (e.g. Deocampo, 2002; Liutkus and Ashley, 2003). Evaporite crystals and possible evaporite nodules are common in the upper part of the succession of facies B1 (Fig. 3), which might suggest a progressive change to drier conditions. Facies B2 is composed of shallowing-upward cycles (Fig. 4) that represent subaqueous deposition in shallow lakes (lower part of the cycles), and dominantly subaerial deposition in littoral areas of the lakes (upper part of the cycles). The latter facies contains a high ichnodiversity of invertebrate trace fossils, associated with numerous desiccation cracks horizons.

Facies association C (68 m thick) is mostly composed of red massive mudstones deposited in a mudflat fringed by coarser-grained sediments of fluvial origin (facies C1) and relatively thick fills of sandy channels with evidence for sheetflood deposition (facies C2). The fluvial channels of facies C2 are thicker and coarser-grained than those of facies A1. Mudflat deposits contain evaporite crystals, possible evaporite nodules, and pedogenic carbonate nodules, suggesting semi-arid climatic conditions and incipient pedogenesis.

Palaeocurrent data display similar orientation for the described facies associations. The mean resultant direction for cross-bedding and cross-lamination readings is N101° ($n=16$) and those of parting lineation is N115° ($n=31$). This information suggests that the predominant fluvial flows were from the west or west-northwest. The orientation of four trackways and two readings of wave ripple crests are roughly perpendicular to the fluvial flows. In consequence, the latter indicators might point to the palaeographic distribution of shallow lacustrine facies (including puddles).

The overall palaeoenvironmental setting represented by the described facies associations is interpreted as a distal, low-gradient fluvio-lacustrine environment sourced from the west in a semi-arid setting, probably comparable with a terminal fan (Kelly and Olsen, 1993). Flows of fluvial origin, including sheetfloods, played a dominant role in the depositional system dynamics. The non-permanent nature of the fluvial flows is indicated by multistory channel fillings (facies A1), the overall tabular geometry of the whole section, dominance of parallel-laminated channel fills, repeated appearance of exposure indicators, and presence of carbonate nodules and evaporite crystals. Mudflats partially eroded by entrenched fluvial channels (facies association C) fringed the depositional lobes, which are composed of distributary channels, associated pond and sheetflood deposits (facies association A). The area between depositional lobes was the site of development of shallow lakes (that suffered marked level changes and frequent subaerial exposure) and low-relief and poorly drained zones located close to the base level similar to wetlands (facies association B). Semi-arid wetland settings are poorly known (Liutkus and Ashley, 2003), although they are a potentially rich source of palaeoclimatic and palaeoenvironmental information.

4. Invertebrate trace fossils

Ichnotaxonomic assignment of the studied invertebrate, vertebrate and plant trace fossils is based on a careful examination of the pertinent literature. About half of the morphological types are left in open nomenclature, which can be attributed to a variety of different reasons. Some morphological types are distinctive enough from any published ichnotaxa; however, the available material is scarce to warrant the proposal of a new ichnotaxon. In other cases, the poor preservation of the specimens precludes any definite assignment. Finally, the ichnotaxonomy of bird-like

Table 1

Description and interpretation of facies associations and component lithofacies from the trace fossil-bearing section of the Santo Domingo Formation

Facies associations	Sedimentary facies		Trace fossil assemblages		
	Lithology and sedimentary structures	Interpretation	Invertebrate and plant	Vertebrate and dubious	Ichnodiversity
A—Fine grained, cross-bedded sandstones and laminated or massive siltstones (sandstone/siltstone ratio=0.7). Plane-convex and tabular sandbodies	A1—Plane-convex sandbodies 0.4–1.5 m thick and 3–15 m wide (width/thickness ratio=6–14). Finning-upward, fine-grained trough cross-bedded sandstone with rip-up clasts. Soft-sediment deformation structures, climbing and current ripples, parallel laminated beds with parting lineation and rare mudcracks	Shallow, ribbon ephemeral channels	Rare: footprint in cross-section		1
	A2—Parallel laminated, cross-laminated or massive siltstones. Common climbing ripples, mud drapes, convolute stratification, mudcracks and raindrop imprints; and occasional wave-rippled tops, wrinkle marks, water-level marks and cut and fill structures. Interbedded thin, fine-grained sandstone beds with parallel lamination or 3D antidunes and parting lineation. Siltstone and sandstone beds pass laterally to climbing or current ripples	Floodplain ponds and proximal sheetflood (or crevasse) deposits	Common: <i>Palaeophycus tubularis</i> , <i>Taenidium barretti</i> . Rare: <i>Diplichnites</i> sp., <i>Helminthoidichnites tenuis</i> , <i>Rusophycus carbonarius</i> , <i>Skolithos linearis</i> , <i>Spongiomorpha carlsbergi</i> , hypichnial bilobed ridges, appendage marks, burrow with brush-like marks, epichnial bilobed ridges	Common: Bird-like footprints type A, small epichnial rounded pits. Rare: footprints preserved in cross-section, tridactyl footprint	15
B—Siltstone-dominated interval (sandstone/siltstone ratio=0.1). Laminated or rippled. Tabular sandbodies	B1—Thinly bedded siltstone with wave cross-lamination or horizontal laminae and mud drapes, occasional raindrop imprints, deformed laminae, and evaporite crystals. Interbedded with less than 0.4 m thick fine-grained and parallel-laminated sandstone beds, internal mud drapes and ripples, deformed laminae. Rare cross-bedded sandstones	Poorly drained floodplain (wetland?) and distal sheetflood deposits	Common: Root trace type A. Rare: <i>Helminthoidichnites tenuis</i> , <i>Spongiomorpha carlsbergi</i> , ? <i>Spongiomorpha</i> sp., imbricated backfilled burrow	Common: footprints preserved in cross-section, tridactyl footprints. Rare: <i>Tetrasauropus</i> sp., bird-like footprints type A, large pentadactyl footprints	10
	B2—Coarsening-upward cycles: siltstone and fine grained sandstone. Siltstone interval (1.5–3 m thick) with undulated lamination, mud drapes, deformed laminae and rare trough cross-lamination. Sandstone interval (1–1.5 m thick) with trough-cross lamination, in addition to mudcracks, parting lineation, flute marks	Shallow freshwater lakes (littoral and deeper facies)	Common: <i>Spongiomorpha carlsbergi</i> , <i>Taenidium barretti</i> , <i>Scoyenia gracilis</i> , <i>Palaeophycus striatus</i> , hypichnial bilobed ridges. Rare: <i>Cochlichnus anguineus</i> , <i>Cruziana problematica</i> , <i>Helminthoidichnites</i>		13

Table 1 (continued)

Facies associations	Sedimentary facies		Trace fossil assemblages		
	Lithology and sedimentary structures	Interpretation	Invertebrate and plant	Vertebrate and dubious	Ichnodiversity
	and rip-up clasts		<i>tenuis</i> , <i>Palaeophycus heberti</i> , <i>Palaeophycus tubularis</i> , epichnial bilobed ridges, root trace type B, scratch marks		
C—Mudstone-dominated interval (sandstone / mudstone ratio=0.4). Fine to medium-grained sandstones and massive mudstones	C1—Red structureless or crudely laminated mudstone and thin parallel- or cross-laminated siltstone or sandstone laminae. Common evaporite crystal pseudomorphs and possible evaporite nodules replaced by calcite. Occasional carbonate nodules, color mottling and foam marks. Intervals with deformed lamination. Thin pyroclastic fall deposits	Evaporitic and pedogenized mudflats + fringing clastic facies	Rare: <i>Helminthoidichnites tenuis</i> , <i>Palaeophycus tubularis</i> , <i>Spongiomorpha carlsbergi</i>	Rare: <i>Dicynodontipus</i> sp., <i>Tetrasauropus</i> sp., bird-like footprints types B and C, large pentadactyl footprints, tridactyl footprints	9
	C2—Up to 7 m thick sandbodies composed of fine to medium-grained sandstone showing erosive bases with rip-up clasts, parallel stratification, 3D antidunes, convolute stratification and rare trough cross-stratification. Common parting lineation. Rare mudcracks and mottled siltstone	Ephemeral channels entrenched in mudflats.	Common: <i>Skolithos linearis</i> . Rare: <i>Diplichnites</i> sp., <i>Palaeophycus tubularis</i> , <i>Taenidium barretti</i>	Rare: <i>Dicynodontipus</i> sp.	5

Also included is the composition and ichnodiversity of trace-fossil assemblages.

footprints will be treated elsewhere (de Valais and Melchor, in preparation).

4.1. *Ichnogenus Cochlichnus Hitchcock, 1858*

4.1.1. Remarks

We follow the definition of the ichnogenus by Stanley and Pickerill (1998). The ichnogenus includes regular sinusoidal burrows and trails, which represent preservational variants of the same type of structure (e.g. Gluszek, 1995; Pickerill and Narbonne, 1995; Buatois et al., 1997; Stanley and Pickerill, 1998).

4.1.2. *Cochlichnus anguineus Hitchcock (1858)*

4.1.2.1. Description. The available material consists of two specimens on one slab (LAR-Ic 62). The narrow horizontal burrows have a regular sinusoidal pattern in

the horizontal plane and slightly undulating in the vertical plane. This ichnogenus includes unlined and smooth traces of curved or straight path. Burrow width is 0.2 mm, trace wavelength is 1.6 mm, and wave amplitude is 0.7 mm. Maximum preserved length is 15 mm. Preserved as convex hypichnia. *Cochlichnus* is crosscut by *Spongiomorpha carlsbergi* (Fig. 6A).

4.2. *Ichnogenus Cruziana d'Orbigny, 1842*

4.2.1. *Cruziana problematica (Schidenwolf, 1921)*

4.2.1.1. Description. This ichnotaxon is represented by one specimen (LAR-Ic 63) preserved as convex hypichnia and composed of two parallel, rounded ridges with an external width of 4.2 mm, separated by a central groove ~0.5 mm wide. The ridges are generally featureless, although some tracts display nearly transverse and

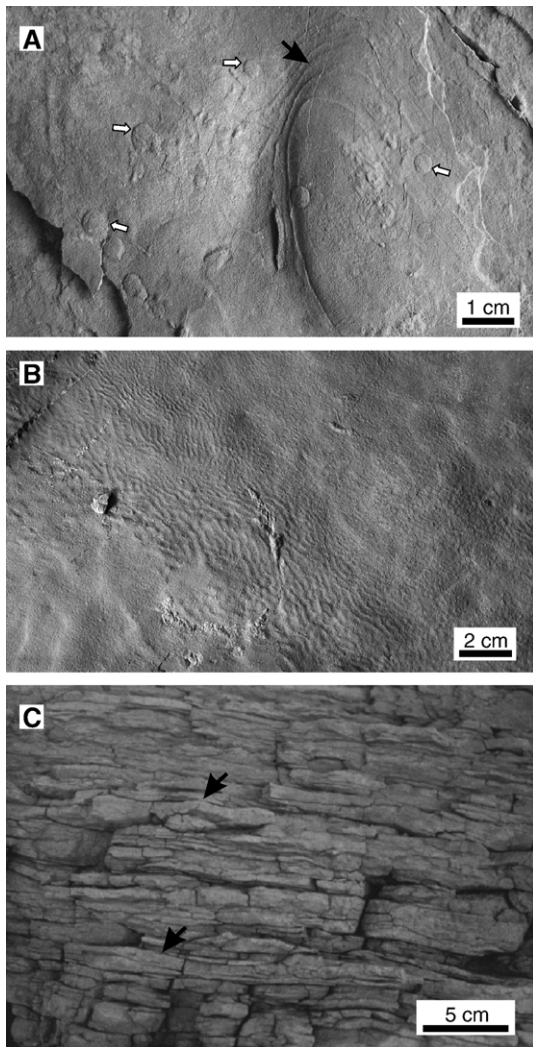


Fig. 5. Selected sedimentary features of the trace-fossil bearing section of the Santo Domingo Formation. (A) Water-level marks (black arrow) and raindrop imprints (small white arrows) from facies A2. (B) Wrinkle marks overprinted on ripples from facies A2. (C) Thinly bedded siltstone with wave cross-lamination or horizontal laminae and mud drapes from facies B1. The arrows point to preserved ripple forms.

fine striae that form an angle of approximately 80° with the midline (Fig. 6B). The path of the trace is straight to slightly curved and the preserved length is 42 mm.

