

# Ichnology of the Late Carboniferous Hoyada Verde Formation of western Argentina: Exploring postglacial shallow-marine ecosystems of Gondwana

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## ABSTRACT

The postglacial interval of the Upper Carboniferous Hoyada Verde Formation of western Argentina contains an ichnofauna dominated by *Psammichnites plummeri* and *Psammichnites implexus*, with minor occurrences of *Ptychopasma vagans*, *Treptichnus bifurcus*, *Lingulichnus verticalis*, *Protovirgularia* isp., *Lockeia* isp., *Palaeophycus* isp., scarce arthropod trackways and some bilobate structures. The particular features of this association indicate a depauperate expression of the *Cruziana* Ichnofacies, and suggest a context that differs from the expected in normal shallow-marine settings (i.e. archetypal *Cruziana* Ichnofacies). Integration of sedimentologic, ichnologic, sequence-stratigraphic and paleontologic data points to a prograding deltaic system influenced by wave action. Trace fossils have been extensively used to recognize stressed brackish-water environments in the late Paleozoic of Gondwana. However, the recognition of stressed settings needs to take into consideration the specific paleogeographic context of glacially influenced Gondwanan settings. A postglacial open sea adjacent to a paleotopographic high is considered as a possible scenario for the Hoyada Verde Formation. In this particular setting, coastal biotas could have been influenced to some degree by the salinity gradient triggered by freshwater release near to melting ice masses stored in highlands and also by freshwater plumes due to longshore currents. Regional factors (e.g. proximity to highlands and climate) may have played an important role in controlling the characteristics of Gondwanan ichnofaunas. This suggests that the distinction between normal-marine and brackish-water settings in glacially influenced environments using trace fossils may not be as straightforward as in non-glacial settings.

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## 1. Introduction

During the late Paleozoic, Gondwana underwent three glacial and deglaciation events recorded in different basins of South America, South Africa, Antarctica, Australia, and India. These events had a major impact on coastal environments, and deglaciation was accompanied by sea-level rises that triggered transgressive phases over Gondwana (López-Gamundí, 1989, 2010; Limarino et al., 2002). However, the direct influences of glacial and deglacial episodes on benthic communities remain largely unexplored (Buatois et al., 2006, 2010).

Trace fossils are useful tools to explore these peculiar ecosystems because they record animal responses to subtle changes in environmental factors (e.g. Seilacher, 1964; Frey and Pemberton, 1985; Pemberton et al., 1992; McIlroy, 2004a; Buatois and Mángano, 2011). As a result, ichnological studies provide detailed information on environmental parameters involved during deposition, and therefore serve as a basis for

sedimentary environment and facies analysis (e.g. Pemberton et al., 1992; McIlroy, 2004a; Buatois and Mángano, 2011).

The Upper Carboniferous Hoyada Verde Formation of Calingasta–Uspallata Basin of western Argentina provides an opportunity to document postglacial ichnofaunas. The aims of this paper are to: (1) present an integrated sedimentologic and ichnologic analysis of the Hoyada Verde Formation; (2) discuss the environmental controls on this ichnofauna; and (3) compare the Hoyada Verde ichnofauna with other examples from the late Paleozoic of Gondwana in order to explore possible latitudinal patterns in trace-fossil distribution and the impact of glaciation on benthic faunas.

## 2. Geologic setting

The postglacial strata analyzed in this paper accumulated in the Carboniferous–Permian Calingasta–Uspallata Basin of western Argentina (Fig. 1). This basin is considered an arc-related basin, and constitutes part of a series of perigondwanic basins developed along the paleo-Pacific active-plate margin (López-Gamundí et al., 1994; Limarino and Spalletti, 2006; López-Gamundí, 2010). The western boundary of these basins was the late Paleozoic volcanic arc, while the eastern boundary was represented by a positive element referred to as the

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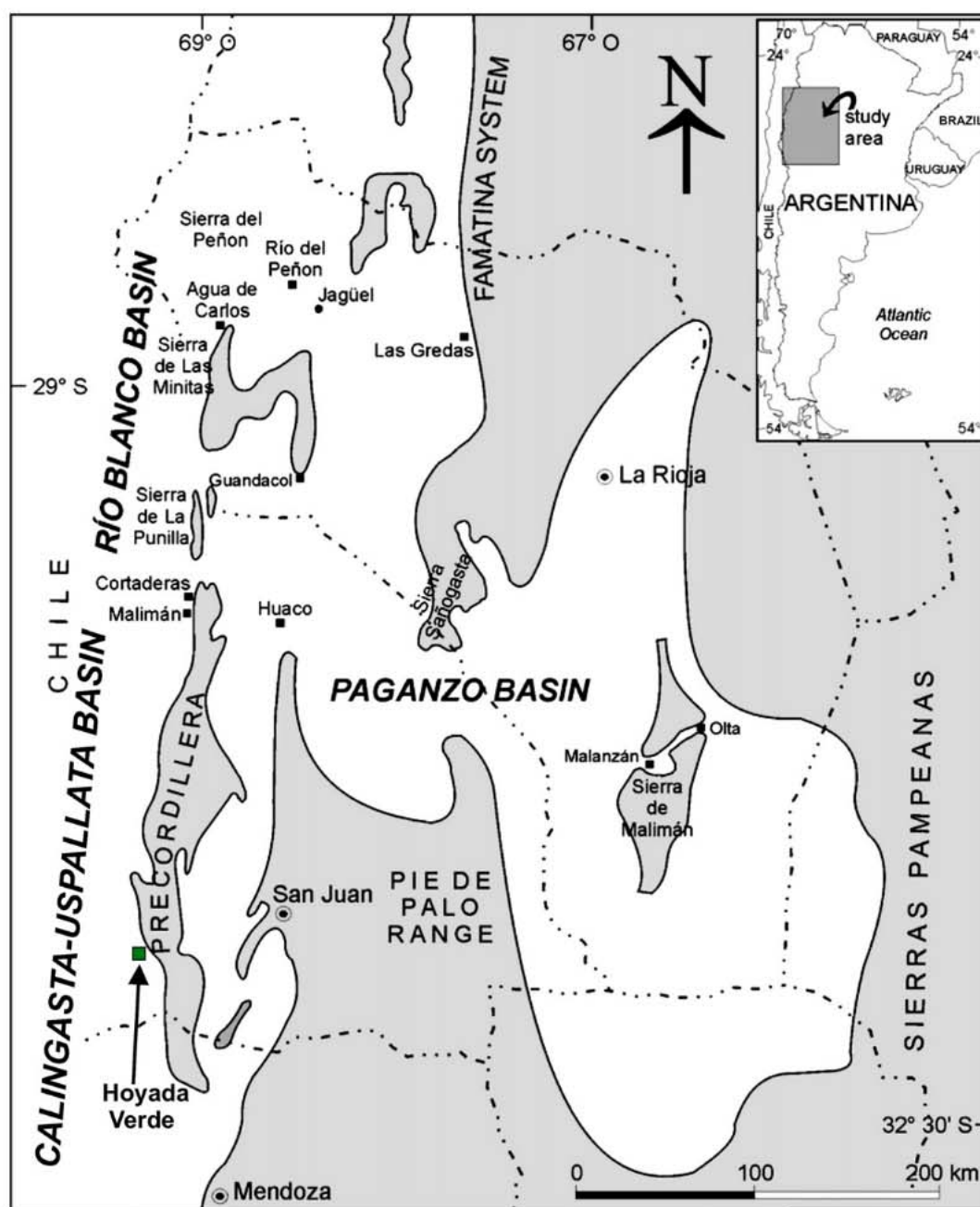


