



# Untold muddy tales: Paleoenvironmental dynamics of a “barren” mudrock succession from a shallow Permian epeiric sea



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## ABSTRACT

During the late Paleozoic, the intracratonic Paraná Basin, Brazil, in central Gondwanaland, was covered by a huge (>1.600.000 km<sup>2</sup>), shallow and isolated epeiric sea. Within the Permian succession, oxygen-deficient facies are commonly recorded in the *Mesosaurus*-bearing Irati Formation (Cisuralian, Artinskian/Kungurian) and the overlying Serra Alta Formation (Guadalupian, Wordian/Capitanian). Barren, dark-grey mudstones are the main facies preserved in this last unit, which has usually discouraged extensive and detailed stratigraphical and paleontological investigations. However, exhaustive sedimentological, taphonomic and paleontological surveys in those deposits reveal a dynamic and complex depositional history. Based on sedimentary fabric, autochthonous to parautochthonous occurrences of shelly benthic invertebrates (bivalves) and the presence/absence of concretion-bearing and phosphate-rich layers, we report variations in the oxygen levels of bottom and pore waters, in bathymetry, sedimentation rates, and changes in benthic colonization. Our data indicate that the deposition of this “apparently barren” mudstone-dominated succession was driven by a complex interplay of variations in sedimentation rate and oxygen pulses tied to tectonic and climate changes. Three distinct populations or invertebrate paleocommunities were recorded, which were adapted to (a) normal background low-oxygen (dysoxic) conditions (*i.e.*, minute infaunal suspension-feeding bivalves associated with the trace fossil *Planolites*), (b) chemically toxic (anoxic/extreme dysoxic) substrates, including gigantic burrowing bivalves (probable chemosymbiotic taxa), and (c) oxic/dysoxic substrates following short-term bottom disruptions.

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## 1. Introduction

Deposits of dark-colored, well-laminated mudstones and shales, usually enriched in organic carbon and pyrite are one of the main records of oxygen-deficient facies in several Paleozoic and Mesozoic sedimentary successions from epicontinental seas (Sageman et al., 1991; Boyer and Droser, 2011). As shown by various authors (*e.g.*, Kauffman, 1984; Oschmann, 1994; Holz et al., 2010), these facies are a record of periods of rising to stable sea-level associated

with transgressive system tracts and early highstands. They are good indicators of long-term stagnant, anoxic to dysoxic conditions, at least at the sediment-water interface (Kauffman and Sageman, 1990; Sageman et al., 1991; Boyer and Droser, 2011, and references therein). Despite the enormous occurrence of exceptionally well preserved fossils in similar lagerstätten (*sensu* Seilacher et al., 1985) these muddy rocks are usually seen as monotonous, fossil-poor deposits, discouraging detailed paleontological analysis (see Sageman et al., 1991). However, as shown by various authors (*e.g.*, Boyer and Droser, 2011), even thin sedimentary successions of dark shales and related oxygen-restricted deposits (mudstones and shales) can record subtle variations in the paleoenvironmental conditions that may be stratigraphically significant at various scales (facies analysis to basin evolution). Yet, by

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adopting the assumptions above (*i.e.*, the notion that dark mudrocks are barren deposits formed within a stagnant basin and tectonic quiescence; see [Seilacher, 1982](#)) several key paleoenvironmental data may be missed. Indeed, as commented by [Kauffmann and Sageman \(1990\)](#), among the main intrinsic paleoenvironmental ideas tied to the dark grey mudstones and black shales is that a) they record relatively long time periods of stagnant waters, b) few or no benthic invertebrates are associated with them, and c) benthic environments remained stable for prolonged time. However, during the early 1990's the seminal papers of [Kauffman and Sageman \(1990\)](#), [Sageman et al. \(1991\)](#), [Tyson and Pearson \(1991\)](#), [Wignall \(1994\)](#), and [Oschman \(1994\)](#) showed that these deposits can be interpreted in much detail. Contrary to traditional beliefs a very dynamic sedimentary history is usually associated with this kind of deposits. In this way, the recognition of variations in the sedimentation patterns in mudstone successions is only possible throughout the integration of physical, biogenic, and chemical data ([Bohacs et al., 2014](#)).

The general scenario depicted above prevailed also in the Gondwana I Sequence ([Milani et al., 2007](#)) of the Paraná Basin, Brazil. During the late Paleozoic, this intracratonic basin was flooded by a large epicontinental sea, with restricted or no connections to the Panthalassa. The last transgressive event is recorded by the dark grey mudstones and black shales of the Permian Serra Alta Formation (Passa Dois Group). However, the above mentioned issues are magnified by local particular factors, such as a) the sedimentary succession developed in an extremely isolated basin ([Runnegar and Newell, 1971](#); [Simões et al., 1998](#)) with variable salinity ([Alessandretti et al., 2015](#)). Thus, typical fully marine invertebrates (*i.e.*, brachiopods, trilobites, echinoderms) or microfossils (*i.e.*, fusulinids) are missing ([Simões et al., 1998](#)), b) sedimentation rates during times of fair-weather were usually low. Consequently, fossil-rich event beds, such as shelly tempestites or tsunamites, are uncommon or misidentified, and c) outcrops of this unit are always deeply weathered and profusely covered by vegetation, hiding or even destroying fossils and sedimentary structures. Therefore, researchers devoted little attention to the fossil-poor, mudstone-dominated deposits of the Passa Dois Group, Paraná Basin, as a kind of “ugly mudstone syndrome”, paraphrasing [Tang \(2000\)](#).

Despite this unexciting scenario, in this contribution the “barren” deposits of the Serra Alta Formation are investigated with an integrated sedimentological, taphonomic, and paleontological approach. Hence, the main goals of this contribution are to provide information on the origin of the fine-grained deposits of the Serra Alta Formation and on the associated paleoenvironmental conditions (*i.e.*, water depth, oxygen content, sedimentation rate), as well as to determine genetic links between the fossil-bearing layers and the associated depositional conditions. We also highlight the advantages of using a multiproxy approach to paleoenvironmental reconstructions of oxygen-deficient mudstone strata.

## 2. Geologic setting

The 50 to 90-m-thick Serra Alta Formation (Guadalupian, 268–259 Ma.), Passa Dois Group, is mainly represented by dark grey mudstones and black shales, also including decimeter-thick layers of fine- to medium-grained sandstones and rare layers of limestones ([Sanford and Lange, 1960](#); [Schneider et al., 1974](#); [IPT, 1981](#); [CPRM, 2006](#); [Meglhioratti, 2006](#); [Holz et al., 2010](#); [Warren et al., 2015](#)). The unit rests on the *Mesosaurus*-bearing Irati Formation and is overlain by the Teresina Formation. In the study area, the central part of the state of São Paulo ([Fig. 1](#)), Brazil, the unit is represented by a thin (~50 m thick) succession of mainly dark grey, laminated mudstones ([Warren et al., 2015](#)). According to

various authors ([Schneider et al., 1974](#); [Araújo, 2001](#); [Meglhioratti, 2006](#)), the Serra Alta Formation is interpreted to have mostly formed in a marine environment below storm wave-base, under predominantly anoxic conditions, during a transgressive event (*i.e.*, the last transgressive event in the geological history of the Paraná Basin, [Milani et al., 2007](#)). In this context, [Holz et al. \(2010\)](#) mentioned that “there are no proximal lithofacies represented in the Serra Alta Formation and it may be inferred that the relatively deep sea surpassed widely the present eastern margin of the basin.”

