



## Sequence stratigraphy and taphonomic signatures of marine invertebrates: A Devonian (Pragian/Eifelian) example of the Paraná Basin, Brazil

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### ABSTRACT

The latest Pragian to the early Eifelian succession of the Devonian of the eastern border of the Paraná Basin (Brazil) is approached integrating taphonomy and sequence stratigraphy, providing new insights to the analysis of intracratonic siliciclastic Paleozoic seas. The high-resolution study of six outcrops revealed a mud-prone succession, composed predominantly of distal tempestites, with minor preservation of foreshore/shoreface depositional systems, and permitted the acquisition of sensible fossil and sedimentary data in relation to environments within the general depositional tendencies of the lowstand (LST), transgressive (TST) and highstand (HST) systems tracts of the succession. The LST has fragmented fossils preserved that indicate proximity to the shoreline; also, can preserve fossils that live in the foreshore/shoreface zone by proximal obrution events. In general, the TST records an epoch of moderate to high faunal diversity, low rates of sedimentation, with occurrence of obrution deposits in its middle part. Concretions with phosphatic animals can be preserved at the maximum transgressive surface, where the calcareous shells are preferentially dissolved. Stringers and rosette orientations below storm wave base are explained by flow lifting of distal muddy turbidity currents. The HST presents higher faunal diversity, with abundance of fragmented valves; sedimentation rates are moderated. Specific lingulid taphofacies displayed a very good correlation with the environmental conditions in each depositional environment. The lingulid taphofacies could be used as a more sensible tool in order to analyze environmental conditions in ancient seas. Therefore taphonomic signatures and biofabrics of the fossils (their occurrences and diversities) showed correlation with the general principles of sequence stratigraphy, and seem to be controlled by the system tracts where they were preserved.

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### 1. Introduction

The Silurian–Devonian succession (Pridolian–Frasnian) that outcrops in the center-east region of the Paraná State (Brazil) is composed of marine siliciclastic deposits. The presumed climate was cold, once this region was localized at about 70–80° of paleolatitude at the deposition time (Cooper, 1977; Scotese and Mckerrow, 1990; Isaacson and Sablock, 1990; Robardet, 2003; Cunha, 2005). In a modern approach the record of this basin is interpreted as dominantly episodic, where only major depositional events are preserved. These events are characterized by shallow, shoreface deposits, and also by deeper waters, offshore deposits

(transitional offshore and offshore deposits) (Zabini et al., 2010). The Devonian paleofauna is composed of marine invertebrates of the Malvinokaffric Realm (sensu Bosetti, 2004; Bosetti et al., 2010).

The present paper focus on the stratigraphic controls, taphonomic signatures and biofabric of that fauna, integrating taphonomic studies with the third-order stratigraphic framework of Devonian succession in the eastern border of the Paraná Basin, southern Brazil.

The fossil distribution, its taphonomic signatures, and its taxonomic diversity were associated with the depositional environments into which they were preserved. Attention is given to lingulid taphofacies, in the sense that they allow environmental sensitiveness and can be used to interpret the environmental conditions by their unique life habit, shell composition and abundance within this Devonian succession.

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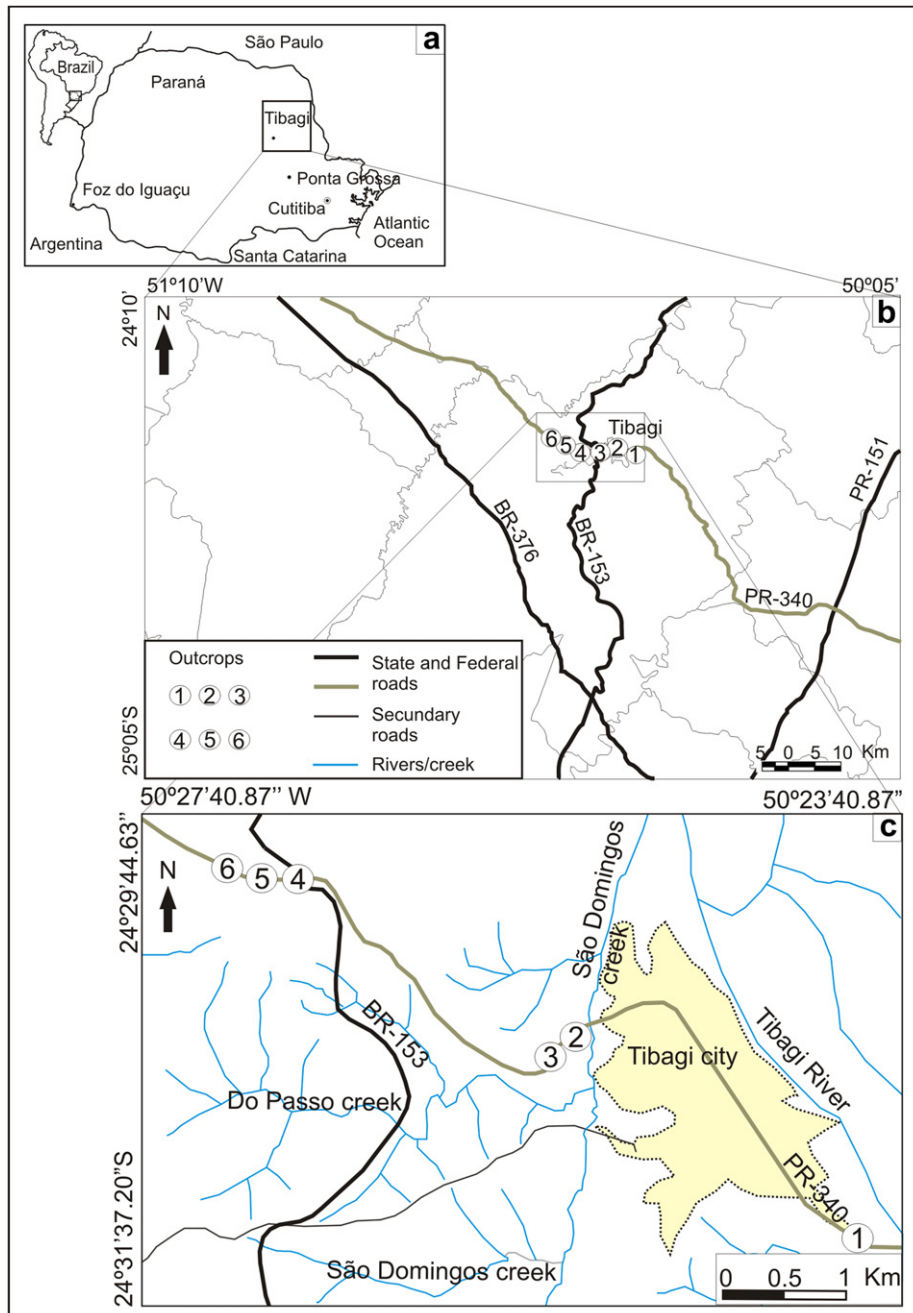
**2. Materials and methods**

**2.1. Acquisition of the material**

The paleontological material was collected from six outcrops (numbered 1–6) that are localized at the PR-340 (from Tibagi city towards Telêmaco Borba city, kilometers 60, 267, 270, 271, and 272) (Fig. 1). Tibagi is situated 222 km N–NW from Curitiba, capital of the Paraná State, Brazil. The fossil material is deposited in the Stratigraphy and Paleontology Lab of the Geosciences Department (DEGEO), Universidade Estadual de Ponta Grossa (UEPG); they are labeled as DEGEO/MPI-1500 to 1501, DEGEO/MPI-0275 to 0599, DEGEO/MPI-1839 to 1902, DEGEO/MPI-2535 to 2659, DEGEO/MPI-3198 to 4147, DEGEO/MPI-4439 to 4450, DEGEO/MPI-4553 to 4555

and DEGEO/MPI-7076 to 7097. Species names were classified accordingly to Clarke (1913).

