

Invertebrate and vertebrate trace fossils from a Triassic lacustrine delta: the Los Rastros Formation, Ischigualasto Provincial Park, San Juan, Argentina

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Abstract. A detailed sedimentologic and ichnologic study of three trace fossil-bearing sections of the Los Rastros Formation (Middle Triassic) at Ischigualasto Provincial Park, San Juan, is presented. This lacustrine unit is mainly sandy, and it is made up of parasequences or shallowing cycles of decametric thickness. Three facies associations were identified, which represent (from bottom to top) open lacustrine, delta front and upper delta plain environments (braided fluvial channel facies). Trace fossils are more abundant in delta front deposits, which show influence of waves and storms. Four ichnofossil assemblages which may reflect environmentally controlled fossilization conditions in lacustrine delta settings were recognized: 1) A subaqueous assemblage of grazing, feeding and locomotion traces from delta front deposits which is comparable to the *Mermia* ichnofacies and occurs in muddy sandstone facies with oscillatory movements. 2) A group composed of fusiform structures (possible chironomid cases), *Cochlichnus anguineus*, and *Palaeophycus tubularis*, that appears to be restricted to moderately shallow water in the upper part of the delta front facies or lowermost delta plain facies. This assemblage can have important paleoenvironmental and paleoecological significance if the origin of the fusiform structures is confirmed. 3) A low diversity assemblage of subaqueous traces which appears in beds with hummocky cross-bedding (*Palaeophycus tubularis* and *Skolithos* isp.). It is attributed to opportunistic organisms that colonized delta front sandstones reworked by storms, and is a continental example of the *Skolithos* ichnofacies. 4) An assemblage recorded from the upper part of parasequences (upper delta plain setting) including tetrapod footprints (*Rhynchosauroides* isp.) and burrows built in partially dehydrated fluvial sediments (*Palaeophycus striatus*), *Palaeophycus tubularis* and horseshoe-shaped structures. This assemblage belongs to a shore environment with fluctuating water levels and occasional subaerial exposure, which is comparable to the *Scoyenia* ichnofacies.

Resumen. TRAZAS FÓSILES DE INVERTEBRADOS Y VERTEBRADOS DE UN DELTA LACUSTRE TRIÁSICO: FORMACIÓN LOS RASTROS, PARQUE PROVINCIAL ISCHIGUALASTO, SAN JUAN, ARGENTINA. Se presenta un estudio sedimentológico e icnológico detallado de tres secciones portadoras de trazas fósiles de la Formación Los Rastros (Triásico Medio), en el Parque Provincial Ischigualasto, San Juan. Esta unidad lacustre es esencialmente arenosa, lacustre y se compone de ciclos somerizantes o parasecuencias de espesor decamétrico. En ellas se han identificado tres asociaciones de facies que representan (de abajo hacia arriba) sedimentación lacustre de costa afuera, de frente deltaico y de planicie deltaica (facies de canal fluvial entrelazado). Las trazas fósiles son más abundantes en depósitos de frente deltaico, que muestran marcada influencia de oleaje y tormentas. Se han reconocido cuatro asociaciones de icnofósiles con distribución litofacial acotada que representarían condiciones de fosilización favorables en ambientes lacustres. 1) Una asociación subácea de trazas de pastoreo, alimentación y locomoción comparable con la icnofacies de *Mermia*; registrada en facies areno-limosas de frente deltaico afectadas por flujos oscilatorios. 2) Una asociación compuesta por estructuras fusiformes (posibles capullos de Chironomidae), *Cochlichnus anguineus* y *Palaeophycus tubularis* que aparece restringida a la parte alta de la asociación de facies de frente deltaico y a la base de aquella de planicie deltaica y tendría importantes consecuencias paleoambientales y paleoecológicas si se confirma la filiación de las estructuras fusiformes. 3) Un conjunto de trazas fósiles subáceas de baja diversidad que aparece en capas con estratificación entrecruzada *hummocky* (*Palaeophycus tubularis* y *Skolithos* isp.). Esta correspondería a organismos oportunistas que colonizaron arenas de frente deltaico re trabajadas por tormentas y constituye un ejemplo continental de la icnofacies de *Skolithos*. 4) Una asociación de la parte alta de las parasecuencias (facies de planicie deltaica superior) que incluye pisadas de tetrapodos (*Rhynchosauroides* isp.), excavaciones construidas en sedimento parcialmente deshidratado (*Palaeophycus striatus*), *Palaeophycus tubularis* y estructuras en forma de herradura. Esta asociación refleja un ambiente costero con fluctuaciones en el nivel de agua y ocasional exposición, que es comparable con la icnofacies de *Scoyenia*.

Key words. Invertebrate ichnofossils. Tetrapod footprints. Lithofacies. Delta. Lacustrine. Ischigualasto-Villa Unión basin.

Palabras clave. Icnofósiles de invertebrados. Pisadas de tetrapodos. Litofacies. Delta. Lacustre. Cuenca Ischigualasto-Villa Unión.

Introduction

Current knowledge on the ichnology of Triassic continental deposits from Argentina is fragmentary and biased to the description of tetrapod footprints (see review in Melchor *et al.*, 2001a). Most of the recent contributions on Triassic invertebrate ichnology

of Argentina have been devoted to different units from the Ischigualasto-Villa Unión basin, including the Los Rastros Formation (Melchor, 1998, 2001; Genise *et al.*, 2000; Melchor *et al.*, 2001b). The tetrapod footprint record of the Los Rastros Formation is scarcer, including the first scientifically described trace fossils from Argentina: the large quadrupedal track *Rigalites ischigualastianus* Huene, 1931 and other poorly documented findings (Alcober, 1993; Leonardi, 1994; Contreras and Bracco, 1998). The Los Rastros Formation has proven to be remarkably rich in trace fossils (mainly those of invertebrates) and deserves a detailed description in a lithofacial and

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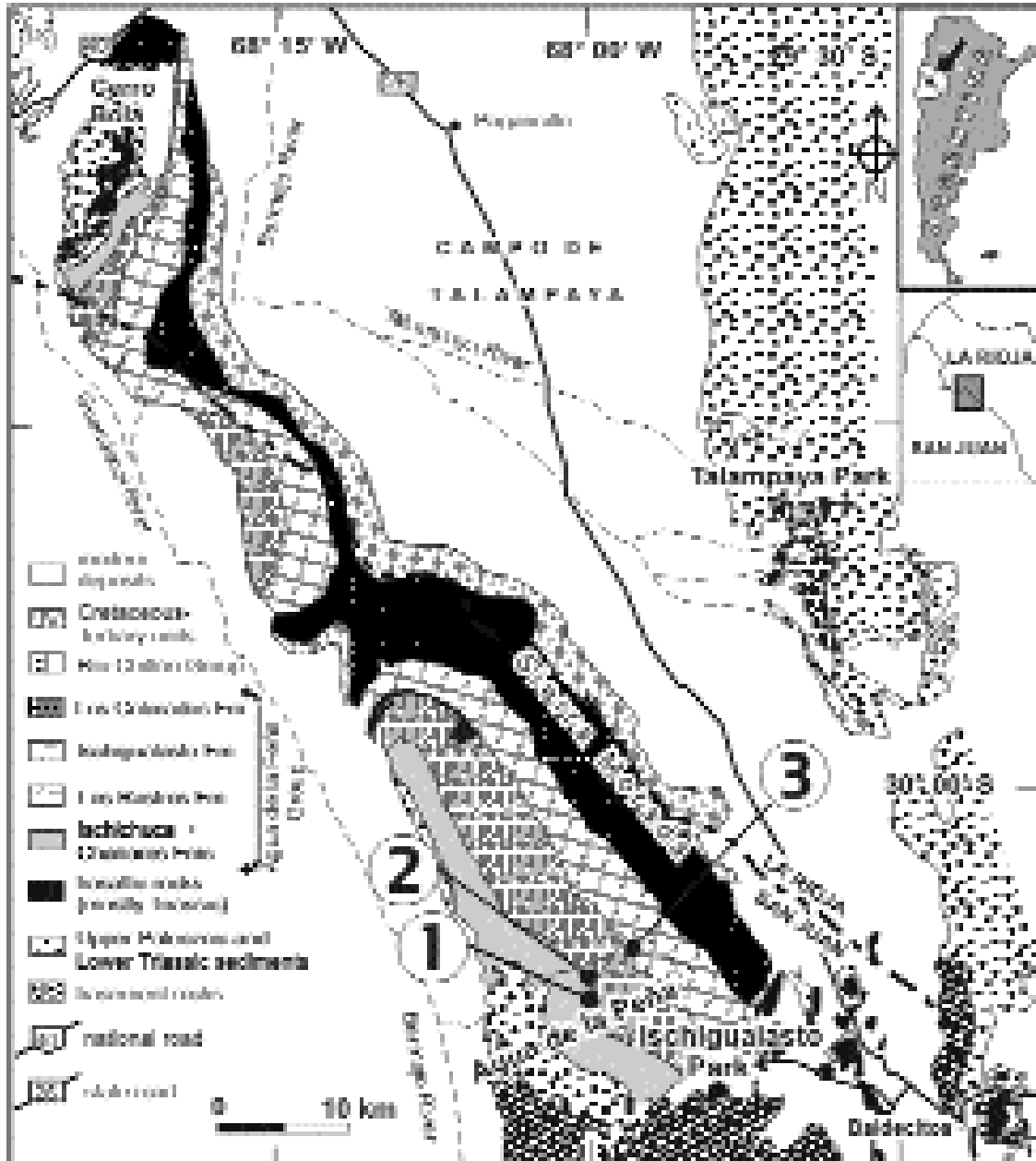