Fig. 6. Invertebrate trace fossils. (A) *Cochlichnus anguineus* (LAR-Ic 62). (B) *Cruziana problematica* (LAR-Ic 63) preserved as positive hyporelief. The arrow points to transverse striae. (C) *Diplichnites* sp. (LAR-Ic 68), preserved as positive hyporelief. (D) *Helminthoidichnites tenuis* (LAR-Ic 46). (E) *Palaeophycus heberti* (LAR-Ic 49). (F) and (G) *Palaeophycus tubularis* (LAR-Ic 51). (F) Scanned thin section through a burrow filling showing possible laminae parallel to the wall, which are also insinuated in (G). (H) Close-up of *Palaeophycus striatus* (LAR-Ic 55). Note striae parallel to the burrow axis. (I) *Rusophycus carbonarius* (LAR-Ic 34). The structureless sediment mass below the *Rusophycus* specimen may represent an associated burrow. (J) Slab with mudcracks and various *Scoyenia gracilis* burrows indicated by arrows (LAR-Ic 35). (K) Detail of the previous slab showing the ornamentation of a specimen of *S. gracilis* cut across by a mudcrack (arrow). (L) Longitudinal thin section through *S. gracilis* showing poorly defined menisci (small arrows) that contain mud chips (dark angular grains) and the burrow boundary and lining (large arrow). (M) Field photograph of *Skolithos linearis* from facies C2. Note widening of burrows in some laminae.

4.3. *Ichnogenus Diplichnites Dawson, 1873*

4.3.1. *Diplichnites isp.*

4.3.1.1. *Description.* This description is based on two collected (LAR-Ic 68 and 70) and one uncollected, poorly preserved trackway. The collected specimens are 26–34 mm long and 5–7 mm wide (external trackway width) and are preserved as convex hypichnia. Individual imprints are comma-shaped, up to 2 mm long and oblique to transverse to the midline (Fig. 6C). The uncollected specimen is larger, the trackway is 80 mm long and 20 mm wide and the individual imprints are 5 mm wide.

4.4. *Ichnogenus Helminthoidichnites Fitch, 1850*

4.4.1. *Helminthoidichnites tenuis Fitch, 1850*

4.4.1.1. *Description.* The available material is seven specimens distributed in six slabs (LAR-Ic 36, 46, 55, 56, 69, 72). Under this ichnospecies are included simple, very fine (0.4–0.8 mm), straight to curved burrows or trails without branching or self over-crossing. They are preserved as convex epichnia, convex hypichnia, and concave hypichnia. Recorded trace length ranges from 11 to 52 mm (Fig. 6D).

4.5. *Ichnogenus Palaeophycus Hall, 1847*

4.5.1. *Remarks*

Following the recommendations of Keighley and Pickerill (1995), *Palaeophycus* is distinguished from *Planolites* by the presence of a burrow lining in the former ichnogenus, which is lacking in *Planolites*.

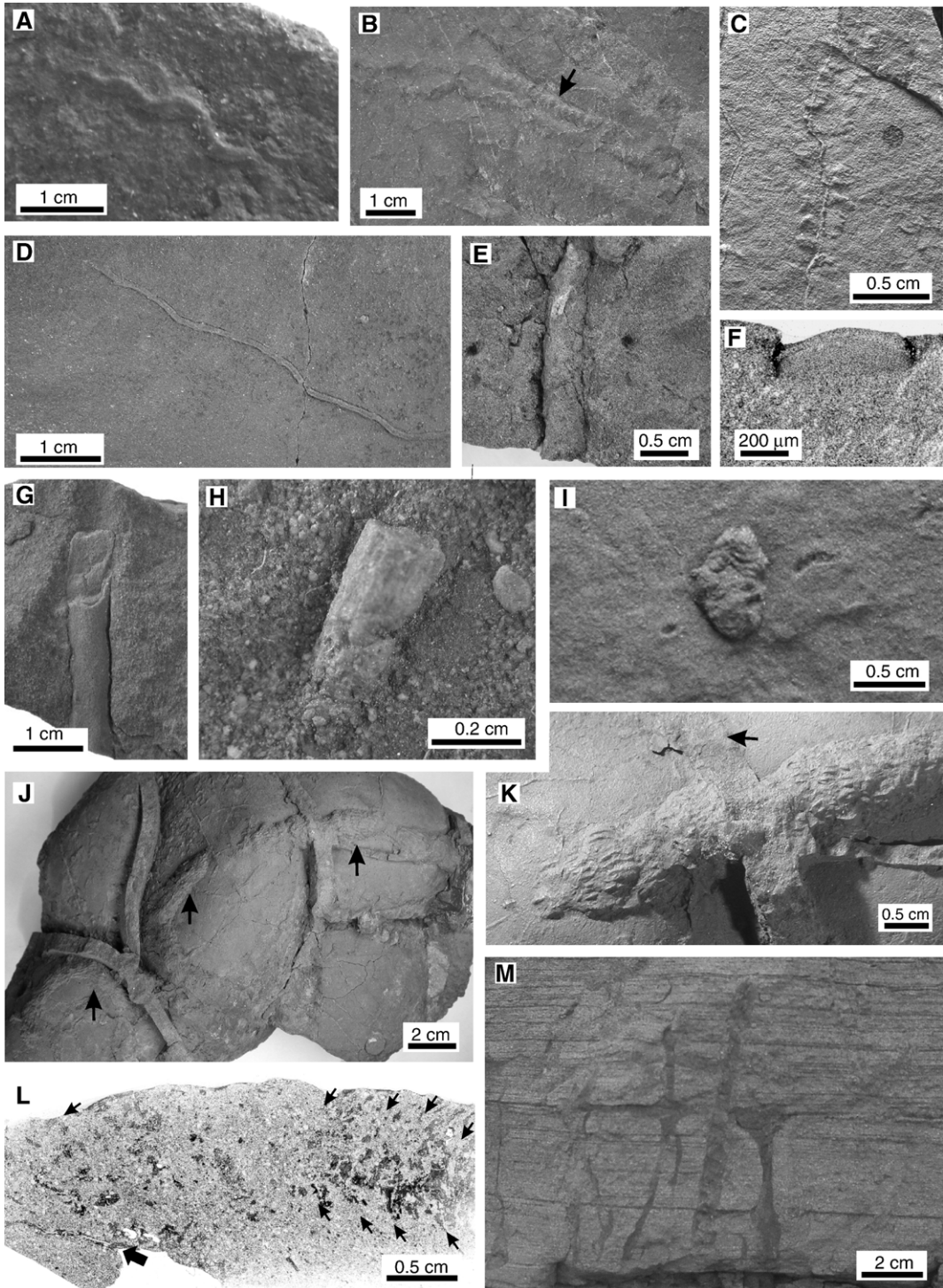
4.5.2. *Palaeophycus heberti (de Saporta, 1872)*

4.5.2.1. *Description.* One specimen (LAR-Ic 49) of a slightly curved, smooth burrow with circular cross-section, usually parallel to bedding, which is characterised by a moderately thick lining. The filling is structureless and similar to host sediment. Preserved as

convex hypichnia. External diameter is 6 mm and preserved length reaches 35 mm. Thickness of lining is ~0.65 mm. The lining is finer-grained than the adjacent material and appears concentrically laminated (Fig. 6E).

4.5.3. *Palaeophycus striatus* Hall, 1852

4.5.3.1. *Description.* This ichnotaxon is represented by several specimens in one slab (LAR-Ic 66). It is



represented by slightly sinuous burrows with circular cross-section, usually lying parallel to bedding plane, characterised by a thin lining and by fine, continuous and parallel striae. Observed burrow diameter ranges from 1 to 2.5 mm and maximum length reaches 20 mm. There are over-crossings between different specimens but true branching is absent. The burrow filling is structureless and, in some specimens, seems to be mineralised by silica. Preserved as convex hypichnia (Fig. 6H).

4.5.3.2. Remarks. *P. striatus* has been commonly (although not exclusively) identified in freshwater facies that display periodic water level fluctuations (e.g., Gierlowski-Kordesch, 1991; Pickerill, 1992; MacNaughton and Pickerill, 1995; Keighley and Pickerill, 1997; Buatois et al., 1997; Melchor et al., 2003).

4.5.4. *Palaeophycus tubularis* Hall, 1847

4.5.4.1. Description. The material includes nine collected specimens in eight slabs (LAR-Ic 44, 45, 47, 48, 50, 51, 52, 53) and six field occurrences. The burrows, of circular or ellipsoidal cross-section, display a straight to slightly sinuous path and are usually arranged parallel and sometimes oblique to bedding. Burrows characterised by a thin, smooth lining and structureless filling, usually identical to the host sediment (Fig. 6G). Some specimens show overlaps between different burrows and no true branching. Preserved as convex hypichnia and as endichnia. Maximum diameter ranges from 1.8 to 8 mm (average 4 mm), maximum observed length is up to 70 mm (Fig. 6F,G).

4.6. *Ichnogenus Rusophycus* Hall, 1852

4.6.1. *Rusophycus carbonarius* (Dawson, 1864)

4.6.1.1. Description. The available material is two specimens (LAR-Ic 34 and 40) composed of two elongated and parallel lobes separated by a marked central groove and preserved as convex hypichnia. The trace is 3–4 mm long, 2–4 mm wide, and ~0.8 mm high. Each lobe displays very fine transverse or oblique striae. The specimen illustrated in Fig. 6I is close to a small mound of structureless sediment.

4.6.1.2. Remarks. The definition of the ichnospecies by Schlirf et al. (2001) is followed. The structureless sediment mound may represent an associated burrow.

4.7. *Ichnogenus Scoyenia* White, 1929

4.7.1. *Scoyenia gracilis* White, 1929

4.7.1.1. Description. Studied material includes two collected specimens (LAR-Ic 35 and 36) and several field occurrences (Figs. 6J,K,L and 9B). They are burrows of irregular course with straight sections connected by curved sections, lacking branching or self crossings, and roughly parallel to bedding (Fig. 6J). The wall is ornamented with longitudinal, parallel and short striae. The burrows display annulations that result of the preferential location of striae at nearly regular intervals, which change the burrow diameter between 9 and 12 mm (Fig. 6K). The burrows show a very fine lining (Fig. 6L) and are preserved as convex hypichnia and endichnia. The internal structure of the burrows is not observed in hand specimens, but a meniscate structure and mud chips in the filling are visible in longitudinal thin-section (Fig. 6L). *Scoyenia* burrows are always associated with mudcracked intervals. Mudcracks crosscut the burrows longitudinally (LAR-Ic 36) or transversely (Fig. 6K).

4.8. *Ichnogenus Skolithos* Haldeman, 1840

4.8.1. Remarks

The preservation of funnel-shaped burrow tops in vertical burrows depends on many factors (including taphonomic and sedimentary processes) and not necessarily reflecting the behaviour of the producer (e.g. Fürsich, 1974; Bromley, 1996; Schlirf, 2000). Although the taxonomy of *Skolithos* burrows is in need of revision, the synonymy of *Monocraterion* Torrell, 1870 under *Skolithos* Haldeman, 1840, as proposed by Schlirf (2000), is herein accepted.

4.8.2. *Skolithos linearis* (Haldeman, 1840)

4.8.2.1. Description. This account is based on several specimens from four field occurrences. Vertical or subvertical burrows showing circular cross-section and uniform diameter (2–7 mm) and occasional rounded ends. Two specimens display a funnel-shaped top, which is about twice as wide as the lower part of the burrow (Fig. 6M), as well as vertical irregular changes in diameter. The maximum measured length is 85 mm. Burrow filling is commonly darker-coloured than the host rock and similar to the overlying sediments. Burrow density is low.

4.8.2.2. *Remarks.* The vertical changes in diameter might indicate adjustment to different sedimentation rates (previous position of the funnel-shaped top) and re-colonization of the newly deposited substrate.

4.9. *Ichnogenus Spongeliomorpha de Saporta, 1887*

4.9.1. *Remarks*

Here we follow the proposal of synonymy of *Steinichnus* under *Spongeliomorpha* by Ekdale et al. (1984), a position also adopted by Bromley (1990, 1996), Bromley and Asgaard (1991), and Pickerill (1992). Melchor and Bedatou (in preparation) will discuss the taxonomy of nonmarine forms of *Spongeliomorpha*.

4.9.2. *S. carlsbergi* (Bromley and Asgaard, 1979)

4.9.2.1. *Description.* The studied material is seven collected specimens from six slabs (LAR-Ic 36–40 and LAR-Ic 62) and other seven observed in the field. Straight to curved, unlined burrows, mostly parallel to bedding preserved as convex hypichnia. Characterised by striae oblique to transverse to the main axis of the trace (from 40° to 90°) that intersect themselves at acute angles (Fig. 7A,B). Cross section is circular to subcircular and the fill is structureless and identical to host rock. Burrow branching is present and the angle ranges from 37° to triple junctions at 120° (Fig. 7C), terminations were not observed; and over-crossings are common. Mudcracks cut across several specimens but in a single specimen the inverse relationship was observed. Diameter varies from 1 to 16 mm (average 8.5 mm, $n=12$) and the maximum preserved length is 97 mm.