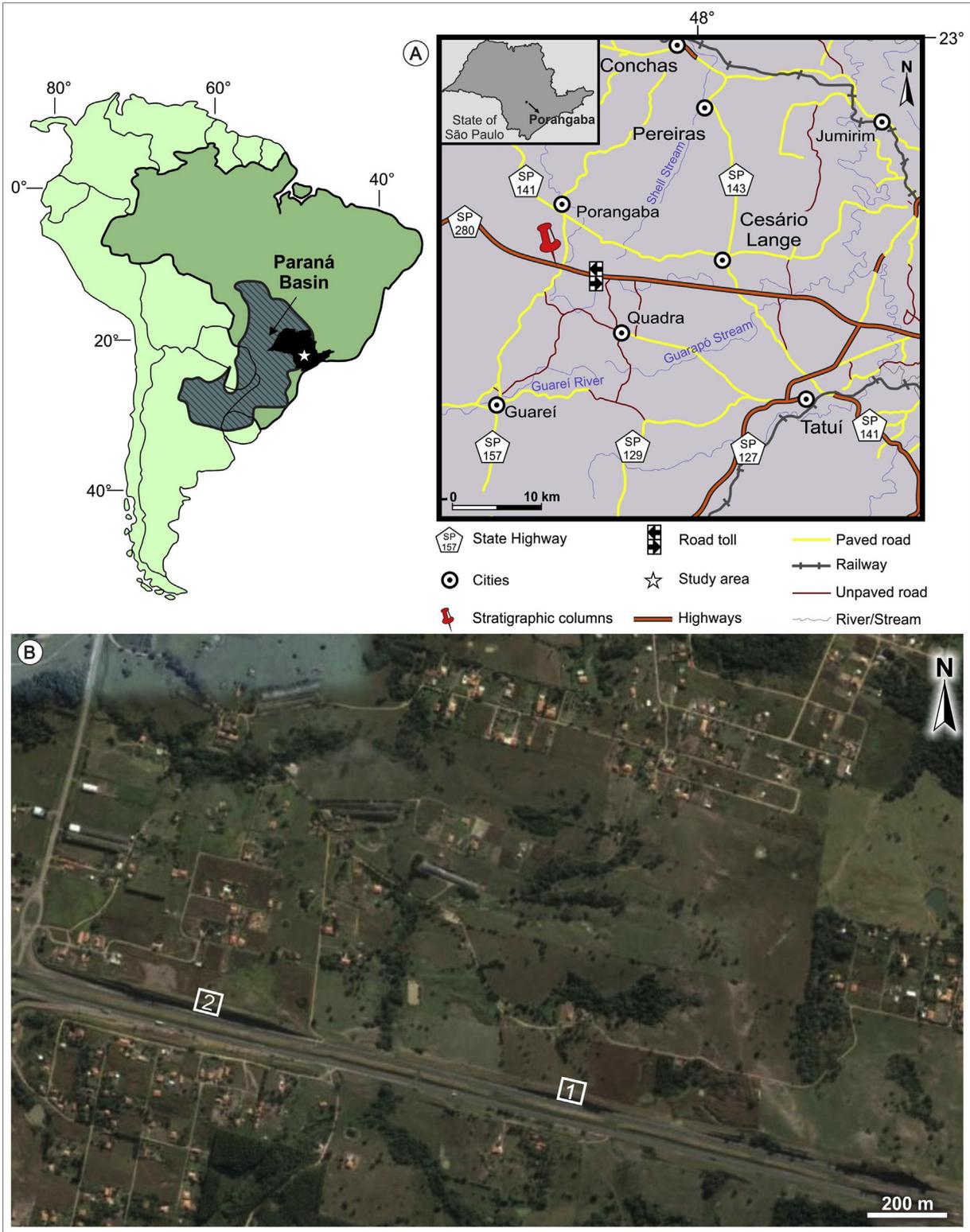
The mudstone intervals of the Serra Alta Formation studied here were selected based on (a) the quality of the exposures, with respect to weathering and plant coverage, and (b) previous interpretations of these fine-grained, dark muddy rocks as offshore, oxygen-deficient facies ([Sousa, 1985](#); [Simões et al., 2000a, b](#); [Warren et al., 2015](#); [Bondioli et al., 2015](#)). The better exposures are road cuts along the SP-280 highway (Castello Branco road), around 8 km to the south of the city of Porangaba ([Fig. 1](#)).

The main investigated outcrop, consists of laminated siltstone (up to 11 m) interbedded with decimeter- to centimeter-thick sandstone and limestone layers, and occasional beds yielding carbonate concretions and phosphate nodules ([Fig. 2](#); [Bondioli et al., 2015](#); [Warren et al., 2015](#)). This is described in detail in Section 4.1 below.

## 3. Methods, samples and terminology

Our integrated approach follows [Kauffman and Sageman \(1990\)](#), [Sageman et al. \(1991\)](#), [Boyer \(2010\)](#), and [Boyer and Droser \(2011\)](#), and encompassed the sub-cm scale investigation of an 11-m-thick succession of the dark grey colored, laminated mudstones and siltstones with subordinate laminated mudstones of the Serra Alta Formation. The bulk sample consists of several (cm- to m-thick) slabs of siltstones, fine-grained sandstones, and phosphate-rich layers, as well as over 66 bivalve specimens, belonging to 7 species (*i.e.*, *Anhemia froesi*, n = 8, *Tambaquyra camargoi*, n = 10, *Maackia contorta*, n = 8, *Ferrazia simplicicarinata*, n = 12, *Houldhausiella elongata*, n = 2, *Barbosaia angulata*, n = 6, *Rioclaroa lefevrei*, n = 3, undetermined, n = 17) and dozens of discoidal carbonate (calcite) concretions. These materials are housed in the scientific collection of the Department of Zoology, Institute of Biosciences, UNESP, Botucatu campus, under the DZP-code. Some rock slabs were sectioned and polished with silicon carbide powder of various grain sizes and digitally imaged using a resolution of 1200dpi in a flatbed scanner.

During the field work, sedimentary facies were distinguished based on lithology, sedimentary structures, bed contacts, geometry, trace fossils and taphonomic signatures of the trace and body fossils (mainly bivalve shells). Bivalve species identification followed [Runnegar and Newell \(1971\)](#) and [Simões et al. \(1997, 2000a, b\)](#). Bivalve paleo-autoecology was inferred based on [Simões et al. \(1998\)](#), [Ghilarci \(1999\)](#) and [Wesseling \(2007\)](#). Trace fossil analysis was based on ichnotaxa identification and bioturbation index (BI), according to [Taylor and Goldring \(1993\)](#), including: BI 0 (no bioturbation); BI 1 (sparse bioturbation, bedding distinct, few discrete traces and/or escape structures); BI 2 (low bioturbation, bedding distinct, low trace density, escape structures often common); BI 3 (moderate bioturbation, bedding boundaries sharp, traces discrete, overlap rare); BI 4 (high bioturbation, bedding boundaries indistinct, high trace density with overlap common); BI 5 (intense bioturbation, bedding completely disturbed - just visible, limited reworking, later burrows discrete), and BI 6 (complete bioturbation, sediment reworking due to repeated overprinting). Taphonomic descriptive terms and parameters are the same as in [Kidwell et al. \(1986\)](#), and [Kidwell and Holland \(1991\)](#). Following [Rhoads and](#)



**Fig. 1.** A. Location map of the study area, near to the city of Porangaba, State of São Paulo; B. Google Earth image (Date: 25/02/2016; Satellite sensor: Landsat) showing the outcrops sampled along the highway cuts, SP-280 (Castello Branco highway).