Fossil data acquisition in the field was organized following a standard collection protocol established to assure standardized and statistically comparable collections, as adopted by several workers (e.g. Simões and Ghilardi, 2000; Bosetti, 2004; Ghilardi, 2004; Zabini, 2007; Zabini et al., 2010). The method consists of the demarcation of grid squares and field sheets, for the acquisition of high-resolution data. Basically the methodology is to set a square in the outcrop, with 3 m wide and 2 m high. This grid is used to materialize an x–y reference system to collect the fossils. Each fossil found is cataloged according to its position on the grid, and its taphonomic characteristics (degree of disarticulation, position relative to the bedding plane, etc.); then the data is entered into a digital spreadsheet.



**Fig. 1.** Maps with the locations of the studied outcrops.

Fossil diversity is expressed using qualitative terminology – low, moderate and high. These terms are defined as follows: low (one or two taxonomic categories), moderate (three to four taxonomic categories); and high (five or more taxonomic categories). The taxonomic categories considered in this paper are as follows: (a) lingulid brachiopods, (b) calcitic brachiopods, (c) trilobites, (d) echinoderms, (e) mollusks, (f) cnidarians, (g) annelids, and (h) plants.

Stratigraphic data was based on Bergamaschi (1999) stratigraphic column. The sections were logged by visual inspection, when sedimentary structures, fossils, sediment grain size and color were described; outcrop details were collected centimeter by centimeter, and local stacking of the outcrops was made with the use of a clinometer.

### 3. Geological settings

The Paraná Basin is a huge intracratonic basin on the South-American platform, located in southernmost Brazil and north/northwestern Uruguay, parts of Paraguay and Argentina (Fig. 2A). The basin covers an area of about 1,700,000 km<sup>2</sup>, has actually a NE–SW elongated shape, and is approximately 1750 km long and 900 km wide. The sedimentary fill of the basin was conditioned by tectonic–eustatic cycles linked to the evolution of the Occidental Gondwana during the Paleozoic and Mesozoic eras.

The prevalence of eustatic–tectonic cycles, which controlled sedimentation in Paraná Basin, has generated a stratigraphic record that is marked by numerous interruptions caused by erosion and non-deposition. Milani et al. (1994, 2007) considered the fill of the basin is constituted of six second-order depositional sequences, ranging in age from Late Ordovician to Late Cretaceous (Fig. 2B). The stratigraphic interval studied herein corresponds to the second sequence of Milani et al. (2007), named as “Paraná Supersequence”, a second-order sequence ranging from the Early to Late Devonian. Based on sequence stratigraphy concepts, Bergamaschi (1999) and Bergamaschi and Pereira (2001) proposed a third-order subdivision for the Silurian–Devonian succession of the Paraná Basin, dividing six sequences labeled sequences A–F.

The stratigraphic and taphonomic study reported in the present paper is based on 80 m thick section overlying the A sequence of Bergamaschi and Pereira (2001) (Fig. 2).

### 4. Results

#### 4.1. Facies and depositional systems

The studied succession is formed mainly of dark-colored mudstones and fine-grained sandstones, with minor portions of medium-grained, and pebbly sandstone, grouped into four main lithofacies. Description and interpretation of these facies are given in Table 1.

The lateral association and vertical succession of these lithofacies as interpreted from outcrop studies led to the identification of four depositional systems, indicative of a paralic to open marine environmental setting. Fig. 3 depicts a summary of sedimentary textures and structures of this depositional gradient, while Table 2 summarizes the characteristics of the systems and shows some examples.

The most proximal depositional system in the studied area is represented by lithofacies S-m (massive or incipiently laminated medium-grained sandstones). The sedimentary structure is mostly obliterated, but when visible, resembles horizontal lamination (swash?) and sometimes trough cross bedding, which are interpreted as indicative of a foreshore and upper shoreface depositional setting. Swaley cross bedding and wavy ripple lamination typically

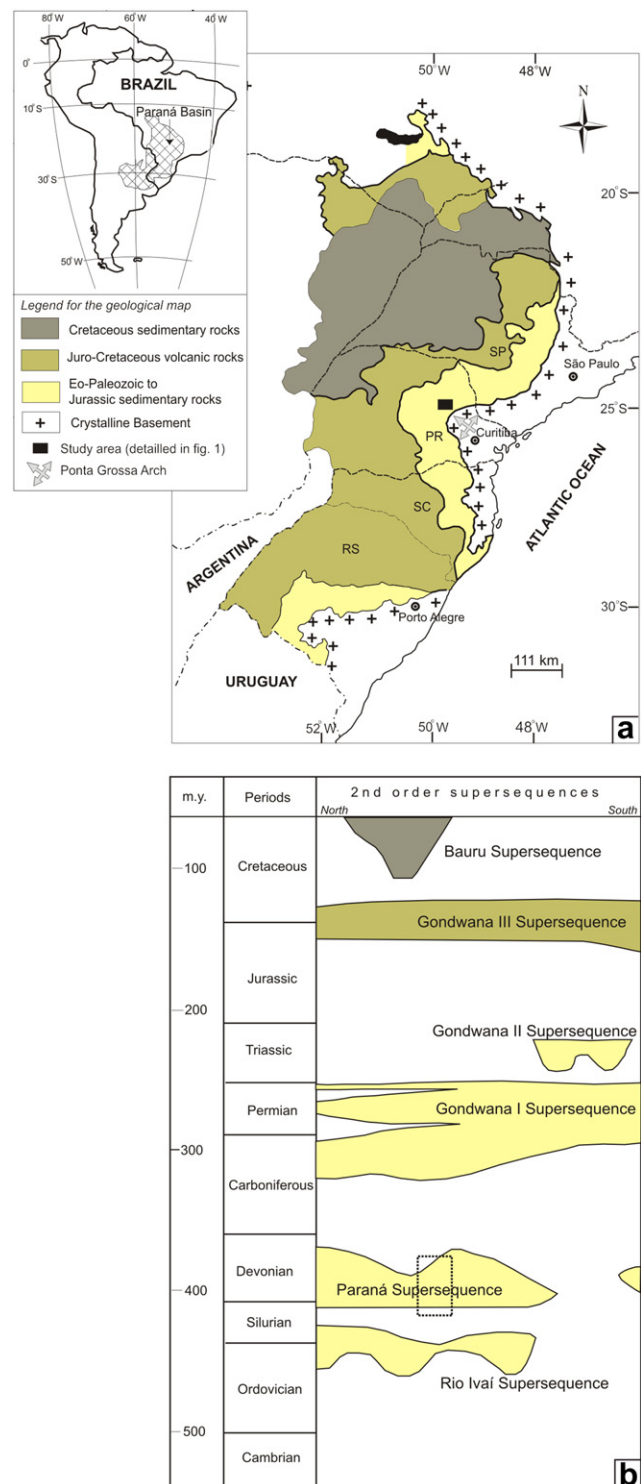






Fig. 2. (A) Location map of the study area in the Paraná Basin record. (B) Studied stratigraphic interval (simplified after Milani et al., 2007). The rectangle indicates the studied interval.

associated to the middle shoreface environment has not been conclusively identified.