Figure 1. Geologic map of the Triassic Ischigualasto - Villa Unión basin showing location of the logged sections (1, 2 and 3). Modified from Romer and Jensen (1966), Stipanovic and Bonaparte (1979), and Alcober (1993) / *Mapa geológico de la cuenca triásica de Ischigualasto - Villa Unión mostrando la localización de las secciones medidas (1, 2 y 3).* Modificado de Romer y Jensen (1966), Stipanovic y Bonaparte (1979) y Alcober (1993).

stratigraphic context. In this contribution, the lithofacies and invertebrate and vertebrate ichnofossils of three selected trace fossil-bearing sections from the Los Rastros Formation at the Ischigualasto Provincial Park, San Juan (figures 1 and 2) are described. This paper presents a combined treatment of the sedimentology and (invertebrate and vertebrate) ichnology at some localities of the Los Rastros Formation, which allows the distinction of four trace fossil assemblages with defined environmental distribution in a lacustrine delta setting. This contribution is not intended as a comprehensive description of the ich-

nology of the Los Rastros Formation at the Ischigualasto Provincial Park, but it can be considered representative of their trace fossil assemblages. The collected material is housed at the Instituto de Geología of the University of San Juan, San Juan, Argentina (INGEO-PI).

Geologic setting

The Ischigualasto - Villa Unión is a rift basin developed on the western margin of southwest Gondwana in Early Triassic times that preserves

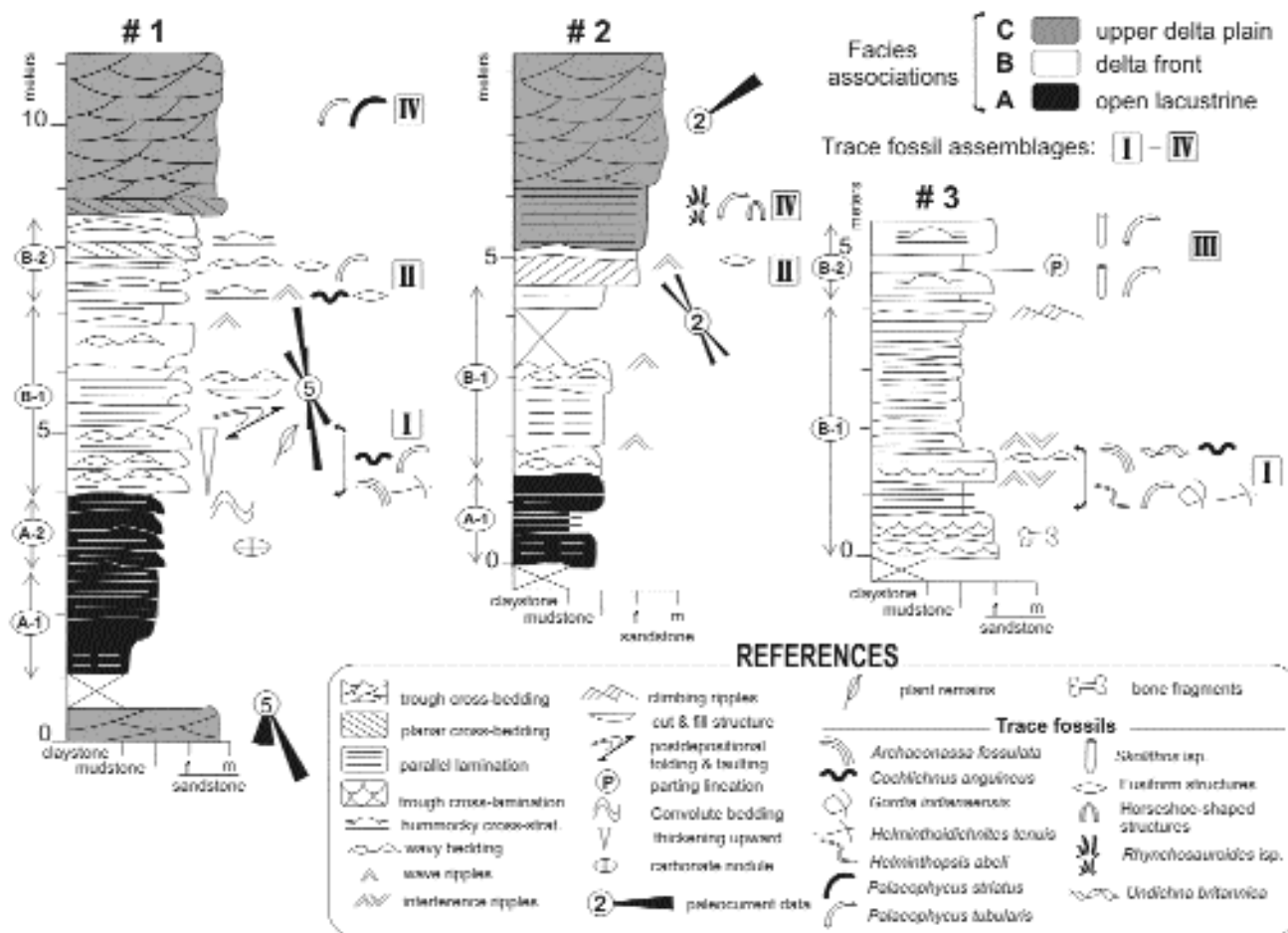


Figure 2. Detailed sedimentologic logs and distribution of trace fossils for measured sections (see coordinates in the text). Every section contains part or a complete shallowing-upward cycle. Component facies are indicated to the left of each section / *Perfiles sedimentológicos detallados y distribución de trazas fósiles en las secciones medidas (ver coordenadas en el texto). Cada sección representa un ciclo somerizante o una parte del mismo. Las facies componentes de las asociaciones de facies se indican a la izquierda de los perfiles.*

sediments from the latest Early Triassic to the Late Triassic (e.g., Uliana and Biddle, 1988; Spalletti, 1999). The filling of this basin is 2500 - 4000 m thick (according to different estimates and localities), entirely continental, and is divided into six major lithostratigraphic units (Stipanovic and Bonaparte, 1979): the Talampaya and Tarjados Formations and the Agua de la Peña Group (which includes the Ischichuca, Los Rastros, Ischigualasto and Los Colorados Formations). The Los Rastros Formation crops out extensively on the southwest border of the basin between the Ischigualasto Provincial Park and Cerro Bola area, and also on the southeast border of the basin, south of Talampaya river canyon at the homonymous national park (figure 1). The main stratigraphic and sedimentologic features of the unit have been reviewed in a number of compilation papers (Bonaparte, 1969; Stipanovic and Bonaparte, 1979; López Gamundí *et al.*, 1989; Kokogíán *et al.*, 1999; Bellosi *et al.*, 2001), although detailed studies are more scarce (Bossi, 1970; López, 1995; Milana, 1998; Rogers *et al.*, 2001). The unit has been dated as

Middle Triassic on the basis of plant remains and stratigraphic relationships (e.g., Stipanovic and Bonaparte, 1979; Spalletti *et al.*, 1999). Its thickness at Ischigualasto Provincial Park was estimated as ranging from 300 to 350 m (López, 1995; Milana, 1998). The Los Rastros Formation records lacustrine sedimentation in a rift system. Most of the sequence is composed of complete parasequences, as those described here (section 3, figure 2), which represent the interplay between changes in the position of progradational, lake-margin lobes or deltas and lake level variations. An autocyclic mechanism (*i.e.* detrital supply), in a stable lake-level has been advocated by Milana (1998) as responsible for the construction and stacking of parasequences. Milana (1998) regarded this unit and the underlying Ischichuca Formation as reflecting continuous sedimentation in the Ischichuca - Los Rastros paleolake. However, at the northwest margin of the basin (near Cerro Bola hill) both units exhibit distinguishing features, which suggest their relation to different depositional episodes. According to Milana and