4.9.2.2. *Remarks.* The specimens of the Santo Domingo Formation are assigned to *S. carlsbergi* on the basis of its general form, type and pattern of striae, the type of fill, and dominant horizontal orientation of the burrow system (Bromley and Asgaard, 1979). Santo Domingo Formation specimens do not show vertical or oblique shafts, however, the burrows described below under ?*Spongeliomorpha* (Fig. 7F) are probably related with *S. carlsbergi*. Bromley and Asgaard (1979) indicated the similarity of *Spongeliomorpha* burrows with modern mole cricket surface burrows (see also Metz, 1990). Modern mud-loving beetles (Heteroceridae) also construct similar burrows (Clark and Ratcliffe, 1989).

The crosscutting relationships between *Spongeliomorpha* burrows and mudcracks suggest that the traces

predate the mudcracks and that were constructed in sediment with water content high enough to preclude crack formation. The single case of a burrow cutting a mudcrack filling may suggest re-submerged sediments. The known records of *S. carlsbergi* are restricted to Late Triassic and Early Jurassic continental deposits (Bromley and Asgaard, 1979; Metz, 1993a,b, 1996; Gillette et al., 2003).

4.9.3. ?*Spongeliomorpha* isp.

4.9.3.1. *Description.* One collected specimen (LAR-Ic 56) and several specimens examined in the field showing circular to oval burrow fillings, vertical or oblique orientation and transversely striated walls. Filling is of slightly coarser grained sediment than host rock and shows small mudstone intraclasts, which are lacking in the host sediment. The diameter ranges between 10 and 15 mm (Fig. 7F).

4.9.3.2. *Remarks.* These structures are comparable with *Spongeliomorpha*, although this assignment is dubious because the visible portion of burrow wall is very small and no connection with horizontal *Spongeliomorpha* burrows was seen. These structures may be comparable to the “striated oblique burrows” reported by Bromley and Asgaard (1979) in connection with *Spongeliomorpha* horizontal networks.

4.10. *Ichnogenus Taenidium Heer, 1887*

4.10.1. *Remarks*

There is no consensus about the ichnotaxonomy of meniscate burrows, in particular about the distinction between *Beaconites* and *Taenidium* (Keighley and Pickerill, 1994; Goldring and Pollard, 1995). In this paper, we follow the definition of Keighley and Pickerill (1994): *Beaconites* possesses a constructed wall, which is lacking in *Taenidium*.

4.10.2. *Taenidium barretti* (Bradshaw, 1981)

4.10.2.1. *Description.* The material described is 21 specimens distributed in 10 collected slabs (LAR-Ic 34, 41, 42, 43, 44, 54, 64, 65, 67, 71) and two specimens observed at the field (Fig. 7D,E,G,H). Straight to sinuous, unlined burrow characterised by a well-defined meniscate backfilling. Menisci are of alternating grain size, well arcuate and its thickness is variable in different specimens, although within each individual it remains uniform (Fig. 7E,J). Commonly the density of menisci is ~6 per cm (width of meniscus 1.5–2 mm), except in

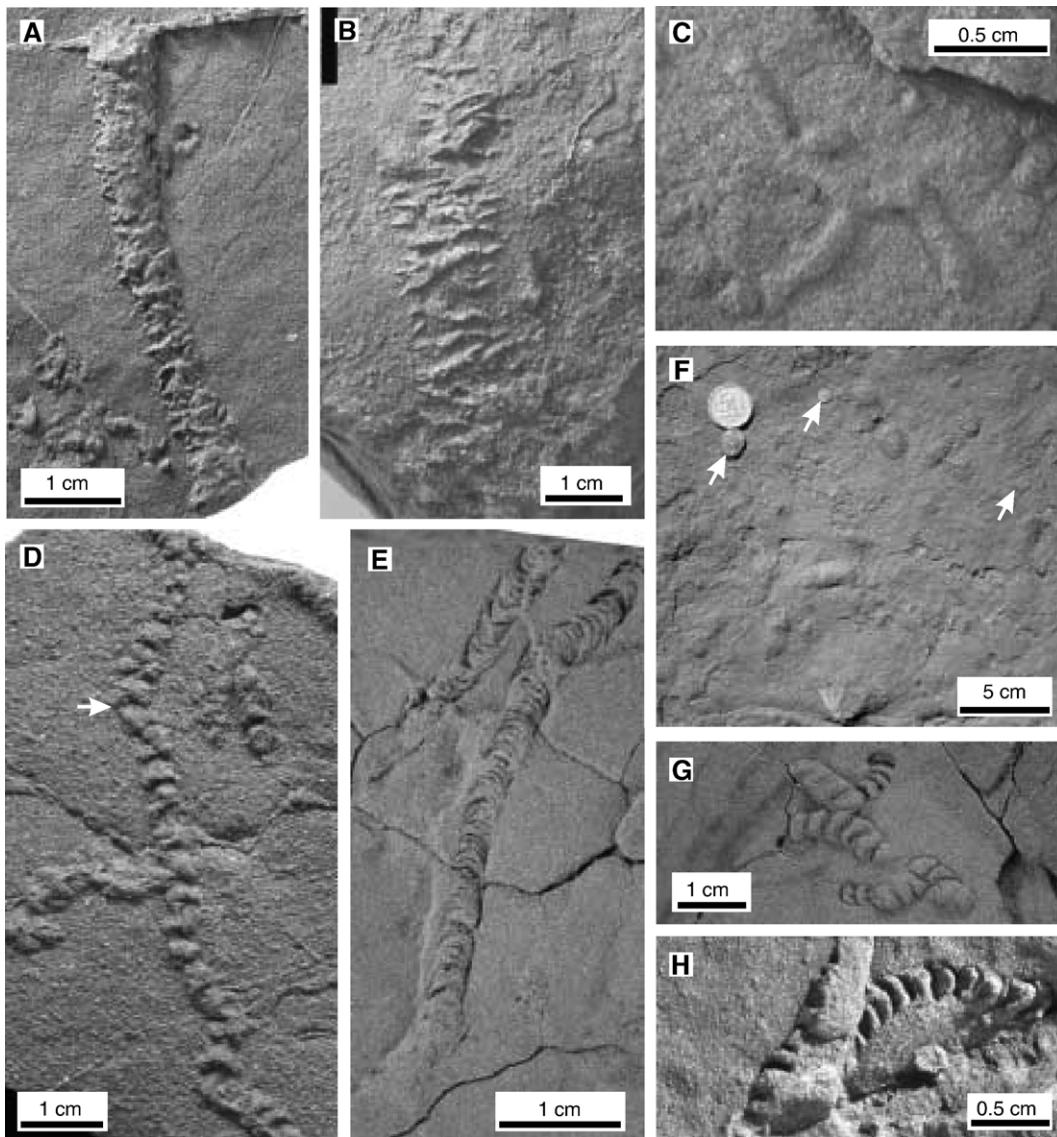


Fig. 7. Invertebrate trace fossils. (A), (B) and (C) *Spongeliomorpha carlsbergi* (LAR Ic-40, 37, and 62, respectively) in sole surfaces. Note branching in (C). (D) Composite specimen that display the sediment pads or pellets of “hypichnial bilobed ridges” above the arrow and a meniscate structure characteristic of *Taenidium barretti* below the arrow (LAR-Ic 71). (E), (G) and (H) *T. barretti* (LAR Ic-43, 44, and 64; respectively). (E) Specimen with tightly packed menisci. (G) and (H) Specimens with thick menisci. Note mudcrack cutting across a *Taenidium* burrow in H. (F) Field photograph of ?*Spongeliomorpha* sp. (arrowed).

LAR-Ic 43, which reaches approximately 15 per cm with meniscus ~ 0.5 mm wide (Fig. 7E). Structure preserved as concave hypichnia, convex hypichnia and convex epichnia. Branching was not observed, whereas some over-crossings are present. Most burrows are sub-horizontal, some are oblique to bedding and others display a change in attitude from horizontal to vertical (LAR-Ic 41). Cross-section is circular to semicircular and the burrow edge usually is undulated. Diameters range from 2 to 8 mm and preserved length ranges

between 3 and 91 mm. One specimen is cut by a desiccation crack (Fig. 7H). Specimen LAR-Ic 71 is a convex hypichnial burrow that in most of the preserved length displays the typical menisci described in other specimens of this ichnogenus, however, one of the ends shows a transition to a pelleted or lobed appearance that resemble the morphology and preservation of the bilobed hypichnial ridge described below (Fig. 7D). This is a composite ichnofossil (Pickerill and Narbonne, 1995).

4.10.2.2. Remarks. The crosscutting relationship observed with desiccation cracks suggests that the substrate was moist when the burrow was constructed, as commonly inferred for *Taenidium* and other meniscate burrows (Frey et al., 1984; D'Alessandro et al., 1987).

The composite specimen LAR-Ic 71 may suggest that the producer of *Taenidium* could be also responsible for the bilobed hypichnial ridges. However, Keighley and Pickerill (1994) mentioned that *Taenidium* preserved in full-relief might present a knobby appearance.

4.11. Appendage marks

4.11.1. Description

The only available material is one slab (LAR-Ic 54) containing tens of apostrophe-shaped marks, preserved in concave epirelief, associated with three-dimensional ripples. The imprints are 0.5–3.7 mm long and 0.2–0.7 mm wide. Some of the marks seem to display a preferential arrangement in couples of imprints, one of them smaller, forming a wide V (angle near but lower than 90°), although not united by its apex (Fig. 8A).

4.11.2. Remarks

The shape and preservation of the marks suggest that they may represent isolated appendage imprints of arthropods. The lack of a definite pattern and the scarcity of the material permit no definite ichnotaxonomic assignment. The paired marks resemble the ichnogenus *Avolatichnium* Walter, 1983, although four bilaterally symmetrical imprints are characteristic of this ichnogenus. The marks described herein differ morphologically from the “appendage marks” by Keighley and Pickerill (1998), which are small rounded pits or larger blade-like prints lacking a preferred pattern.

4.11.3. Burrows with brush-like features

4.11.3.1. Description. A single specimen of hypichnial burrow (LAR-Ic 67) having a curved to slightly meandering path and fill similar to host. Some parts of the burrow filling display fine parallel ridges of very low relief that follow the axis of the burrow. Burrow diameter is 3.7 mm and the cross-section seems to be circular. This trace displays brush-like features that form an oblique angle with the axis of the burrow and are arranged in an alternate pattern. They are roughly triangular, curved outward and elongated, showing the

distal end rounded and containing internal thin laminae arranged oblique to the margin of the brush-like features. There are, at least, three groups of these features (Fig. 8B).

4.11.4. Remarks

The most significant aspect of this structure is the brush-like marks. They may represent probes of the producer during construction of the burrow.

4.12. Epichnial bilobed traces

4.12.1. Description

This category includes two specimens (LAR-Ic 30 and 58) that are similar to the “hypichnial bilobed ridges” described below, but the mode of preservation is different. They are essentially bilobed and composed of two rows of epichnial sediment pads or hypichnial elliptical depressions. LAR-Ic 58 shows a 3-mm-wide central groove, which is darker than the rest of the trace, flanked by two poorly preserved sediment-pad rows (each up to 4 mm wide). LAR-Ic 30 (Fig. 8C) is a trace 12 mm wide and 47 mm long, preserved as concave hypichnia. It is composed by two 4-mm-wide rows of oval to elliptical depressions separated by a low central ridge, which is 4 mm wide.

4.12.2. Remarks

“Epichnial bilobed traces” and “hypichnial bilobed ridges” might represent preservational variants of the same type of structure. “Epichnial bilobed traces” resemble surface burrows of mole crickets (Orthoptera: Gryllotalpidae) and the variegated mud-loving beetle (Coleoptera: Heteroceridae) (e.g. Chamberlain, 1975; Clark and Ratcliffe, 1989; Metz, 1990).