Fig. 1. Late Carboniferous paleogeography of perigondwanic basin of western Argentina, showing the location of the Hoyada Verde area. Modified from Salfity and Gorstovich (1983).

"Protoprecordillera" (Amos and Roller, 1965; López-Gamundí et al., 1994; Limarino et al., 2006; Henry et al., 2008). The Protoprecordillera was a mountain chain that separated the mostly marine Calingasta–Uspallata Basin from the Paganzo Basin (Fig. 1), which was dominated by continental sedimentation. However, the presence of marine deposits in some areas of the Paganzo Basin indicates the existence of a breach in the Protoprecordillera during the Late Carboniferous–Early Permian (López-Gamundí et al., 1992; Desjardins et al., 2010).

The Hoyada Verde Formation of the San Eduardo Group, originally described by Mésigos (1953), constitutes one of the best-known glaciogenic units of the basin (López-Gamundí, 1989, 1991). It crops out in the eastern flank of the basin (western side of Precordillera) in the locality of Sierra de Barreal, San Juan Province, Argentina. The basal relationships of the Hoyada Verde Formation are still unknown, and the unit is erosively overlain by the nonmarine strata of the Tres Saltos Formation of the Pitul Group (Buatois and Limarino, 2003).

### 3. Sedimentary facies

The deposits analyzed are exposed on the western flank of the Hoyada Verde anticline, where they form up to 230 m-thick sedimentary succession (Fig. 2). Based on lithology, physical sedimentary structures, geometry, bed boundaries and fossil content, seven sedimentary facies have been recognized in the succession studied (see also López-Gamundí, 1983; Mángano et al., 2003).

#### 3.1. Facies A: parallel-laminated mudstone

This facies occurs in the lower part of the unit, and consists of up to 45 m-thick of green to greenish gray parallel-laminated mudstone with abundant carbonatic concretions. Dispersed pebbles are locally present. Mésigos (1953) reported gastropods and plant remains, and González (1981) mentioned the presence of glendonite. Recently, Cisterna and





the *Levipustula* Fauna, which is mainly dominated by brachiopods, bivalves, bryozoans, and echinoderms; gastropods, conularids and wood remains represent accessory elements. Based on the paleoecologic signatures of this fauna, Cisterna (1999) and Alonso-Muruaga (2007) characterized the mudstone interval as formed in an open-shelf environment with low sedimentation rate.

### 3.6. Facies F: parallel-laminated mudstone and ripple cross-laminated very fine-grained sandstone

Facies F grades upward from the fossiliferous mudstone (Facies E), and consists of about 25 m of poorly fossiliferous parallel-laminated mudstone interbedded with very fine-grained sandstone. Sandstone displays climbing-ripple cross-lamination, sub-horizontal lamination and quasi-symmetrical ripples. *Psammichnites plummeri* and *Psammichnites implexus* are very common on ripple tops, increasing in abundance towards the upper part of the interval. *Lingulichnus verticalis*, *Palaeophycus* isp. and *Treptichnus bifurcus* are locally present. The ripples were produced by oscillatory and combined flows. This interval represents quiet-water sedimentation only interrupted by minor tractional and oscillatory currents, reflecting deposition below fair-weather wave base, but above storm wave base (Mángano et al., 2003).

### 3.7. Facies G: ripple cross-laminated very fine- and fine-grained sandstone

This facies is made of about 28 m of very fine- and fine-grained sandstone, and occurs gradationally on top of the interbedded mudstone and sandstone unit (Facies F). Sedimentary structures are similar to those of Facies F, but ripples display higher amplitudes and wavelengths. Mudstone is represented by thin layers. *Psammichnites plummeri* and *Psammichnites implexus* are common in fine-grained sandstone, while *Ptychoplasma vagans*, *Lockeia* isp., *Protovirgularia* isp. and arthropod trackways are less common. *Lingulichnus verticalis* and *Treptichnus bifurcus* locally occur in very fine-grained sandstone. This facies represents sedimentation right above fair-weather wave base (Mángano et al., 2003). The top of the interval is erosively truncated by the Tres Saltos Formation (Buatois and Limarino, 2003).

## 4. Facies associations and sequence-stratigraphic framework

The Hoyada Verde sedimentary facies are grouped into three facies associations, representing the transition from glacial to post-glacial conditions (López-Gamundí, 1990, 2010) (Fig. 2). Facies A, B and C are included within facies association 1, which represents glacial-marine proximal deposits. This facies association has been regarded by López-Gamundí (1990, 2010) as the Glacial facies association. From a sequence-stratigraphic perspective, this facies association represents the lowstand systems tract.

