DOI: 10.1590/2317-4889201820180021

ARTICLE

Paleoenvironments of a regressive Devonian section from Paraná Basin (Mato Grosso do Sul state) by integration of ichnologic, taphonomic and sedimentologic analyses

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ABSTRACT: *Studies that integrate ichnologic, taphonomic and sedimentologic data result in more accurate paleoenvironmental inferences than isolated approaches. Most of paleontological studies regarding Devonian from Paraná Basin were conducted in the southern part of the basin (Paraná state), precluding taphonomic or ichnologic studies to the northern part, and even its macrofossils content is understudied. This study analyzes paleoecologic and depositional conditions represented by trace fossils, macrofossils and sedimentary facies in a regressive Devonian section from Paraná Basin, Mato Grosso do Sul state, Brazil. Seven ichnofabrics (*Macaronichnus, Psammichnites, Arenicolites-Skolithos, Cylindrichnus-Skolithos, Zoophycos, Rhizocorallium-Palaeophycus, *and* Chondrites *ichnofabrics) and three taphofacies (T1: parautochthonous to allochthonous preservation; T2: Autochthonous preservation; and T3: time-averaged autochthonous to allochthonous association) were diagnosed. The studied sections are positioned in a highstand systems tract (HST) exhibiting dominance of sandy facies, and four sub-environments were defined: foreshore; shoreface; storm-dominated shoreface to transitional offshore; and offshore. The dominance of foreshore to shoreface settings in a HST corroborates a shallower context in relation to the southern part. However, similarities in the facies and ichnofacies stacking, as well in the macrofossil content suggest that the hypothetical division between two sub-basins (Apucarana and Alto Garças Sub-basins) was not complete until early Emsian.*

KEYWORDS: *Ichnofacies; Taphofacies; Tempestites; Devonian; Sub-Basins.*

INTRODUCTION

The distribution of the trace fossil associations is controlled by biologic and environmental parameters, making them useful for paleoecologic, depositional and paleoenvironmental analyses (*e.g.*, Pemberton & Frey 1984, Bottjer *et al.* 1988, Savrda & Bottjer 1986, Ekdale & Lewis 1991, Savrda 1998). In the same way, taphonomic signatures are controlled by environmental processes, allowing inferences regarding depositional regimes (*e.g.*, Brett & Baird 1986, Speyer & Brett 1986, 1988). The integration of these tools result in more accurate depositional inferences. However, studies integrating ichnological and taphonomic analysis applied to sedimentological, stratigraphical, palaeoenvironmental and palaeoecological inferences are still rare (*e.g.*, Henderson & McNamara 1985, Bromley & Asgaard 1991, Reolid *et al.* 2014, Sedorko *et al.* 2018a).

The Devonian macrofossils from Paraná Basin have been widely studied under different approaches, such as taxonomy (*e.g.*, Clarke 1913, Kotzian 1995, Leme *et al.* 2004, Scheffler & Fernandes 2007a, 2007b, Scheffler *et al.* 2013, Richter *et al.* 2017), biogeography (Melo 1988) and

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Manuscript ID: 20180021. **Received on:** 03/02/2018. **Approved on:** 09/26/2018.

taphonomy (Simões *et al.* 2009, Rodrigues *et al.* 2003, Bosetti *et al.* 2011, 2012, 2013, Zabini *et al.* 2010, Horodyski *et al.* 2014). However, most of those studies were developed in the south part of the Paraná Basin (Paraná State, Brazil, Fig. 1A), and ichnologic studies were conducted under ichnotaxonomic approach (see Sedorko *et al.* 2013 for a synthesis). The strata from the northern basin preclude taphonomic or ichnologic studies, and even the macrofossils content is understudied, especially in Mato Grosso do Sul state, Brazil (see Scheffler *et al.* 2010 for a synthesis). In this sense, this study aims to:

1. infer the paleoecologic and depositional conditions to Devonian strata in the northern Paraná Basin;
2. record the Malvinokaffric fauna in this regressive succession;
3. compare the stratigraphic stacking and macrofossil content represented by coeval deposits from south part of the basin (Paraná state).

MATERIALS AND METHODS

Two sections (referred as MS14 [19°24'41.91"S; 54°58'59.92"W; datum WGS84] and MS 18/19 [19°26'16.37"S; 55°0'2.41"W; datum WGS84] were prospected considering their sedimentologic, ichnologic and taphonomic features. These sections crop out at Rio Negro municipality (Mato Grosso do Sul state, Brazil; Figs. 1A and 1B).

The sedimentologic analysis considered textures, primary sedimentary structures, geometry of beds and macrofossil content. The trace fossil analysis took into account the ichnofabric characterization and the quantification of the bioturbation. The amount of bioturbation was expressed based on bioturbation scale (BS), as proposed by Reineck (1963), ranging from 0 (no bioturbated) to 6 (completely bioturbated). Finally, taphonomic analysis followed the techniques as proposed by Simões & Ghilardi (2000), with vertical control of the fossil content, as well their taphonomic signatures. The collected skeletons were classified as univalved, bivalved or multielement, and all observable taphonomic signatures were verified according to the criteria established by Speyer & Brett (1986, 1988), but only articulation and fragmentation were diagnosed. Lack of abrasion, corrosion, rounding, bioerosion, encrustation, and partial dissolution were also considered for paleoenvironmental interpretation, as well packing and relative position to the bedding plane (Suppl. Tab. A1).

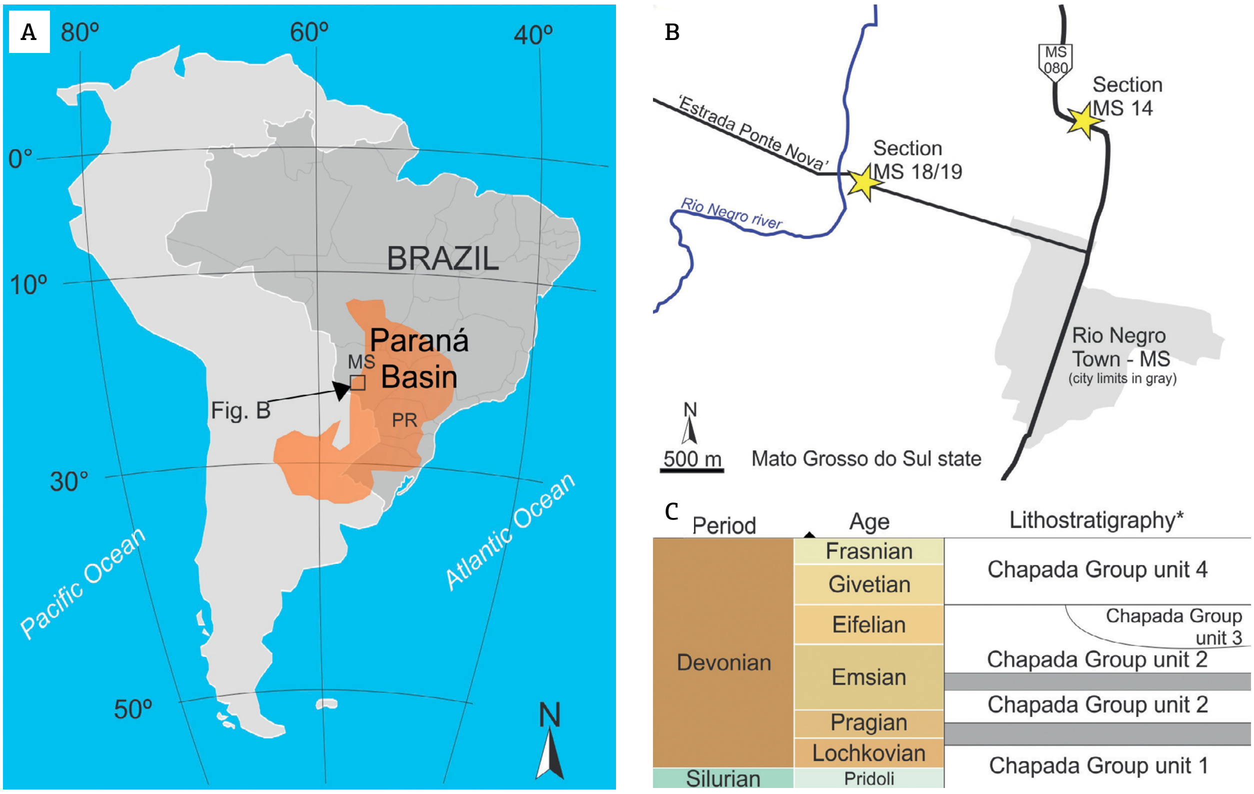

Figure 1. Geographic and stratigraphic context of studied sections. (A) Position of studied sections in the Paraná Basin; (B) geographic position of studied outcrops close to Rio Negro Town (MS); (C) general lithostratigraphy, ages and sequences of Devonian strata in northern basin; studied sections are positioned in the lower Chapada Group unit 2.