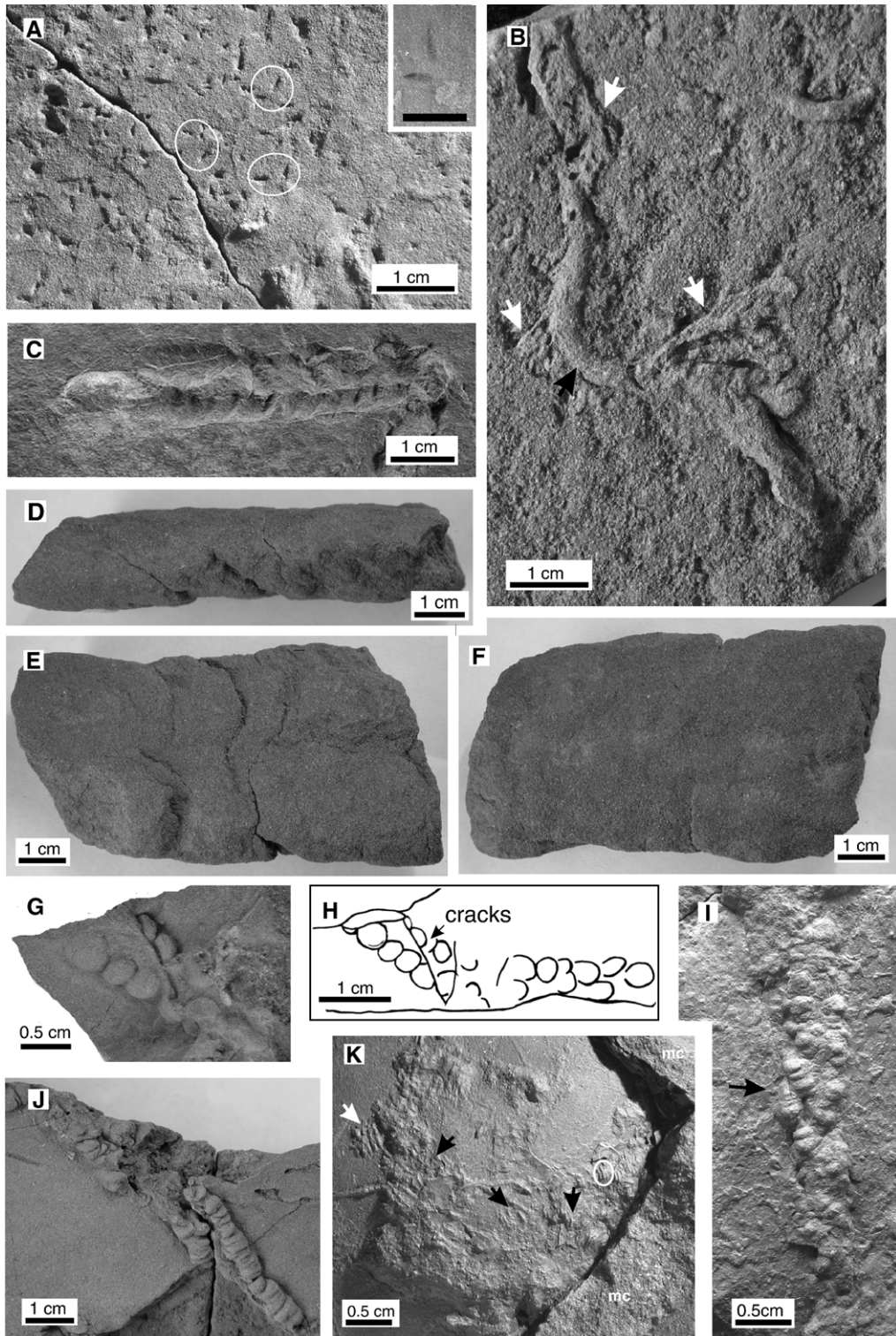
4.13. Imbricated backfilled burrow filling

4.13.1. Description

Straight burrow filling (LAR-Ic 61) composed of a series of juxtaposed and flattened pads of fine-grained sandstone. Sediment pads are neither arcuate nor meniscate and show uniform thickness (Fig. 8D). The cross section of the burrow is kidney-shaped and flattened in a direction perpendicular to its long axis because one side contains a marked groove and the opposite is convex to flat (Fig. 8E,F). The convex side of the burrow filling displays the chevron-like outline of the sediment pads. As the only available specimen was not found in situ, the hosting material and the original orientation of the structure is uncertain. Total width of trace is 44 mm, height is 17 mm (width/height

ratio=2.59), and preserved length reaches 80mm. The central groove is 6mm wide and 2mm deep. Sediment pads are 5 to 10mm thick. One weathered specimen

observed at the field was arranged at a low angle to bedding (about 10°) and the central groove was apparently oriented upward.



4.13.2. Remarks

The available material is insufficient for a complete characterisation of the trace fossil and precludes an adequate ichnotaxonomic treatment. This structure probably represents an active backfilling of a burrow. It is distinguished from other meniscate backfilled ichnotaxa because it lacks true menisci and for the kidney-shaped cross-section, which might shed light on producer affinity. The only comparable burrow casts found in the literature are some of the “type L burrows” described from Triassic floodplain deposits of Antarctica by Miller et al. (2001). The imbricated backfilled burrow fill from the Santo Domingo Formation share a similar size, width/height ratio, and the presence of a central groove and surficial chevron-like marks with some of the “type L burrows” from Antarctica. The main differences are that the central groove is located in the lower part of the burrow and that the internal structure does not seem to be imbricated in the Antarctic specimens (Miller et al., 2001). In particular, the central groove in burrow casts is considered as indicative of tetrapod origin by Miller et al. (2001). Other possible similar burrow fillings are those assigned to *T. barretti* by Gouramanis et al. (2003) from Silurian cross-bedded channel deposits of Australia.

4.14. Hypichnial bilobed ridges

4.14.1. Description

This trace fossil type includes five specimens (LAR-Ic 31, 32, 33, 59-a,b, and 60) (Fig. 8G,H,I,J). Typically curved or straight, hypichnial ridge composed of two rows of small, imbricated sediment pads with elliptical or flattened spherical form, which are arranged with alternate or parallel pattern (Fig. 8I,J). Within each specimen, the sense of inclination of sediment pads is uniform (Fig. 8J). Sediment pads display different degree of flattening or deformation. Rows are separated by an irregular groove 1 or 2 mm wide. Some sediment pads display fine concentric striae. In some cases (LAR-Ic 31 and 33), the sediment pads are arranged in a less regular form and compose no rows, instead they are located in the embayment or empty space between the

adjacent pads (Fig. 8H,I). Trace width ranges from 8 to 13 mm and preserved length from 47 to 75 mm. Sediment pads are 2–4 mm long and 1–3 mm wide (intermediate and short axis, respectively). The density of sediment pads is 3 to 6 per cm.

4.14.2. Remarks

Studied specimens display morphological differences that might reflect contrasting water saturation of the substrate. This bilobed structure probably was constructed by an arthropod and the formation of sediment pads could be the result of sideward and downward movements of appendages of the producer during burrowing (Buatois and Mángano, 2004, personal communication). The traces showing rounded, thicker and well-spaced pads and occasional surface striae (Fig. 8I) would reflect a sediment with lower water content than the traces with flattened and closely spaced pads, and smooth surface (Fig. 8J). The uniform inclination of sediment pads within each trace (Fig. 8J) possibly can be used to infer the direction of displacement of the producer, assuming that it was an arthropod. It is envisaged that the producer was moving in the direction opposite to the dipping of imbricated sediment pads. The trace can be made during locomotion, feeding or a combination of these behaviours.

4.15. Scratch marks

4.15.1. Description

Groups of two to four, short, parallel striae preserved as convex hyporelief in surfaces with mudcracks found in a single slab (LAR-Ic 29). One end of the group is more deeply imprinted. Striae are about 1–1.5 mm long and 0.2 mm wide; whereas groups of striae are less than 1 mm wide. They appear randomly arranged although some groups of striae are roughly parallel each other (Fig. 8K).

4.15.2. Remarks

Similar groups of striae can be identified in the ornament of *S. gracilis*, especially at burrow terminations (compare Figs. 6K and 8K), and in some of the

Fig. 8. Invertebrate trace fossils. (A) Bedding plane with numerous appendage marks, some of them paired (circled), preserved as concave epirelief (LAR-Ic 54). The inset displays a close-up of a pair of marks (the bar is 5 mm long). (B) Burrow with brush-like features preserved as convex hyporelief (LAR-Ic 67). The white arrows point to brush-like features and the black arrow indicates striae on burrow boundary. (C) Epichnial bilobed trace preserved as concave hyporelief (LAR-Ic 30). (D), (E) and (F) Views of imbricated backfilled burrow filling (LAR-Ic 60) showing lateral (D), convex (E) and grooved (F) sides. (G), (H), (I) and (J) Hypichnial bilobed ridges. (G) Elliptical to rounded sediment pads (LAR-Ic 59). (H) Sketch from a field photography of a partially collected specimen. The trace pictured in (G) corresponds to the left part of the sketch. (I) Sediment pads with scratch marks (arrowed). (J) Note imbrication of sediment pads in the same direction (LAR-Ic 60). (K) Scratch marks in mudcracked sole surface. The arrows and the ellipse indicate some of the groups of striae (LAR-Ic 29). Compare circled striae with those pictured in Fig. 10(B). mc = mudcrack filling.

specimens of hypichnial bilobed ridges (Fig. 8I). This shared key morphologic element suggests a common producer, probably an arthropod with sclerotized appendages, for these traces. The “scratch arrays” described by Morrissey and Braddy (2004) for the Lower Old Red Sandstone of Wales are similar to the studied scratch marks.

5. Vertebrate tracks

Part of the vertebrate tracks of the Santo Domingo Formation has been treated ichnotaxonomically by Melchor and de Valais (2006). In this contribution, a complete description of the vertebrate ichnofauna is offered, including material collected more recently. Except for the bird-like footprint types A and B, the remaining vertebrate tracks are considered as transmitted tracks or undertracks.

5.1. *Ichnogenus Dicynodontipus von Lilienstern, 1944*

5.1.1. *Dicynodontipus isp.*

5.1.1.1. Description. The material includes one collected specimen (LAR-Ic 1) and two tracks measured at the field. They are rounded pentadactyl footprints with a broad, sub-circular to sub-triangular sole and short digit impressions that commonly lack claw marks. The collected footprint is 36mm wide and 43mm long. The field specimens belong to a poorly preserved trackway. The latter tracks are larger and nearly isometric (110mm wide, 115mm long) (Fig. 9A).

5.2. *Tetrasauropus Ellenberger, 1972*

5.2.1. *Tetrasauropus isp.*

5.2.1.1. Description. A plaster cast of a manus-pes set (MPEF-IC 234) and several uncollected footprints measured at the field (one trackway and three isolated footprints) are described under this ichnogenus. The manus-pes set cast (MPEF-IC 234) belongs to the same trackway measured at the field. The pes is large (up to 300mm long and 135mm wide), sub-triangular, tetradactyl, plantigrade, and deeply imprinted. Digit imprints are short and frequently difficult to distinguish. The manus is smaller and subcircular, measuring from 120 to 150mm in diameter and showing at least three short digit impressions. The manus imprint is often less deeply impressed and may be preserved as a rounded

featureless mark or be missing. A single measured trackway has a pes pace angulation of 149° (Fig. 9B).

5.3. *Bird-like footprints*

Three bird-like footprint morphologies have been found in the succession. De Valais and Melchor (in preparation) will deal in detail with the ichnotaxonomy of these footprints.

5.3.1. *Bird-like footprint type A*

5.3.1.1. Description. The material of this ichnogenus is abundant and includes about 30 slabs that form a mosaic from a single track-surface containing several hundred footprints (LAR-Ic 5) and 3 separate slabs (LAR-Ic 6 to 8) from other stratigraphic intervals. These bird-like footprints were preliminary described by Melchor et al. (2002). They compose bipedal trackways, typically with small tetradactyl footprints (average length: 27mm) that display three digits directed forward and one (hallux) backward. The imprints of digits are slender with claw marks, the imprint of digit III is the longest, and those of digits II and IV are subequal. The footprints are almost symmetrical, wider than long, and the digits converge in a rounded sole. The average divarication of digit imprints II–IV is 115°. These footprints usually occur with high density and a seemingly random pattern in, at least, two track horizons (Fig. 9C).

5.3.2. *Bird-like footprint type B*

5.3.2.1. Description. Small bipedal trackway composed of seven small, typically tetradactyl footprints (LAR-Ic 74). Pace angulation ranges from 102° to 114°, stride length is ~32mm, and footprints display an inward rotation (8–22°). Individual footprints are 16–19mm long (including hallux imprint) and 15 to 17mm wide. The footprints have very slender and curved digit imprints; the hallux imprint is straight, backward-directed and accounts for ~40% of the footprint length. Some digit imprints display phalangeal pads, while most of them have claw marks. No webbing was observed (Fig. 9D).