Facies association 2 consists of facies D and E, representing fully marine shelf deposits. Facies D is considered to be part of the early postglacial transgressive systems tract (TST), whereas Facies E is considered the maximum flooding interval that accumulated during a later phase of the transgression (López-Gamundí, 1989, 2010; López-Gamundí and Martínez, 2003). A maximum flooding surface (MFS) occurs near the top of this mudstone interval. This MFS has been recognized in different places of the basin (Limarino et al., 2002). The presence of the brachiopod *Levipustula levis* in these deposits indicates a Serpukovian to Bashkirian age (González, 1985; Taboada, 1997; Cisterna, 1999; Simanaukas et al., 2001; Cisterna et al., 2002).

Facies association 3 comprises facies F and G, forming a coarsening- and thickening-upward interval that reflects progradation of a shoreline weakly affected by storms. This interval is included within the highstand systems tract (López-Gamundí and Martínez, 2003; López-Gamundí, 2010).

Facies associations 2 and 3 represent the retreat of ice masses, and constitute the Postglacial facies association of López-Gamundí

(1990). The erosional surface that is present in the top of the succession corresponds to a sequence boundary (SB), resulting from the incision of a fluvial valley filled with deposits of the overlying Tres Saltos Formation (Buatois and Limarino, 2003; López-Gamundí and Martínez, 2003).

## 5. The Hoyada Verde body-fossil fauna

The Hoyada Verde Formation contains marine invertebrates of the *Levipustula* Fauna, which is included in the *Levipustula levis* Zone (Amos and Roller, 1965). This fauna is relatively diverse, and consists of brachiopods, bivalves, bryozoans, gastropods and crinoids (Taboada and Cisterna, 1996; Sterren, 2003; Cisterna and Sterren, 2010). Cisterna and Sterren (2008, 2010) recognized two associations of this invertebrate fauna in the Hoyada Verde Formation: the “Intraglacial *Levipustula* Fauna” present in mudstone interbedded with diamictite in the lower part, and the “Postglacial *Levipustula* Fauna” in the upper part of the section (see Fig. 2). The former is scattered within thick mudstone packages of the Glacial facies association, displaying scarce and poorly diversified invertebrate fauna (e.g. brachiopods, bivalves and annelids, accompanied by gastropods, ostracods and fragmentary bryozoans) of small size. This fauna reflects environmental stressed conditions, probably related to the low temperatures in areas close to the glacier (Cisterna and Sterren, 2008, 2010).

In contrast, the “Postglacial *Levipustula* Fauna” is present in the postglacial mudstone (Fig. 2) of the upper part of the section (Facies E), displaying relatively higher abundance and diversity. Cisterna (1999) and Alonso-Muruaga (2007) documented the vertical distribution of the benthic fauna in the postglacial mudstone interval (Facies E). Three types of paleocommunities were recognized. The bivalve-dominated paleocommunities, mainly composed by the *Streblochondria* sp.–*Palaeolima retifera* association, are characterized by relative low diversity and low abundance. The bryozoan paleocommunities are dominated by *Fenestella* sp., and exhibit the lowest diversity but high abundance. The brachiopod-dominated paleocommunities, characterized by the *Costuloplicia leonicensis*–*Kitakamithyris* sp.–*Levipustula levis* association, display the highest diversity and abundance of the three.

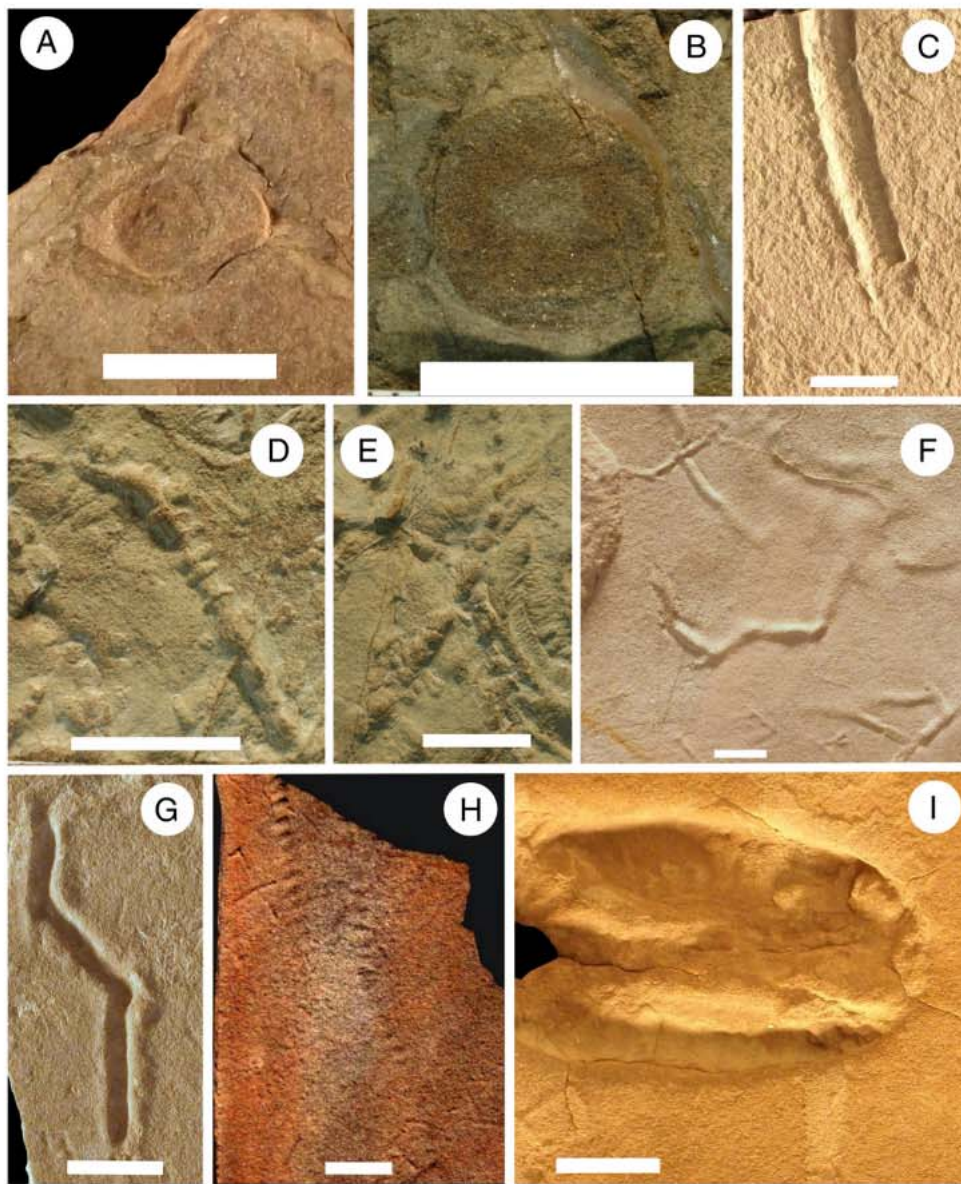
The bryozoan and brachiopod paleocommunities are well represented in most of the interval, while the bivalve paleocommunities are mainly confined to the lowest levels. The replacement of bivalve paleocommunities by bryozoan communities indicates a decrease in sedimentation rate and current intensity as a result of sea-level rise (during the last stage of the transgressive systems tract). Maximum depth, and minimum energy and sedimentation rate during maximum flooding were characterized by the development of bryozoan paleocommunities (Alonso-Muruaga, 2007). The replacement of bryozoan paleocommunities by brachiopod paleocommunities represents an increase in food supply during the highstand. Towards the top of the interval, the benthic faunal content decreases. The last paleocommunity recorded is dominated by bryozoans, but with poor abundance, in marked contrast with those of the maximum flooding, reflecting more unstable conditions and probably more sediment supply. This occurrence may represent faunal restrictions as a response to shallowing. Finally, a “barren interval” separates the uppermost paleocommunity recorded from the first occurrence of trace fossils in the upper part of the interval (see Fig. 2).