GEOLOGICAL SETTING

The Paraná Basin is a huge intracratonic basin that covered the southern portion of Brazil and adjacent areas during the pre-Cenozoic eras. This basin was originally a gulf opened to the Panthalassa (Zalán *et al.* 1990, Milani 1992), changing to an intracratonic depression in the interior of Gondwana probably during Upper Devonian (Milani 1997). Six supersequences compose the basin sedimentary fill, which was influenced by tectonic-eustatic cycles related to the evolution of the Western Gondwana, from Late Ordovician to Late Cretaceous (Milani *et al.* 2007). Ramos (1970) and Pereira *et al.* (1998) proposed the existence of two depocenters during the Early Paleozoic and the differentiation of two sub-basins, Alto Garças (north) and Apucarana (south). However, Milani *et al.* (1998, 2006, 2007) argued that the difference in thickness of Devonian strata are product of differential preservation beneath the sub-Pennsylvanian unconformity.

At least in the south part of the basin, the Paraná Supersequence spans in age from Lower Silurian (Sedorko *et al.* 2017) to Middle Devonian (Grahn *et al.* 2013) in outcrops, with Upper Devonian ages preserved only in subsurface (Bergamaschi 1999, Grahn *et al.* 2013, Sedorko *et al.* 2018c). Grahn *et al.* (2013) used microfossil zonation to correlate the ages of the lithostratigraphic units from southern basin (referred by them as Apucarana sub-basin) and northern (Alto Garças sub-basin). There is no consensus in relation to the exact position of south pole during Emsian, but during Emsian the basin was possibly positioned between 70 and 80º South (Isaacson & Sablock 1990, Isaacson & Diaz Martinez 1994, Witzke & Heckel 1988, Scotese & McKerrow 1990, Kent & Van Der Voo 1990, Torsvik & Cocks 2013).

In Mato Grosso do Sul state (northern basin), Brazil, the Paraná Supersequence is composed of four lithostratigraphic units, named Chapada Group units 1, 2, 3 and 4 (Grahn *et al.* 2013, Fig. 1C).

The Chapada Group unit 1 contains the basal marginal-marine and shallow marine sandy deposit and is mostly correlated with Furnas Formation from southern part of the basin (Grahn *et al.* 2013). The lower and middle units of Furnas Formation were deposited during Lower Silurian, based on its trace fossils with ichnostratigraphic value (Sedorko *et al.* 2017).

The Chapada Group unit 2 is composed by a basal conglomerate capped by purple-red sandstone interbedded with siltstones and shales, overlapped by fine- to medium-grained grayish to reddish sandstones, ranging from Early Pragian to Eifelian (Grahn *et al.* 2010). Pioneering descriptions of the macrofossil content in this unit attributed affinities to the Malvinokaffric Realm (Melo 1988). Grahn *et al.* (2013) identified a gap within Chapada Group unit 2, dividing this unit in lower and upper parts. The lower part was correlated with Ponta Grossa Formation (*sensu* Grahn *et al.* 2010, 2013, or Jaguariaíva Member *sensu* Lange & Petri 1967), while the upper part corresponds to lower São Domingos Formation (*sensu* Grahn *et al.* 2013, or São Domingos Member *sensu* Lange & Petri 1967). Outcrops here studied are inserted in lower Chapada Group unit 2 (Ponta Grossa Formation or Jaguariaíva Member; Pragian to Early Emsian) considering their stratigraphic relations overlapping the Chapada Group unit 1 and the macrofossil content.

The Chapada Group unit 3 crops out only in the northeast border of the basin (Andrade & Camarço 1980, Melo 1988). This unit is characterized by reddish medium- to coarse-grained sandstones interbedded with conglomeratic sandstones, interpreted as shallow marine to wave-dominated deltaic environments (Andrade & Camarço 1980, Grahn *et al.* 2010). This unit was deposited during Early Emsian to Eifelian and was interpreted as the proximal equivalent of the upper Chapada Group unit 2, correlated to São Domingos Formation and its Tibagi Member from southern part of the basin (*sensu* Grahn *et al.* 2010, 2013).

Finally, the Chapada Group unit 4 consists of dark-gray shales interbedded with sandstones and siltstones. The base of this unit is related to the maximum flooding surface in the Eifelian-Givetian boundary (Assine 2001, Grahn *et al.* 2010). This unit is correlated with the upper São Domingos Formation (*sensu* Grahn *et al.* 2013) from southern part of the basin.

RESULTS

Six sedimentary facies, seven ichnofabrics, and three taphofacies were diagnosed in the studied section. Their vertical disposition characterizes a regressive pattern, as suggested by the dominance of sandy facies to the top of the sections and the ichnofabrics stacking, as further presented (Figs. 2 and 3).

Macaronichnus ichnofabric (Fig. 4A) is characterized by horizontal to sub-horizontal, straight to meandering, cylindrical burrows with a mantle and core reflecting grain segregation by the tracemaker. Only few plant fragments occur associated with this ichnofabric (no defined taphofacies), and the bioturbation scale is low to moderate (BS 2-3). *Macaronichnus* occurs as simple ichnofabric, reflecting the activity of a single ichnocoenosis, and is preserved in horizontal stratified (Fig. 5A) or wave cross-laminated (Fig. 5B), well sorted, fine- to medium-grained sandstones (Sw and Sh facies; Tab. 1).

Psammichnites ichnofabric (Fig. 4B) is characterized by straight to meandering, horizontal, flat traces preserved in negative epirelief (trail preservation) on bedding