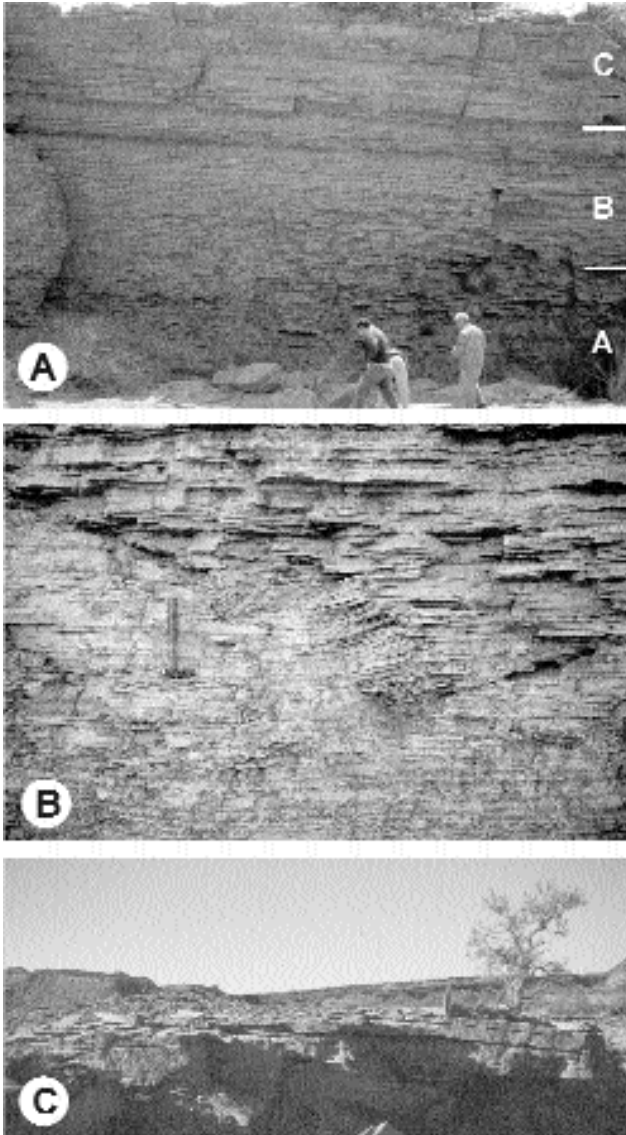


Figure 3. Views of selected lithofacies / *Vistas de litofacies seleccionadas.* **A,** Field photograph of section 1 displaying the approximate vertical distribution of described facies associations (A, B, and C) / *Foto de campo de la sección 1 mostrando la distribución vertical aproximada de las asociaciones de facies descritas (A, B y C).* **B,** Close-up view of facies association A showing the transition between facies A-1 and A-2 / *Vista de detalle de la asociación de facies A mostrando la transición gradual entre facies A-1 y A-2.* **C,** Hummocky cross-bedding from top of section 3 / *Estratificación entrecruzada "hummocky" del techo de la sección 3* Hammer is 0.35 m long / *El martillo tiene 0,35 m de largo.*

Alcober (1994), the Los Rastros Formation represents a single prograding, coarsening-upward sequence developed in a shallow lake of the Ischigualasto half-graben.

Fieldwork for this study was conducted in the exposures of the Los Rastros Formation at Ischigualasto Provincial Park, San Juan province. Two sections were logged close to state road 150 (in construction during the 2000-2001 fieldwork between Baldecitos and Jachal) at two locations in the neighbourhood of the south margin of the Agua de La Peña canyon

(section 1: 30° 09' 25" S; 67° 57' 29" W and section 2: 30° 09' 11" S; 67° 58' 19" W) and the remaining section was measured at the entrance of the same canyon (section 3: 30° 05' 33" S; 67° 56' 04" W; see figures 1 and 2). From a stratigraphical standpoint, the first two sections belong to non-correlative tracts from the lower third, and the remaining section is fairly close to the top of the formation. Consequently, the sections in figure 2 are not laterally equivalent.

Sedimentary facies

Description

The Los Rastros Formation is a sandstone-dominated succession showing a general coarsening-upward trend. It is composed of stacked, shallowing-upward cycles or parasequences (1 in figure 2 and figure 3.A) containing four distinct trace fossil assemblages. The studied coarsening and thickening-upward cycles are up to 10.5 m thick and change up-section in color from olive gray (5Y4/1, 5Y3/2) to yellowish or light gray (5Y7/2, N7). Facies changes are gradational or occasionally sharp. Channel sandstone beds may display a flat, slightly erosive base. Parasequences are divided into three facies associations (figure 2), which are not present in all sections. *Facies association A* is composed by laminated claystone and mudstone (figure 3.B). Two facies were distinguished: facies A-1 (up to 1 m thick) consists of claystone with thin lamination and laminated siltstone, where no bioturbation was observed. Facies A-2 comprises laminated sandy mudstone arranged in 3-4 cm thick laminae that display a fining-upward trend, with occasional convolute bedding and scattered carbonate concretions. Isolated, wedge-shaped sandstone with low angle cross-bedding and non-erosive bases is found interbedded with the sandy mudstone.

Facies association B is composed of centimetre-thick, heterolithic cyclic beds arranged in tracts up to 5.5 m thick. It includes two distinctive facies (figure 2). Facies B-1 are coarsening-upward (mudstone to laminated fine-grained sandstone), 0.1 m to 0.25 m sub-cycles, displaying wavy bedding, trough cross-lamination, wave and interference ripples, cut and fill structures, and plant debris. This tract can be affected by soft-sediment deformation (overturning and inverse faulting) and its degree of bioturbation is low to moderate. Fragments of long bones were recognized at section 3. Facies B-2 includes heterolithic and sandy hummocky cross-bedding. Rare, large (up to 15 m in diameter, 0.5 m thick), isolated heterolithic hummocks are composed of laminated fine-grained sandstone and mudstone with wave ripples on their tops, which are capped by massive mud-

stone. Wavelength of symmetrical ripples is 6 - 11 cm and their height is less than 1 cm. Amalgamated, sandy hummocky cross-bedding is composed of fine-grained sandstone and displays occasional parting lineation. The apparent diameter of each hummock can reach up to 2 m (figure 3.C).

Facies association C includes decimetre-thick sandstone beds with cross-bedding. In the lower part of the association the most common structures are isolated sets of low angle planar cross-bedding (up to 0.30 m thick), which can show oscillation ripples on their tops (ripple wavelength = 11 cm, height = 1 cm). The facies association commonly culminates with thick beds of parallel laminated or trough cross-bedded, medium to fine-grained sandstone showing an upward increase in set thickness. Paleocurrent data from trough cross-bedded sandstone display a low dispersion (40° , $n = 5$). Parallel laminated sandstones contain tetrapod footprints.

Interpretation

Facies arrangement in the described parasequences indicates shallowing upward conditions at a ramp-type margin of the lacustrine basin (Milana, 1998). Although clinofolds were not identified in the analysed outcrops, large prograding surfaces were previously mentioned in sandy intervals up to 2.5 m thick from the same unit and geographic area (Milana, 1998). These features suggest a Gilbert-type delta dominated by fluvial sedimentary supply and wave-storm reworking.

Non-bioturbated, thinly laminated claystone and mudstone (facies A-1) represent moderately deep and open lake conditions. This interval records the lake bottom and lower prodelta environments, where deposition from settling was probably regulated by fluvial supply. Laminated and fining-upward sandy mudstone (facies A-2) was accumulated by pulsatory detrital inputs (underflows) probably linked to fluvial flooding or storm events. Disruption of rhythmic accumulation by non-erosive, isolated wedge-shaped sand bodies is due to sediment removal at the delta front probably as a storm effect.

The middle heterolithic interval (facies association B), including rhythmites, corresponds to the delta front environment. Constant wave reworking beneath storm/wave base depth was the prevalent process. Paleocurrent data from wave crest measurements indicate that prevailing wind direction during deposition of the lower part of the unit was NNW-SSE (sections 1 and 2, figure 2). Sustained prograding conditions are also revealed by coarsening-upward subcycles (facies B-1). A lake margin supply is evidenced by the presence of transported allochthonous plant debris in this association. Episodes of high sedi-

mentation rate also led to instability on the delta front slope, producing soft-sediment deformation of rhythmic beds. Prevailing oscillatory water movements were affected by sporadic stronger currents, producing small erosive structures (cut-and-fill structures). Rare sandstone hummocks uniformly draped by mudstone (section 1, figure 2) indicate a depth above storm wave base punctuated by periods dominated by settling from suspension. The relatively high vertical form index (wavelength/height) of the associated symmetrical ripples suggests that deposition occurred at a moderately high orbital velocity (about 0.7 m/s) with orbital diameter ranging from 1-2.5 m (Allen, 1984). This evidence coupled with the position of these hummocky beds within the parasequence suggest that deposition occurred in water depth lower than a few meters (*cf.* Greenwood and Sherman, 1986). Greenwood and Sherman (1986) demonstrated that hummocky cross-stratification can be produced and preserved in very shallow water (< 2 m) in a lacustrine setting. Conversely, these structures have a low preservation potential in shallow marine basins (Duke, 1985). Sandy hummocky cross-bedding (sections 1 and 3, figure 2) indicates large oscillatory waves of storm origin, which reworked sandy deposits (possibly distributary mouth bar sediments) at the upper delta front environment. There is no direct evidence about the water depth of its formation. Their appearance in different stratigraphic positions and localities (lower and upper part of the unit, sections 1 and 3) suggests deltaic sedimentation of higher energy than previously documented for this unit and location (*cf.* Milana, 1998), while the succession of the formation at Talampaya National Park is also storm-dominated (Melchor, 2001). Hummocky cross-bedding is more common in marine sequences, though it has been recorded in some lacustrine sequences (*e.g.*, Eyles and Clark, 1986, 1988; Dam and Surlyk, 1993; Basilici, 1997; Artabe *et al.*, 1998; Melchor and Herbst, 2000). In particular, Spalletti (1997) also described hummocky cross-bedding from a delta front environment of the Triassic Llantenes Formation (Mendoza, Argentina).