This shallow-water depositional system is spatially associated with a lower shoreface system (or transitional offshore system, as called by some authors), formed by a facies association composed of fine-grained sandstones with hummocky (HCS) bedding

**Table 1**

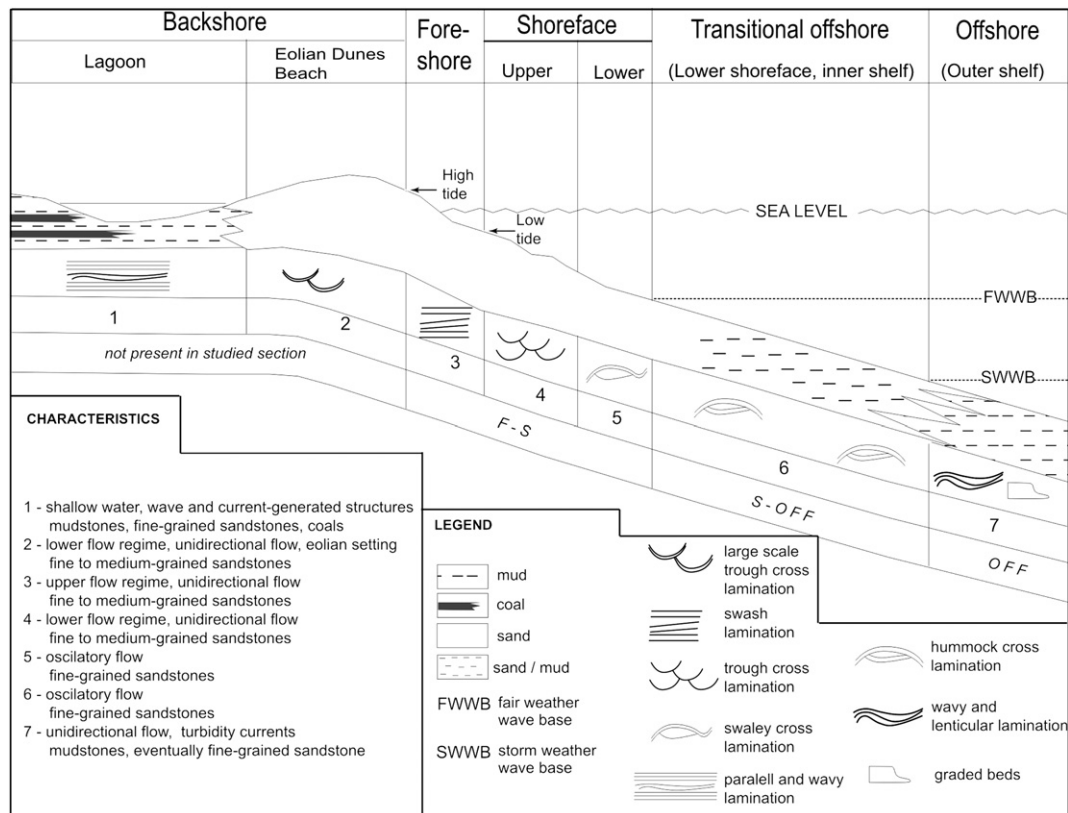
Lithofacies of the studied Devonian succession. The table provides each facies, their descriptions, the sedimentary processes involved in their formation, and one representative photograph each.

Facies code	Facies	Description	Sedimentary process	Photo
M	Mudstone	Dark-gray to black massive, sometimes with very fine-grained sand intervals, occasionally with concretions	Settling of suspended sediments, deposition below SWB, hemipelagic sedimentation with contribution of muddy to sandy turbidity currents	
MS	Sandy mudstone	Dark-gray to black mudstone with very fine-grained sandstone forming graded beds	Settling of suspended sediments, deposition close or below FWWB, emplaced by muddy to sandy turbidity currents	
S-hcs	Sandstone	Yellowish, fine-grained sandstone with hummocky cross bedding, sometimes with outsized pebbles	Oscillatory flows, deposition between SWB and FWWB	
S-m	Sandstone	Yellowish, medium-grained sandstone, massive or showing incipient parallel and laminated trough cross bedding (?)	Upper and lower flow regime, unidirectional flows (?)	

(lithofacies S-hcs) and by sandy mudstones sometimes forming graded beds (lithofacies MS). The S-hcs facies is indicative of oscillatory flows, with deposition between storm (SWB) and fair weather wave base (FWWB) and represent the more proximal part of the shoreface-offshore transition. The MS facies, sometimes forming graded beds, represents the more distal part of the

shoreface-offshore transition and was originated by the settling of suspended sediments, deposition close or below FWWB, emplaced by sand-mud and muddy turbidity currents. The typical offshore depositional system is formed by dark mudstones (M lithofacies), representing settling of suspended sediments (hemipelagic sedimentation) in a depositional environment below SWB, with





**Fig. 3.** Summary of the sedimentary characteristics of a typical paralic to open marine environmental setting. F-S, S-OFF and OFF designate the depositional systems mapped in the study area and summarized in Table 2.

contribution of muddy turbidity currents, indicated by the incipient graded beds associated with the massive mudstones.

#### 4.2. Sequence stratigraphy

Due to the limitation of the stratigraphic dataset (only composite profile, no boreholes, and no seismic data) we have chosen to divide the studied succession into the basic three-fold scheme of system tracts as depicts the sequence stratigraphy classic model (i.e. Posamentier and Vail, 1988). No other stratigraphic elements (such as the falling stage systems tract and its limiting surfaces) were added. The nomenclature of the stratigraphic surfaces, however, follows the modern tendencies (e.g. Catuneanu et al., 2009, 2010). Insofar, the surface that separates the lowstand (LST) and the transgressive system tracts (TST) is labeled the “maximum regressive surface” (MRS) instead of the previous designation “transgressive surface”. The surface separating the transgressive (TST) and the highstand system tracts (HST) is labeled “maximum transgressive surface” (MTS).

In order to recognize sequence boundaries and geometric system tracts within the studied succession, two criteria were used:

- contacts between facies indicative of deep-water and shallow-water settings, recording a base-level fall and a conceptual sequence boundary (i.e., a unconformity or its correlative conformity); and
- vertical variations of facies in order to detect retrogradational and progradational stacking patterns.

Based upon these criteria and following/modifying the label scheme of Bergamaschi and Pereira (2001) the following third-order sequences have been recognized (Fig. 4).

*Sequence A* – represented by the topmost Furnas sandstone (a shallow marine to fluvial sandstone which underlies the studied succession in the entire study area); not detailed in the present paper because no fossils have been encountered in the top of that sequence.




*Sequence B* – (consists of LST, TST and HST in approximately 26 m) a foreshore/upper shoreface sandstone body marks the LST of this sequence, followed by a retrogradational stacking pattern (TST) culminating with a several meters thick muddy section where the MTS of the sequence is marked. This stratigraphic level shows centimeter-large mudstone concretions. The highstand systems tract (HST) is marked by regressive sedimentation marking a slight progradational pattern.

*Sequence B1* – (consists of TST, and HST in approximately 28 m) its base is marked by a shoreface sandstone sharply overlying a lower shoreface to offshore sediments, indicating a base level drop which is interpreted as a third-order sequence boundary. No lowstand deposits are mapped in that sequence, only retrogradational to progradational patterns can be recognized; these are separated by a muddy section where the MTS is marked.

*Sequence B2* – (consists of LST and HST in approximately 6 m) the base is again marked by a shoreface sandstone sharply overlying a lower shoreface to offshore sediments, indicating a base level drop followed by shoreface progradation, interpreted as a LST. A MRS separates that system tract from a TST characterized by fine sandstones and mudstones from the shoreface-offshore transition. The MTS as well as the HST are not present because the TST of sequence B2 is truncated by the boundary of the next sequence.