Morse (1971), Sageman et al. (1991), Tyson and Pearson (1991), Wignall (1994), and Boyer and Droser (2011), we adopted the tripartite model of relative bottom-water oxygenation, which recognizes the following depositional conditions: a) aerobic (fully

oxygenated,  $\text{ml O}_2/\text{l H}_2\text{O} > 2$ ), b) dysaerobic (reduced oxygen; moderate:  $\text{ml O}_2/\text{l H}_2\text{O} = 2-1$ ; severe:  $\text{ml O}_2/\text{l H}_2\text{O} = 1-0.5$ ; extreme:  $\text{ml O}_2/\text{l H}_2\text{O} = 0.5-0$ ), and c) anaerobic (completely devoid of bottom-water oxygen,  $\text{ml O}_2/\text{l H}_2\text{O} = 0$ ).

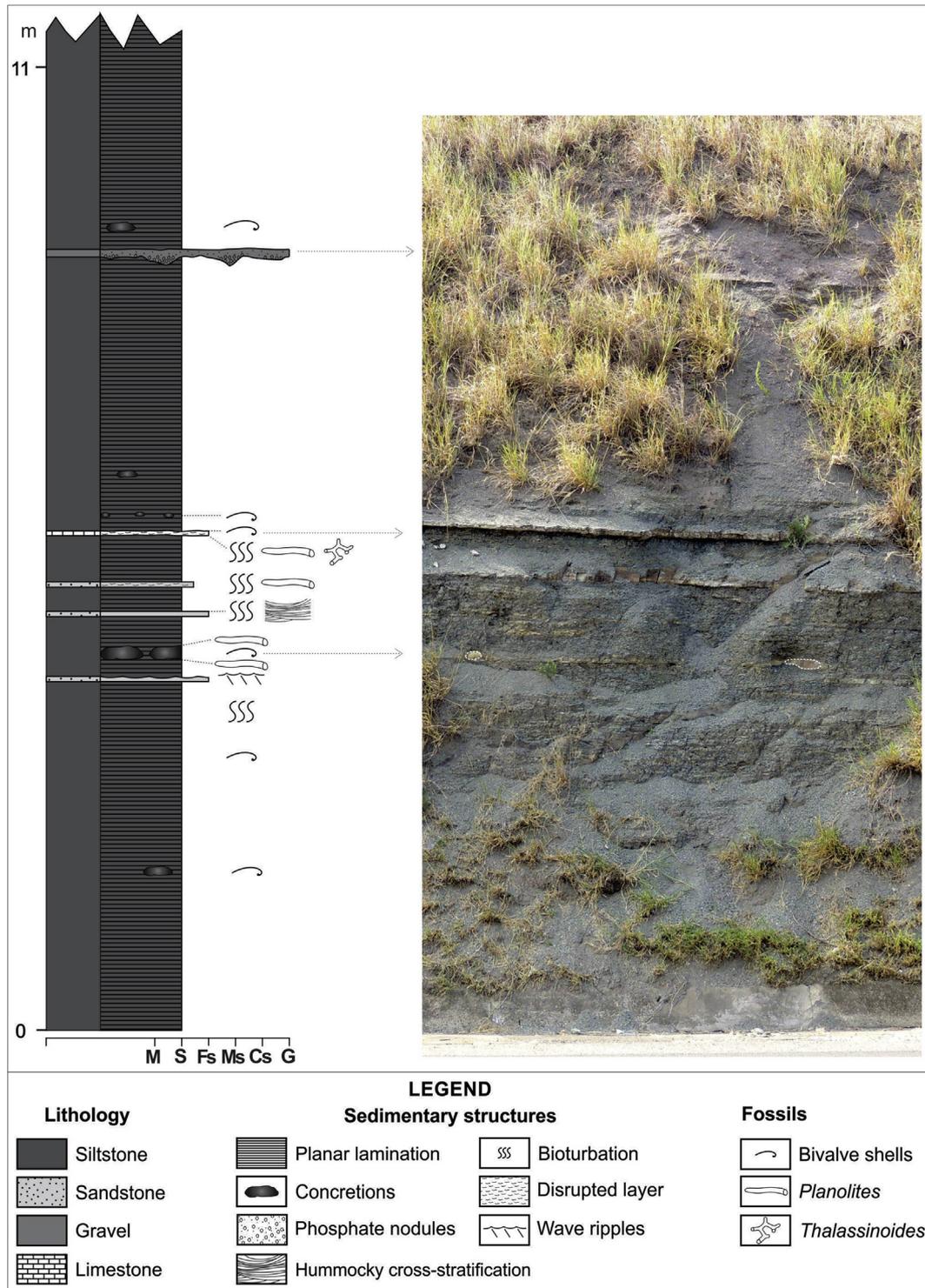


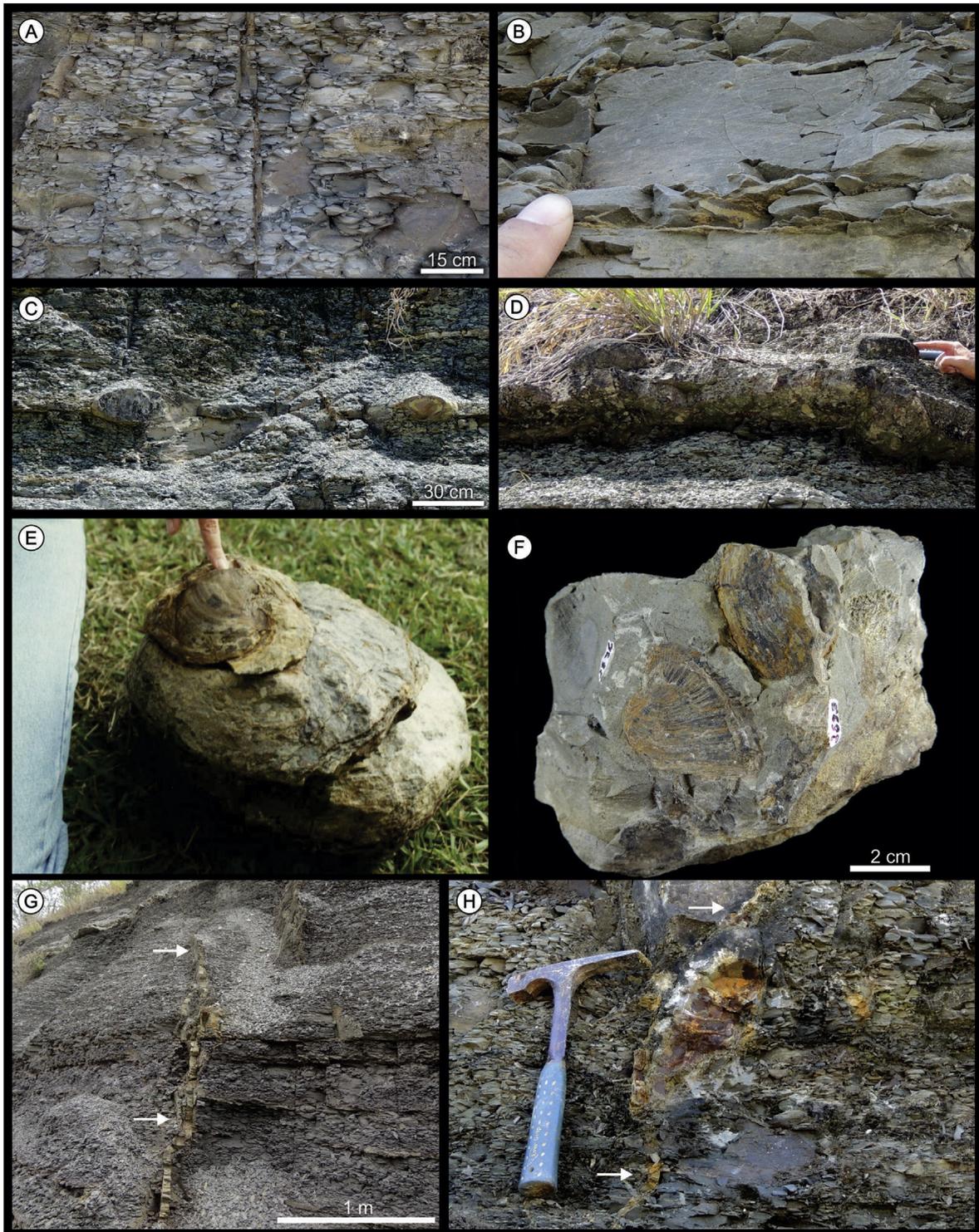
Fig. 2. Section of the basal part of the Serra Alta Formation, km 160.7, SP-280 (Castello Branco highway), State of São Paulo.