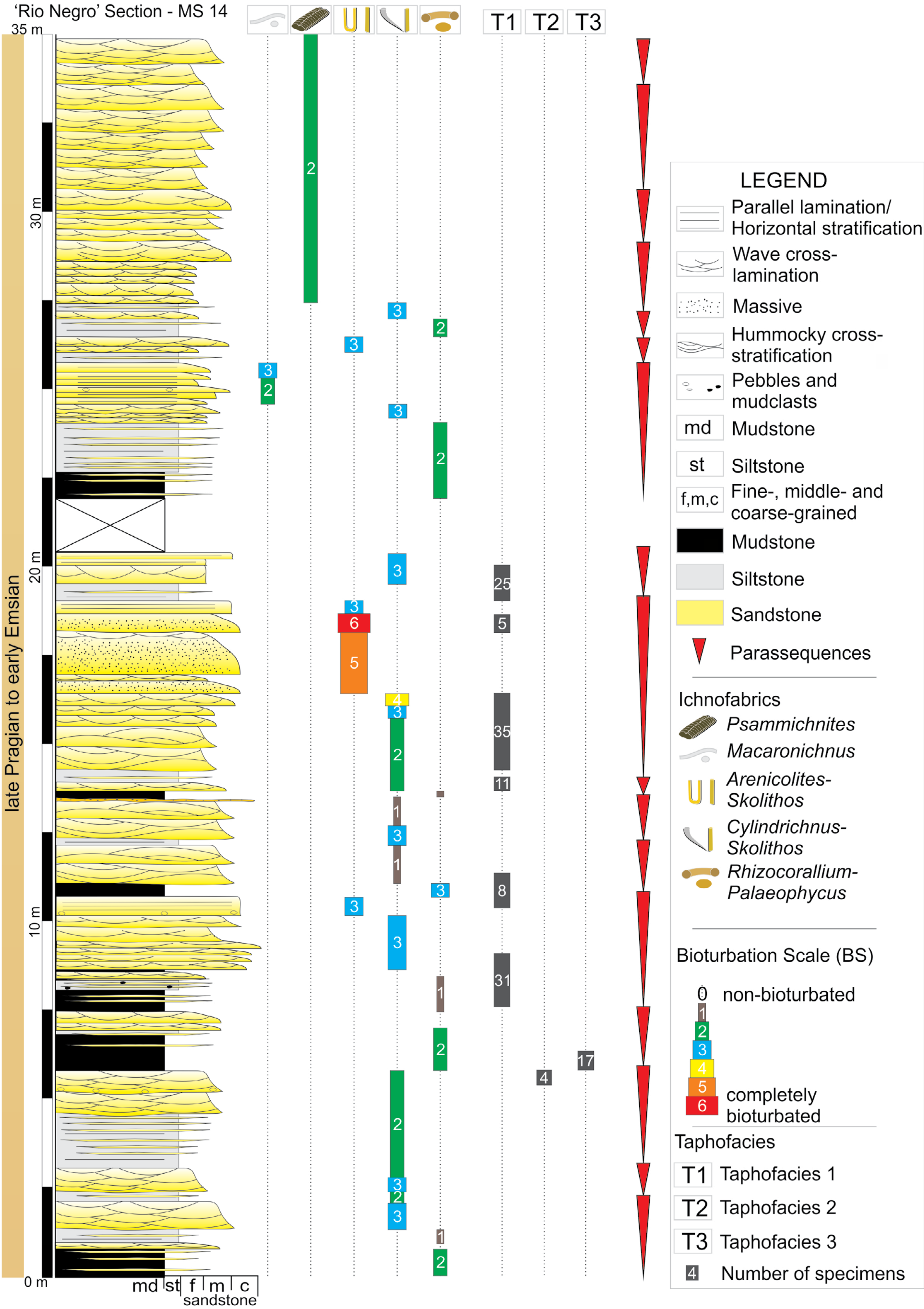

Figure 2. Sedimentologic profile, ichnofabric distribution and taphofacies from outcrop MS 14.

planes, internally ornamented by a faint meniscate backfill. *Skolithos*, *Arenicolites*, *Diplocraterion*, *Palaeophycus*, and *Macaronichnus* are locally preserved, characterizing this ichnofabric as composite, and with no associated macrofossils. The *Psammichnites* ichnofabric is preserved at wave cross-laminated fine-grained sandstones (Sw facies; Tab. 1), with low bioturbation scale (BS 2).

The *Arenicolites-Skolithos* ichnofabric (Fig. 4C) is composed by vertical burrows, simple or U-shaped, locally with *Cylindrichnus*, *Rosselia*, *Rhizocorallium*, *Diplocraterion*, and

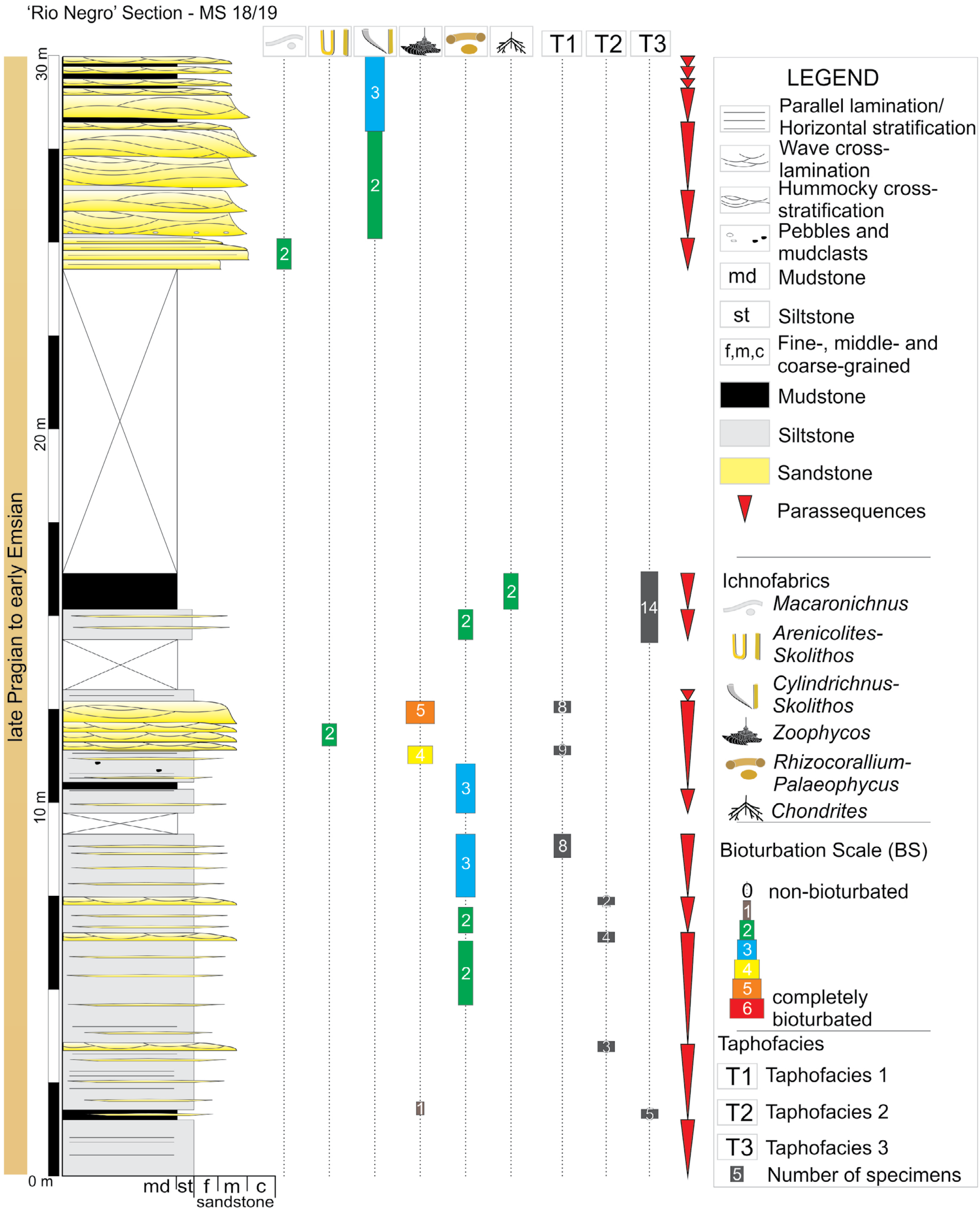

Figure 3. Sedimentologic profile, ichnofabric distribution and taphofacies from outcrop MS 18/19.

Palaeophycus, with bioturbation scale variably expressed, being normally low to moderate (BS 3-4), but occasionally high (BS 5-6). In the rare levels with macrofossils, they occur disarticulated, few fragmentated, parallel or oblique in relation to bedding-plane, being composed of conulariids and mollusks bivalves, which characterizes the Taphofacies 1 (Tabs. 2 and 3). This composite ichnofabric is preserved in several sandstones facies (Shcs, Sm, Sw, and Sh; Fig. 5 and Tab. 1).