*Sequence C* – only the base of this sequence is present in the study area. The base is marked by a foreshore/upper shoreface sandstone, interpreted as the LST of this sequence, followed by

**Table 2**  
Depositional systems of the study area and correlated facies.

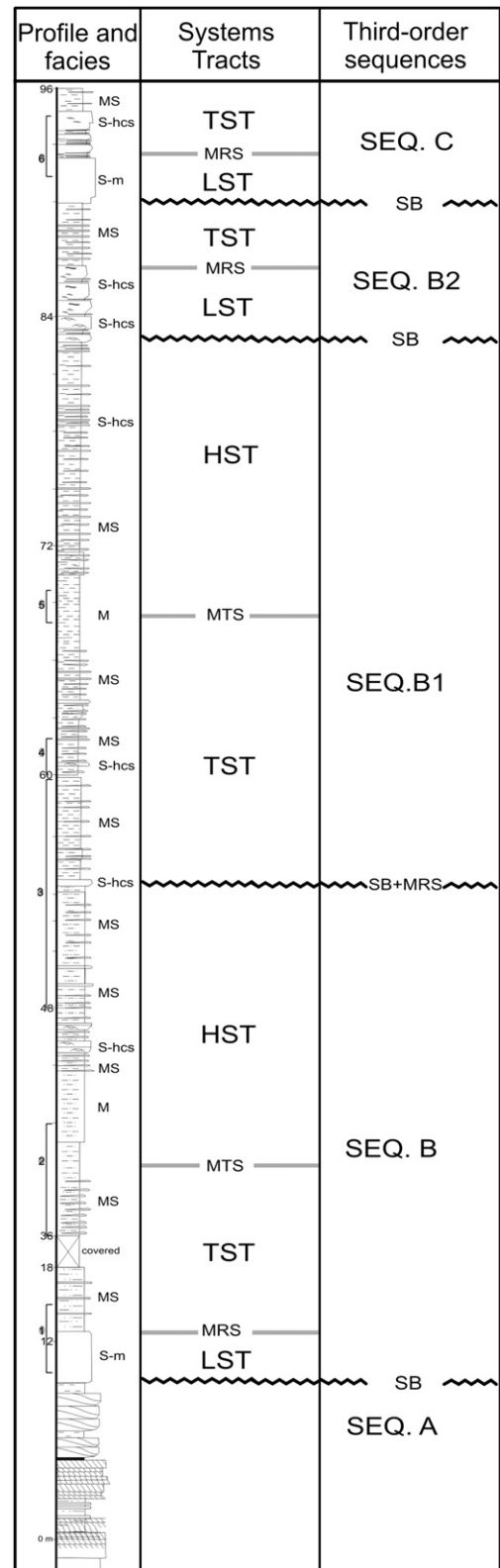
Depositional system	Facies	Photo
F-S	Foreshore –upper shoreface S-m	
S-Off	Lower shoreface (transitional offshore) S-Hcs, some MS	
Off	Offshore M	

a few meter thick section with retrogradational stacking pattern, marking the initial TST of that sequence. The MTS as well as the HST are not mapped because the end of the profile.

Based upon biostratigraphic data, mostly acritarchs, chitinozoan and miospores (e.g. Grahn et al., 2000, 2010), the base of the studied succession has a latest Pragian age (~407 m.y.), while the top, marked by the lowermost portion of sequence C, and has an Early Eifelian age (~395 m.y.). Insofar, the rocks of the 80 m of the composite profile record a time span of approximately 8 m.y., and each of the analyzed sequences (B, B1, B2) has an average duration of 2.8 million years, a duration compatible with third-order cycles as recorded by several authors (e.g. Vail et al., 1991; Catuneanu, 2006).

### 4.3. Taphofacies

Taphofacies are based on the orientation and disposition of shell material within the stratigraphic horizon and on distinct suites of taphonomic signatures, which are imprinted on shell material as a result of physical, chemical and biological processes. The processes controlling these various attributes are potentially unique to and, thus, characteristic of, a particular environment



**Fig. 4.** Composite stratigraphic profile of the study area, based upon field work and integrating data provided by Bergamaschi (1999) and Bergamaschi and Pereira (2001) showing main sedimentary facies (see also Table 1), and the sequence stratigraphic interpretation as discussed in Section 4.2. LST = lowstand system tract, TST = transgressive system tract, HST = highstand system tract, MSR = maximum regressive surface, MTS = maximum transgressive surface; and SB = sequence boundary. Brackets with numbers at left designate the stratigraphic interval of the outcrops studied in detail.

**Table 3**  
Taphonomic and taxonomic descriptions of the fossils and the relative species richness of each outcrop. Additionally, systems tract and facies of each outcrop are also provided. Note that the descriptions are given from the base to the top, following the stratigraphic position of each analyzed point.

Outcrop number/ approximate thicknesses	Systems tract/ referred sequence	Correlated facies	Relative species richness	Taphonomic and taxonomic description of the fossils
6 (top)/2 m	TST/Seq. C	S-m; S-hcs	Moderate	Fragments of <i>Spongiophyton</i> (plant debris), Calmoniidae pygidium, and fragments of conulariids.
6 (base)/3 m	LST/Seq. C	S-m	Low	Only lingulids in life position were found.
5 (middle)/5 m	TST (MST)/Seq. B1	M	Low	Bivalve mollusks disarticulated (? <i>Janeia</i> sp.); ? <i>Bucaniella</i> sp. gastropods as impressions, oriented as stringers; <i>Tentaculites crotalinus</i> concordant to the bedding plane, sometimes oriented.
4 (complete)/2 m	TST/Seq. B1	MS; S-hcs	Moderate	Great numbers of lingulid valves (complete or fragmented) arranged in rosettes or stringers; <i>T. crotalinus</i> concordant to the bedding plane, not oriented; <i>Orbiculoidea</i> sp. concordant to the bedding plane also occur in great amounts. Bivalve mollusks (? <i>Pleurodapis</i> sp.) with valves open (butterfly).
3 (top)/6 m	TST/Seq. B1	MS	Moderate	Great amount of fragmented and complete lingulid valves; <i>Orbiculoidea</i> sp. concordant to the bedding plane occur in great proportions; bivalve mollusks also occur; complete but disarticulated valves of <i>Derbyina whitiorum</i> and <i>Australocoelia tourteloti</i> have sparse occurrences.
3 (base)/6 m	HST/Seq. B	MS; S-hcs	High	Great amount of fragmented lingulid valves; complete valves and very rarely lingulids in life position also occur; <i>Orbiculoidea</i> sp. concordant to the bedding plane; dispersed scolecodont pieces; complete and disarticulated valves of bivalve mollusks; <i>T. crotalinus</i> concordant to the bedding plane, not oriented; very sparse occurrence of complete <i>Australospirifer</i> sp. valves and of articulated carpoid echinoderms.
2 (top)/3 m	TST (MST)/Seq. B	M	Moderate	Great amount of life positioned lingulids preserved in concretion; impressions of fragmented lingulid valves; articulated <i>A. tourteloti</i> ; Calmoniidae carcasses (torax; torax and pygidium; complete carcasses).
2 (base)/3 m	TST/Seq. B	MS	High	Dispersed scolecodonts, complete valves of <i>Australospirifer</i> sp. and ? <i>Australostrophia</i> sp., complete but disarticulated <i>A. tourteloti</i> ; <i>T. crotalinus</i> concordant to the bedding plane, not oriented; complete and fragmented lingulid valves; lingulid ichnofossils (? <i>Lingulichnus inclinatus</i> ); articulated bivalve mollusks (? <i>Nuculites</i> sp.); complete Homalonotidae extended carcasses.
1 (top)/2 m	TST/Seq. B	MS	Low	Great numbers of lingulids in life position; <i>A. tourteloti</i> in life position.
1 (base)/3 m	LST/Seq. B	S-m	–	No fossils found.