5.3.2.2. Remarks. These footprint are distinguished from other described bird-like tracks because of its low pace angulation, noticeable rotation of footprints toward the midline, curvature of digit imprints II and IV, and comparatively large hallux imprints (compare Fig. 9C and D).

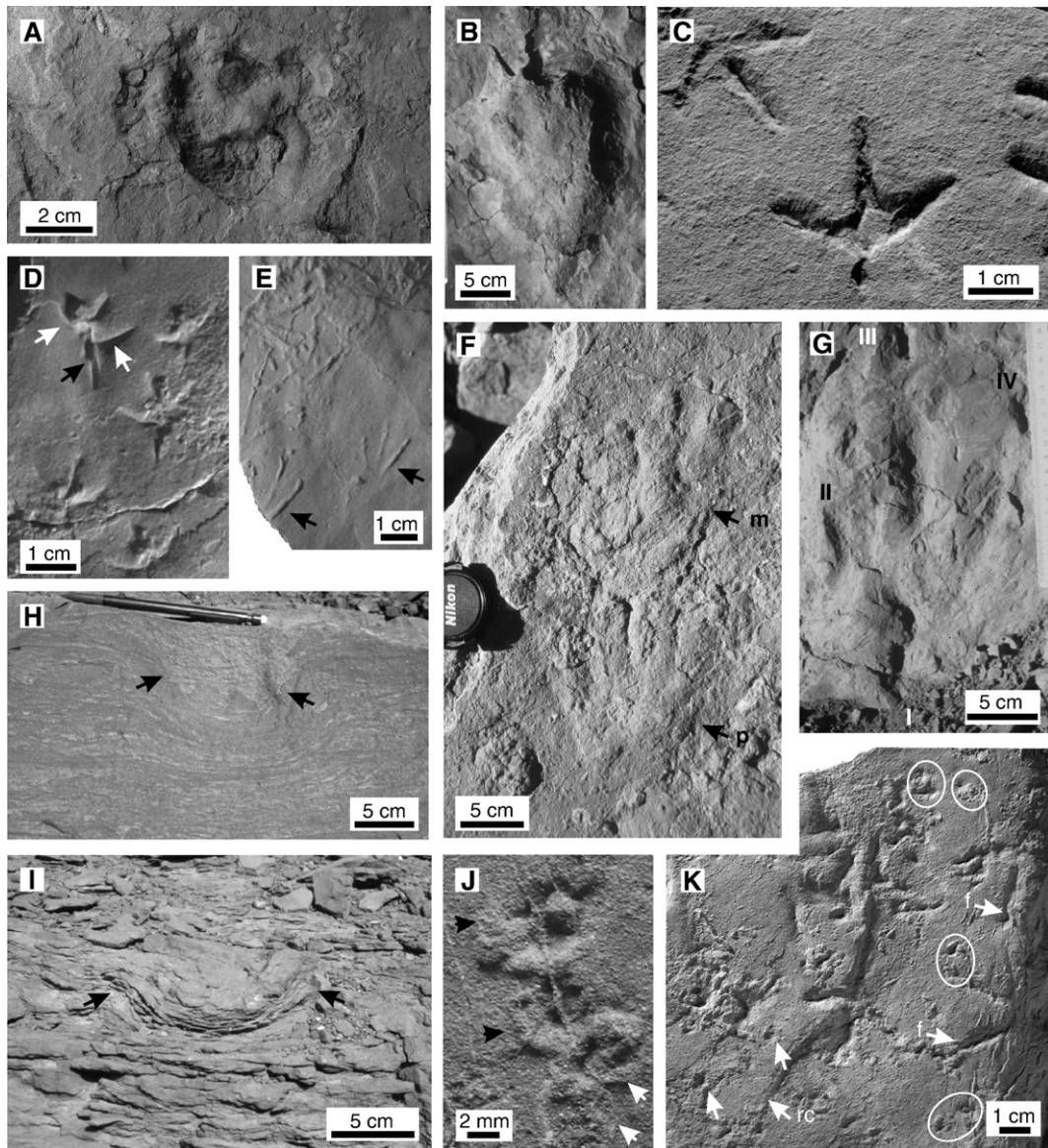


Fig. 9. Traces of vertebrates and traces of dubious affinity. (A) *Dicynodontipus* isp. (LAR-Ic 1). (B) Pes assigned to *Tetrasauropus* isp., preserved as convex hyporelief. Uncollected field specimen. (C), (D) and (E) Bird-like footprints. (C) Two isolated tracks assigned to “bird-like footprints type A”, preserved as concave epirelief (LAR-Ic 5). (D) Trackway of “bird-like footprints type B” (LAR-Ic 74). Note curved imprints of digits II and IV (white arrows) and long digit I imprint (black arrow). (E) Isolated footprints assigned to “bird-like footprints type C” (arrows point to two discrete footprints). Specimen LAR-Ic 10. (F) Large pentadactyl footprints preserved as convex hyporelief (uncollected field specimen). m=manus, p=pes. (G) Field photography of tridactyl footprint preserved as negative epirelief. I, II, III, IV: imprints of digits. (H) and (I) Field views of footprints preserved in cross-section. The arrows point to the margins of a conical “U-shaped” shaft. Note deformed laminae below the shaft in H. (J) and (K) Small epichnial rounded pits (LAR-Ic 68) preserved as concave epirelief. (J) Close-up of two pairs of pits. The pits indicated with the black arrows display a marginal ridge on the left side. The white arrows point to another possible pair. (K) Rippled bedding plane with numerous small epichnial rounded pits (arrows and circles) associated with bird-like footprints type A (f). The arrows point to isolated pits, the circles to pair of pits. rc=ripple crest.

5.3.3. Bird-like footprint type C

5.3.3.1. Description. The material assigned to this bird-like footprint type is, at least, two moderately preserved tetradactyl transmitted footprints that seem

to belong to different trackways (LAR-Ic 10), displaying a faint posterolateral hallux imprint. Footprints are 16–19 mm long and 12–15 mm wide. Digit imprints are very slender, can show phalangeal pads and claw marks, and do not join in a sole mark, which is

missing. Divarication of digits II–IV ranges from 42° to 44° and the angles between digits II–III and III–IV are similar (Fig. 9E).

5.4. Large pentadactyl footprints

5.4.1. Description

The material of this footprint type includes a plaster cast (MPEF-IC 229) and one uncollected manus-pes set. The uncollected specimen (Fig. 9F) is a manus-pes set of semiplantigrade to digitigrade quadrupedal and pentadactyl tracks showing thick and straight digit imprints and marked pads. Digit imprint length decreases from II to V, the possible imprint of digit I is considerably reduced. Size of footprints measured parallel to digit III is 160mm long by 120mm wide for the manus; and 140mm long by 130mm wide for the pes. Divarication of digit imprints II–V is 18° and 28° for manus and pes, respectively. The distance between manus and pes imprints is 20mm. Specimen MPEF-IC 229 is a deep undertrack comparable to the manus imprint of the uncollected specimen.

5.4.2. Remarks

The pes impression is similar to some chirotheriid tracks (especially *Brachychirotherium* sp.), but the manus is considerably larger than the typical for this group of tracks.

5.5. Tridactyl footprints

5.5.1. Description

Under this designation are described one collected specimen (LAR-Ic 9), a plaster cast of a field specimen (MPEF-IC 228) and two trackways measured at the field. LAR-Ic 9 corresponds to a partial tridactyl footprint showing only two well-preserved digit imprints. These isolated footprints are 80mm long, display low divarication angle between digits, clear phalangeal pads and claw marks. MPEF-IC 228 is a plaster cast of a poorly preserved tridactyl footprint showing a posterolateral hallux imprint. Without considering the hallux, the total length/width ratio is 1.4 (length 210mm, width 150mm), whereas the footprint length with the hallux reaches 265mm. Digit imprints are of similar width and display long claw marks. Relative digit lengths are III>IV>II (190mm, 150mm and 87mm), clear and rounded metatarsal impression. Divarication between digits II and IV is 52° and between I and III is 165°. The hallux imprint is 29mm long and 6mm wide (Fig. 9G).

The trackways measured at the field are composed of three and four poorly preserved tracks. The footprints are approximately 120mm long and 90mm wide. The pace angulation ranges from 170° to 180° and the pace length is 400–500mm.

5.6. Footprints preserved in cross-section

5.6.1. Description

The material comprises tens of specimens observed in the field. This type of trace fossil includes structures preserved in exposures dominantly transverse to bedding in laminated intervals. These structures are composed of a group of deformed (and/or faulted) laminae that defines a concave upward, conical or U-shaped shaft, which is overlain by undeformed and curved laminated sediments that fill the shaft and surrounding sediments. The base of the shaft is horizontal or curved downward. The laminae surrounding the shaft commonly terminate against it. The structure can be symmetric or asymmetric (compare Fig. 9H,I). These structures are 60–200mm deep, the lower part of the shaft is 20–130mm wide and the upper part of the shaft is 30–270mm wide.

5.6.2. Remarks

These structures are interpreted as footprints in cross-section by comparison with similar recent structures (e.g. van der Lingen and Andrews, 1969; Allen, 1989, 1997). They were also recorded in many fossil examples (e.g. Agenbroad, 1984; Loope, 1986; Smith et al., 1993; Lea, 1996; Loope et al., 1998; Nadon, 2001; Ashley and Liutkus, 2002; Difley and Ekdale, 2002; Fornós et al., 2002; Paik et al., 2004). These structures represent the result of application of a load by an animal foot that induces deformation and faulting of the underlying sediments and the posterior filling of the produced downfold by sediments (e.g. van der Lingen and Andrews, 1969; Allen, 1989). The extent of deformation of the sediment is related to the sediment consistency. The depth of these structures can be used to infer the relative substrate consistency (e.g. Allen, 1989; Nadon, 2001; Manning, 2004).

6. Plant traces

6.1. Root trace type A

6.1.1. Description

Numerous uncollected vertical and cylindrical empty structures of uniform diameter (about 1mm or less) that

display downward bifurcation. The maximum vertical length of individual traces reaches 30 mm. They commonly occur in large number at selected stratigraphic intervals in laminated siltstones with evaporite nodules (Fig. 10A).

6.2. Root trace type B

6.2.1. Description

A single tubular and branched structure about 55 mm long and 33 mm wide, preserved as convex hypichnia in slab LAR-Ic 35. The cross-section of the structure seems to be sub-circular and ranges from 1.5 to 0.5 mm. Successive branches consistently display smaller cross-section diameter. The structure is mostly developed on a bedding plane, although locally it cut the plane. Branching angle ranges from 70° to 90°. Root trace type B is associated with mudcracks and *S. gracilis* (Fig. 10B).

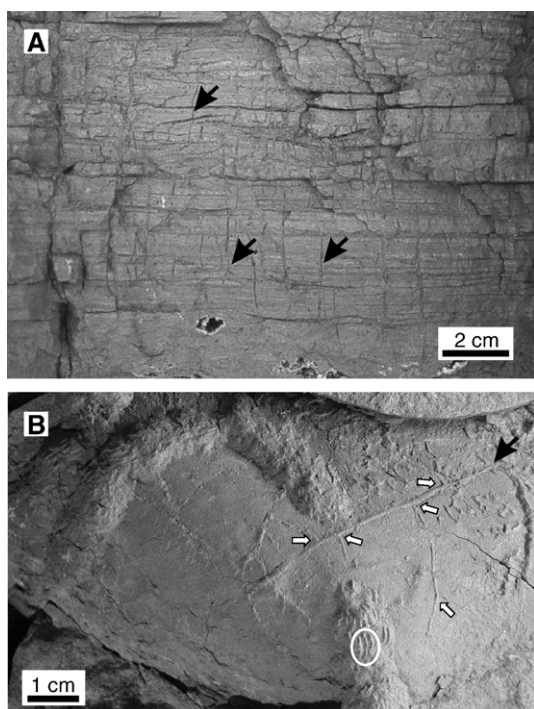


Fig. 10. Plant trace fossils. (A) Field view of numerous root traces type A (the arrows point to some specimens) in parallel laminated siltstones of facies B1. (B) Root trace type B (black arrow) and *Scoyenia gracilis* burrows on mudcracked sole surface (LAR-Ic 35). Note the progressive decrease in width of the central axis of the root trace and branching points (white arrows). The ellipse points to group of striae in *S. gracilis* that resemble the morphology of scratch marks. In this slab, *Scoyenia* burrows seem to “avoid” the root trace.

6.2.2. Remarks

This structure is considered as a root trace because of the branching pattern and distal reduction in diameter of the “tubes”. It is distinguished from mudcracks by its sub-circular cross-section and because the tubes locally intersect the bedding plane.