## 6. Composition and characteristics of the ichnofauna

The Hoyada Verde Formation ichnofauna is present in the sandstone deposits of facies F and G. Trace fossils are described alphabetically.

*Lingulichnus verticalis* Hakes, 1976: Vertically to near vertically oriented sediment-filled tubes with subcircular to elliptical cross sections (Fig. 3A, B). Concentric laminae are present, surrounding a well-defined cylindrical center. Preserved as full-relief structures. Burrows are 5.3–10.2 mm wide and 10.6–18.5 mm long. *Lingulichnus*





**Fig. 3.** Ichnofauna of the uppermost strata of the Hoyada Verde Formation. (A) *Lingulichnus verticalis*. View towards the top of the bed. Note the elliptic outline. (B) *Lingulichnus verticalis* on bed sole. (C) *Palaeophycus* isp. preserved as positive hyporelief. (D) *Protovirgularia* isp. preserved as positive hyporelief. (E) *Ptychoplasma vagans* preserved as positive hyporelief. Note the presence of *Psammichnites plummeri* towards the right side of the picture. (F) *Treptichnus bifurcus* preserved as positive hyporelief. (G) *Treptichnus bifurcus* preserved as negative epirelief. (H) Trackway indet. Preserved as positive hyporelief. (I) Bilobate structure. All scale bars are 1 cm long.

represents the dwelling structure (Domichnion) of a lingulide brachiopod (Hakes, 1976; Szmuc et al., 1977; Zonneveld and Pemberton, 2003).

*Lockeia* isp.: Elongate, relatively small oval to almond-shaped structures preserved as positive hyporelief. Length is 3.9–2.9 mm, and width is 2.3–1.5 mm. *Lockeia* is interpreted as a resting structure (Cubichnion) of bivalves (Seilacher and Seilacher, 1994; Mangano et al., 1998, 2002a).

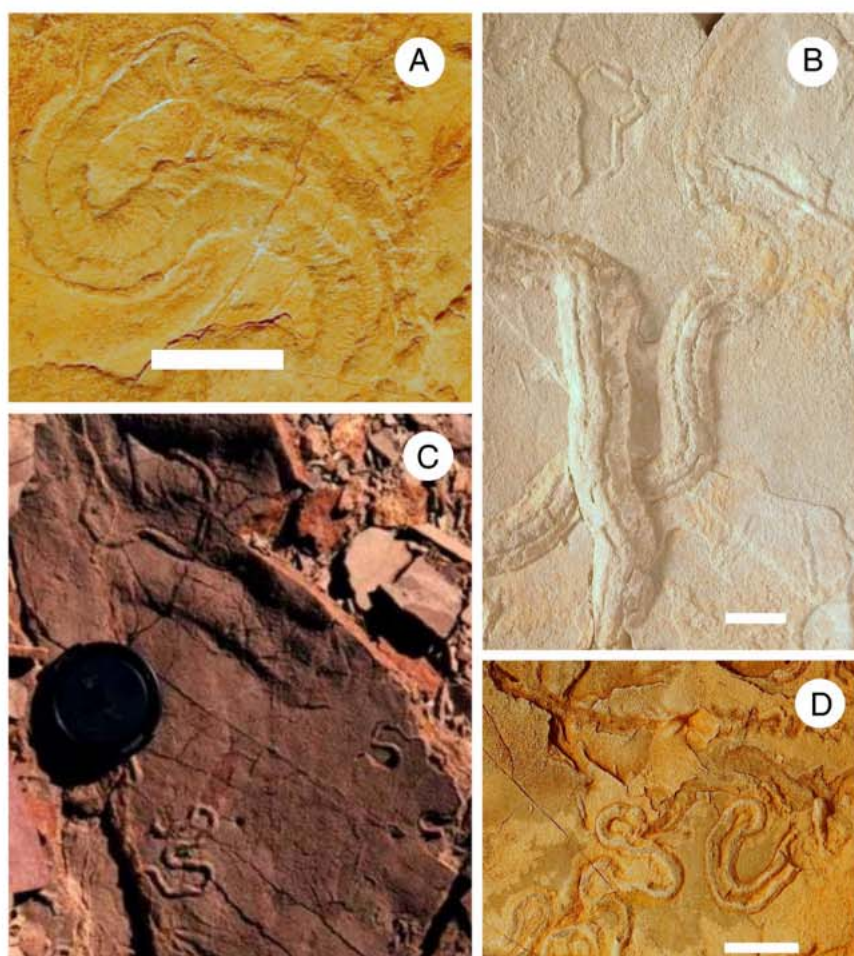
*Palaeophycus* isp.: Horizontal to subhorizontal, unbranched, straight to gently curved, thinly lined, smooth-walled subcylindrical burrows (Fig. 3C). Burrow II is identical to the host rock. Burrows are 4.8–5.8 mm wide, and up to 36.0 mm long. Preserved as positive hyporelief. *Palaeophycus* is a dwelling structure (Domichnion) of a suspension feeder or active predator (Pemberton and Frey, 1982).