The *Cylindrichnus-Skolithos* ichnofabric (Fig. 4D) is dominated by vertical structures, with funnel-shape or circular apertures, locally with *Arenicolites*, *Diplocraterion*, *Rhizocorallium*, *Palaeophycus*, *Lingulichnus*, and *Rosselia*, presenting low bioturbation scale (BS 1-3), to locally moderated (BS 4). The associated macrofossils are predominantly disarticulated, few fragmented, parallel or oblique in relation to bedding-plane. In this association, two preservation modes occurs, which were grouped in two taphofacies. The most recurrent association of macrofossils is characterized by dominance of disarticulated (bivalved) and predominantly parallel-oriented fossils in relation to the bedding-plane. This association is characterized by the presence of brachiopods infaunal lingulids (Fig. 6A) *Orbiculoidea* (Fig. 6C), *Australocoelia*, *Australospirifer*, conulariids, *Tentaculites* and

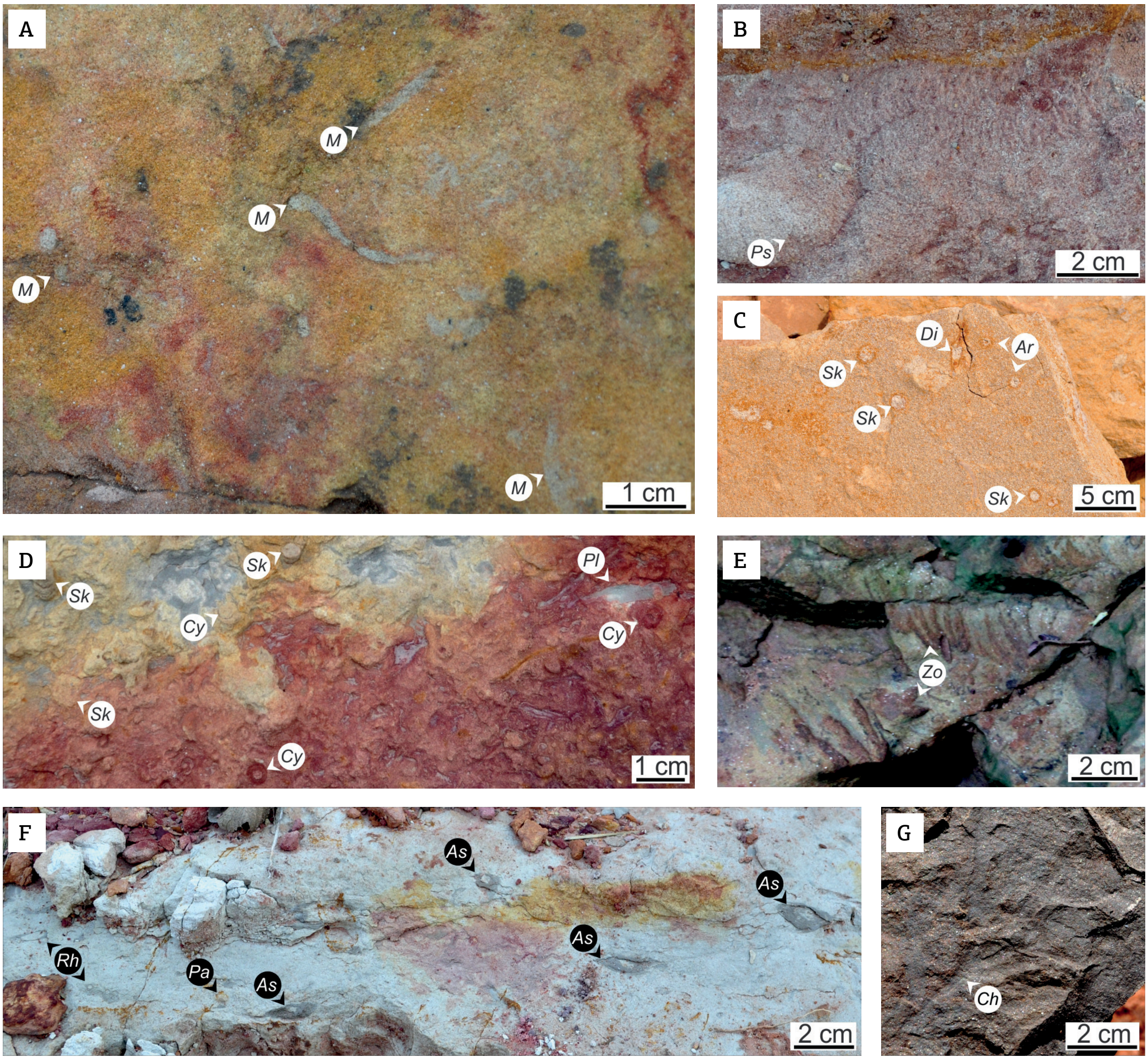

Figure 4. Ichnofabrics from lower Chapada Group unit 2 in Rio Negro (MS). (A) *Macaronichnus* (*M*) ichnofabric in bedding-plane view. (B) *Psammichnites* (*Ps*) ichnofabric in bedding-plane view. (C) *Arenicolites-Skolithos* (*Ar* and *Sk*) ichnofabric with *Diplocraterion* (*Di*) in bedding-plane view. (D) *Cylindrichnus-Skolithos* (*Cy* and *Sk*) ichnofabric with *Planolites* (*Pl*) and other indistinct trace fossils in bedding-plane view. (E) *Zoophycos* (*Zo*) ichnofabric in bedding-plane view. (F) *Rhizocorallium-Palaeophycus* (*Rh* and *Pa*) ichnofabric with *Asterosoma* (*As*) in oblique view in relation to the bedding-plane. (G) *Chondrites* (*Ch*) in bedding plane view.

trilobites, which were grouped as Taphofacies 1. In the other hand, the occurrences of whole and articulated fossils, vertically oriented in relation to bedding plane indicating *in situ* position, is composed of *Australospirifer* (Figs. 6D and 6E) and infaunal lingulids (Fig. 6F). This association was grouped as Taphofacies 2 and is preserved in sandy facies (Tab. 2). The *Cylindrichnus-Skolithos* ichnofabric is very frequent in the MS 14 section, being preserved in all facies, but mudstones (Fig. 2).

The *Zoophycos* ichnofabric (Fig. 4E) is characterized by planar U-shaped morphology or few helical *spreiten* burrows, parallel to inclined in relation to bedding-plane, with marginal tube and central shaft occasionally preserved. *Palaeophycus*, *Asterosoma* and *Rhizocorallium* are subordinate structures, characterizing a composed ichnofabric. The bioturbation scale is moderate (BS 4-5), or locally low (BS = 1), and the associated shelly fauna occurs in two preservation modes. The fossil content is characterized by disarticulated, no fragmentated fossils, parallel or oblique in relation to bedding-plane, being composed of infaunal lingulids, *Orbiculoidea* and *Australospirifer*, which was grouped as Taphofacies 1. In the other hand, occurrences of conulariids and *Orbiculoidea* (Fig. 6H) with a mixture of articulated and disarticulated brachiopods, without signal of fragmentation, dissolution or abrasion, both inclined- and parallel-oriented in relation to the bedding-plane were grouped as Taphofacies 3. In the level T3 is preserved, *Zoophycos* occurs as monospecific ichnofabric with low intensity (BS = 1). *Zoophycos* ichnofabric is preserved in siltstones or in fine-grained sandstones with hummocky cross-stratification (F and Shcs facies; Tab. 1).

The *Rhizocorallium-Palaeophycus* ichnofabric (Fig. 4F) is characterized by dominance of U-shaped horizontal traces with spreiten and unbranched horizontal cylindrical burrows. The associated structures are *Asterosoma*, *Rosselia*, *Diplocraterion*, *Cylindrichnus*, *Chondrites*, *Planolites*, and *Skolithos*. Although the relatively high ichnodiversity, this ichnofabric has low bioturbation scale (BS 1-3). The macrofossils are also preserved in two patterns. The dominance