## 4. Results

### 4.1. Description of the rock succession

As mentioned above, the sampled intervals of the Serra Alta Formation in the study area were selected to represent a range of relative oxygen levels throughout the dysoxic muddy (barren) facies (see Bondioli et al., 2015; Warren et al., 2015). The section

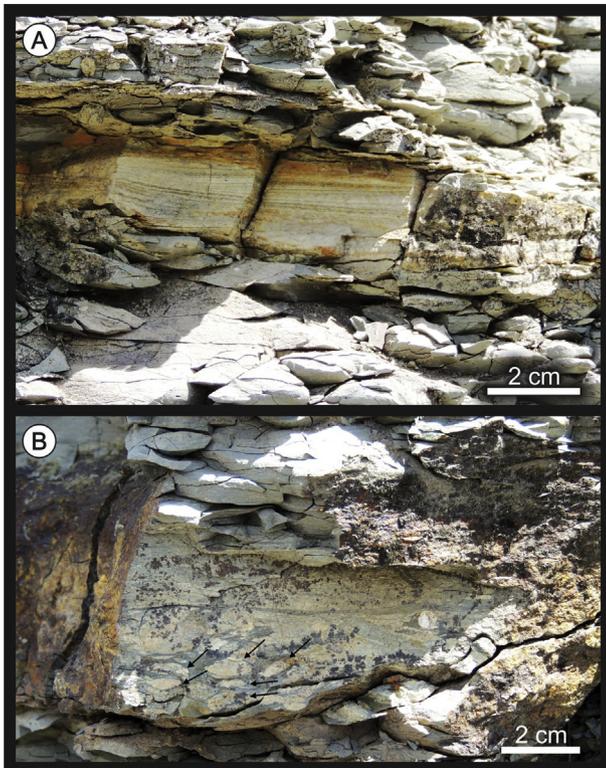
starts with a 3.5-m-thick package of non-bioturbated (BI 0), dark greenish-grey siltstones and subordinate laminated mudstones (BI 0) (Figs. 2 and 3). Rare, minute bivalve shells are dispersed in the matrix. Shells are either disarticulated or articulated (closed or splayed) and belong to suspension-feeding, infaunal bivalves (*Barbosaia angulata*, *Ferrazia simplicicarinata*, *Holdhausiella elongata*, *Rioclaroa lefevrei*, *Tambaquyra camargoi*, *Maackia contorta*). Isolated, discoidal, carbonate concretions also occur in this fossil-



**Fig. 3.** A-B. Dark grey siltstones of the basal portion of the Serra Alta Formation. C-F. Details of part of the two main carbonate concretion-bearing horizons. C. Large concretions, which are found in the lowermost carbonate concretion-bearing horizon; D. Small carbonate concretions found in the upper concretion-rich horizon; E-F. Bivalve shells (*Tambaquyra camargoi*) within a carbonate concretion; G. Clastic dike cutting across the mud rock (white arrows); H. A clastic dike (white arrows) in detail.

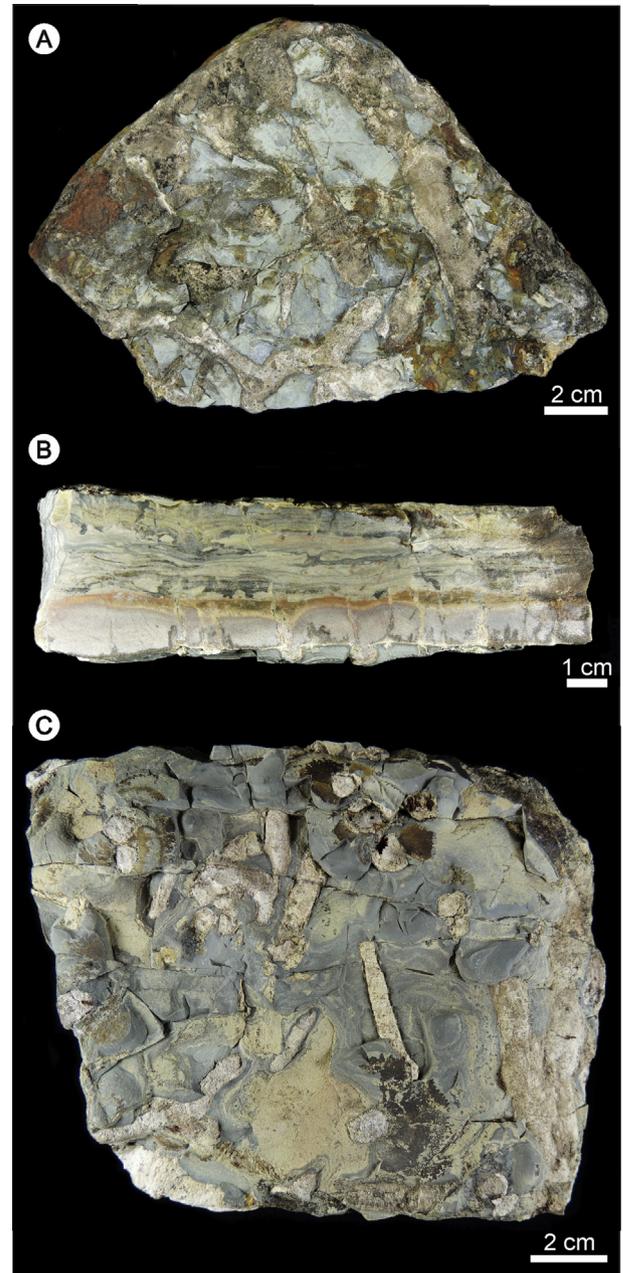
poor deposit. Above this level, a 7-cm-thick layer of fine-grained sandstone with current ripples (Fig. 2) and low levels of bioturbation (BI 2–3) occurs. These are succeeded by a 60-cm-thick bed of dark grey laminated siltstone (BI 0) including a conspicuous horizon with calcite or siderite (rare) concretions. These concretionary bodies (CB's, sensu Selles-Martinez, 1996) range in size

from a few centimeters to almost a meter (Figs. 3 and 4). In cross-section, the larger concretions are oval-shaped or lenticular, while the smaller ones are spherical (Fig. 3). This concretion-rich horizon can be laterally traced for almost a kilometer (Fig. 1). Uncompacted or compressed, closed articulated bivalve shells are abundant within the concretions. Some bivalve shells can be very large (Fig. 3)