The upper sandstone interval (facies association C) reveals a subsequent increase of energy and sedimentation rate in a shallower environment. Trough cross-bedded sandstone facies accumulated in distributary channels of the delta plain. The absence of fine-grained deposits and lateral accretion surfaces, together with low paleocurrent dispersion, points to a braided fluvial system where preservation of subaerial floodplain fines was not favored. Progradation of fluvial sands upon delta front sediments would have been continuous (*i.e.* not driven by sudden lake-level changes) or non-energetic due to the lack of erosive soles in channel bodies. Temporary subaerial ex-

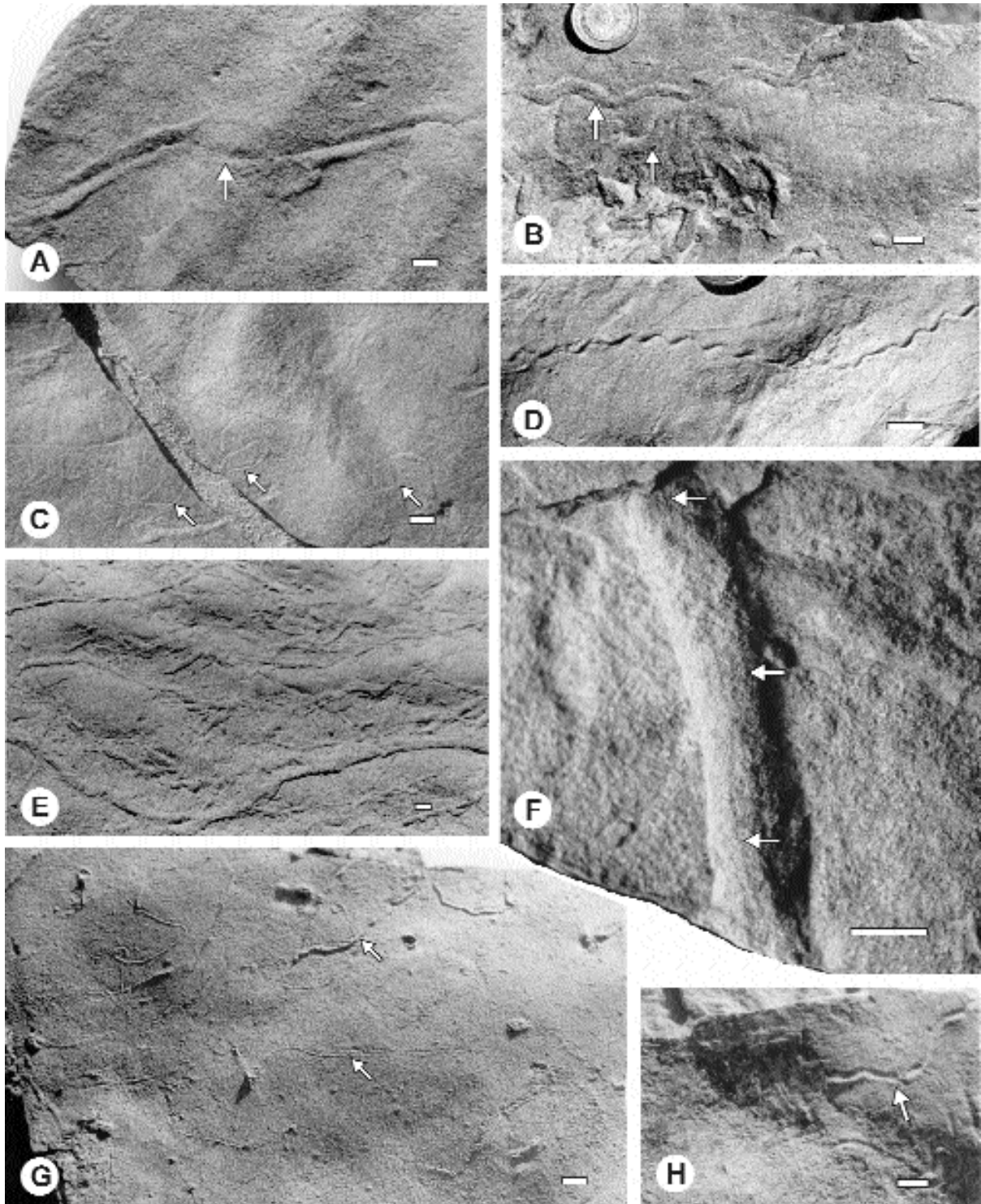


Figure 4. Invertebrate trails and burrows / *Pistas y excavaciones de invertebrados*. **A**, *Archaeonassa fossulata* on ripple marked bedding plane. Arrow indicates partial interruption of trace on ripple crest (INGEO-PI 636) / *Archaeonassa fossulata* en plano de estratificación con ondulas. La flecha indica parcial interrupción de la traza en la cresta de la óndula (INGEO-PI 636). **B, D**, Two burrows (arrows in B) and one trail (D) assigned to *Cochlichnus anguineus*. The upper arrow indicates a small levee / *Dos excavaciones (flecha en B) y una pista (D) asignadas a Cochlichnus anguineus*. La flecha superior indica un pequeño albardón. **C**, *Gordia indianaensis* (three specimens arrowed) / *Gordia indianaensis* (se indican tres especímenes). **E**, Top of trough cross-bedded set of facies association C showing abundant specimens of *Palaeophycus tubularis* / *Techo de set con estratificación entrecruzada en artesa mostrando abundantes especímenes de Palaeophycus tubularis*. **F**, *Palaeophycus striatus* on the same bedding plane as in figure E. Thin, parallel striations are arrowed (INGEO-PI 637) / *Palaeophycus striatus* en el mismo plano de estratificación que aquel de la figura E. Las delgadas estriaciones paralelas son indicadas por flechas (INGEO-PI 637). **G**, *Helminthoidichnites tenuis* (arrows) and probable *Gordia indianaensis* (upper left) / *Helminthoidichnites tenuis* (flechas) y probable *Gordia indianaensis* (arriba a la izquierda). **H**, *Helminthopsis abeli* (arrowed) / (señalado por la flecha). Scale bars = 1 cm / *Barras = 1 cm*.

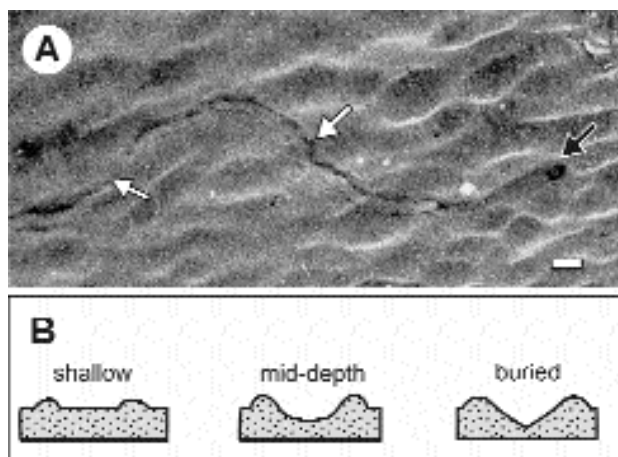


Figure 5. Modern traces of *Buccinanops* (Gastropoda: Nassariidae) in medium-grained sand / *Trazas actuales de Buccinanops* (Gastropoda: Nassariidae) en arena mediana. **A.** View of the trace (white arrows) produced by motion at medium depth or in the subsurface (center and left) and at the sand/water interface (near the gastropod). The producer is 10 mm long and 6.5 mm wide (black arrow). Scale bar = 1 cm / *Vista de la traza (flechas blancas) producida por movimiento a profundidad intermedia debajo de la arena (centro e izquierda) y en la interfase arena/agua (próximo al gastrópodo). Barra = 1 cm.* **B.** Schematic cross-section profiles of traces produced at different depths in relation to the sediment/water interface: surface trail (left), mid-depth trail (center), and shallow collapsed burrow (right). Not to scale / *Perfiles transversales esquemáticos de trazas producidas a distintas profundidades con relación a la interfase sedimento/agua: pista superficial (izquierda), pista de profundidad intermedia (centro) y excavación somera colapsada (derecha). Sin escala.*

posure of channel bars is evident because of the presence of the tetrapod footprints in these fluvial facies. Paleocurrent data for the lower part of the unit (sections 1 and 2, figure 2) suggest that distributary channels transported sediments toward the NE and SE.

Parasequences described in this study display some distinguishing features in relation to those described by Milana (1998). The lower muddy - heterolithic interval is similar to the fine member of Milana's type A parasequences, while the upper sandstone interval is partially comparable to Milana's sandstone member. An important difference described here is the noticeable evidence of wave and storm events, which suggest a large and windy lake (Talbot and Allen, 1996). This feature also implies that storm events affected delta front topography, distributing fine-grained sands supplied by distributary channels. Consequently, we can infer a progradational, fluvial dominated and wave / storm influenced lacustrine delta model.

Systematic ichnology

Invertebrate trace fossils

Ichnogenus *Archaeonassa*
Fenton and Fenton, 1937

Archaeonassa fossilata

Fenton and Fenton, 1937

Figure 4.A

Description. Straight to sinuous, horizontal, epichnial traces consisting of a median groove flanked by rounded ridges. Cross-section of median groove in the form of a flattened "V". Width of the trace ranges from 11 mm to 13.5 mm. Ridges about 4 mm wide with a maximum measured relief of 1.5 mm. Length of traces is up to 215 mm, although showing interruptions in its continuity, usually where they intersect a ripple crest (figure 4.A). Some specimens show overcrossing.

Material. Five specimens measured, one collected (INGEO-PI 636).