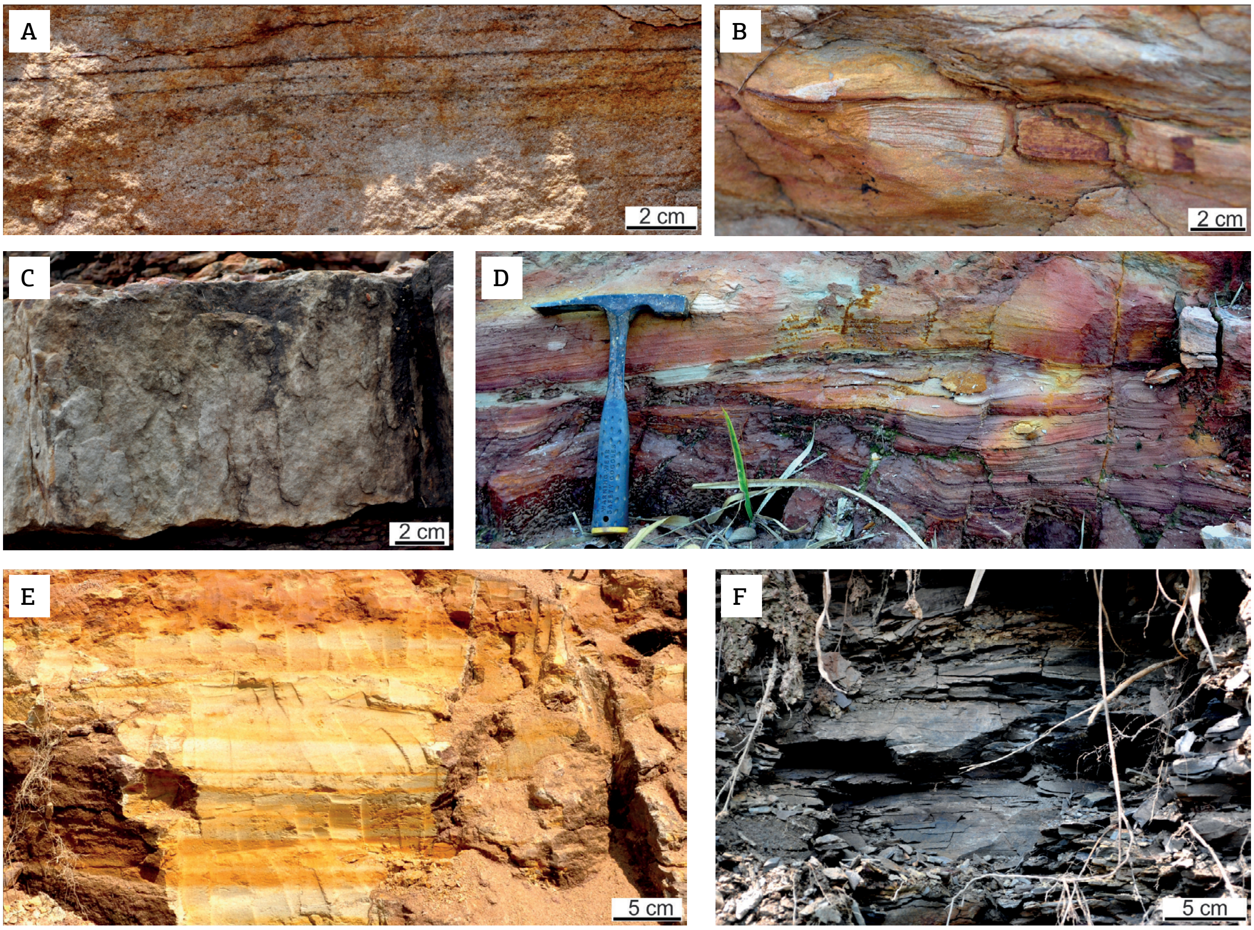

Figure 5. Facies and macrofossils from lower Chapada Group unit 2 in Rio Negro (MS). (A) Middle-grained sandstone with horizontal stratification (Sh facies). (B) Wave cross-laminated fine-grained sandstone (Sw facies). (C) Massive middle-grained sandstone (Sm facies). (D) Hummocky cross-stratified very fine-grained sandstone (Shcs facies). (E) Parallel laminated siltstone interbedded with very fine-grained sandstones (F facies). (F) Mudstone with high organic content (M facies).

of disarticulated and non-fragmented macrofossils, oblique or parallel to the bedding plane, mostly composed of *Orbiculoidea*, *Tentaculites*, trilobites, infaunal lingulids, *Australocoelia*, *Derbyina* (Fig. 6B), brachiopods and mollusks bivalves were grouped as Taphofacies 1. In the other hand, a mixture of articulated and disarticulated brachiopods *Schuchertella*, *Orbiculoidea*, infaunal lingulids, crinoids (Fig. 6I) and *Craniops* with no fragmentation, dissolution or abrasion, both vertical- and parallel-oriented in relation to the bedding-plane were grouped as Taphofacies 3. This ichnofabric is preferentially preserved in siltstones and mudstones (F and M facies; Tab. 2).

Finally, the *Chondrites* ichnofabric (Fig. 4G) is characterized by a branched system of small excavations, mostly vertically oriented and filled by darker material than the host rock, associated to simple horizontal excavations (*Planolites*).

Table 1. Sedimentary facies and inferred processes from studied sections.

Facies code and figure	Texture	Sedimentary structures	Geometry	Sedimentary process	Ichnofabrics	Taphofacies
Sh (Fig. 5A)	Middle-grained sandstone	Horizontal lamination	Lenticular	High energetic unidirectional flows above fair-weather wave-base	*Macaronichnus*, *Arenicolites-Skolithos*	Absent
Sw (Fig. 5B)	Fine- to coarse-grained sandstone	Wave cross-lamination	Lenticular	Oscillatory flows generated above fair-weather wave-base	*Psammichnites*, *Cylindrichnus-Skolithos*	T1 and T2
Sm (Fig. 5C)	Coarse- to middle-grained sandstone	Massive to faint wave cross-stratification	Lenticular	Oscillatory flows with fast deposition storm-generated above fair-weather wave base	*Arenicolites-Skolithos*	Absent
Shcs (Fig. 5D)	Very fine- to fine-grained sandstone	Hummocky cross-stratification	Lenticular	Oscillatory flows storm-generated, between storm and fair-weather wave-base	*Zoophycos*	T1
F (Fig. 5E)	Siltstone locally interbedded with very fine-grained sandstones	Parallel lamination	Tabular	Decantation episodically disrupted by storm flows below storm wave-base, in outer shelf context	*Rhizocorallium-Palaeophycus*	T1 and T3
M (Fig. 5F)	Mudstone locally interbedded with very fine-grained sandstones	Parallel lamination	Tabular	Decantation episodically disrupted by storm flows below storm wave-base, in outer shelf context	*Chondrites*	T3

Table 2. Composition of recurrent ichnofabrics from studied sections.

Ichnofabric	BS	Accessory ichnogenus	Associated taphofacies
Macaronichnus	1-2	Absent	Absent
Psammichnites	1-3	*Skolithos*, *Palaeophycus*, *Arenicolites*, *Diplocraterion*, *Macaronichnus*	Absent
Arenicolites- Skolithos	3-4, locally 5-6	*Cylindrichnus*, *Rosselia*, *Rhizocorallium* *Diplocraterion*, *Palaeophycus*	T1
Cylindrichnus-Skolithos	1-3, locally 4	*Arenicolites*, *Diplocraterion*, *Rhizocorallium*, *Palaeophycus*, *Lingulichnus*, *Rosselia*	T1, T2
Zoophycos	3-4	*Palaeophycus*, *Asterosoma*, *Rhizocorallium*	T1
Rhizocorallium, *Palaeophycus*	1-3	*Rosselia*, *Asterosoma*, *Diplocraterion*, *Cylindrichnus*, *Chondrites*, *Planolites*, *Skolithos*	T1, T3
Chondrites	2	*Planolites*	T3

The bioturbation scale is low (BS 2), and the associated shelly fauna is composed of *Orbiculoidea*, infaunal lingulids, trilobites (Fig. 6G), *Tentaculites*, *Craniops*, and *Cryptonella*. This association is characterized by articulated and disarticulated skeletons, few fragmented, both vertical- and parallel-oriented in relation to the bedding-plane, which were grouped as Taphofacies 3. This ichnofabric is preserved in mudstones with parallel lamination rarely disrupted by thin lenses of very-fine grained sandstones (M facies, Fig. 5F; Tab. 1).

DISCUSSION

Integrated sedimentologic, ichnologic and taphonomic analysis resulted in recognition of four main depositional contexts, named from proximal to distal paleoenvironments: foreshore, shoreface, storm-dominated shoreface to transitional offshore, and offshore (Fig. 7).

5.1 Foreshore

This sub-environment is characterized by high energetic flows, which is corroborated by the dominance of sandstones with horizontal cross-stratification. In this sub-environment, the erosion or non-preservation of shallow-tiers is common. High energetic conditions also difficult the colonization of the upper levels of the substrates, and only deep-tiers structures are preserved, for example, *Macaronichnus* (Howard & Frey 1984, Saunders 1989). This ichnogenus is common near the upper shoreface/foreshore contact (Pemberton *et al.* 2001, Saunders 1989, Saunders & Pemberton 1986, Saunders *et al.* 1994) and has been used as indicator of cold waters (Quiroz *et al.* 2010). The presence of this ichnogenus in high paleolatitude of the Paraná Basin during Lower Devonian corroborates the affinity by cold waters.