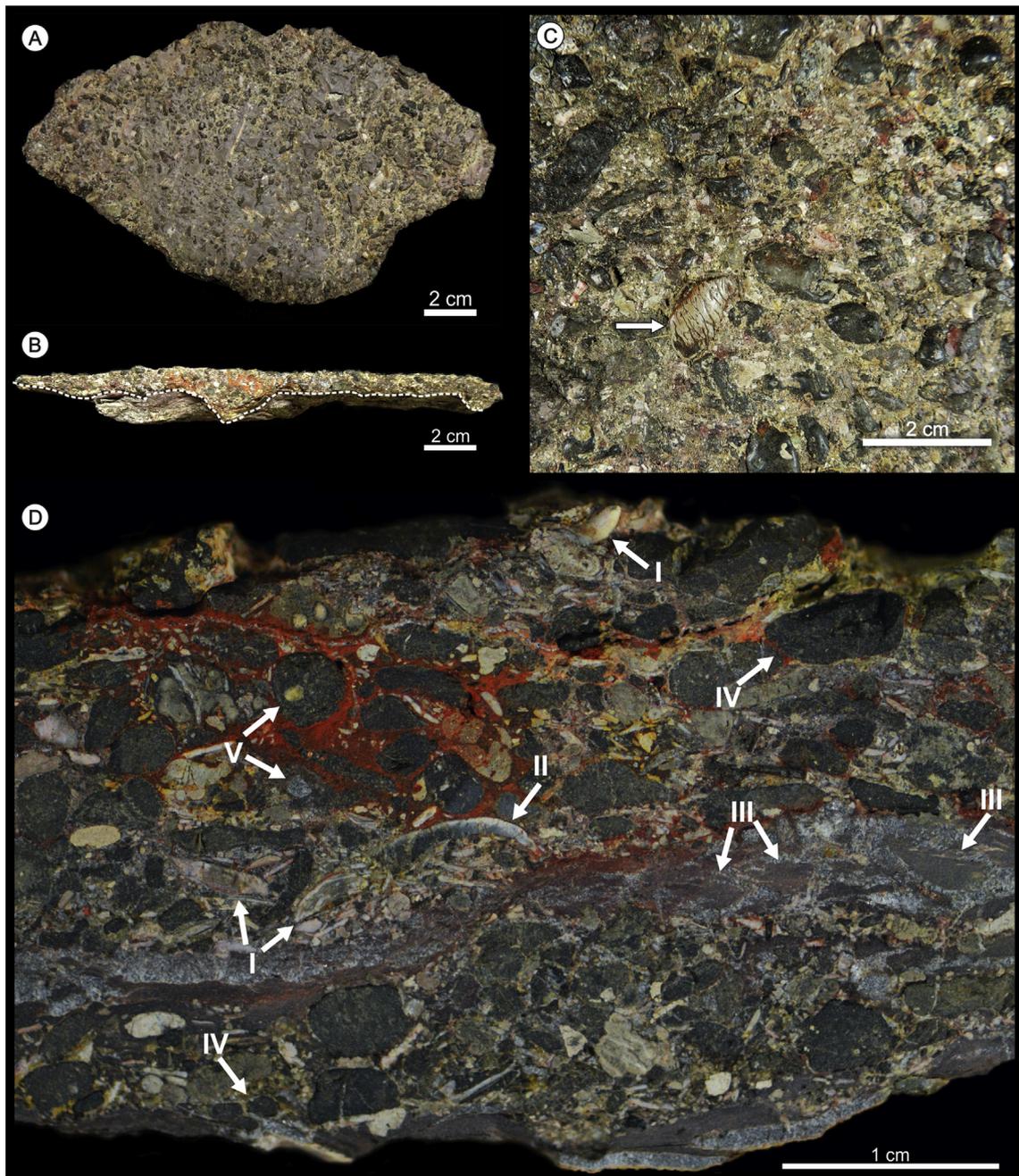
**Fig. 4.** A. Decimeter-thick intercalation of fine-grained sandstone with low angle cross-stratification. Note the sharp basal contact; B. Bioturbated silty sandstone intercalated between laminated siltstones. Note the presence of large burrows (black arrows) at the base of the layer.

and are attributed to suspension-feeding bivalves (e.g., *Tambaquyra camargoi*). Isolated *Planolites* traces (BI 1) are also found in association with these carbonate concretions. Above this level, the siltstone (BI 0) is overlain by dm- to cm-thick, fine-grained sandstone beds. Two of them deserve attention due to their contacts, geometry, and bioturbation index. The lowermost one is located only 35 cm above the concretion horizon and is represented by a mm- to cm-thick fine-grained sandstone showing a sharp and erosional base, normal grading and small scale hummocky cross-stratifications (Fig. 4). These sandstone beds can be laterally traced for several meters. They lack bioturbation or are only densely bioturbated at their top. *Planolites* seems to be the main trace fossil, being either small (mm) or large (cm) in size. BI is zero at the base of the sandstone and 2 or 3 at its top. This sandstone is succeeded by 35-cm-thick laminated dark grey siltstones with a 3-cm-thick, highly bioturbated (BI 4) and silicified silty/muddy sandstone layer. Trace fossils are mainly represented by *Planolites*, which are larger at the base than at the top of the bed (largest diameter ~1,15-cm; smallest diameter ~0,29-cm). In cross-section, the burrows are slightly to moderately compacted (Fig. 4). Above this, a 47-cm-thick package of dark grey, laminated siltstone occurs (BI 0), which is succeeded by a ~20-cm-thick limestone bed (Fig. 5). As shown by Matos (2016), this is a highly silicified (microcrystalline quartz), brecciated limestone. The silicification probably occurred very early in the diagenesis, and not much carbonate was left. At the top of the bed, microbial lamination is clear visible. At the base of the limestone *Thalassinoides*-like burrows and *Planolites* are found (Fig. 5), which are slightly compressed in cross-section. This limestone bed is overlain by planar laminated siltstones. These lithotypes are succeeded by a 5.1-m-thick package of siltstone including a well-defined, fossil-rich calcareous concretion horizon similar to that



**Fig. 5.** A ~20-cm-thick brecciated limestone with microbial lamination at the top. A. *Thalassinoides* burrows at the base of the limestone. B. Cross-section of the same sample. Note the lamination at the top C. *Planolites* isp. from the same bedding plane as in A.