Remarks. In the assignment of the Los Rastros specimens to *Archaeonassa*, we followed the review of the type material by Yochelson and Fedonkin (1997). Most of the forms assigned to *Archaeonassa* by Buckman (1994) are not comparable with the material described herein (especially because of the presence of ornamentation in grooves and ridges) and they may not belong to that ichnogenus. The type material comes from the marine sequence of the Middle Cambrian Mount Whyte Formation (British Columbia, Canada). The remaining occurrences of the ichnogenus are from Carboniferous rocks of shallow marine to freshwater environments: tidal facies of the Lower Carboniferous Mullaghmore Sandstone Formation, Ireland (Buckman, 1994) and fluvial deposits of the Tupe Formation, Argentina (Buatois and Mángano, 2002). The traces illustrated by Turner (1978) as *Scolicia* isp. from fluvial facies of the Late Triassic Molteno Formation of South Africa also are comparable to *Archaeonassa*. Yochelson and Fedonkin (1997) interpreted the type material of the ichnogenus as an endichnial burrow excavated just below the sediment/water interface. This interpretation explains common interruptions in the trace observed in the type material and also in part of the material described here. All the remaining occurrences were considered as surface trails (e.g., Häntzschel, 1975; Buckman, 1994; Buatois and Mángano, 2002). Observations on the traces produced by the extant marine gastropod genus *Buccinanops* d'Orbigny 1841 in the tidal sandy beach of the San Matías gulf, Río Negro province, Argentina (about 40° 50' L.S.) provide some insights on the possible origins of *Archaeonassa* (figure 5.A). This gastropod produces different traces depending on the depth of movement in relation to the sand/water interface. All observations were made during low tide with the gastropods in motion underwater. Main trace differences are related to their cross-section profile (figure 5.B). When the gastropod progresses above the sandy

bottom it leaves a shallow flattened trail flanked by two small rounded ridges. The trail left when the gastropod progresses partially covered with sand displays a flattened U profile flanked by rounded ridges. In contrast, the displacement of the gastropod completely covered by sand (about 1 cm below the sediment/water interface) produces a trace with higher relief, showing an open "V" profile, flanked by two marked ridges. In this case, the "trail" is in fact a collapsed shallow burrow. All traces have a curved, irregular path and may display self-overcrossing. These observations suggest that traces similar to *Archaeonassa* can be produced both as surface trails and shallow burrows and indicate the potential usefulness of the cross-sectional profile to distinguish between these modes of formation (figure 5.B). Other modern traces of similar morphology have also been attributed to gastropods or bivalves in marine and continental settings (e.g., Walter *et al.*, 1973; Kitchell *et al.*, 1978; De, 2000).

Ichnogenus *Cochlichnus* Hitchcock, 1858

Cochlichnus anguineus Hitchcock, 1858

Figures 4.B, 4.D

Description. Horizontal trails and burrows with a regular sinusoidal pattern preserved as concave or convex epirelief. Burrows are unlined, although some specimens display small levees. Trace path is straight or slightly curved. In the measured material trails are always smaller than burrows. Trails (n=4) are 1.2 - 2.2 mm wide, wavelength is 9.5 - 11 mm, and wave height 3.3 - 4.6 mm. In contrast, measurements for burrows (n= 4) are: 2.9 - 4.2 mm (width), 21 - 26 mm (wavelength), and 7.3 - 10 mm (wave amplitude). Maximum observed length is 200 mm.

Material. Seven specimens measured in the field (sections 1 and 3) and one collected (INGEO-PI 681).

Remarks. This ichnogenus has been recently discussed by Rindsberg (1994), Gluszek (1995), and Stanley and Pickerill (1998). Rindsberg (1994) proposed to distinguish sinusoidal trails under *Cochlichnus* and sinusoidal burrows under the new ichnogenus *Cymataulus*. Nevertheless, most recent authors include both trails and burrows within *Cochlichnus* (e.g., Gluszek, 1995; Buatois *et al.*, 1997; Stanley and Pickerill, 1998). *Cochlichnus* has been reported from different marine and continental environments in deposits ranging from Precambrian to Recent (Fillion and Pickerill, 1990). It is commonly interpreted as a grazing (pascichnia) or locomotion trace (repichnia). Metz (1998) recently discussed the potential trace makers for *Cochlichnus* and concluded that, besides worm and worm-like animals, nematodes and insect larvae of Diptera were important producers. Additionally, cyclostomatid Agnatha and leeches were considered as potential producers by Gluszek (1995). The

large size variability of the specimens from fluvial floodplain facies of the Upper Carboniferous of Poland studied by Gluszek (1995) was explained either as reflecting different producers or a single producer passing through different growth stages. Buatois *et al.* (1997) distinguished two size populations of *Cochlichnus* from floodplain facies of the Permian La Golondrina Formation of Patagonia, which were interpreted as reflecting colonization of soupy/soft (large *Cochlichnus*) and soft substrates (small *Cochlichnus*). In the studied material, there is no evidence of different substrate water content between large and small forms of *Cochlichnus*. Despite the low number of specimens measured, the identified size populations probably reflect different producers or different growth stages of a single producer.

Ichnogenus *Gordia* Emmons, 1844

Gordia indianaensis (Miller, 1889)

Figure 4.C

Description. Small, thin (1 mm), horizontal, simple, sharply angled trails displaying self-overcrossings and preserved as concave epireliefs. Trail segments are regularly straight or slightly curved and commonly joined by angles of about 140°-160°. Traces form semicircular paths of approximately 20 mm in diameter.

Material. Three specimens measured in the field from section 3.

Remarks. The ichnospecies *Haplotichnus indianaensis* Miller, 1889 was relocated within *Gordia* by Buatois *et al.* (1998). This ichnospecies is characterized by thin trails displaying self-overcrossing and sharply angled segments. It is interpreted as a grazing trail (pascichnia) of surface feeding organisms and has been previously reported only from Carboniferous lacustrine to marginal marine environments (Buatois *et al.*, 1998).

Ichnogenus *Helminthoidichnites* Fitch, 1850

Helminthoidichnites tenuis Fitch, 1850

Figure 4.G

Description. Small, thin, unbranched, simple, straight or curved trails and burrows lacking self-overcrossing. Diameter of trace up to 1 mm, maximum preserved length 80 mm. Specimens occur as concave or convex epirelief.

Material. Five specimens measured in the field (sections 1 and 3).

Remarks. Buatois *et al.* (1998) emended the diagnosis of the ichnogenus to include only simple, unbranched, nonmeandering traces lacking self-overcrossing (see also Schlirf *et al.*, 2001). It is interpreted as a grazing trace (pascichnia) probably produced by arthropods or worm-like animals. *Helminthoidichnites* has been recorded in Precambrian to Mesozoic ichnofaunas, from marine and continental settings (Buatois *et al.*, 1998).