(Brett and Baird, 1986; Meldahl and Flessa, 1990; Callender et al., 1992; Brett, 1995).

The faunal diversity of this Devonian epeiric sea is considered low (Melo, 1985; Bosetti et al., 2010), in the sense that few species occur in the same beds, and in great numbers; nevertheless, these fossils do not necessarily share their life position, habits, shell composition, and shape. For this reason it would be too demanding to distinguish distinct and complex taphofacies encompassing all types of bioclasts without making it too difficult to comprehend; it is known that each bioclast will respond differently to the same environmental conditions (Speyer and Brett, 1986; Meldahl and Flessa, 1990; Brett, 1995). Although such complex taphofacies are not impossible to be established, we here suggest that the detailed description of one type of bioclast in particular can represent specific environments without compromising the general evolution model of the preserved events. In fact, lingulid taphofacies, in this case, represent extremely well the environmental conditions.

Another related aspect is the almost completely absence of corrosion, abrasion, and bioerosion in the studied fossils. Until now, only a small number of fossils have demonstrated to be bioeroded (Clarke, 1913, 1921; Zabini, 2007). No abrasion and corrosion have been related to these fossils until the present moment.

As can be noted from the described taphocoenosis (Table 3), lingulids occurred in almost every outcrop analyzed, and, generally,

in reasonable numbers (at least 25 per grid square). Their abundance contributes to the visualization of a great variety of occurrence modes suggesting several environmental aspects. Two main lingulid taphofacies can be described (Fig. 5):

*Tf1* – Lingulids concordant to the bedding plane; disarticulated valves, complete or fragmented; shells chaotically distributed or arranged as stringers or rosettes.

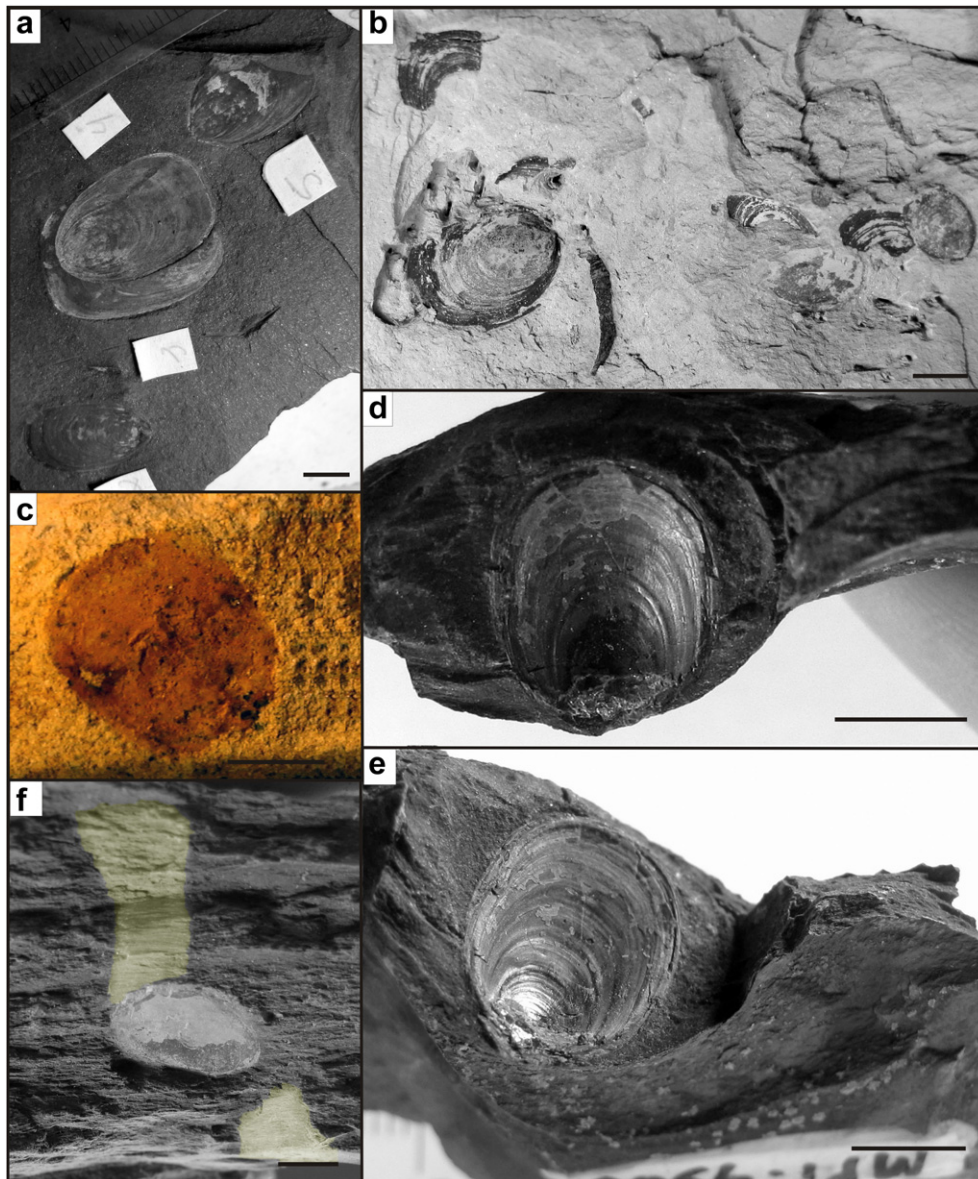
This taphofacies was already described in Zabini et al. (2010). It can occur from the shoreface to the distal transitional offshore settings, associated with minor numbers of lingulids in life position. The degree of fragmentation increases within the increase of depth (being higher in the distal part of the transitional offshore). Stringers and rosette oriented valves can occur below the SWB, most commonly at the distal part of the transitional offshore, and at the offshore.

*Tf2* – life positioned lingulids; articulated and with complete valves; can be associated with their traces (ichnofossils produced by lingulids).

This taphofacies can be subdivided into two categories, as follows.

*Tf2a* – lingulids fossilized as impressions or molds. These lingulids in life position occur from the proximal shoreface to the transitional offshore. There is a preference for the shoreface settings.





**Fig. 5.** The lingulid taphonomic signatures. Photographs (a, b) represent Tf1, with lingulid valves concordant to the bedding plane and preserved complete or fragmented; (c, d) represent Tf2a, with lingulids preserved in life position, as molds. (C) Shows a lingulid associated with its trace (highlighted); (e, f) represent Tf2b, i.e., a concretion bearing a life positioned lingulid. Scale bars equal 5 mm.

*Tf2b* – lingulids fossilized in concretions, with their three dimensions preserved. This type of fossilization probably represents preservation at the MTS. The period with sediment starvation influences the eodiagenesis and lead to the formation of concretions and the preferential dissolution of calcitic shells. This taphofacies occurs below the SWB, for this reason, muddy turbidity currents are thought as the main events that preserved these fossils.

For each outcrop that had a representative number of lingulids, these 3 taphofacies can be assigned. Different lingulid taphofacies (Tf1, Tf2a, and Tf2b) are represented in percentages in Fig. 6. In each outcrop analyzed the graph shows the variations of lingulid taphonomic signatures that comprehend one of the 3 proposed taphofacies. In addition, Fig. 7 shows the variation of sample size in each outcrop.