recorded at the base of the section. Higher in the section, a 0.7-3-cm-thick layer of phosphatic particles occurs (Fig. 6) and can be laterally traced for over 1 km (see also Simões and Rohn, 1996). This layer includes a dense concentration of rounded phosphatized particles, which range from fine sand- to pebble-sized grains. Bioclasts, such as paleoniscoid scales and teeth and petalodont remains, bone and shell fragments, coprolites and/or enterospores are all mixed with indeterminate phosphate particles and intraclasts. Elongated clasts are preferentially N-S oriented (Simões and Rohn, 1996). In thin-section, pyrite nodules and allochems (i.e., peloids) are observed (Simões and Rohn, 1996) as well as pervasive cementation by  $\text{CaCO}_3$ , partially replaced by silica. The basal contact of this layer is sharp and erosional with scour and fill



**Fig. 6.** Phosphate-rich layer at the top of the section. A. Plan-view, showing phosphate nodules of various sizes (sand to pebble). B. Note the sharp and erosional base. C. Phosphate nodules of various sizes associated with large (cm) bone remains (white arrow). D. Polished, thin-section showing the complex nature of the phosphate-rich layer. Note the presence of small, bone (I) and shell fragments (II), and intraclasts (III). Phosphate nodules of distinct sizes (IV) are also visible as well as nodules with different nuclei (V).

structures, and its upper contact is also sharp (Simões and Rohn, 1996) (Fig. 6). Towards the top, the section is composed of a monotonous succession of laminated, dark-grey (or reddish when weathered) siltstones. Finally, both outcrops are cut by abundant clastic dikes (Fig. 3G–H).

#### 4.2. Biostratigraphy

In the section of the dark-grey mudstones of the Serra Alta Formation, shells of the suspension-feeding bivalve *Tambaquyra camargoi* are abundant and associated with valves of *Barbosaia angulata*. This indicates that the investigated succession is part of

the *Barbosaia angulata*-*Anhembia froesi* Association Biozone (sensu Rohn, 1994).

The stratigraphic distribution of the bivalve species assigned to that biozone is restricted to the base of the Serra Alta Formation (see also Holz et al., 2010, Fig. 11). Indeed, in some sections where rocks of the Serra Alta Formation are well exposed, such as those cropping out south of the city of Piracicaba (Simões et al., 2000b), shells of *Tambaquyra camargoi* are found only a few meters (~5 m) above the last limestone beds of the underlying Irati Formation (Simões et al., 2000b). Thus, the studied rocks are locally placed in the basal part of the Serra Alta Formation, approximately 9 m above the local, erosional contact (diastem) with the underlying Irati

Formation, considering the stratigraphic information available in Sousa (1985) and Warren et al. (2015).

## 5. Discussion

As discussed in detail below, the barren mudstones presumably constitute deposits generated by suspension settling sometimes under the influence of episodic sedimentation in distal (mainly offshore) portions of a siliciclastic-dominated shallow interior sea. Our multiproxy analysis indicates that this offshore facies had a very dynamic and complex sedimentary history, punctuated by high energy events (storm flows and/or shock-induced waves). These are suggested by (a) the presence of several layers with smothered articulated (closed/splayed) bivalve shells; (b) fine-grained sandstones with low angle cross-stratification (i.e., small scale hummocky cross-stratification); (c) clastic dikes (Fig. 3G–H) and tabular brecciated limestone with injection structures (see also Matos, 2016); and (d) layers of coarse-grained (sand to pebble) phosphate nodules between laminated siltstones. These may suggest extreme variations of some environmental conditions, such as bottom oxygenation, sedimentation rate, water depths, and tectonic activity. Among these, however, depletion in oxygen is the most widespread environmental condition observed, as described below.

### 5.1. Interpretation of the sedimentological and trace fossil signal

As shown in Fig. 2, the laminated siltstones predominate within the investigated section. They were deposited under conditions of calm water and oxygen-deficient bottoms (Warren et al., 2015). As discussed below, discrete layers of sandstones are interpreted to record sediment influx from more proximal areas in to distal, deeper settings. Within the studied section, bioturbation and discrete trace fossils display a scattered distribution (Fig. 2), occurring in high densities and low diversity in some preferred intervals. In general, the bioturbation index is low (see above) and the simple burrows (*Planolites*) are the most common trace fossil in the dark grey laminated siltstones, the bioturbation index is usually 0 to 1 and body fossils are normally absent. Abundant traces and/or highly bioturbated sediments are always recorded in close association with event beds, invariably the tabular sandstone layers. The presence of burrowing organisms in these beds may indicate the opportunistic colonization of the seafloor after event sedimentation. Indeed, the rare, isolated presence of *Planolites* in siltstones is a good indicator of low oxygen content of the taphonomically active zone (TAZ, sensu Davies et al., 1989). In a recent study, Boyer and Droser (2011, p. 506) showed that along a bathymetric gradient encompassing oxic to anoxic bottoms in Devonian epeiric seas, small isolated *Planolites* are recorded in the distal part where extreme dysoxic conditions to anoxic prevailed.

The highly bioturbated (BI-4) layer of silicified silty sandstone shows the presence of small (mm) to large (cm) *Planolites* tubes. In polished cross-sections, the tubes are extremely compacted indicating that the traces were emplaced in a water-saturated soft bottom. Large (cm) individual tubes are recorded at the base of this layer and are succeeded by smaller (mm) ones. This may indicate variations in oxygen content within this layer with the higher values associated with the large individuals. *Planolites* seems to be the only identifiable ichnofossil, but as noted by Boyer and Droser (2011, p. 504) presence and abundance of other traces in those offshore facies are difficult to distinguish. For example, *Thalassinoides* is indistinguishable from large *Planolites* when the branching points are not exposed. The end of these conditions is marked by the disappearance of the traces and return of oxygen-deficient conditions. These prevailed during the day-by-day sedimentation

of the overlying laminated (non-bioturbated) siltstones. Similarly, the opportunistic benthic colonization of storm-influenced layers is well documented at the highly bioturbated top of the sandstone bed with low angle cross-stratification. It indicates that the benthic activity was intense during times of decreased sedimentation rates and better oxygenation (aerobic), after deposition of the sandstones by high-energy events (Buatois et al., 2011).

The presence of *Thalassinoides* and *Planolites* at the base of the limestone bed (Fig. 5) records again the opportunistic colonization of bottoms by infaunal benthos, probably under aerobic and low sedimentation rate conditions (Boyer and Droser, 2011). Finally, at the top of the section, laminated siltstones prevail indicating the return of oxygen-depleted conditions at the sea floor. Phosphate-rich layers are a noteworthy sedimentological and diagenetic feature of this interval (see Section 5.3.).