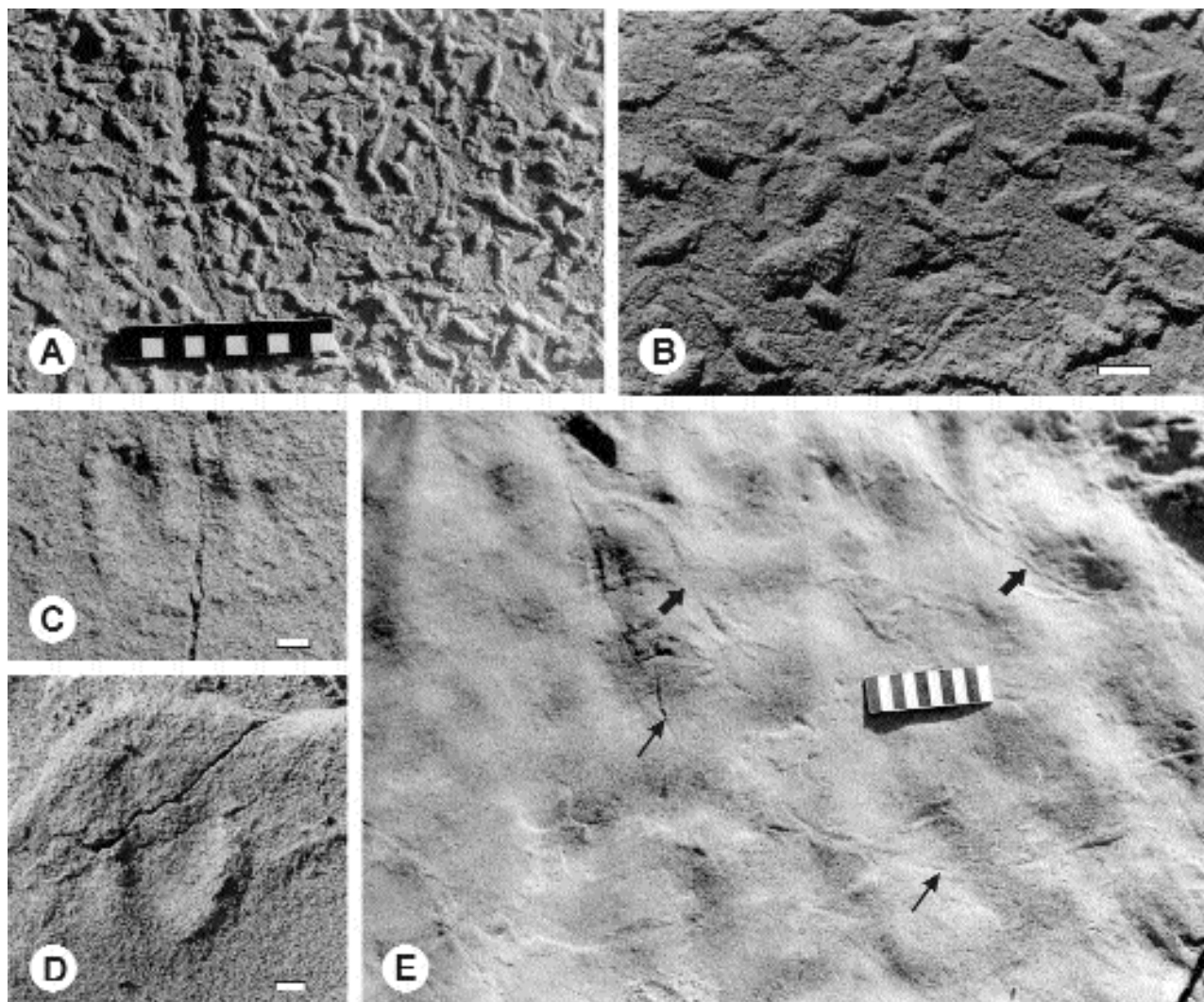


Figure 6. Fusiform structures, horseshoe-shaped structures, and fish trails / *Estructuras fusiformes, estructuras en herradura y pistas de peces.* **A, B,** Sole with abundant fusiform structures (A) and their close-up view (B) / *Base de estrato con abundantes estructuras fusiformes (A) y detalle de las mismas (B).* **C, D,** Horseshoe-shaped structures on bedding plane of parallel-laminated medium-grained sandstone. Note sand crescent on the lower part of figure D / *Estructuras en forma de herradura en plano de estratificación de arenisca mediana con estratificación paralela. Notar rebaba de arena en la parte inferior de la figura D.* **E,** Field photograph of *Undichna britannica* on bedding surface with interference ripples. Thin arrows indicate a nearly complete specimen and thick arrows point to other cross-cut, incomplete trails that also may belong to the same ichnogenus / *Fotografía de campo de Undichna britannica en plano de estratificación con ondulas de interferencia. Las flechas delgadas indican un ejemplar casi completo y las flechas gruesas apuntan a otras pistas cruzadas incompletas que pueden pertenecer al mismo icnogénero.* Divisions of large scale and scale bars = 1 cm / *Divisiones de la escala mayor y de las barras = 1 cm.*

Ichnogenus *Helminthopsis* Heer, 1877
Helminthopsis abeli Książkiewicz, 1977

Figure 4.H

Description. Meandering to winding, horizontal, unbranched trail preserved as concave epirelief. The trail is 4 mm wide and 56 mm long.

Material. A single specimen measured at the field.

Remarks. The ichnotaxonomy of *Helminthopsis* has recently been reviewed by Han and Pickerill (1995) and Wetzel and Bromley (1996), though both studies reach partially different conclusions. *Helminthopsis* is considered as a grazing trail produced by deposit feeding organisms. It has been recorded from deep marine to freshwater environments. In continental

settings the most probable producers are arthropods and nematodes (Buatois *et al.*, 1998). *Helminthopsis abeli* is not common in continental settings (Keighley and Pickerill, 1997).

Ichnogenus *Palaeophycus* Hall, 1847
Palaeophycus striatus Hall, 1852

Figure 4.F

Description. Straight, subcylindrical, thinly lined burrow displaying delicate, parallel, longitudinal striations. Burrow fill identical to host. A single specimen (8.4 mm in diameter and 89 mm long) preserved as convex epirelief.

Material: INGENO-PI 637.

Remarks. Preservation of thin striations is indicative of burrowing in stiff or desiccated substrates (e.g., Buatois *et al.*, 1997). In addition, the presence of a host lithology of fine grain size to cast the striations and subsequent differential weathering of host and lining lithotypes are also recognized as significant factors (Maples and Suttner, 1990). *Palaeophycus striatus* has been commonly identified in freshwater facies that display periodic water fluctuations (e.g., Gierlowski-Kordesch, 1991; Pickerill, 1992; MacNaughton and Pickerill, 1995; Keighley and Pickerill, 1997; Buatois *et al.*, 1997), although it also occurs in outer shelf facies (e.g., Maples and Suttner, 1990).

Palaeophycus tubularis Hall, 1847

Figure 4.E

Description. Straight to slightly sinuous, subcylindrical, thinly lined, smooth burrows preserved as convex epirelief or hyporelief. Burrows commonly oriented parallel to bedding plane. Burrow fill identical to host sediment, diameter commonly falls in two size classes: 2-3 mm and 6-8 mm, maximum recorded diameter is 12 mm. Burrows show overlap but no true branching was observed. Maximum preserved length is 260 mm.

Material. Tens of specimens measured in the field from all sections.

Remarks. This trace is the most abundant of all described ichnotaxa. *Palaeophycus* represents passive infilling of open dwelling burrows of predaceous or suspension-feeding organisms (Pemberton and Frey, 1982). The ichnogenus has been reported from a wide range of environmental settings and varies in age from Precambrian to Recent.

Ichnogenus ***Skolithos*** Haldeman, 1840

Skolithos isp.

Description. Subvertical, smooth, unlined, cylindrical burrows ranging from 4 mm to 6 mm in diameter, which display massive filling similar to host. Maximum observed length is 20 mm. This trace occurs in hummocky cross-bedded sandstone beds, sometimes in large number.

Remarks. The complete morphology of the traces identified as *Skolithos* was not observed, which precluded its ichnospecific assignation. This ichnogenus has been reported from a wide variety of marine and continental environments, commonly from high-energy sediments. Its age ranges from Precambrian to Recent (e.g., Fillion and Pickerill, 1990).

Fusiform structures

Figures 6.A, 6.B

Description. Fusiform to oval-shaped, smooth structures, tapering or rounded at both ends, somewhat

depressed in cross-section. The range of observed length is 14 -17 mm and that of diameter is 4-6 mm. The structures display an elliptical cross-section about 4 - 6 mm wide and 3 - 4 mm high. Preserved as convex epirelief or convex hyporelief. The structure is composed by fine-grained sandstone enclosed in mudstone or sandstone. In some cases, these individual structures are extended to form short, horizontal tubes up to 85 mm in length, which may join with others to give a branched pattern. These traces commonly occur in large numbers on bedding planes, either lacking a preferred orientation or showing two main orientations at a straight angle. In some cases they lie mainly on ripple troughs, whereas in others they are found on ripple crests. In both cases they can be found oriented parallel or perpendicular to ripple-mark crests.

Material. Hundreds of specimens measured at the field a few tens collected (INGEO-PI 638) from sections 1 and 2.

Remarks. These traces were first reported by Genise *et al.* (2000) as possible cases of Chironomidae and will be described in detail elsewhere. The preservation of similar traces with convex relief both in top and bottom of beds requires further explanation. The structures preserved on bed tops probably are constructed. For those structures preserved in soles it is probable that, in most instances, the cases were constructed in a muddy substrate. Currents of greater energy can wear away part of the mud bed with cases and subsequent deposition cast with sandstone some of them. They are thus preserved as sole structures in sandstone beds.

Similar structures have been described by Gierlowski-Kordesch (1991) as "fusiform burrows" from ephemeral alluvial facies of the Jurassic East Berlin Formation (eastern USA). It is possible that these traces have been misidentified in the past as a highly bioturbated texture. Individual traces resemble the ichnogenus *Lockeia* James, 1879, although it lacks the almond-shaped form, is more elongated than that ichnogenus, and lacks connection with vertical shafts. Its preservation on bed tops further rule out its comparison with *Lockeia*. Mángano *et al.* (1998) documented alignment of *Lockeia* specimens that resemble the horizontal tubes described herein, although their cross-section is not elliptical as in our specimens. The morphology of fusiform structures also partially resembles inorganic structures such as syneresis cracks, sole marks, and crystal pseudomorphs. They are distinguished from the former by their oval cross-section (as opposed to wedge-shaped in cracks) and lack of a polygonal pattern. Sole marks are distinguished from fusiform structures by its common asymmetrical form and preferred orientation. Crystal