*Protovirgularia* isp.: Imbricated relatively small chevron-like structures preserved as positive hyporeliefs (Fig. 3D). Width is 1.6–2.4 mm. Intergradations with *Lockeia* are common. *Protovirgularia* has been interpreted as a locomotion trace (Repichnion) (Mángano et al., 2002a).

*Psammichnites plummeri* (Fenton and Fenton, 1937): Predominately horizontal, sinuous to meandering trails bearing a distinct median ridge and ne, crenulated transverse ridges (Fig. 4A). Trace II is similar to the host rock, and meniscate internal structures are poorly to moderately preserved. Trace width remains relatively constant within specimens. A well-developed marginal fringe is locally present. Overcrossing of the trails is common. Trace width is 6.2–6.4 mm. Median ridge is 0.8–0.9 mm wide. Transverse ridges are 0.5–1.0 mm wide. In some slabs, *P. plummeri* is preserved as hypichnial crests with a distinctive three-lobed structure with two parallel furrows along the trace (Fig. 4B). *Psammichnites plummeri* is a grazing trace (Pascichnion) of deposit feeders (Mángano et al., 2002b).

*Psammichnites implexus* (Rindsberg, 1994): Horizontal to subhorizontal, highly sinuous or meandering trails with a smooth structure and a sharp median ridge, preserved as positive epireliefs (Fig. 4C, D). In many cases, the ridge is locally present. Trace II is similar to host rock. Trace width remains relatively constant within specimens, but tends to broaden at turns. Trace width is 1.9–4.5 mm. *Psammichnites*





**Fig. 4.** Ichnofauna of the uppermost strata of the Hoyada Verde Formation. *Psammichnites plummeri* and *Psammichnites implexus*. (A) *Psammichnites plummeri* preserved at the sole of sandstone. Note the median ridge and fine, crenulated transverse ridges. (B) *Psammichnites plummeri* preserved as positive hyporelief as a three-lobed structure with the two median furrows. (C) *Psammichnites implexus* preserved as positive epirelief in the top of a sandstone (lens cover diameter is 55 mm). (D) Close-up view of the meandering pattern of *P. implexus* (positive epirelief). All scale bars are 1 cm long.

*implexus* is a grazing trace or Pascichnion of deposit feeders (Mángano et al., 2002b).

*Ptychoplasma vagans* Fenton and Fenton, 1937: Irregularly meandering or looping, discontinuous hypichnial crests containing a series of elongate mounds. The mounds are arranged in a rosary pattern (Fig. 3E). Overcrossing of specimens is common. Individual mounds are 1.7–3.7 mm wide and 2.1–7.8 mm long. The structure resembles serial occurrences of *Lockeia*. This structure has been interpreted as a bivalve locomotion trace (Uchman et al., 2011).

*Treptichnus bifurcus* Miller, 1889: Simple or zigzag, straight or slightly curved segments with small projections at the angle of juncture (Fig. 3F, G). Segments consist of horizontal and thin burrows preserved as positive hyporeliefs or negative epireliefs. Individual segments are 1.5–2.5 mm wide and 6.2–14.1 mm long. *Treptichnus bifurcus* represents a feeding structure (Fodinichnion) (Häntzschel, 1975; Buatois and Mángano, 1993). Identical structures in these deposits were referred to as bryozoan polygonal traces by Peralta et al. (1997).

Trackway indet: Horizontal structure preserved as positive hyporelief formed by two subparallel rows of elliptical imprints with their larger axis arranged slightly oblique (transversal) to the axis of the trackway (Fig. 3H). Width of imprints is 1.0–1.5 mm. Distance between rows is about 6.0 mm. This structure may represent a locomotion trace (or Repichnion) of an arthropod.

Short bilobate structure: Coffee-bean structure preserved as an epichnial furrow. Structure is elongated with an elliptical outline and

a wide ridge separating the smooth lobes (Fig. 3I). The structure is 44.7 mm long and 23.4 mm wide. No striae are visible. Although is not possible to assign to a specific ichnotaxa, this structure may represent a resting trace or Cubichnion.

The Hoyada Verde ichnofauna is characterized by the dominance of horizontal trace fossils and subordinate presence of vertical and inclined structures. Different ethological categories are present, including locomotion, feeding, resting and dwelling structures. In terms of trophic types, the ichnofauna is dominated by trace fossils of mobile deposit feeders and subordinate presence of permanent domiciles of suspension feeders. Ichnodiversity is low to moderate, and trace fossils become more abundant towards the uppermost interval of the formation. Low to moderate abundance characterizes facies F, with dominance of *Psammichnites plummeri* and *Psammichnites implexus*. The uppermost deposits corresponding to facies G exhibit sporadically more dense assemblages, which are also dominated by the two ichnospecies of *Psammichnites*. Most of the trace fossils are restricted to bedding planes, whereas shallow vertical structures are scarce and only locally present. Bedding plane bioturbation index or BPBI (Miller and Smail, 1997) varies from 1 to locally 4, whereas vertical bioturbation index (Taylor and Goldring, 1993) ranges from 1 to 2. All these features indicate dominance of shallow tiers, resulting in very low or virtual absence of vertical bioturbation. The preservation of these trace fossils is also favored by the local presence of very thin sandstone–mudstone interfaces.