7. Traces of dubious affinity

7.1. Small epichnial rounded pits

7.1.1. Description

The material comprises several specimens in two slabs (LAR-Ic 5 and 68) and tens of specimens observed in the field. They are small rounded to oval pits, commonly paired, with a raised margin of variable height and preserved as negative epichnia (Fig. 9J). Maximum and minimum diameter is 5–7 mm and 4 mm, respectively. The depth of the traces is less than 1 mm. They appear on bedding surfaces in large number (up to 0.2 pits/cm²), associated with bird-like footprint type A and current ripples (Fig. 9K).

7.1.2. Remarks

The raised rims of these surface structures suggest that they were produced by displacement of moist sediment due to the pressure applied by an object. They strongly resemble modern or fossil pecking marks produced by some birds (e.g. Swennen and van der Baan, 1959; Erickson, 1967; Frey and Pemberton, 1986, 1987; Yang et al., 1995). A slightly open bill, while pecking the substrate to catch a prey, may produce paired pits (Swennen and van der Baan, 1959).

8. Trace-fossil assemblages

The trace-fossil assemblages discussed in this paper are composed of the invertebrate, vertebrate and plant ichnofossils recovered from particular sedimentary facies (Table 1). Each trace-fossil assemblage is a composite of individual occurrences of ichnotaxa in beds of the same sedimentary facies. Some of them can be considered the work of a community of organisms, or ichnocoenoses in the sense of Bromley (1990, 1996). The identification of fossil communities is uncertain in most cases (e.g. Pickerill, 1992; Keighley and Pickerill, 2003), in part due to time averaging and scarcity of crosscutting relationships (McIlroy, 2004). Identification of ichnocoenoses (sensu Ekdale, 1988; Bromley, 1990, 1996) in the studied case is generally uncertain, in consequence, it

is more accurate to consider the associations described herein as trace-fossil assemblages. The “ichnocoenoses” recognised by Keighley and Pickerill (2003) are comparable to trace fossil assemblages, as defined herein.

The taxonomic composition and ichnodiversity of trace-fossil assemblages of the different sedimentary facies of the Santo Domingo Formation is summarised in Table 2. Table 3 lists the possible producers of the studied trace fossils. These assemblages are described below grouped according to the

hosting facies (Buatois and Mángano, 1996, 2004) and distinguishing between fluvial channel (facies A1 and C2), overbank (facies A2 and B1) and shallow lacustrine (facies B2 and C1) settings. When possible, the definite trace fossil-bearing strata within a sedimentary facies (subfacies) are distinguished along with the interpreted subenvironment of occurrence (Table 2). For example, trace fossils in facies A2 occur in floodplain ponds but this facies also include associated sheetflood deposits, which lack trace fossils.

Table 2

Quantitative composition of the trace-fossil assemblages arranged in three major settings: fluvial channel, overbank, and shallow lacustrine

Trace fossils	Trace fossil assemblages					
	Fluvial channel		Overbank		Shallow lacustrine	
	Ephemeral channel (A1 + C2)	Floodplain pond (A2)	Poorly drained floodplain (B1)	Nearshore lacustrine (B2)	Mudflat (C1)	
<i>Invertebrate trace fossils</i>						
<i>Cochlichnus anguineus</i>				1		
<i>Cruziana problematica</i>				1		
<i>Diplichnites</i> isp.	2	2				
<i>Helminthoidichnites tenuis</i>		2	1	1	1	
<i>Palaeophycus heberti</i>				1		
<i>Palaeophycus striatus</i>				3		
<i>Palaeophycus tubularis</i>	2	7		2	1	
<i>Rusophycus carbonarius</i>		2				
<i>Scoyenia gracilis</i>				3		
<i>Skolithos linearis</i>	4	2				
<i>Spongiomorpha carlsbergi</i>		2	1	7	1	
? <i>Spongiomorpha</i> isp.			1			
<i>Taenidium barretti</i>	1	6		4		
Appendage marks		1				
Burrow with brush-like features		1				
Epichnial bilobed traces		1		1		
Imbricated backfilled burrow filling			1			
Hypichnial bilobed ridges		2		3		
Scratch marks				1		
<i>Vertebrate tracks</i>						
<i>Dicynodontipus</i> isp.	1				1	
<i>Tetrasauropus</i> isp.			1		1	
Bird-like footprints type A		10	2			
Bird-like footprints type B					1	
Bird-like footprints type C					1	
Large pentadactyl footprints			1		1	
Tridactyl footprints		1	3		1	
Footprint preserved in cross-section	1	2	10			
<i>Plant trace fossils</i>						
Root trace type A			3			
Root trace type B				1		
<i>Dubious traces</i>						
Small epichnial rounded pits		5				

Table 3
Possible producers of trace fossils

Trace fossils	Possible producer	Source
<i>Invertebrate trace fossils</i>		
<i>Cochlichnus anguineus</i>	Insect larvae	Metz (1987)
<i>Cruziana problematica</i>	Freshwater crustacean	Bromley and Asgaard (1979)
<i>Diplichnites</i> isp.	Unidentified arthropod,	
<i>Helminthoidichnites tenuis</i>	nematomorphs or insect larvae	Buatois et al. (1997, 1998)
<i>Palaeophycus heberti</i>	Unknown invertebrate	Pemberton and Frey (1982)
<i>Palaeophycus striatus</i>	Unknown invertebrate	Pemberton and Frey (1982)
<i>Palaeophycus tubularis</i>	Unknown invertebrate	Pemberton and Frey (1982)
<i>Rusophycus carbonarius</i>	Freshwater crustacean	Bromley and Asgaard (1979)
<i>Scoyenia gracilis</i>	Decapods, insects, polychaetes, millipedes, undetermined arthropods	Olsen (1977), Bromley and Asgaard (1979), Frey et al. (1984), D'Alessandro et al. (1987), Retallack (2001)
<i>Skolithos linearis</i>	Insects, spiders, crustaceans	Stanley and Fagerstrom (1974), Bromley and Asgaard (1979), Ratcliffe and Fagerstrom (1980), Scourse (1996)
<i>Spongeliomorpha carlsbergi</i>	Terrestrial insect (larvae?)	Bromley and Asgaard (1979), Metz (1990, 1993a, 1996), Clark and Ratcliffe (1989)
<i>Taenidium barretti</i>	Insects, earthworms	Bown and Kraus (1983), Frey et al. (1984), Retallack (1990), Buatois and Mángano (1996), O'Geen and Busacca (2001)
Appendage marks	Unidentified arthropod	This paper
Burrow w/ brush-like features	Unknown	This paper
Epichnial bilobed traces	Arthropod (insect?)	This paper
Imbricated backfilled burrow filling	Unidentified vertebrate?	Miller et al. (2001)
Hypichnial bilobed ridges	Insects? (same as for <i>Scoyenia</i>)	This paper
Scratch marks	Insects? (same as for <i>Scoyenia</i>)	This paper
<i>Vertebrate tracks</i>		
<i>Dicynodontipus</i> isp.	Therapsid	Haubold (1984)

Table 3 (continued)

Trace fossils	Possible producer	Source
<i>Tetrasauropus</i> isp.	Prosauropod dinosaur	Ellenberger (1972), Haubold (1984), Lockley and Hunt (1995)
Bird-like footprints type A	Small theropod?	Melchor et al. (2002)
Bird-like footprints type B	Unknown vertebrate	This paper
Bird-like footprints type C	Unknown vertebrate	This paper
Large pentadactyl footprints	Unknown vertebrate	This paper
Tridactyl footprints	Theropod dinosaur	Haubold (1984)
Footprint preserved in cross-section	Unidentified vertebrates	This paper
<i>Plant trace fossils</i>		
Root trace type A	Herbaceous plants	Retallack (1983), Bockelie (1994)
Root trace type B	Unknown	This paper
<i>Dubious traces</i>		
Small epichnial rounded pits	Small theropod?	This paper

8.1. Fluvial channel assemblages

8.1.1. Ephemeral fluvial channel assemblage (facies A1 + C2)

These assemblages display the lowest ichnodiversity, although the associated overbank assemblage of facies A2 records the highest ichnodiversity of the studied assemblages (Table 1). Only a footprint preserved in cross-section was recorded in shallow, ephemeral ribbon channels (facies A1). This footprint occurs within the channel fill and is suggestive of non-permanent fluvial flows. The assemblage from coarser-grained, ephemeral channels (facies C2) includes five ichnotaxa (Tables 1 and 2) and is dominated by vertical dwelling burrows (*S. linearis*) and rare arthropod trackways (*Diplichnites* sp.), simple burrows (*P. tubularis*), meniscate burrows (*T. barretti*) and vertebrate footprints (*Dicynodontipus* sp.). Except for *Skolithos*, trace fossils occur in the upper part of the channel fill (Fig. 3) and are thus likely produced during the abandonment phase. Comparable assemblages were described by Demathieu and Wycisk (1990), Schlirf et al. (2001) and Keighley and Pickerill (2003). The ephemeral channel assemblage share some elements with overbank assemblages (as noted by Buatois and Mángano, 2004), although the latter assemblages are much more diverse.

8.2. Overbank assemblages

8.2.1. Floodplain pond assemblage (facies A2)

The overbank assemblage of facies A2 shows 15 trace fossil types that are recorded from intervals interpreted as floodplain ponds (Table 1). They are dominated by simple or meniscate burrows (*P. tubularis* and *T. barretti*, respectively) and by bird-like footprint type A and associated small rounded pits. At least, two densely trampled track surfaces with bird-like footprint type A were recognised (Fig. 3). In addition, this assemblage includes arthropod resting (appendage marks), feeding (*R. carbonarius*), and locomotion traces (*Diplichnites* isp.); vertical burrows (*S. linearis*); epichnial bilobed traces and hypichnial bilobed ridges; simple trails (*H. tenuis*); burrows with scratches (*S. carlsbergi*); burrows with brush like marks, and footprints preserved in cross-section. Crosscutting relationships are scarce but some general relationships regarding the sequence of colonization of the ponds can be recognised, using the interval exposed at 1650m of the section (Fig. 3), and partly based on speculations about the relative sharpness of burrow walls or imprints (e.g. Buatois et al., 1997) and on the sedimentary features of the hosting sediments. This interval is envisaged as a small and shallow (i.e. less than 20–30mm deep) pond of sheetflood origin emplaced in a low-relief landscape. The occupation of the pond by different animals probably was immediate after the original sheetflooding event and accompanied the partial desiccation of the pond. The absence of mudcracks suggests that complete desiccation did not occur and that the lifetime of the pond did not exceed a few days. However, part of the pond was sufficiently long-lived to enable the development of algal mats, as indicated by the presence of wrinkle marks. The large number and random pattern of bird-like footprint type A and of associated small rounded pits overprinted on small current ripples, suggest the feeding activities of unknown vertebrates (possibly small theropods) on the newly formed pond (Melchor et al., 2002). Soft or moist pond deposits recorded the activities of the producers of *H. tenuis*, *T. barretti* and those of the epi- and hypichnial bilobed traces, which may have been potential prey for the producers of bird-like footprints. It is possible that the latter were also feeding on small arthropods, whose traces are represented by *Diplichnites* isp., *R. carbonarius*, and appendage marks. The sharpness of appendage marks and of scratch marks in *Rusophycus* probably reflects a partially desiccated substrate. Ornamented *Spongeliomorpha* burrows were possibly excavated in a dehydrated (firm?) substrate, although this inference is

only based on the presence of scratches on the burrow walls. *Skolithos* burrows cut the laminae containing bird-like footprints, for this reason it is uncertain if this trace was produced by a member of the same community. In conclusion, the floodplain pond assemblage is characterised by the largest diversity of trace fossil types and by abundant bird-like footprint type A. Its composition can be compared with the Tertiary ichnofauna from the Fildes Peninsula, West Antarctica (Covacevich and Lamperein, 1970; Covacevich and Rich, 1982; Jianjun and Shuonan, 1994); as well as, with the Cretaceous ichnofauna of the Jindong Formation, Korea (Lockley et al., 1992) (Table 2).