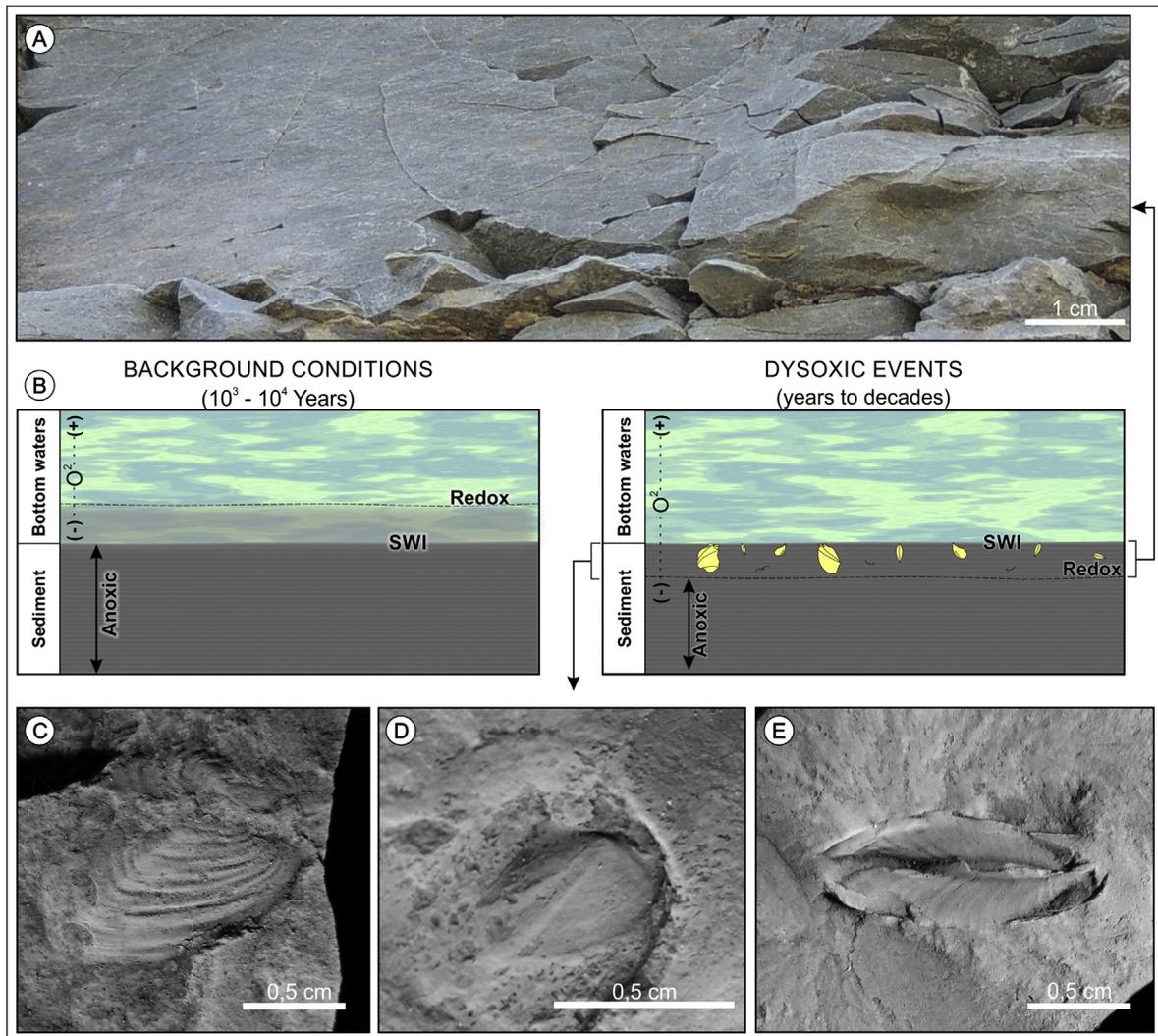
### 5.2. Interpretation of the body fossil signal

Fig. 2 shows the scattered distribution of the body fossils, mainly represented by a low diversity shelly fauna of bivalve mollusks, within the columnar section. Their presence in discrete horizons may be due to shell dissolution in confined mud horizons, as well as to stress conditions related to the oxygen-deficient sea floor.

The presence of bivalves in some layers of the laminated siltstones, mainly as articulated (closed or splayed) valves, without signs of abrasion and bioerosion is a good indicator that they were autochthonous to parautochthonous (sensu Kidwell et al., 1986). Very small (mm), articulated shells in the basal, laminated siltstones (Fig. 7), belonging to infaunal suspension-feeding species such as *Barbosaia angulata* and *Rioclaroa lefevrei*, may represent taxa adapted to low-oxygen conditions, belonging to a low diversity community. Indeed, these bivalves are absent in coeval paleocommunities, living in better more favorable oxygenated environments (Simões et al., 1998), such as those found in contemporary shallow-water deposits of the laterally equivalent Corumbataí Formation. The latter bivalves may represent pioneer members of a benthic community adapted to low-oxygen conditions (Kauffman and Sageman, 1990) inhabiting the top layer of the substrate. Hence, their absence in several horizons of the siltstones (Fig. 2) may indicate extremely dysoxic or anoxic conditions precluding colonization even by members of a community adapted to background reduced-oxygen conditions (Fig. 7).

Other noteworthy body fossils are those large (“gigantic”) bivalves, some with unusual morphologies (see Runnegar and Newell, 1971), including *Tambaquyra camargoi* and *Anhembia froesi* (Simões et al., 1998, 2000a, b). They are mainly documented in two well-defined horizons of laminated, dark grey siltstones in the mid portion of the studied section (Figs. 2, 3 and 8) (Simões et al., 2000b; Bondioli et al., 2015), usually associated with the discoidal carbonate concretions. Shells of these species are enormous (104.5 mm of maximum length) or ten times larger than those contemporary ones found in the siltstones below (Fig. 7). *Tambaquyra camargoi* may be rare and represented only by small shells (20.8 mm of maximum length) in contemporary shallow-water bivalve assemblages (Matos et al., 2013). This suggests their preferential adaptation to low-oxygen substrates (see also Kauffman et al., 2007; Edelman-Furstenberg and Kidwell, 2015).

The large size of these shells and their abundance at some horizons of the laminated mudstones is a striking feature of the studied interval of the Serra Alta Formation. Some authors suggested that both *Tambaquyra* and *Anhembia* are good Permian candidates for chemosymbiotic bivalves (Ghilardi and Simões, 2000, 2002; Matos et al., 2013; Matos, 2016). For example, *Anhembia* resembles *Arconaia lanceolata*, a living chemosymbiotic



**Fig. 7.** A. Siltstone from the basal part of the Serra Alta Formation where small bivalve shells are disperse (see below); Note in B, how a dysoxic event allowed low-oxygen adapted taxa to inhabit the uppermost layer of the substrate (modified from Berrocoso et al., 2008). C-E. Examples of small bivalves found in the laminated siltstone. C. Articulated *Houdhausiella elongata* specimen in butterfly posture (DZP-2282); D. Disarticulated valve of *Barboisa angulata* (DZP-2267); E. Articulated undetermined bivalve (DZP-2277). SWI= Substrate-water interface.