## 7. Environmental implications of body- and trace-fossil distribution

The vertical distribution of body and trace fossils was controlled by substantial changes in environmental parameters, which in turn reflect the depositional evolution of the unit. The vertical variation in the body-fossil content between Facies D and E indicates an increase in sediment clastic input (higher sedimentation rate) and hydrodynamic energy (Alonso-Muruaga, 2007). The passage into Facies F is characterized by a decrease in the abundance of body fossils and by the first appearance of trace fossils.

In spite of the possible preservational problems (e.g. poor visibility of trace fossils in mudstone deposits, body-fossil preservational biases), the relative absence of body fossils and the presence of trace fossil in Facies F indicate an important faunal replacement parallel to shallowing. Diverse communities dominated by a shelly invertebrate fauna, as indicated by the body-fossil record, occupied deeper-water and low-energy settings, namely shelf to offshore environments, while a soft-body fauna, illustrated by the trace fossils, was present in shallower water and low- to moderate-energy settings.

The ichnofauna indicates dominance of detritus and deposit feeders, and reflects the accumulation of organic detritus in the sediment under moderate- to low-energy conditions. Suspension feeding is recorded locally, indicating some water agitation and currents that helped to keep some food particles in the water column.

Available evidence indicates that the Hoyada Verde ichnofauna shows affinities with the *Cruziana* Ichnofacies. This ichnofacies is characterized by dominance of horizontal traces of mobile organisms and subordinate presence of vertical and inclined permanent structures, wide variety of ethologic categories, dominance of deposit and detritus feeding traces and limited participation of suspension feeders and predators, and high ichnodiversity and abundance (MacEachern and Pemberton, 1992; MacEachern et al., 1999; Buatois and Mángano, 2011). This ichnofacies occurs environmentally from slightly above the fair-weather base to the storm wave base, in a zone ranging from the lower shoreface to the lower offshore in wave-dominated seas. This is consistent with previous sedimentologic interpretations (Buatois and Limarino, 2003; Mángano et al., 2003). However, the assemblage also displays some features that differ from those of the archetypal *Cruziana* Ichnofacies (see MacEachern et al., 1999). These features are: low ichnodiversity, sporadic distribution of trace fossils with localized high abundance, impoverishment of suspension-feeding trophic types and very low bioturbation intensities with primary lamination dominating over biogenic reworking. Accordingly, the Hoyada Verde ichnofauna represents a stressed expression of the *Cruziana* Ichnofacies, and indicates a context that departs from that expected in normal shallow-marine settings (MacEachern and Pemberton, 1994; MacEachern et al., 2005). Mángano et al. (2003) noted this situation based on the occurrence of the two ichnospecies of *Psammichnites* in dense assemblages of very low diversity, and deposition within a prograding deltaic system was suggested.

The effects of deltaic influence on benthic fauna were summarized by MacEachern et al. (2005); controlling factors include heightened sedimentation rates, water turbidity, salinity changes (freshets), episodic sediment gravity deposition, hyperpynical flows, and phytodetrital pulses. In deltas and associated strandplains, the vertical influx and deposition decrease laterally away from the sites of vertical input, such that deltaic stresses may be very localized (MacEachern et al., 2005; Hansen and MacEachern, 2007; Buatois et al., 2008, 2012). Water turbidity is especially important because suspended river-borne mud clogs the filter-feeding apparatus of suspension feeders, therefore resulting in an impoverishment or direct suppression of the *Skolithos* Ichnofacies (Gingras et al., 1998; MacEachern et al., 2005). In the present case, elements of the *Skolithos* Ichnofacies are scarcely distributed, being represented by shallow-tier ichnotaxa (e.g. *Lingulichnus*). Low ichnodiversity reveals a stress factor due to reduced salinity, and allows

distinction from nondeltaic strandplain, shoreface successions (McIlroy, 2004b; MacEachern et al., 2005; Buatois et al., 2008; MacEachern and Bann, 2008; Buatois et al., 2012). Salinity exerts a significant control on the distribution, abundance, and type of organisms in marginal-marine settings (Remane and Schlieper, 1971; McLusky, 1989). In addition to ichnodiversity, the degree of bioturbation of deltaic deposits shows departures from that typical of nondeltaic settings, ranging from low to moderate in prodelta and delta front (Bann and Fielding, 2004; Bann et al., 2004). Reduced bioturbation favored preservation of very thin tempestites that otherwise would have been destroyed by the infauna under fully marine conditions (Buatois et al., 2008). Moreover, the sporadic occurrences of trace-fossil suites in high densities may reflect more stable conditions between depositional events. In addition, Buatois et al. (2008) pointed out that the scarcity of suspension feeders, rather than total absence seems to be the norm in wave-dominated deltas, in contrast to more stressful river-dominated ones.

Accordingly, the integration of sedimentologic and ichnologic information suggests that the upper interval of the Hoyada Verde Formation represents progradation of a wave-influenced deltaic system (Fig. 5). Facies F is regarded as deposited in a prodelta subenvironment, characterized by general impoverishment of bioturbation intensities, reduced ichnodiversity and abundances, and limited opportunistic colonization of tempestites by elements of the *Cruziana* Ichnofacies. The prodelta setting graded seaward into a shelf environment represented by facies E. Facies G is considered as deposited in a distal delta front, characterized by a stressed shallow-infaunal community, dominated by opportunistic deposit-feeding organisms (e.g. *Psammichnites plummeri* and *P. implexus*), with few suspension feeders. Although no evidence of distributary channels is preserved, the fluvial system recorded in the overlying Tres Saltos Formation may reflect incision of former distributary channels as a response to sea-level fall (see Fig. 5).

## 8. Discussion: evaluating the controls on late Paleozoic shallow-marine Gondwanan ichnofaunas

Marine ichnofacies represent archetypal facies models based upon recurrent ichnologic assemblages (Seilacher, 1967, 1978; Frey and Pemberton, 1984, 1985; Buatois and Mángano, 2011). The Hoyada Verde ichnofauna and its depositional framework may be compared with some other examples from the late Paleozoic of Gondwana in order to explore similarities and differences with respect to archetypal ichnofacies. This allows evaluating not only depositional controls, but also potential latitudinal variations in trace-fossil distribution and the impact of the glaciation on coastal and shallow-marine benthic faunas.