8.2.2. Poorly drained floodplain assemblage (facies B1)

The trace-fossil assemblage recovered from a poorly drained floodplain setting (Table 1) is distinguished by the dominance of footprints preserved in cross-section and subordinate tridactyl footprints and root traces type A (Table 2). Other ichnofossils include the tracks of large animals (*Tetrasauropus* isp. and large pentadactyl footprints); small bird-like footprint type A, the endichnial ornamented burrow *S. carlsbergi*, simple trails (*Helminthoidichnites*), and imbricated backfilled burrow of possible vertebrate origin. The significant aspect of this trace-fossil assemblage is the recurrence of deeply imprinted footprints observed in cross-section associated to deformed stratification and finely laminated siltstones with mud drapes. These features reflect a moderately high moisture content of the floodplain sediments (e.g. Nadon, 2001; Difley and Ekdale, 2002) and weak, intermittent aqueous currents. Other traces from this assemblage formed in soft (possibly subaqueous) substrates are *H. tenuis* and *P. tubularis*. Except for the footprints in cross-section, for which direct evidence is lacking, the remaining footprints were likely imprinted in a subaerial, partially desiccated setting, as indicated by associated raindrop imprints, mudcracks, and ornamented burrows (*S. carlsbergi*). Similarly, intervals where deeply imprinted footprints are lacking that either display imbricated backfilled burrow filling associated with *S. carlsbergi* or fine root traces (type A) in conjunction with evaporite nodules, suggest a substrate with lower water saturation than those containing abundant footprints preserved in cross-section. It is not certain if the former intervals represent periods of drier climatic conditions or better-drained areas of the floodplain. To summarise, the assemblage from poorly drained floodplain settings is distinguished by the recurrence of deeply penetrating footprints observed in cross-section. In this

regard, it is comparable with Maastrichtian dinosaur trampled beds from Utah described by Difley and Ekdale (2002), which were interpreted as produced in wet/soft mud of seasonal wetlands in floodplain depressions or close to anastomosing rivers, predominantly with high water tables.

8.3. Shallow lacustrine assemblages

8.3.1. Nearshore lacustrine assemblage (facies B2)

The nearshore lacustrine assemblage is only recorded in the upper sandstone interval of the typical shallowing-upward cycles of facies B2, which are interpreted as subaqueous to subaerial shoreline lacustrine deposits (Fig. 4). This is a high ichnodiversity assemblage (thirteen trace fossil types) dominated by striated and/or meniscate burrows (*S. carlsbergi*, *T. barretti*, *P. striatus*, *S. gracilis*), which are commonly associated with mudcracks, and hypichnial bilobed ridges. The assemblage also includes simple burrows (*C. anguineus*, *H. tenuis*, *P. tubularis*), lined burrows (*P. heberti*), *C. problematica*, scratch marks, epichnial bilobed ridges and root traces type B. No vertebrate tracks were found in this assemblage (Table 2).

Crosscutting relationships between trace fossils and between trace fossils and mudcracks, in conjunction with the presence or absence of mudcracks in the intervals with trace fossils allow to reconstruct the history of colonization of this shallow lacustrine setting, especially in relation to water-level changes and varying substrate consistency. Mudcracks cross cut *Spongeliomorpha* (the most common relationship), *Scoyenia* (Fig. 6J,K) and *Helminthoidichnites*; although a single specimen of *Spongeliomorpha* is located within a mudcrack filling. *Spongeliomorpha* was found intersecting *Helminthoidichnites* and *Cochlichnus* burrows and *Scoyenia* cutting *Helminthoidichnites*. In addition, epichnial bilobed traces, hypichnial bilobed ridges, *C. problematica*, and *P. heberti* are not associated with mudcracks. *Cochlichnus*, *Helminthoidichnites*, *Taenidium*, and probably epi- and hypichnial bilobed traces, and root traces type B; would have been constructed in soupy to soft substrates with the highest water saturation (Buatois et al., 1997). The ornamented burrows *Spongeliomorpha*, *Scoyenia* and *P. striatus*, in addition to scratch marks and possibly hypichnial bilobed ridges with striated sediment pads, were constructed in a moist substrate that was firm or cohesive enough to cast the scratches made by hard parts of the producing organisms. Continued desiccation led to the formation of mudcracks that intersected the previously mentioned burrows. The location of some mudcracks along

previous *Spongeliomorpha* burrows suggests a possible control on mudcrack emplacement (Baldwin, 1974; Kazanci et al., 2001). Successive desiccation/wetting cycles of the lacustrine shoreline sediments are indicated by the stacking of two or more mudcracked surfaces, by the existence of cracks of contrasting width (from less than 1 mm to 10 mm), and by a single *Spongeliomorpha* burrow excavated in a mudcrack filling.

As discussed above, *S. gracilis* burrows, some hypichnial bilobed ridges and scratch marks share the presence of three short, parallel striae of similar size. This shared element is possibly indicative of a single producer for these traces, which may reflect different burrowing strategies in response to varying substrate consistency. The scratch marks are interpreted as probes to assess the consistency of the substrate, in the case pictured in Fig. 8K the animal probably stopped burrowing because the substrate was too firm. The construction of *Scoyenia* burrows would be related to the ideal condition of the substrate for excavation. Hypichnial bilobed ridges were possibly constructed in substrates with higher moisture content, as suggested by deformed sediment pads (Fig. 8J) and occasional preservation of striae (Fig. 8I). In addition, the producer of *Scoyenia* seems to avoid roots as suggested by a burrow that is apparently deflected in the proximity of a root trace (Fig. 10B).

The relatively thick lining of *P. heberti* could indicate reinforcement of the burrow walls, either to give greater stability in a sediment with high water content or to prevent from water loss in a desiccated sediment (deep burrows in desiccated substrate?). Although no crosscutting relationships were identified, it is considered that the second alternative is more compatible with the outlined environmental setting.

In consequence, the nearshore lacustrine assemblage is typified by a high ichnodiversity and by dominance of striated and/or meniscate burrows (*S. carlsbergi*, *T. barretti*, *P. striatus*, *S. gracilis*). Some examples of similar trace-fossil assemblages are the Triassic Rusophycus and *Scoyenia* ichnocoenoses from Greenland described by Bromley and Asgaard (1979), the Late Triassic lacustrine assemblages from the Passaic Formation of Pennsylvania (Metz, 1996), and the Rusophycus versans ichnocoenosis from Late Triassic ephemeral lacustrine deposits of Germany (Schlirf et al., 2001).

8.3.2. Mudflat assemblage (facies C1)

The mudflat assemblage displays moderate ichnodiversity (nine trace fossil types) and no dominant ichnotaxa, although records the largest number of

vertebrate track types ($n=6$). The invertebrate traces include simple (*H. tenuis*, *P. tubularis*) and ornamented burrows (*S. carlsbergi*). The recorded vertebrate tracks are *Dicynodontipus* isp., *Tetrasauropus* isp., bird-like footprint types B and C, large pentadactyl footprints, and tridactyl footprints. Both vertebrate and invertebrate trace fossils were mostly recorded from a few beds from the coarser-grained intervals (siltstone and fine-grained sandstone) that are considered as the fringing clastic facies of the mudflat, which were deposited by sheet-flooding events. Playa-lake settings represent stressful environmental conditions and the faunal and floral diversity is typically low (e.g. Townsend et al., 2002; Buatois and Mángano, 2004). The association of the trace fossils to marginal clastic facies might indicate that the periods of flooding created better preservational conditions for trace fossils or that these events were related to reduced stress (e.g. lower salinity) and increased the availability of food or prey resources (e.g. Scrivner and Bottjer, 1986; Gierlowski-Kordesch, 1991; Buatois and Mángano, 2004).

The large variety of vertebrate track types recorded in the mudflat assemblage is in accordance with the inferred high preservation potential of vertebrate tracks in mudflats of playa-lakes (e.g. Scrivner and Bottjer, 1986).

9. Implications for continental ichnofacies

The five described trace-fossil assemblages encompass thirty morphological types. Fifty-three percent of these trace fossil types were recorded from a single assemblage and 27% from two additional assemblages (Table 2). Only 20% of the recorded trace fossil types occur in three or four of the assemblages, including *H. tenuis*, *P. tubularis*, *S. carlsbergi*, *T. barretti*, footprints preserved in cross-section and tridactyl footprints (Table 2). The latter trace fossil types are considered as facies-crossing elements. The complete ichnofauna, individual trace-fossil assemblages, and the facies-crossing elements from the Santo Domingo Formation contain the distinctive trace fossils of the Scoyenia ichnofacies (sensu Frey et al., 1984; Frey and Pemberton, 1987; Buatois and Mángano, 1995, 1998). The proposal for emendation of the Scoyenia and Mermia ichnofacies and the procedures used by Keighley and Pickerill (2003) are not followed here because a number of problems are found. These authors observed that some nonmarine ichnocoenoses exhibited components that occur in the Mermia and Scoyenia ichnofacies and they suggested that a more strict definition of both ichnofacies is needed. Essentially, Keighley and Pickerill

(2003) excluded ichnotaxa typical, although not exclusive, of the Mermia ichnofacies (sensu Buatois and Mángano, 1995, 1998) from the Scoyenia ichnofacies, without considering if they compose a single suite (or ichnocoenosis) or not. The proposed set of morphological groupings of trace fossils (Table 1, Keighley and Pickerill, 2003) is not fully objective, as the category VIII includes vertebrate and invertebrate trackways, which do not share a common morphology but a common behavioural meaning (locomotion). In addition, it is generally accepted that the morphology of (invertebrate) trace fossils is a reflection of behaviour (e.g. Bromley, 1990, 1996), these behavioural inferences are the more informative aspect of a trace fossil assemblage that give clues about a set of environmental conditions. Finally, the recognition of each ichnofacies by Keighley and Pickerill (2003) is made on the basis of the presence of individual ichnotaxa or morphological groupings instead of comparing the suites, ichnocoenosis or assemblages of trace fossils, and without distinguishing dominant from subordinate ichnotaxa.

The outlined distribution of trace fossil types and the differences between the trace-fossil assemblages of the Santo Domingo Formation emphasise the potential for subdivision of the Scoyenia ichnofacies (e.g. Bromley and Asgaard, 1979), probably defining ichnosubfacies (sensu Seilacher, 1974). However, such a proposal cannot be undertaken without further detailed studies that consider sedimentary facies, invertebrate, vertebrate and plant trace fossils in combination, along with an analysis of recurrent patterns of these trace fossils in different environments included in the Scoyenia ichnofacies. This approach is the most informative as an aid in the understanding of the palaeoecological meaning and potential relationships between animal and plant communities and the depositional setting (e.g. Goldring, 1993).

Tetrapod tracks cannot be treated as a single morphologic/behavioural category as proposed in the original definition of the Scoyenia ichnofacies (Seilacher, 1967) and subsequent usage, as that approach convey little palaeoecological or palaeoenvironmental information. This aspect is exemplified in the trace-fossil assemblage from floodplain ponds, where the essential element is the presence of bird-like footprint type A, although other track types were recorded (Table 2). The apparent recurrence of bird tracks in shoreline (both lacustrine and marine) environments was noted by Lockley et al. (1994), who proposed the “shorebird ichnofacies”. The association of bird tracks with shoreline environments gives some insights about the

possible categorisation of vertebrate traces. In addition to integrating vertebrate with plant and invertebrate ichnofossils, the definition of each vertebrate ichnofacies is in need of revision in order to demonstrate its temporal and geographic recurrence and association with definite sedimentary facies (see criticism by McIlroy, 2004). As a consequence of applying of the suggested procedures, most vertebrate ichnofacies will become subdivisions of the Scoyenia ichnofacies (Lockley et al., 1994), but also encompassing the associated invertebrate and plant trace fossils. The “shorebird ichnofacies” (Lockley et al., 1994) and the “red bed ichnofacies” (Hunt et al., 1995) are examples of proposed vertebrate ichnofacies that might be integrated to the Scoyenia ichnofacies as ichnosubfacies.

Despite the current difficulty of finding repetitive patterns of trace fossils in different sedimentary facies, some trace-fossil assemblages contain two characteristic suites of trace fossils (sensu Bromley, 1975, 1990) that are linked to changes in substrate consistency and water saturation, generally coupled to base level changes. Buatois and Mángano (2002, 2004) proposed that the Scoyenia ichnofacies includes a “pre-desiccation suite” with structures lacking ornamentation (e.g. *Taenidium*, *Beaconites*) and developed in a soft substrate and a “desiccation suite” typified by striated traces (e.g. *Scoyenia*, *Spongeliomorpha*) that crosscut the former. The superposition of these suites has been recognised as a composite ichnofabric (Buatois and Mángano, 2004) linked to the desiccation of a water-lain sediment. The distinction of these suites stresses the importance of water availability for continental trace fossil distribution and occurrence (Bromley and Asgaard, 1979, 1991; Gierlowski-Kordesch, 1991). Partially similar ichnocoenoses have been considered by Keighley and Pickerill (2003) and Kim et al. (2005) as representatives of separate ichnofacies and the resulting palimpsest trace-fossil assemblage as a composite of two or more ichnofacies (e.g. Mermia–Scoyenia composite). It is agreed that the distinction of composite or mixed ichnofacies should be based on crosscutting relationships but none of the examples from the Carboniferous of eastern Canada studied by Keighley and Pickerill (2003) satisfy this criterion. For example, the ichnocoenosis C of Keighley and Pickerill (2003; Table 2), presented as a case of the Mermia–Scoyenia composite ichnofacies, contains four trace fossils that belong to the Scoyenia ichnofacies (*C. problematica*, *R. carbonarius*, cf. *R. carbonarius*, and plug-shaped burrows) and a single ichnotaxa (*Helminhopsis hieroglyphica*) considered as a representative of the Mermia ichnofacies. In the cases of composite ichnofacies discussed, no

evidence suggesting an overprinting of different groups of trace fossils (i.e. suites) is presented.