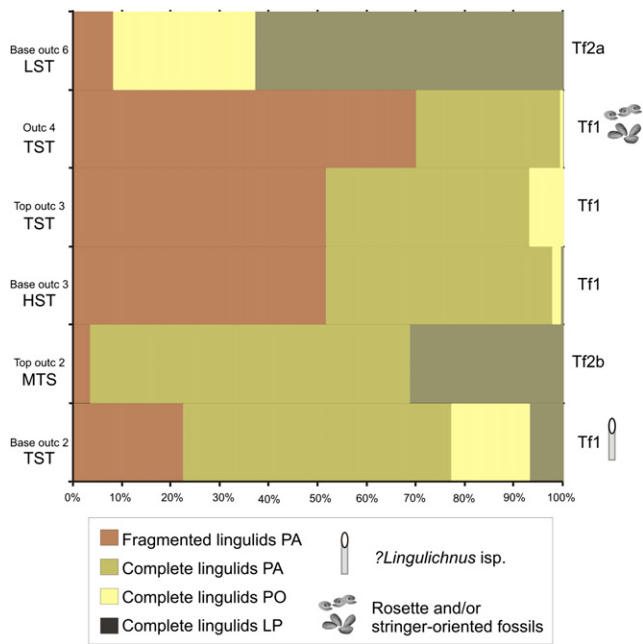
Accordingly to Simões et al. (2010) the fossil record of the TST tends to follow this order (Simões et al., 2000, 2001): (a) megafossils are more common and more volumetrically important at the

base and the inferior medium part of the tract; (b) to the top, the megafossils became scarce; (c) at the top, in the sediments that form the MTS, the megafossils should be almost completely absent, occurring only in the condensed section, in the form of inarticulated brachiopods, preserved in concretions; and (d) obrution deposits with infaunal or epifaunal benthonic, suspensivore, macroinvertebrates, preserved in life position are notably common at the medium portion of the TST.

## 5. Discussion: integration between stratigraphic framework and the taphonomic signatures

Four sequences were recognized in an 80 m profile. Within these sequences lowstand, transgressive and highstand system tracts were preserved, as well as the MRS and the MTS. The faunal diversity and taphonomic signatures of the fossils are a result of the environmental conditions during the time of deposition.

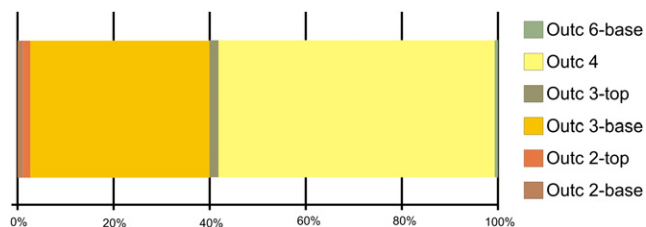




**Fig. 6.** Percent variations of lingulid taphonomic signatures in each outcrop, and correspondent lingulid taphofacies. Note that the association with *?Lingulichnus* isp. and the orientation of lingulid valves occur only in outcrops 2 (base) and 4, respectively. Outcrop position denotes real stratigraphic position.

Although we have depicted only lingulid taphofacies, it is clear that the fossil diversity found in each outcrop also resembles the conditions of each depositional environment and its stratigraphic position (Table 4, Figs. 8 and 9). Yet, the study of lingulid taphofacies demonstrated a great relation within the sequence stratigraphic framework, and can be used as a tool to interpret different environmental conditions. Lingulids are one of the best fossils to describe taphonomic conditions (Emig, 1986; Kowalewski, 1996). Their abundance and their intrinsic properties (such as organo-phosphatic carapace, bivalved shell, infaunal life habit) are probably the best to imprint environmental variations, at least in Paleozoic siliciclastic seas. Also, lingulids are the most well-known Malvinokaffric fossils of the Paraná Basin, once they have been the focus of intense research in the last decade (Quadros, 1987; Bosetti, 1989; Zabini, 2007; Zabini et al., 2010). Moreover, lingulids in general have been the subject of many scientific researches worldwide in the last decades (Kowalewski, 1996; Kowalewski and Flessa, 1996; Williams, 1997; Williams et al., 1994; Emig, 1997) the result is substantial knowledge in lingulid biology, life-habits, and on some aspects of their environmental preferences.

Hereafter there is the summed-up integration of sequence stratigraphy and the taphonomic signatures of the fossils found along the studied succession (Table 4 and Fig. 8):



**Fig. 7.** Variation of sample size in each outcrop referred in Fig. 6.

### 5.1. Lowstand system tract

This system tract is characterized by low accommodation rates and shallowing water. There is proximity to the shoreline, and a stacking progradational pattern.

The LST has an unusual fossil record, with lingulids preserved in life position; the progradational stacking pattern usually implies in reworking of the sediments deposited in proximal environments. Nevertheless, the LST is composed of fine to medium-grained massive sandstones, with *in situ* lingulids and followed by mudstones with HCS, plants and conulariids both fragmented. These fossils represent the proximity to the shore, and their fragmentation represents the high energy of this environment. The mudstones probably denote the event that preserved the *in situ* lingulids.

### 5.2. Transgressive system tract

This system tract is characterized by increasing accommodation rates and increasing water depths. The shoreline is transgressive and the stacking pattern is retrogradational.

Overall, at the very base of the TST, fossils are mostly represented as complete valves in low diversity communities (occurrence of *Australocoelia tourteloti* and lingulids, both in life position – top of outc 1, Fig. 8). The early TST stages also consist of disarticulated shells of *Orbiculoidea* sp., bivalve mollusks and other infaunal lingulids occurring complete or fragmented; *Derbyina whitiorum* and *A. tourteloti* occur very rarely as disarticulated valves (top of outc 3, Fig. 8). These signatures reflect the relatively high energy, and the lower sedimentation rates, occurring during the transition between the LST (proximity of shoreline) and the increase of the coastal encroachment during the TST.

At the middle of the TST, a variety of fossils occur, such as complete and articulated *Australospirifer* sp. and *?Australostrophia* sp., disarticulated *A. tourteloti*; disoriented *Tentaculites crotalinus*, parallel to the bedding plane; articulated bivalve mollusks and complete Homalonotidae carcasses; lingulids are present in life position, and concordant to the bedding plane. The high diversity found is a reflection of the low energy and of the environment stability. *?Lingulichnus inclinatus* (sensu *Zonneveld et al., 2007; Zabini and Bosetti, 2010*) could also be recognized, demonstrating some events of higher sedimentation rates. The presence of some reworked bioclasts and the occurrence of lingulid shells oriented in rosette and stringers represent the presence of bottom currents (base of the outc 2 – Fig. 8).

### 5.3. Maximum transgressive surface

The MTS is formed during a time of maximum transgression, and it represents a change from retrogradational to progradational stacking patterns.

At this point there is a great amount of lingulids in life position preserved in concretions; in other levels of the outcrop there are also the preservation of articulated *A. tourteloti*, associated with the presence of Calmoniidae carcasses (torax, torax-pygidium, and complete carcasses), disarticulated bivalve mollusks, sometimes oriented *T. crotalinus* and gastropod shells parallel to the bedding (top of the outc 2 and outc 5, Fig. 8).

At the MTS the preservation of thin sediment layer during long timespans allows some diagenetic reactions to occur. In this case, phosphatized-lingulid bioclasts were preserved, and other calcitic or carbonated bioclasts were selectively destroyed. Rosette and stringers oriented shells are also found in this environment.