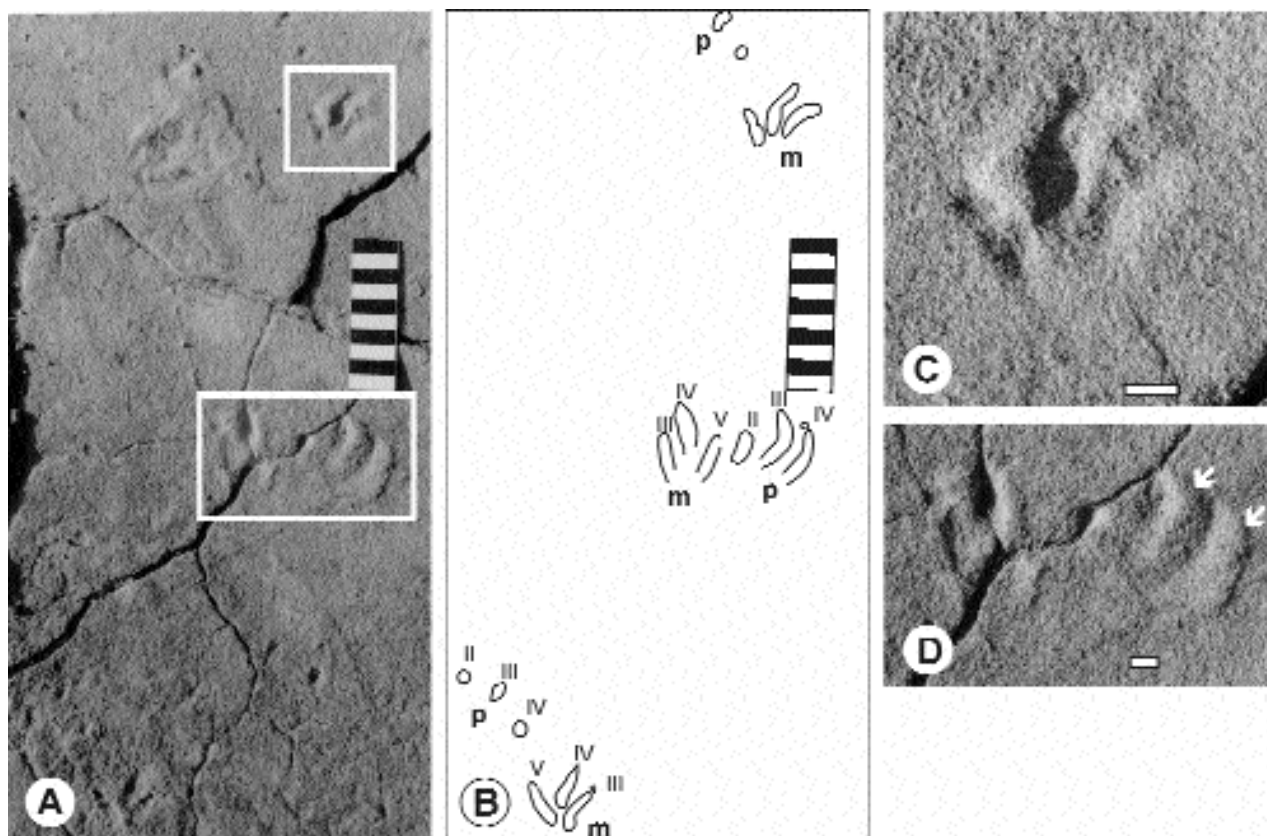


Figure 7. Tetrapod track assigned to *Rhynchosauroides* isp. / Rastro de tetrápodo asignado a *Rhynchosauroides* isp. **A**, Field photograph of complete track showing three pes-manus couples. Squared areas correspond to figures C and D / Fotografía de campo del rastro completo mostrando tres pares pies-manos. Las áreas recuadradas corresponden a las figuras C y D. **B**, Drawing of the previous figure. p = pes, m = manus, II to V = digit impressions. Note probable claw marks in manus of the lower couple and pes of the intermediate couple of footprints / Diagrama de la figura previa. p = pie, m = mano, II a V = impresiones de dígitos. Notar probables marcas de garras en la mano del par inferior y el pie del intermedio. **C**, **D**, Close-up view of manus (from third couple, part of INGEO-PV 041) and intermediate pes-manus couple (see location on figure A). Arrows in D indicate sand crescents in the outer part of pes digits III and IV / Detalle de la mano (del tercer par, parte de INGEO-PV 041) y par pie-mano del par intermedio (ver localización en figura A). Las flechas en D indican rebabas de arena en la parte externa de los dígitos III y IV del pie. Divisions of larger scale and scale bars = 1 cm / Divisiones de la escala mayor y barras = 1 cm.

pseudomorphs after gypsum also may display a fusiform outline, but are distinguished by their planar faces and common overlap (cf. Astin and Rogers, 1991; Finkelstein *et al.*, 2001).

Horseshoe shaped traces Figures 6.C, 6.D

Description. Shallow, horizontal, horseshoe or “U”-shaped trace preserved as concave epirelief. Trace width 35 - 42 mm and length 51 - 60 mm. “U” arms parallel, showing similar width (16 - 20 mm), and with sharp distal ends. A sand crescent is present in the rounded end of one specimen.

Material. Two specimens measured at the field from section 2.

Remarks. Lockley *et al.* (1994) reviewed several occurrences of U or horseshoe-shaped traces in the stratigraphic record, concluding that many of them are inorganic structures (current crescents) and others could be attributed to the ichnogenus *Rhizocorallium* Zenker, 1836. However, as discussed below, there are many other biogenic structures with a sim-

ilar gross morphology. A further potential comparison can be made with the ichnogenus *Fuersichnus* Bromley and Asgaard, 1979, with some xiphosurid traces (e.g., Miller, 1982; Chisholm, 1985; Eagar *et al.*, 1985; Romano and White, 1987; Buatois and Mángano, 1993), and with the ichnogenus *Herradurichnus* Poiré and del Valle, 1996. Metz (1987) also described small (less than 18 mm wide), modern trails with elliptical to horseshoe-shaped outlines produced by scarab beetles. The material herein described can be distinguished from current crescents by a sharp termination of U arms and from *Rhizocorallium* by the absence of *spreiten* between the arms (cf. Lockley *et al.*, 1994). *Fuersichnus* was also defined as *spreiten* burrows (Bromley and Asgaard, 1979), although the ichnospecies *F. striatus* Buatois, 1995 lacks this structure and shows a general outline similar to the material herein described. Xiphosurid traces, mainly *Limulicubichnus* Miller, 1982 and *Selenichnites* Romano and Whyte, 1990, are similar in general outline. *Limulicubichnus* commonly display a serrate/elongated posterior margin or associated ap-

pendage markings, features that are lacking in our material. *Selenichnites* is the more closely related form, especially because of its anterior rounded margin and markedly convex lunate shape (Romano and Whyte, 1987; Trewin and McNamara, 1995). Other morphologically akin traces interpreted as resting/feeding structures of limulids are the "rhomboidal traces" described by Buatois and Mángano (1993), but they are distinguished from the material described here by their angular outline. Traces assigned to *Herradurichnus* are much smaller and bilobed (Poiré and Del Valle, 1996) and its ichnotaxonomic status is in need of re-evaluation. The modern trails described by Metz (1987) are smaller and show an irregular form. We conclude that the scarce material available does not allow an ichnotaxonomic assignment, although the most closely related forms are either prosoma casts of xiphosurids included under *Selenichnites* or, less likely, horizontal U burrows resembling *Fuersichnus*. The specimen with a rim of sand can also correspond to a deep undertrack of a tetrapod footprint.

Vertebrate trace fossils

Ichnogenus ***Rhynchosauroides*** Maidwell, 1911

Rhynchosauroides isp.

Figure 7

Description. Narrow, digitigrade trackway of a quadrupedal tetrapod with high pace angulation, preserved as natural casts and composed of three manus-pes couples (figures 7.A, 7.B). Manus and pes footprints are tridactyl with curved digit imprints.

Manus footprints lie on the midline and are arranged always behind and toward the midline in relation to pes footprints. Track width 180 mm, pace angulation of manus 175°, pace angulation of pes 124°, preserved track length 580 mm. Stride length (manus)= 470 mm, pace (manus) = 225 - 245 mm. Positive (outward) divarication of pes (8°) and negative (inward) divarication of manus (10°) in relation to midline. Pes impression includes the three central digits displaying increasing length from II to IV, footprint wider (65 mm) than long (43 mm), total divarication of 11°. Only a single nearly complete pes impression was seen (figure 7.D), the remaining two are preserved as sets of three rounded to elliptical depressions (ca. 10 mm in size). Pes digits III and IV can display sand crescents on their outer margins (figure 7.D). Manus prints also show three digit impressions with digits III and IV curved inward and digit V nearly straight and directed outward, footprint length ranging from 57 - 44 mm, and width from 41 - 47 mm (figure 7.B). Divarication of digits III-V varies from 63° and 67°, III-IV = 22°-26°, and IV-V = 52° (n=2). A single trackway was found preserved on a weathered surface of medium-grained sandstone with parallel lamination and probably corresponds to transmitted traces (undertracks). Phalangeal pads were not seen except in manus digit IV, which displays two pads. Claw marks not preserved except in pes digit IV (figure 7.B).

Material. A single trackway measured at the field from section 2. Collected material includes: one slab containing the third manus-pes couple (INGEO-PV 041) and a plaster of Paris cast of the second manus-pes set of the same trackway.

Table 1. Summary of the main features of trace fossil assemblages/Resumen de las principales características de las asociaciones de trazas fósiles.

| Trace-fossil assemblage | Lithofacies | Sedimentary environment | Ichnofossils | Paleoecology / ethology |
|-------------------------|---|---|---|--|
| I | Wave-rippled sandstones and mudstones. Soft - sediment deformation structures (facies B-1). | Middle delta front. | <i>Palaeophycus tubularis</i> <i>Cochlichnus anguineus</i> <i>Helminthoidichnites tenuis</i> <i>Archaeonassa fossulata</i> <i>Gordia indiaensis</i> <i>Undichna britannica</i> <i>Helminthopsis abeli</i> | Moderate ichnodiversity, shallow horizontal trail and burrows. Simple grazing, feeding or locomotion strategies. |
| II | Sandstones and mudstones, isolated hummocks, planar cross-stratification (facies B-2) | Upper delta front / lower delta plain setting. | Fusiform structures <i>Cochlichnus anguineus</i> <i>Palaeophycus tubularis</i> | Low ichnodiversity, feeding and dwelling structures in shallow water. |
| III | Amalgamated hummocky cross-stratification (facies B-2). | Upper delta front. Distributary mouth bar sands reworked by storm events. | <i>Palaeophycus tubularis</i> <i>Skolithos</i> isp. | Low ichnodiversity, opportunistic community. Deposit and suspension feeding behavior. |
| IV | Parallel laminated and trough cross-bedded sandstones (facies C). | Upper delta plain. Braided distributary channels. Subaerial exposure. | <i>Rhynchosauroides</i> isp. Horseshoe-shaped structures <i>Palaeophycus striatus</i> <i>Palaeophycus tubularis</i> | Low ichnodiversity, Locomotion and feeding structures. |