Although less common, other ichnofabric associated to sandstones with horizontal cross-stratification is *Arenicolites-Skolithos* with moderate bioturbation scale

Table 3. Taphofacies and their main characteristics from studied sections.

Characteristic	Taphofacies 1	Taphofacies 2	Taphofacies 3
Macrofossil content (number)	*Orbiculoidea* (40), *Australospirifer* (21), infaunal lingulids (17), *Conularia* (11), *Australocoelia* (8), *Tentaculites* (8), *Schuchertella* (7), Bivalvia (7), Trilobite (4), *Derbyina* (4), Crinoids (2), Brachiopod (2), Gastropoda (1) = 132 (total)	*Australospirifer* (11), *Australocoelia* (1), infaunal lingulids (1) = 13 (total)	infaunal lingulids (15), *Orbiculoidea* (13), trilobites calmonids (4), conularids (3), crinoids (3), *Craniops* (2), *Tentaculites* (2), *Schuchertella* (1), *Cryptonella* (1) = 44 (total)
Percentage of articulated skeletons	33.6% (113D/38A/19U)	92.3% (1D/12A)	38.6% (27D/17A)
Percentage of fragmented	17.4% (23F)	7.7% (1F)	15.9% (7F)
Abrasion	Absent	Absent	Absent
Corrosion	Absent	Absent	Absent
Rounding	Absent	Absent	Absent
Bioerosion	Absent	Absent	Absent
Encrustation	Absent	Absent	Absent
Partial dissolution	Absent	Absent	Absent
Position in relation to the bedding plane	Parallel 84.8% (112P), inclined 12.9% (17I), vertical 2.3% (3V)	Parallel 7.7% (1P), inclined 7.7% (1I), vertical 84.6% (11V)	Parallel 72.7% (32P), inclined 6.8% (3I), vertical 20.5% (9V)
Packing density	Dispersed	Dispersed	Dispersed
Inferred sedimentation rate	Low	High	Low
Genetic process	Onshore fair-weather deposition	Onshore storm-deposition	Offshore fair-weather deposition

D: disarticulated; A: articulated; U: univalved skeleton; F: fragmented; P: parallel-oriented in relation to the bedding-plane; I: inclined-oriented in relation to the bedding-plane; V: vertical-oriented in relation to the bedding-plane. Obs.: *the numbers inside parenthesis indicate the number of macrofossils.*

(BS 3) and low ichnodiversity (*Skolithos*, *Arenicolites* and *Diplocraterion*). This ichnofabric attests the preservation of shallow-tier structures in high energetic conditions, allowing the inference of less erosive processes or higher depositional frequency if compared to *Macaronichnus* ichnofabric (*e.g.*, MacEachern & Pemberton 1992). The presence of conulariids and mollusks bivalves also indicates lesser residence time in the taphonomically active zone (*e.g.*, Olszewski 1999) than that represented in the *Macaronichnus* ichnofabric.

The general absence of macrofossils in foreshore deposits is interpreted to be result of destructive processes associated to high energetic conditions, the high residence time of the organisms, and to the nature of coarse-grained substrates, commonly permeable and saturated with oxygenated pore water, factors that are not conducive for body fossil preservation. The subordinated presence of plant fragments corroborates the interpretation of reworking by waves in proximal areas.

Shoreface

This sub-environment is characterized by dominance of oscillatory flows, as expressed by the occurrence of sandstones with wave cross-lamination. In those beds, *Psammichnites* ichnofabric is preserved, with shallow-tier structures (*Arenicolites*, *Skolithos*, *Diplocraterion*, *Palaeophycus*, and *Psammichnites*) in low intensity and low ichnodiversity. Although highly

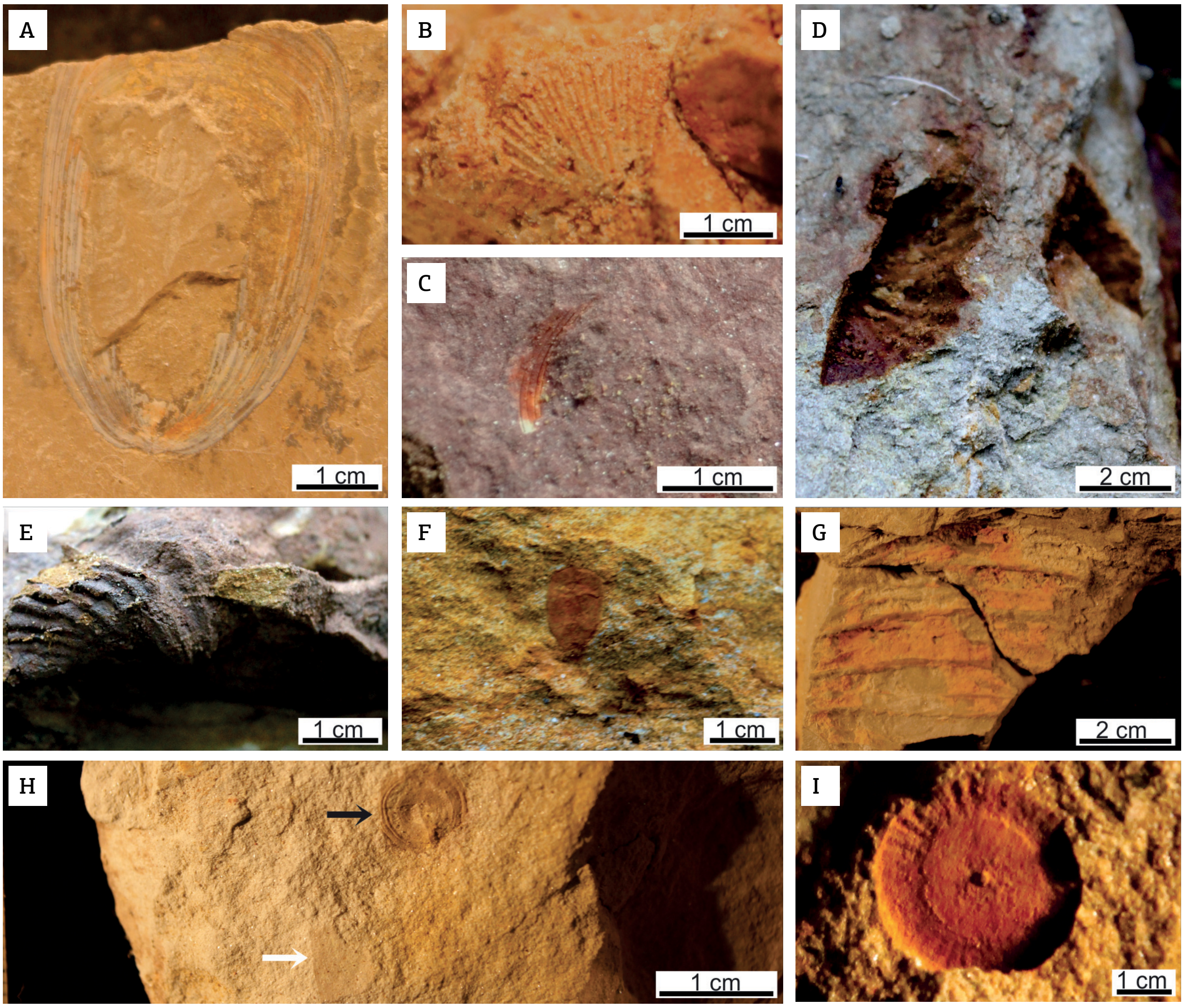

Figure 6. Macrofossil content of studied sections representing Taphofacies 1: (A) whole, disarticulated lingulid parallel-oriented in relation to the bedding-plane; (B) whole, disarticulated *Derbyina* parallel-oriented in relation to the bedding-plane; (C) fragmented *Orbiculoidea* parallel-oriented in relation to the bedding-plane; Taphofacies 2: (D-E) *in situ Australospirifer* vertically oriented in relation to the bedding-plane; (F) *in situ* infaunal lingulid inclined in relation to the bedding-plane); Taphofacies 3: (G) thorax of trilobite parallel-oriented in relation to the bedding-plane; (H) whole, articulated *Orbiculoidea* (black arrow) and fragmented infaunal lingulid (white arrow) parallel-oriented in relation to the bedding-plane; (I) disarticulated crinoid columnal parallel-oriented in relation to the bedding-plane).

energetic, this sub-environment is less erosive than the foreshore, allowing preservation of few shallow-tier structures. *Macaronichnus* locally overprint the shallow-tier structures, which is interpreted as the result of the vertical migration of the ichnocoenosis (autocomposite ichnofabric *sensu* Savrda 2016). The absence of macrofossils probably is consequence of high energetic conditions and low sedimentation rates resulting from fair-weather conditions, which increase the residence time in the interface water-sediment, as discussed to the foreshore setting.