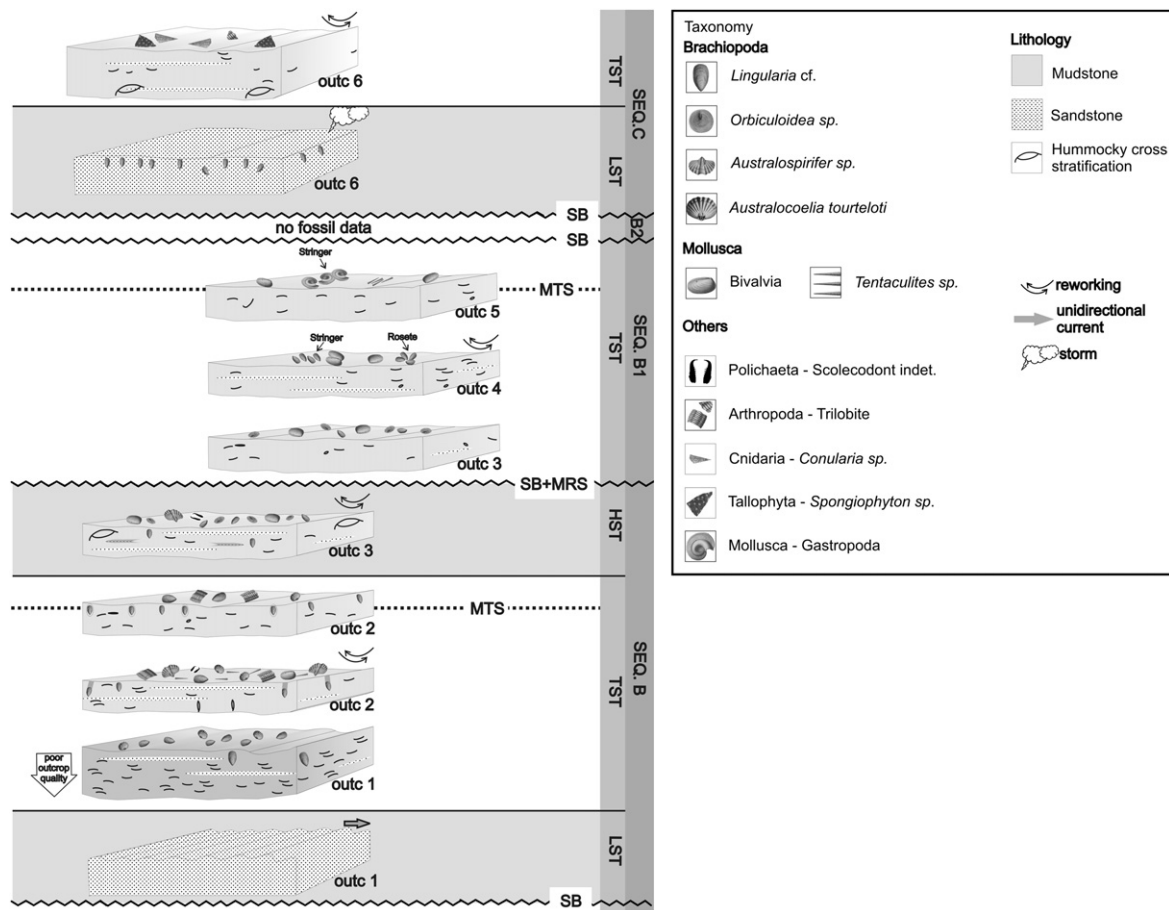
The eventual occurrence of shells in stringers and rosettes below the SWB raises two questions: (1) the origin of currents capable of reorient fossils in a low energy environment, and (2) the strengths

**Table 4**  
Main taphonomic characteristics of the systems tracts and their interpretations.

Systems tracts	Characteristics	Taphonomic signatures	Interpretation
Lowstand system tract	Low accommodation rates, progradational stacking pattern. Shallowing water, proximity of clastic shoreline	Low diversity of Malvinokaffric biota; usually lingulids disarticulated and concordant to the bedding planes; plant and conulariid fragments	Plant fragments indicate shoreline proximity; disarticulated invertebrates indicate depositional environment with high energy level
Transgressive system tract	Increasing accommodation rates, retrogradational stacking patterns, increase of the water depth, transgressive shoreline	Moderate to high diversity of Malvinokaffric biota, trilobite fragments, disarticulated calcitic brachiopods, life positioned lingulids, lingulids concordant to the bedding planes, oriented, lingulid traces; at MTS: lingulids in mudstone concretions	Increasing water depths and lower environmental energy levels increase the diversity of the fauna, rapid storm events cause eventual obrution of <i>in situ</i> fauna; before and at MTS: deep water, low energy, below SWB, muddy turbidity currents align body fossils
Highstand system tract	Decreasing accommodation rates, agradational to increasingly progradational stacking pattern. Regressive shoreline	High diversity of Malvinokaffric biota, few lingulids in life position, most lingulids disarticulated, fragmented and concordant to the bedding planes, not oriented	Shoreline proximity and increasing energy levels cause disarticulation and fragmentation on invertebrate remains

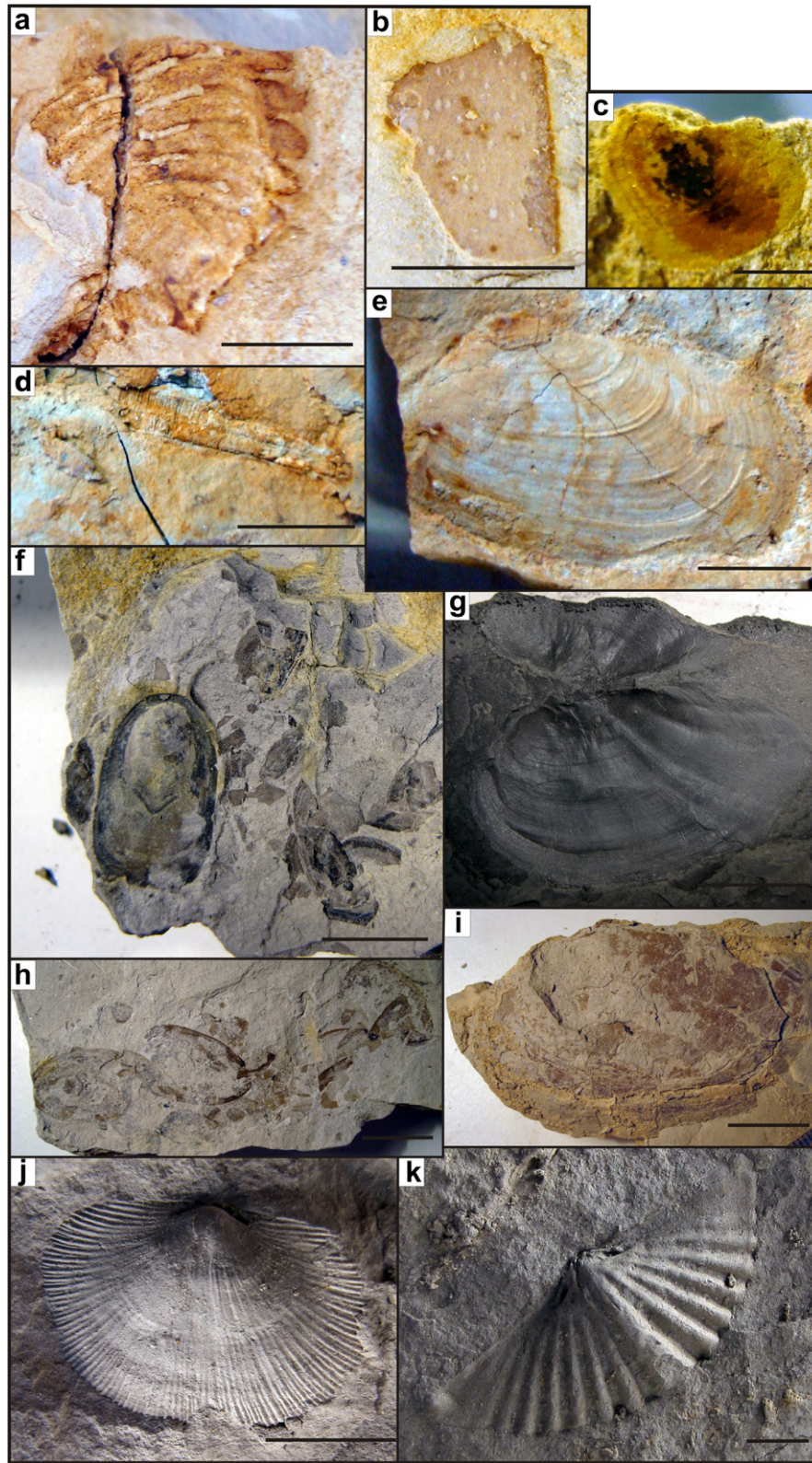
of this current in order to align 1 to 2 cm sized shells. The first aspect can be tentatively solved by the sedimentological process involved: the muddy transitional offshore facies is probably linked with the storm-triggered, distal muddy turbidity currents (as interpreted from the graded beds, discussed before). The incoming turbidity current can carry mostly mud and fine-grained sand (the only sand texture available in the studied system). While leaving the sandy portion behind and beginning to deposit the muddy portion, the currents may have become more buoyant, and ascended as plumes in a process known as sediment flow lifting,