Remarks. The presence of digitigrade footprints with curved, slender digit imprints of different length and high pace angulation suggest assignment of this track to the Triassic, lizard-like, and widespread ichnogenus *Rhynchosauroides* Maidwell, 1911. Other common features of this ichnogenus recorded in the studied material are: overstep of the manus by the pes, pes footprints less impressed than manus footprints, and low total divarication of pes footprints (Baird, 1957, 1964; Demathieu, 1970). The Triassic vertebrate ichnogenus *Rotodactylus* Peabody, 1948 is morphologically similar, but our material lacks the impression of digit V directed backward in both manus and pes that is typical of that ichnotaxon. There are more than 20 named ichnospecies of *Rhynchosauroides* (cf. Maidwell, 1911; Baird, 1957, 1964; Haubold, 1966, 1971; Demathieu, 1970; Holst *et al.*, 1970; Demathieu and Saiz de Omenaca, 1977; Demathieu and Leitz, 1982; Fuglewicz *et al.*, 1990; Ptaszynski, 2000). Some ichnospecies were diagnosed either on the basis of scarce/poorly preserved material or distinguished by subtle morphological differences, which suggest that the ichnogenus is in need of a comprehensive revision. Of the named ichnospecies, *R. bavaricus* Demathieu and Leitz, 1982 is similar to the material herein described, mainly by the presence of tridactylous footprints, large pace angulation and general arrangement of manus and pes footprints. However, the poor preservation of the single trackway found precludes a more precise assignation. The gleno-acetabular distance (= body length) of the trace maker is estimated as 235 mm (calculated as half of stride length). *Rhynchosauroides* has been attributed to the Sphenodontidae (Baird, 1957) and is a common ichnotaxa in Triassic to Early Jurassic assemblages from Europe and North America (e.g., Haubold, 1971; Lockley and Hunt, 1995). This is the first record of *Rhynchosauroides* from South America (cf. Leonardi, 1994).

Ichnogenus *Undichna* Anderson, 1976

Undichna britannica Higgs, 1988

Figure 6.E

Description. Pair of sinusoidal trails arranged out of phase and preserved as concave epirelief. Wavelength is 184 mm and wave amplitude 67 mm, maximum preserved length 490 mm (figure 6.E).

Material. Only two nearly complete specimens were recognized in wave-rippled surfaces from section 3 (not collected). Other disconnected, intertwined sinusoidal trails can belong to this ichnotaxa also.

Remarks. The presence of a couple of sinusoidal, intertwined grooves allows us to assign these traces to *Undichna*, in particular to *U. britannica*. Other morphologically related *Undichna* ichnospecies are *U. consulca* Higgs, 1988; *U. radnicensis* Turek, 1989; *U.*

tricosta Lu and Chen, 1998; and *U. quina* Trewin, 2000. However, additional features that typify these ichnotaxa are lacking in our material. *Undichna* has been recorded from freshwater to shallow marine environments, ranging in age from Carboniferous to Recent (e.g., Higgs, 1988; Melchor and Cardonatto, 1998; Gibert *et al.*, 1999). *Undichna britannica* is interpreted as trails left by the caudal and anal fins of fishes swimming close to the bottom (Higgs, 1988).

Distribution of trace fossils

Figure 2 displays the detailed stratigraphic distribution of the ichnofossils described in this study and Table 1 summarizes the main features of the recognized trace fossil assemblages. No trace fossils were identified in open lacustrine mudstone (facies association A). The apparent absence of ichnofossils in underflow deposits of facies A-2 contrasts with their high abundance and diversity in similar facies from the same unit at the Gualo area, Talampaya Park, recently reported by Melchor (2001). These differences are probably related to subtle variations in lacustrine or deltaic processes or preservation conditions between both areas (located ca. 30 km apart). Most of the material described here occurs in facies association B (delta front mudstone and sandstone). In this association, trace fossils are preferentially preserved on wave-rippled tops of the intermediate part of delta front succession (trace fossil assemblage I). This assemblage displays a moderate ichnodiversity and is dominated by shallow subhorizontal trails or burrows, suggesting simple grazing, locomotion or feeding behavior; including (in approximate order of abundance) *Palaeophycus tubularis*, *Cochlichnus anguineus*, *Helminthoidichnites tenuis*, *Archaeonassa fossulata*, *Gordia indianaensis*, *Undichna britannica*, and *Helminthopsis abeli*. Ichnofossils commonly occur in higher density on ripple troughs than in ripple crests. This differential preservation may suggest that organisms preferentially exploited the finer-grained, and potentially richer in organic matter, sediments of ripple troughs. This assemblage is comparable with the *Mermia* ichnofacies, which is characteristic of fine-grained sediments from well-oxygenated, low-energy, permanently subaqueous zones of lacustrine basins (Buatois and Mángano, 1995a).

Fusiform structures occur in association with *Cochlichnus anguineus* and *Palaeophycus tubularis* in the upper part of delta front facies or lowermost delta plain facies (trace fossil assemblage II), associated to storm and wave structures. This assemblage may indicate a resident fauna (common high density of fusiform structures), whose preservation potential was increased by erosion and casting of the traces during storm events. The possible chironomid origin

of fusiform structures is potentially a very useful environmental indicator because the different genera of chironomids are strongly controlled by ecological factors. Micromorphological comparisons in progress among these trace fossils and different modern chironomid cases will clarify the actual affinities of these structures and yield precise data on their paleoecological significance.

Trace fossil assemblage III is exemplified by the presence (sometimes with moderate to high density) of simple subhorizontal and vertical burrows assigned to *Palaeophycus tubularis* and *Skolithos* isp. in beds with amalgamated hummocky cross-bedding of facies association C (section 3, figure 2). This ichnofauna may represent colonization of a newly deposited substrate in relatively shallow water by an opportunistic community of deposit and suspension feeders. Similar assemblages have been described from other high-energy lacustrine settings (cf. Buatois and Mángano, 1998). This assemblage is considered as a continental example of the *Skolithos* ichnofacies in a high-energy deltaic setting.

The remaining recognized trace fossil assemblage (IV in figure 2) includes lacertoid footprints (*Rhynchosauroides* isp.), horseshoe-shaped structures, *Palaeophycus striatus* and *P. tubularis* from the upper part of parasequences (facies association C). The presence of thin striations in *P. striatus* from channel sandstones indicates that the burrows were excavated in a partially dehydrated substrate. This is concurrent with the presence in this interval of tetrapod footprints that suggest, at least, temporary subaerial exposure of fluvial sediments of the upper delta plain. From a conceptual perspective this assemblage can be compared with the *Scoyenia* ichnofacies, mainly because of the evidence of fluctuating water levels in a fluvial-lacustrine setting, which led to subaerial exposure and later trampling by vertebrates.

The Carboniferous lacustrine - deltaic deposits of the Agua Colorada Formation from Catamarca province (Argentina) described by Buatois and Mángano (1993, 1995b) display similar sedimentologic and ichnologic features. This lacustrine succession has less influence of oscillatory flows, greater participation of deposits generated by turbidity currents and underflows, and lacks indications of subaerial exposure. In particular, the Carboniferous ichnocoenosis from sandy and muddy turbidity currents and continuous underflows (ichnocoenosis B, C, and D of Buatois and Mángano, 1993, 1995b) are comparable to our trace fossil assemblage I (Table 1). Nevertheless, this assemblage occurs in shallower facies, displays a lower ichnodiversity and was not recorded in the associated underflow deposits. A further difference is the absence in the Agua Colorada Formation of an ichnocoenosis comparable with our trace fossil as-

semblage IV. An additional example for comparison is the Devonian lacustrine / fan delta sequence described by Pollard *et al.* (1981), but in this case trace fossils were only recorded from distributary channel deposits and are dominated by arthropod trails and tracks. Furthermore, Metz (2000) also recorded the occurrence of *Mermia* and *Scoyenia* ichnofacies from shallow lacustrine shoreline deposits of the Triassic Passaic Formation (Pennsylvania, USA).

Conclusions

Sedimentologic analysis of three trace fossil - bearing sections from the Los Rastros Formation at Ischigualasto Provincial Park allowed the recognition of open lacustrine, delta front and upper delta plain environments. Typically, the facies are arranged in coarsening-shallowing upward parasequences that display a defined vertical distribution of ichnofossil assemblages.

The trace fossil association is of moderate to high diversity and includes four distinctive assemblages, which may reflect environmentally controlled fossilization conditions in lacustrine delta settings (cf. Buatois and Mángano, 1998):

a) A subaqueous assemblage of grazing, feeding and locomotion traces from delta front deposits, which is comparable with the *Mermia* ichnofacies (trace fossil assemblage I).

b) A group composed of fusiform structures (possible chironomid cases), *Cochlichnus anguineus*, and *Palaeophycus tubularis* that appears to be restricted to moderately shallow water in the upper part of the delta front facies or lowermost delta plain facies (trace fossil assemblage II).

c) A high energy, subaqueous assemblage with trace fossils attributed to opportunistic organisms in probable distributary mouth bar sandstone reworked by storm events (upper delta front setting), which is comparable with the *Skolithos* ichnofacies (trace fossil assemblage III).

d) A group of ichnofossils recorded in the upper part of parasequences (upper delta plain facies) including tetrapod footprints and burrows constructed in partially dehydrated fluvial sediments, which is comparable to the *Scoyenia* ichnofacies (trace fossil assemblage IV).

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