Using the terminology of Keighley and Pickerill (2003), it is argued that the Scoyenia ichnofacies is composite by definition or subsequent usage (e.g. Frey et al., 1984), as it is characteristically linked to floodplain water bodies and shallow lacustrine settings showing frequent inundation and exposure.

Pre-desiccation and desiccation suites (Buatois and Mángano, 2002, 2004) can be consistently distinguished using crosscutting relationship between different ichnotaxa (e.g. Buatois et al., 1996; Buatois and Mángano, 2002, 2004). Other indicators such as relative definition of burrow margins (i.e. clear burrow margins indicate firmer substrates than poorly defined ones), the degree of sharpness of invertebrate impressions (sharp vs. blurred imprints), and deformation of lamination of the hosting sediment (e.g. Buatois et al., 1997; Keighley and Pickerill, 2003; Morrissey and Braddy, 2004; Kim et al., 2005) are much less reliable and sometimes subjective. Similarly, it is not certain what range of substrate consistency is adequate for preservation of striated burrow walls. Preservation of striae is commonly taken as indicative of burrowing in a firm or desiccated substrate. However, modern mole cricket burrows are constructed in moist sediments despite displaying striae (Metz, 1990). The potential of preservation of these scratches in modern burrows is uncertain; however, it is envisaged that cohesive mud and/or fine-grained sediment saturated in saline brines might help to preserve these features in the fossil record. For these reasons, it is considered that the assumption that ornamented burrows indicate firm or desiccated substrates should be contrasted with independent evidence in each case study. When the trace-fossil assemblage includes tetrapod footprints, some speculations concerning the consistency of the substrate can be drawn from the degree of preservation of anatomical details and the depth of the impressions (e.g. Peabody, 1948; Scrivner and Bottjer, 1986; Haubold et al., 1995). Except for crosscutting relationships, the exact meaning of the mentioned criteria (e.g. preservational variants of tetrapod footprints vs. substrate consistency), as well as the influence of algal mats on track preservation, should be tested by neoichnological studies (e.g. Chamberlain, 1975; Clark and Ratcliffe, 1989; Cohen et al., 1993; Allen, 1997; Manning, 2004).

Examples of pre-desiccation and desiccation trace fossil suites can be identified in the trace-fossil assemblages studied herein (Table 4). In particular, the nearshore lacustrine trace-fossil assemblage is considered

the best example because the suites are distinguished by crosscutting relationships. In this assemblage, the presence of one ornamented burrow in a mudcrack filling is indicative of rewetting of a desiccated substrate. This is an example of a potentially complicating factor for identification of the mentioned suites of trace fossils, although a large sample size would allow recognition of these relationships. Two additional examples are the poorly drained floodplain and floodplain pond trace-fossil assemblages, although they are considered less reliable because the suites are distinguished using features like presence of deep vertebrate tracks, ornamented burrows and sharpness of invertebrate imprints (Table 4).

In addition to Buatois et al. (1996), previously described examples where these suites were recognised with confidence are scarce and are generally not based

on crosscutting relationships (Table 4). The example from the Late Pleistocene flash-flood sediments of Namibia described by Smith et al. (1993) is considered tentative because recognition of the ichnogenus *Termitichnus* in this ichnofauna has been disputed (Genise et al., 2000). Metz (1996) described a Late Triassic lake shoreline assemblage from the Newark Supergroup that display a number of surface grazing trails typical of the Mermia ichnofacies, although the author highlighted that *Scoyenia* was the most common ichnotaxon. The *Scoyenia* and *Rusophycus* assemblages from the Triassic of Greenland described by Bromley and Asgaard (1979) are entirely composed of striated trace fossils (*C. problematica*, *Rusophycus eutendorfensis*, *S. gracilis*, *S. carlsbergi*, and striated oblique burrows) and the softground (pre-desiccation) suite is apparently missing.

Table 4
Examples of trace-fossil assemblages that display pre-desiccation and desiccation suites

Trace fossil assemblage	Pre-desiccation suite	Desiccation suite	Distinguishing criteria
Nearshore lacustrine (this study)	<i>Cochlichnus anguineus</i> , <i>Helminthoidichnites tenuis</i> , <i>Taenidium barretti</i> , epichnial bilobed traces, hypichnial bilobed ridges, root traces type B	<i>Palaeophycus striatus</i> , <i>Palaeophycus heberti</i> , <i>Spongeliomorpha carlsbergi</i> , <i>Scoyenia gracilis</i> , scratch marks	Crosscutting relationships
Poorly drained floodplain (this study)	Deeply imprinted footprints, <i>Helminthoidichnites tenuis</i> , <i>Taenidium barretti</i> , <i>Palaeophycus tubularis</i> , <i>Dicynodontypus</i> isp., bird-like footprints type A, large pentadactyl footprints, Tridactyl footprints	<i>Spongeliomorpha carlsbergi</i> , ? <i>Spongeliomorpha</i> isp., imbricated backfilled burrow filling, root traces type A	Depth of tracks, burrow ornamentation
Floodplain pond (this study)	<i>Helminthoidichnites tenuis</i> , <i>Diplichnites</i> isp., <i>Taenidium barretti</i> , epichnial bilobed traces, bird-like footprints type A, small rounded pits	<i>Spongeliomorpha carlsbergi</i> (<i>Rusophycus carbonarius</i> , appendage marks)	Crosscutting relationships, burrow ornamentation, sharpness of imprints
Sheetflood deposits (Smith et al., 1993)	<i>Skolithos linearis</i> , <i>Taenidium satanassi</i> , <i>Planolites</i> isp., invertebrate trail	Pellet-filled chambers and burrows, pellet-lined burrows, rhizoconcretions (?= <i>Termitichnus</i>), <i>Chondrites</i> -like traces, <i>Monomorphichnus</i> -like tracks	Crosscutting relationships
Desiccated floodplain (Buatois et al., 1996)	<i>Taenidium barretti</i> , <i>Didymaulichnus lyelli</i> , <i>Palaeophycus tubularis</i> , <i>P. striatus</i>	Meniscate striated traces	Crosscutting relationships, burrow ornamentation
Closed lake shoreline (Metz, 1996)	<i>Cochlichnus anguineus</i> , <i>Didymaulichnus lyelli</i> , <i>Helminthopsis</i> isp., <i>Mermia carickensis</i> , <i>Palaeophycus alternatus</i> , <i>P. tubularis</i> , <i>Planolites annularis</i> , <i>P. beverleyensis</i> , <i>Treptichnus bifurcus</i> , <i>T. pollardi</i>	<i>Scoyenia gracilis</i> , <i>Spongeliomorpha carlsbergi</i> , reptile footprints (?)	Burrow ornamentation
Track ichnoconosis # 6 (Melchor and Sarjeant, 2004)	<i>Batrachichnus salamandroides</i> , Swimming trace type A, <i>Palaeophycus</i> isp., arthropod locomotion traces	<i>Scoyenia</i> isp.	Burrow ornamentation, swimming trace
Trackway-bearing ichnoconosis # 4 (Kim et al., 2005)	<i>Beaconites antarcticus</i> , <i>Beaconites coronus</i> , <i>Cochlichnus anguineus</i> , <i>Planolites beverleyensis</i> , <i>Taenidium barretti</i>	<i>Diplichnites</i> ispp.	Burrow boundary, sharpness of imprints

10. Conclusions

Detailed sedimentological analysis of the trace-fossil bearing strata from the Santo Domingo Formation (Fig. 2) suggests that this part of the succession was deposited in an ephemeral fluvio-lacustrine system probably comparable with a terminal fan. Three facies associations were recognised, each composed of two sedimentary facies (Table 1, Figs. 3 and 4). Facies association A includes shallow, ribbon ephemeral channels (facies A1) and floodplain ponds and proximal sheetflood deposits (facies A2). Facies association B is comprised of poorly drained floodplain (wetland?) and distal sheetflood deposits (facies B1) and shallow freshwater lakes (facies B2). Facies association C includes playa-lake mudflats (facies C1) and ephemeral channels entrenched in playa-lake mudflats (facies C2).

Thirty invertebrate, vertebrate and plant trace fossil types were identified ichnotaxonomically. The analysis of the distribution of these trace fossil types in the six sedimentary facies allows determination of five distinctive trace-fossil assemblages that can be grouped in fluvial channel, overbank, and shallow lacustrine settings (Tables 1 and 2). The distinctiveness of the trace-fossil assemblages is established owing to the high ichnodiversity in the assemblages. The fluvial channel setting is represented by an impoverished ephemeral channel assemblage (facies A1 and C1). Overbank settings yielded a high ichnodiversity floodplain pond assemblage (facies A2) typified by abundant bird-like footprint type A, and a poorly drained floodplain assemblage (facies B1) that is distinguished by the recurrence of deeply penetrating footprints. Crosscutting relationships of the floodplain pond assemblage permit documentation of the progressive colonization during desiccation of a shallow floodplain pond. Shallow lacustrine settings encompass a diverse near-shore lacustrine assemblage (facies B2) characterised by dominance of striated and/or meniscate burrows and a mudflat assemblage (facies C1) showing moderate ichnodiversity and the largest variety of vertebrate track types.

The ichnofauna of the Santo Domingo Formation and each component trace-fossil assemblage are considered as representative of the Scoyenia ichnofacies. It is illuminating that the facies-crossing elements (*H. tenuis*, *P. tubularis*, *S. carlsbergi*, *T. barretti*, footprints preserved in cross-section and tridactyl footprints) include the essential components of the Scoyenia ichnofacies (Seilacher, 1967), which underscore the validity and usefulness of that ichnofacies in a broad sense. Compositional and lithofacial differences of the

trace-fossil assemblages from the Santo Domingo Formation also highlight the viability of identification of ichnosubfacies within the Scoyenia ichnofacies. For example, the poorly drained floodplain assemblage is potentially distinctive and can be linked to tetrapod trampling in substrates with relatively high water saturation, like wetlands (e.g. Ashley and Liutkus, 2002; Difley and Ekdale, 2002). Further case studies that integrate facies analysis and describe in detail invertebrate, vertebrate and plant trace fossils are necessary in order to define recurrent patterns of distribution of all types of trace fossils in distinct lithofacies of periodically exposed and inundated continental settings.

At present, it is envisaged that the subdivision of the Scoyenia ichnofacies can be based on two grounds: a categorisation of vertebrate tracks and distinction of suites of trace fossils related to a desiccating substrate. These subdivisions should always be made considering the whole suite or assemblage of trace fossils, instead of the occurrence of individual traces. Some of the trace-fossil assemblages from the Santo Domingo Formation and examples from the literature suggest that a grouping of tetrapod tracks might enhance the palaeoecological and palaeoenvironmental meaning of the association of trace fossils. The existence of this grouping of vertebrate tracks is partially highlighted by the proposed vertebrate ichnofacies (e.g. Lockley et al., 1994). As a consequence of the re-analysis of recurrent vertebrate ichnocoenoses and blending with associated invertebrate and plant trace fossils, some vertebrate ichnofacies will probably become subdivisions of the Scoyenia ichnofacies (e.g. “red bed” and “shorebird” ichnofacies).

A further significant division of the Scoyenia ichnofacies could be based on the presence of contrasting suites of trace fossils in a desiccating substrate: a “pre-desiccation suite” with structures lacking ornamentation and developed in a soft substrate and a “desiccation suite” typified by striated traces that crosscut the former (Buatois and Mángano, 2002, 2004). These trace fossil suites can be recognised in three of the trace-fossil assemblages of the Santo Domingo Formation and in other potential examples from the literature. The most reliable criterion for recognition of these trace fossil suites is determination of crosscutting relationships between trace fossils and between trace fossils and sedimentary structures. The exact meaning of other potential and less reliable criteria; such as definition of burrow walls, sharpness of invertebrate impressions, depth and anatomical details of tetrapod tracks; should be confirmed by neoichnological studies.

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