Other ichnofabric preserved in this context is *Cylindrichnus-Skolithos* ichnofabric. Although vertical forms produced by suspension-feeder organisms are the main signature of this ichnofabric, there are some detritus-feeding structures preserved (*e.g.*, *Rhizocorallium* and *Rosselia*), indicating short moments of lesser energetic conditions. This ichnofabric expresses the alternation of the Skolithos and the Cruziana ichnofacies in lower shoreface zone (*e.g.*, MacEachern & Pemberton 1992, Buatois *et al.* 2007).

In some levels, massive sandstones with faint wave cross-stratification (Sm facies) are preserved. The massive characteristic can be both caused by high biogenic activity within the substrate, marked by *Arenicolites-Skolithos* ichnofabric, as well by fast deposition after storm events. The dominance of suspension-feeding habits associated to high bioturbation scale indicate low depositional rates under energetic conditions in shoreface environment (Pemberton *et al.* 2001). Depending on the depositional rates, two taphofacies can be associated to these sandstones with wave cross-lamination:

1. T1, with disarticulated organisms indicating a reworked assemblage under minor sedimentation rates;
2. T2, represented by *in situ* organisms recording rapid burial (*Australospirifer*) associated to storm events close to the fair-weather wave base.

The T1 is here representing relatively longer resident period in the taphonomic active zone under lower accommodation rates, as expected in prograding trends. In this sense, it is hard to infer if either the different taphonomic modes associated in a single bed is result of variable hydrodynamic flows or if they are indicating a time-averaged assemblage (*e.g.*, Kidwell 1997). In the other hand, the T2 is representing rapid deposition, as expected when the accommodation space is relatively higher or during intense storm events and higher sedimentation rates

To western India, Fürsich & Oschmann (1993) recognized nine genetic types of fossil concentrations in Jurassic deposits of the pericratonic basins of Kachchh and Rajasthan. Although from different basin type and age,

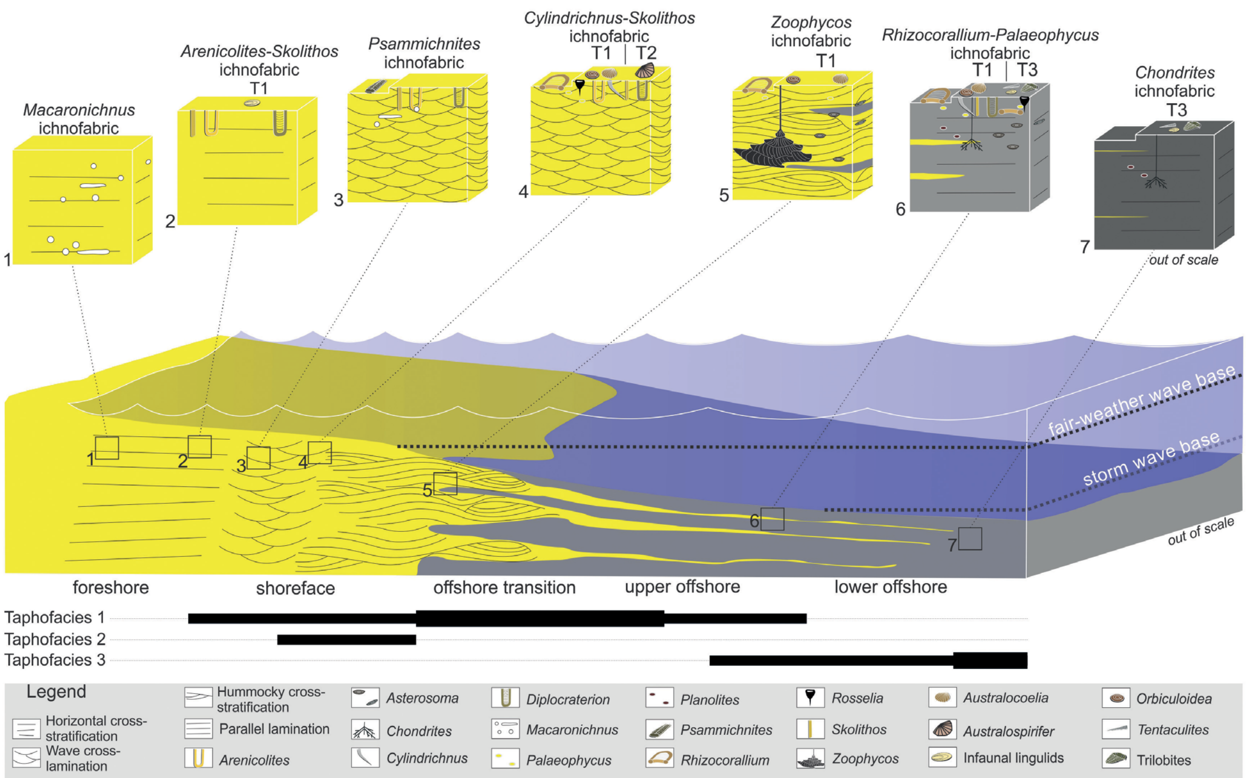

Figure 7. Paleobathymetric context of high-stand systems tract (HST) deposits in northern Paraná Basin, Brazil, inferred by integrated ichnofabric, taphofacies and sedimentologic analyses.

these concentrations have similar signatures with the here identified taphofacies. Thus, the Taphofacies 1 has similarities with the "distal tempestites (type 4)" (*sensu* Fürsich & Oschmann 1993), showing evidences of transport, moderate sorting, and dominance of small-sized fossils. In the other hand, the Taphofacies 2 has common signatures with the so-called "storm-wave concentrations (type 2)" (*sensu* Fürsich & Oschmann 1993), grouping well-preserved, monospecific *in situ* fossils associations. A similar taphofacies was also diagnosed to coeval strata in the southern Paraná Basin (Taphofacies B of Sedorko *et al.* 2018a), representing storm-generated fossil assemblages.

Storm-dominated shoreface to transitional offshore

This sub-environment is the most recurrent in the studied section, characterized by a mixture of decantation and traction in the sea bottom, expressed by sandstones with hummocky cross-stratification interbedded with siltstones, or mudstones disrupted by thin sandstones lenses (Shcs, F and M facies). Due to this mixture, different ichnofabrics are associated to this context, such as *Cylindrichnus-Skolithos*, *Zoophycos* and *Rhizocorallium-Palaeophycus* ichnofabrics.

As previous discussed, *Cylindrichnus-Skolithos* ichnofabric indicates the mixture of suspension- and detritus-feeding strategies, in this case possibly resulting from the alternation of storm and fair-weather conditions. The *Zoophycos* ichnofabric expresses preferential deposit-feeding strategies, but the depleted character of this ichnofabric (low diversity: *Asterosoma*, *Rhizocorallium*, *Palaeophycus* and *Zoophycos*) indicates some stressful condition, possibly related to storm events. Recently, a similar context of *Zoophycos* dominance was reported in the south part of the basin, which was interpreted as differential preservation of deep-tier structures due to high frequency storms and erosion of shallow tiers under low accommodation space regimes (Sedorko *et al.* 2018b).

Rhizocorallium-Palaeophycus ichnofabric is the most diverse, although presenting low bioturbation scale (BS 1-3). The variability of feeding strategies (*i.e.*, suspension-feeding: *Diplocraterion*, *Skolithos* and *Cylindrichnus*; detritus-feeding: *Rhizocorallium*, *Rosselia*, and *Asterosoma*; and deposit-feeding: *Chondrites* and *Planolites*) indicates environmental stable conditions, allowing colonization of all tiers (*e.g.*, Ekdale & Mason 1988, Savrda & Bottjer 1989). The scarcity of bioturbation can be explained by relatively high sedimentation rates or because some taphonomic filter, such as the predominance of soup substrates, precluding visibility of previous structures (*e.g.*, Ekdale 1985).