when parts of turbidity current lift up from the substratum on which it flows due to buoyancy reversal. The process has been initially described by Stow and Wetzel (1990) and Sparks et al. (1993) as an explanation for the deposition of distal graded-mud facies (hemiturbidites). During the lifting phase, the turbidity flow gradually decreases velocity and stops. It is possible that during that phase, these currents had strength enough to align the bioclasts on the sea floor, while most of the mud was lifted and deposited days or weeks later, covering the aligned bioclasts with hemipelagic mud. Insofar, the location of that signature must be



**Fig. 8.** Scheme of the major environmental conditions that lead to the formation of the studied succession, and the correspondent systems tracts and sequences. “Outc” plus number refers to each part of the analyzed outcrop. MTS = maximum transgressive surface, MSR = maximum regressive surface, SB = sequence boundary, and TS = transgressive surface. The sequences are delimited to the right. Other symbols are defined in the caption.





**Fig. 9.** Fossil diversity and taphonomic signatures in several prospected outcrops. (a) Torax-pygidium of a Calmoniidae trilobite, found at outcrop 6-top. (b) *Spongiophyton* fragment found at outcrop 6-top. (c) Life positioned lingulid, found at outcrop 6-base. (d) Mollusca, *Tentaculites crotalinus*, found at outcrop 5. (e) Mollusca *?Janeia* sp. found at outcrop 5. (f) Lingulid valves, complete or fragmented (representing Tf1), collected in outcrop 4. (g) Mollusca *?Pleurodapis* sp. found at outcrop 4 (valves in butterfly). (h) Lingulid valves, complete or fragmented (Tf1) collected in outcrop 3-base. (i) Mollusca found at the base of outcrop 3. (j) Brachiopoda *?Australostrophia* sp. collected at the base of outcrop 2, along with *Australospirifer* sp. (k). Scale bars equal 1 cm.



marking the approximate zone of lifting, i.e., the zone where current began to suspend the mud in the column while orienting the shell clusters at the bottom.

Additionally, the turbidity flow can explain the presence of fragmented shells in the offshore zone. Distal settings are considered lower energy environments, therefore, the related taphonomic signatures expected to be found are complete valves. However, our data indicate that the more distal the environment, the more fragmented lingulid shells occur. As discussed by Kowalewski (1996), extant lingulid shells found concordant to the bedding surface are very fragile, and can be fragmented even in low-energy waters. Hence, these currents were probably able to transport, fragment and arrange lingulid valves.

The second problem concerns the strengths of the muddy turbidite current to align 1–2 cm sized shells. Lingulids and gastropods can have low body density after death because of putrefaction; disarticulated lingulid valves are also extremely light, so the weight would be no problem for these currents to align these bioclasts.

#### 5.4. Highstand system tract

It is characterized by decreasing accommodation rates and a regressive shoreline. The stacking pattern is aggradational to increasingly progradational.

The beginning of the HST has similar environmental conditions to the base of the TST (i.e. base level is still raising), although they represent inverse conditions: in the HST there is the gradual decrease of the accommodation space. The fossil diversity is lower in the HST when compared to the base of the TST. At the HST there is the occurrence of *Orbiculoidea* sp. valves parallel to the bedding, disarticulated valves of bivalve mollusks, not oriented *T. crotalinus*. Dispersed scolecodont pieces also occur, and very rarely, there is the preservation of complete *Australospirifer* sp. These signatures are attested by reworking of bottom sediments (and of the bioclasts). Lingulids appear as extremely fragmented valves; this is explained by the relatively high energy environment with moderate sedimentation rates, capable of fragmenting lingulid fragile valves, but also capable of preserving complete and articulated carpod echinoderms (base of outc 3, Fig. 8).

## 6. Conclusions

Taphonomic signatures and biofabrics of the fossils show a good correlation with the general principles of the sequence stratigraphy; their occurrences and diversities seem to be controlled by the systems tracts where they were preserved. These aspects now improve the model proposed by Simões et al. (2010) in the sense that they expand the knowledge of the events associated with bioclast aspects not only on TST, but also on HST and LST.

The detailed and high-resolution study of the six outcrops revealed sensible data in relation to depositional environments within the general tendencies of the system tracts. Despite of being a succession dominated by mud, composed predominantly of distal tempestites, the Devonian succession also has preserved foreshore/shoreface environments with *in situ* bioclasts; these were preserved by proximal muddy turbidity currents.

The lingulid taphofacies display a very good correlation with the conditions in each depositional environment, and can be used as a more sensible tool in order to analyze environmental conditions in Paleozoic epeiric seas. Lingulids were the chosen fossils not only because they are chitinophosphatic bivalved, infaunal brachiopods, but also because they have extant counterparts that give important taphonomic clues about the way their valves react to different environmental processes after death. Additionally, lingulids are one

of the most well studied Paraná Basin Malvinokaffric invertebrates. Although the interpretation of the complete paleo-scenario, with the use of all macrofossils found should not be disregarded, lingulids are more completely understood in respect to life-habit, environmental preferences, and biology.

Although biostratigraphic events collaborate to different taphonomic signatures, intrinsic factors (e.g. chemical composition of the shell, life habit among others), allied to diagenetic processes also can govern the distribution of the bioclasts on the fossil record. This could be noted with the preferential preservation of lingulid-bearing concretions at the MTS.

The fossil distribution and diversity along the succession varied by the elapsed time and/or by the depositional environments that were preserved, and this is also attributed to the own environmental preferences of each taxa.

With the results here obtained, the model proposed by Simões et al. (2010) is enhanced, as follows: HST represents higher faunal diversity moments, with abundance of disarticulated and fragmented valves; sedimentation rates are moderated; the LST has lower faunal diversity, and presents fragmented fossils, indicating proximity to the shoreline; also, can preserve fossils (in life position) that live in the foreshore/shoreface zone by proximal obrution events. The TST base usually has low to moderate diversity, representing a moment of transition and reworked fossils. The TST middle part and top is described as a moment of medium to high faunal diversity and lower rates of sedimentation. Obrution deposits mark the MTS, preserving concretions with phosphatic animals and selectively dissolving calcitic shells. Stringers and rosette fossil-orientation (below SWB) occur at the TST and are explained by flow lifting of distal muddy turbidity currents.

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