Buatois et al. (2006, 2010) documented the impact of freshwater discharge due to melting during the postglacial transgression in Gondwanan fjord settings. These authors described ichnofaunas typical of freshwater environments representative of the *Mermia* Ichnofacies. In the Paganzo Basin of western Argentina, these ichnofaunas occur in the Upper Carboniferous Guandacol Formation, which contains glacially influenced deposits towards the base, which are overlain by transgressive mudstone (Limarino and Césari, 1988; López-Gamundí and Martínez, 2000; Limarino et al., 2002; López-Gamundí, 2010; Schatz et al., 2011). Prograding deltaic deposits transitionally cap the flooding interval. The occurrence of these ichnofaunas above the transgressive mudstone represents an example of extreme freshwater discharge into the fjord due to melting of the nearby glaciated areas (Buatois et al., 2006, 2010). This indicates a control directly related to the proximity of ice masses and, as such, reflects the peculiarities of the Gondwanan context.

The Lower Permian Pebley Beach Formation from the Sydney Basin, Australia records accumulation in shallow-marine to coastal environments at the close of the late Paleozoic Gondwanan ice age (Bann et al., 2004). Although previous interpretations suggested inner- to outer-shelf and slope environments, re-evaluation by these



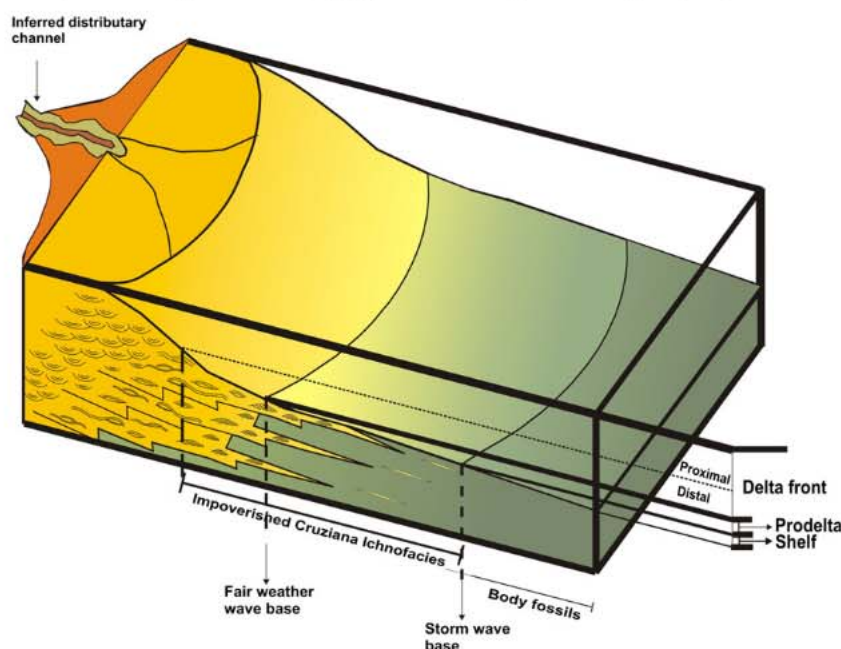


Fig. 5. Deltaic facies model showing distribution of the ichnofauna and body fossils with their respective environmental ranges.

authors indicated alternation of brackish-water estuarine facies and open-marine deposits instead. Brackish-water and fully marine intervals are, to some extent, lithologically and sedimentologically similar, but display profound ichnologic differences, namely bioturbation intensity and the characteristics of the trace-fossil assemblages. In general, the fully marine deposits contain trace-fossil suites that display moderate to intense bioturbation, high ichnodiversity, specialized feeding and grazing behaviors, and uniform distribution of ichnogenera. All these characteristics reflect climax communities in stable environments. In particular, offshore deposits display diverse trace-fossil assemblages and complex mixtures of structures produced by deposit feeding and grazing behaviors, illustrating the archetypal *Cruziana* Ichnofacies. Shoreface intervals contain trace-fossil assemblages with robust, complex deposit- and detritus-feeding structures, which reflect a more proximal expression of the *Cruziana* Ichnofacies, indicating well-oxygenated, open-marine settings. In contrast, deltaic successions contain diverse but sporadically distributed trace-fossil suites that record proximal expressions of the *Cruziana* Ichnofacies. Estuarine deposits contain extremely impoverished ichnological suites, with significantly reduced degrees of bioturbation intensity, variability in the distribution of the individual ichnogenera, and dominance of a few simple forms with elements that reflect simple feeding strategies of trophic generalists. The last characteristic indicates low diversity expressions of the mixed *Skolithos*–*Cruziana* Ichnofacies.

In the same vein, Bann and Fielding (2004) compared non-deltaic shoreface and subaqueous delta deposits in various Lower to Upper Permian formations of Australia. These authors noted that offshore to shoreface deposits contain high ichnodiversity, uniform lateral and, to a lesser extent, vertical distribution of bioturbation, and significant number of structures with different feeding and grazing behaviors that reflect diverse expressions of distal, archetypal and proximal *Cruziana* Ichnofacies, respectively. Abundant food material and stable conditions in well-oxygenated fully marine setting were envisaged. In contrast, ichnological signatures of the subaqueous-delta deposits consist of low-diversity trace-fossil assemblages (one or two ichnotaxa), bioturbation sporadically distributed showing low intensity, and the assemblage represents a stressed expression of the *Cruziana* Ichnofacies, with largely absent or rare elements of the *Skolithos* Ichnofacies. Prodelta deposits exhibit a general dominance of the primary fabric

over biogenic reworking, and relatively diverse trace-fossil suites with individual ichnospecies reduced in size and sporadically distributed throughout the interval. In contrast, offshore deposits show high and uniformly distributed bioturbation intensities and very diverse trace-fossil suites. Distal delta-front deposits contain a stressed infaunal community dominated by opportunistic deposit feeder organisms, with rare burrows of suspension feeders. This is different from shoreface deposits, which contain a well-diversified trace-fossil assemblage that represents a proximal expression of the *Cruziana* Ichnofacies.