The macrofossils associated to this sub-environment were grouped as Taphofacies 1, with disarticulated and few fragmented fossils indicating minor reworking before final burial in transitional offshore settings. In siltstones and mudstones, the macrofossil assemblage is more diverse (T3; Tab. 3), with a mixture of *in situ* (*Orbiculoidea* and infaunal lingulids) and transported organisms (*Schuchertella*, *Craniops*, and infaunal lingulids), suggesting a time-averaged assemblage, at least in 5th or 6th order. Time-averaging is the process that accumulates organic remains from different time intervals, sometimes expressing repeated burial/exhumation cycles as result of sediment reworking (Kidwell 1997). In this sense, the apparent diversity can be a taphonomic artifact resulting from accumulation of different biocoenosis, but the magnitude of this time-averaging is not accessible by this study.

Offshore

This sub-environment is characterized by dominance of decantation, expressed by gray to dark mudstones only locally disrupted by very-fine grained sandstones (M facies). In this sub-environment, both *Chondrites* and *Zoophycos* ichnofabric occur with low density of trace fossils and representing deposit-feeding habits (*e.g.*, *Chondrites*, *Zoophycos*, and *Planolites*), which allow the interpretation of stressed conditions, possibly associated to dysoxic substrates (Savrda & Botjer 1989). The associated macrofossils (Taphofacies 3) might be representing a time-averaged assemblage, as suggested by the dominance of disarticulated shells, which can be linked to long residence time as consequence of starvation periods (Kidwell 1997).

The Taphofacies 3 has similar signatures of the "condensed concentrations (type 9)" of Fürsich & Oschmann (1993), or with the "Taphofacies C" of Sedorko *et al.* (2018a), the last identified to coeval strata from southern Paraná Basin. These concentrations are described as grouping different taphonomic signatures in the skeletal elements due to *in situ* reworking and the highest time involved. These concentrations tend to be very diverse and highly time-averaged, even that the magnitude of time is not accessible to that Devonian strata.

STRATIGRAPHICAL CORRELATIONS WITH SOUTH PART OF THE PARANÁ BASIN

The studied sections are inserted in the lower Chapada Group 2 (Pragian-Emsian), correlated in age with Ponta Grossa Formation from southern basin (*sensu* Grahn *et al.* 2013), based on the macrofossil content and palynological data. The prograding pattern observed in the studied sections is characterized by upward dominance of shoreface to foreshore environments, which allows to correlate these sections with the high-stand systems tract (HST) of the Siluro-Devonian Sequence from Paraná state (Sedorko *et al.* 2018c). As previously discussed, in the studied sections predominate shoreface to foreshore paleoenvironments, in a general onshore setting. In the other hand, even the HST in the southern basin (Paraná state; Fig. 1A) is represented mostly by transitional offshore to lower shoreface deposits (e.g. Sedorko *et al.* 2018a, 2018b, 2018c). These strata in Paraná state exhibit dominance of expressions of the Cruziana ichnofacies (Sedorko *et al.* 2018c), while in Mato Grosso do Sul state dominates expressions of the Skolithos ichnofacies (this study).

The shallower character of the north part might be a passive response to its position in the basin, closer to the border (Ramos 1970, Assine 1996). To Goiás state, Assine (1996) reported the absence of fine-grained rocks covering the sandstones of the Furnas Formation, which conducted him to infer that the Tibagi Member overlays the Furnas Formation. In studied region, late Pragian to early Emsian mudstones were previously reported in Rio Verde do Mato Grosso, overlaying the sandstones of Chapada Group unit 1 (Furnas Formation) (*e.g.*, Carvalho *et al.* 1987, Melo 1988, Becker-Kerber *et al.* 2017). Some palynological studies in "Paleosul-02-RV-MT" corroborate a late Pragian to early Emsian age for the rocks in this region (Mendlowicz Mauller 2007, Mendlowicz Mauller *et al.* 2009, Grahn *et al.* 2010). These data support the inference of a similar stacking of the Pragian to Emsian strata in the whole basin, but in a general shallower setting to the northern basin.

The Lower Devonian macrofossil content is also similar both in Mato Grosso do Sul and Paraná states. Except by fish remains only preserved in southern part of the basin (*e.g.*, Richter *et al.* 2017), all groups are distributed in the basin, corresponding to the typical association of the Malvinokaffric Realm (dominance of brachiopods *Orbiculoidea*, lingulids, *Australospirifer*, *Australocoelia*, *Schuchertella*, with subordinated mollusks bivalves and gastropods, tentaculitids, conulariids and crinoids). The decline in diversity during the Middle Devonian (Eifelian), as observed by Bosetti *et al.* (2012), was not yet observed in Mato Grosso do Sul state.

Thus, the dominance of proximal environments in Devonian strata of the Mato Grosso do Sul region, especially in Rio Negro municipality, is related to its proximal context in the border of the basin. The presence of the Três Lagoas, Campo Grande Arch (*c.f.* Northfleet *et al.* 1969), geographically close to the study area, was not clear in our study. However, the virtual absence of middle Devonian strata in the study region do not allow to conclude that this high was not active in posterior times. The similarities in the facies and ichnofacies stacking in Paraná and Mato Grosso do Sul states and the similar macrofossil content suggest that the division between two sub-basins was not complete during late Pragian to early Emsian. However, the problem regarding the division of the Paraná Basin in two sub-basins during Devonian needs more detailed studies to be elucidated.

CONCLUSIONS

Seven ichnofabrics (*Macaronichnus*, *Psammichnites*, *Arenicolites-Skolithos*, *Cylindrichnus-Skolithos*, *Zoophycos*, *Rhizocorallium-Palaeophycus*, and *Chondrites* ichnofabrics) and three taphofacies (T1: parautochthonous to allochthonous preservation with evidence of moderate transport; T2: autochthonous preservation, indicating rapid burial; and T3: time-averaged association with autochthonous to allochthonous preservation) were diagnosed in Devonian strata from lower Chapada Group unit 2 (Ponta Grossa Formation, *sensu* Grahn *et al.* 2013), in Rio Negro (MS). The studied sections are mostly positioned in a HST and exhibit upward dominance of sandy facies representing shoreface to foreshore settings, with local occurrences of transitional offshore to offshore context.

Four sub-environments were defined by integration of ichnologic, taphonomic and sedimentologic analyses: foreshore (*Macaronichnus* and *Arenicolites-Skolithos* ichnofabrics); shoreface (*Psammichnites*, *Arenicolites-Skolithos*, *Cylindrichnus-Skolithos*, associated to T1 and T2); storm-dominated shoreface to transitional offshore (*Cylindrichnus-Skolithos*, *Zoophycos* and *Rhizocorallium-Palaeophycus* ichnofabrics associated to T1 and T3); and offshore (*Chondrites* and *Zoophycos* ichnofabrics associated to T3). The dominance of foreshore to shoreface settings in HST of the Pragian to Emsian strata in northern basin corroborates a shallower context in relation to the south part. Similarities in the facies and ichnofacies stacking, as well in the macrofossil content, suggest that the division between two sub-basins was not complete during late Pragian to early Emsian. Additional studies are needed to evaluate the stratigraphic distribution of the macrofossils in middle Devonian strata in the northern Paraná Basin, as well the existence of two sub-basins during this time.

ACKNOWLEDGEMENTS

DS thanks Henrique Parisi Kern, Rodrigo Scalise Horodyski, Jorge Villegas-Martín, Samuel Henrique Noll, Tiago Girelli, and Mateus Vargas for the valuable suggestions. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), through Finance Code 001; by Programa de Suporte à Pós-Graduação de Instituições de Ensino Particulares (Prosup)/Instituições Comunitárias de Educação Superior (Prosuc) 88887.154071/2017-00 and

CSF-PVE-S Program 88887.129752/2016-00. This research was also supported by National Council for Scientific and Technological Development (CNPq), under the number 474952/2013-4.

SUPPLEMENTARY DATA

Supplementary data associated with this article can be found in the online version: Suplementary Table A1.

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