In another unit of the Sydney Basin, the Lower Permian Wasp Head Formation, McCarthy (1979) recorded relatively diverse trace-fossil assemblages. These ichnoassemblages are mainly composed of feeding and dwelling structures, illustrating the *Cruziana* and *Skolithos* Ichnofacies in shoreface and foreshore environments, respectively. Overall, the Wasp Head Formation ichnofauna shows similarities to the ichnofaunas described by Bann et al. (2004) and Bann and Fielding (2004).

Mángano and Buatois (2004) documented low-latitude Carboniferous marginal- to shallow-marine ichnofaunas from the North American Midcontinent. These authors recognized that normal open-marine environments display high diversity and abundance of trace fossils, whereas more stressed environments (bays settings and estuarine transitions) show a relatively lower ichnodiversity and variable abundance. Although the geological and latitudinal context of these ichnofaunas is in sharp contrast with that of the Australian assemblages, similar general trends in trace-fossil distribution across a salinity gradient occur in both.

The examples of North America Midcontinent and Australia indicate that the occurrences of impoverished and non-impoverished ichnofaunas may reflect changes in ecological parameters at the scale of environments and subenvironments. However, other examples from Gondwana show some departures with respect to this pattern. The Lower Permian Talchir Formation of India comprises an ice-marginal glaciomarine succession containing deposits that show direct connection to ice masses (Chakraborty and Bhattacharya, 2005; Sarkar et al., 2009). The Talchir Formation contains impoverished trace-fossil assemblages consisting of vertical and horizontal trace fossils attributed to the *Skolithos* and *Cruziana* Ichnofacies. These occurrences represent the activity of a depauperate marine fauna under



harsh ecologic conditions due to the establishment of a brackish-water environment that resulted from the influx of glacier meltout freshwater during climatic amelioration. In this particular case, the main control inferred in the occurrence of the ichnofauna is directly related to the proximity to glaciers and their melting. This is different from the Australian ichnofaunas, which occur in facies not directly linked to glaciers.

Although the Hoyada Verde Formation contains glacial deposits, trace fossils are present in the non-glacial part, above shelf deposits with a diverse marine fauna. This indicates that in relatively deeper-water settings (shelf), normal-marine conditions occurred during the postglacial transgression. The reinterpretation of the highstand deposits as deltaic in origin may explain the establishment of an impoverished assemblage of the *Cruziana* Ichnofacies, due to an increase in stress conditions. However, the emplacement of a stressed environment should be also understood within the framework of a specific paleogeographic context, namely a high-latitude postglacial open sea adjacent to the paleotopographic high (López-Gamundí et al., 1994; López-Gamundí, 1997; Henry et al., 2008; Domeier et al., 2011). Taking into account this particular Gondwanan setting, some mechanisms can be inferred. Freshwater discharges coming from the ice stored in the highlands, due to a combination of high latitude and altitude (Isbell et al., 2011), may have affected the marine realm, mainly during climatic amelioration. In this scenario, a salinity gradient controlled by the distance to freshwater areas near ice masses was established within this postglacial sea. Discharges would not have been strong enough to dilute the salinity of more distal and deep-water areas, such as offshore-shelf settings, owing to their relative emplacement away from the ice masses. This is different from what is envisaged in the more proximal fjord settings of the Paganzo Basin where the freshwater influence can be strong even in relatively deeper-water settings (Buatois et al., 2006, 2010). Therefore, the dilution of normal-marine salinity in the Hoyada Verde area may have taken place in shallow-water settings, not only in deltas but also in their associated strandplains. In this model, non-deltaic shallow-marine environments could have been also influenced to some degree by the salinity gradient and by freshwater plumes due to longshore currents, impacting on the nearby benthic faunas.

If the inferred role of adjacent ice masses is correct, Gondwanan ichnofaunas were influenced not only by standard local environmental parameters at the scale of environments and subenvironments, but also by regional factors (e.g. proximity to highlands and climate). If this is the case, the distinction between normal-marine and brackish-water settings is probably not as straightforward as in non-glacial settings.

## 9. Conclusions

The postglacial ichnofauna of Hoyada Verde Formation is mainly composed of *Psammitichnus plummeri*, and *Psammitichnus implexus*, and minor occurrences of *Lingulichnus verticalis*, *Ptychoplasma vagans*, *Treptichnus bifurcus*, *Lingulichnus verticalis*, *Protovirgularia* isp., *Lockeia* isp., *Palaeophycus* isp., scarce arthropod trackways and some bilobate structures. The ichnofauna is characterized by the dominance of horizontal trace fossils and subordinate presence of vertical and inclined structures of mobile deposit feeders and suspension feeders. Ichnodiversity is low to moderate. Most of the trace fossils are restricted to the bedding planes, whereas shallow vertical structures are scarce and only locally present, indicating dominance of shallow tiers.

The Hoyada Verde ichnofauna illustrates the *Cruziana* Ichnofacies, which environmentally occurs from slightly above the fair-weather base to the storm wave base, in a zone ranging from the lower shoreface to the lower offshore in wave-dominated seas. However, low ichnodiversity, sporadic distribution of trace fossils with localized high abundance, impoverishment of suspension-feeding trophic types and very low bioturbation intensities with primary fabric dominating over biogenic reworking indicate a depauperate expression of *Cruziana* Ichnofacies, suggesting a context that depart from normal shallow-marine settings.

Integration of sedimentologic, ichnologic, sequence-stratigraphic and paleontologic data suggests a prograding deltaic system influenced by wave action. A review of the literature on late Paleozoic ichnofaunas suggests that the paleogeographic context (e.g. proximity with the ice, presence of a nearby topographic high) played an important role. High freshwater discharge from the adjacent ice areas in the highlands may have considerably affected coastal biotas during postglacial times. Accordingly, associated strandplains may have been also influenced to some degree by the salinity gradient due to melting of the ice caps and by freshwater plumes due to longshore currents. If this is the case, Gondwanan ichnofaunas were influenced not only by the standard local environmental factors that operate at the scale of subenvironments, but also by regional factors. This environmental scenario suggests that the distinction between normal-marine and brackish-water settings in glacially influenced environments using trace fossils may not be as straightforward as in non-glacial settings.

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