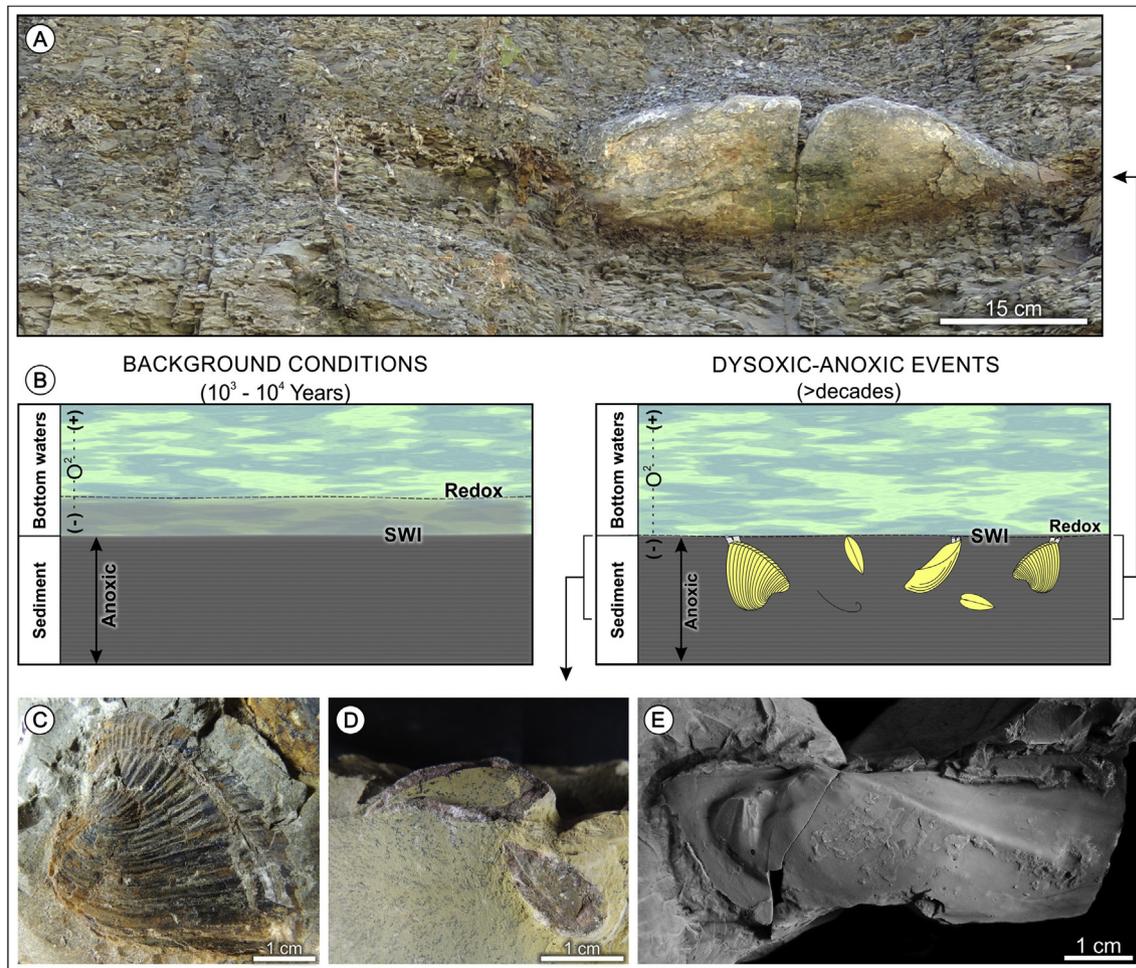
bivalve (Savazzi and Peiyi, 1992). Articulated shells of *Tambaquyra camargoi* are ten times larger than the vast majority of co-existing non-chemosymbiotic infaunal bivalves (see Oschmann, 1994 for similar examples in Jurassic co-occurring chemosymbiotic and non-chemosymbiotic bivalve faunas, and Edelman-Furstenberg and Kidwell, 2015, for modern examples). Indeed, because of their higher oxygen demands, abundance, size of individuals and diversity of benthic communities decreases with decreasing oxygen levels (Boyer and Droser, 2011). Therefore, an explanation for the abundance of large-size bivalves in oxygen-deficient mudstones or black shales is the faster growth of chemosymbionts. Indeed, chemosymbiosis commonly results in accelerated growth rates in bivalves (Kauffman et al., 2007, p.71), which may house sulfide or methane oxidizing bacteria in the gills and/or mantle tissues. As discussed by Kauffman and Sageman (1990), the “necessary organic carbon is produced through internal bacterially moderated physiological/chemosymbiotic processes”. In these conditions, these bivalves are able to colonize otherwise chemically toxic settings around the boundary between to extremely dysaerobic (=exaerobic) to anoxic zone (Savrdá, 1992; Savrdá and Bottjer 1986; Wignall, 1994; Boyer and Droser, 2007; Edelman-Furstenberg and

Kidwell, 2015) or at vent springs (Kauffman and Sageman, 1990; Oschmann, 1994; Kauffman et al., 2007).

In our case study, the interpretation that the horizons with gigantic shells of *Tambaquyra* and *Anhembia* were anaerobic or extremely dysaerobic is also supported by the recent found that these shells show negative  $\delta^{13}\text{C}$  values ( $-6.1\text{‰}$ ), suggesting colonization of oxygen-depleted, organic rich substrates and a probable chemosymbiotic (at least facultatively) mode of live (see Matos, 2016). Finally, the association of bivalves with chemoautotrophic organisms in anoxic sediments, mostly in deep sea environments, is a well-known feature of the evolutionary history of this molluscan class (e.g., see Taylor and Glover, 2000, 2005, 2010; Savazzi and Peiyi, 1992; Wesseling, 2007; Kauffman et al., 2007; Taylor et al., 2014).

### 5.3. Interpretation of the phosphatogenesis and the early diagenetic signal

As shown in Fig. 2, carbonate (calcite) concretions can be found at several levels of the section, but they are much more common in two distinct intervals. The formation of these eodiagenetic



**Fig. 8.** A. Dark grey siltstones with carbonate concretions. B. Extremely dysoxic bottoms colonized by large chemosymbiotic bivalves (modified from Berrocoso et al., 2008). C–E. Bivalves found within carbonate concretions. C. *Tambaquyra camargoi* (DZP-2896). D. Cross-section view of two articulated bivalves within a concretion. E. Disarticulated specimen of *Anhemia froesi* (DZP-2889). SWI= Substrate-water interface.

concretions has been discussed in detail by Bondioli et al. (2015). As mentioned above, articulated bivalve shells are common in the nuclei of these concretions, suggesting that they are associated with event layers (Bondioli et al., 2015). Indeed, as recently revealed by the detailed study of Brett et al. (2012), concretionary horizons in offshore facies are a record of event deposition of fine-grained sediments, which smother the benthos followed by periods of prolonged low sedimentation rates with the organic-rich layers situated at the sulfate reduction zone. The formation of the carbonate concretion in the sulfate reduction zone is favored by the rapid burial of organic matter and gaps in sedimentation, which allows sufficient time for concretions to grow (Brenchley and Harper, 1998). Hence, each concretionary layer may represent an individual obrution deposit or a record of rapid, episodic deposition of fine-grained sediments, followed by a period of non-deposition or starvation prior to sediment cementation and compaction (Brett et al., 2012).

Above the interval with carbonate concretions, a 5.1-m-thick package of laminated siltstone occurs (Fig. 2). These are non-bioturbated or contain discrete, isolated horizontal burrows (BI 0–1). Thus, as for other parts of the section, this is mainly formed offshore under oxygen-deficient conditions.

The most striking feature in the studied deposit is the presence of dense concentrations of phosphate nodules and biogenic remains in some layers (Fig. 6). As shown by John et al. (2002),

phosphate-rich layers such as those described here, may result from local phosphogenesis processes leading to the formation of phosphatized particles (Meghioratti, 2006, p. 98). As discussed by Brett and Baird (1986), the phosphatization process is normally linked to restricted, organic-rich microenvironments. According to these authors, abrupt burial of the organic matter followed by an extensive period of minimal sedimentation and/or erosion provide enough time for phosphatization. Phosphate formation probably also requires prolonged stability of an oxidizing microzone overlying anoxic sediment in which phosphate is released from organic matter and hydroxides in its dissolved form (see also Li and Schieber, 2015, p. 58). After the formation of the phosphate-rich sediments (i.e., as laminae, lenses or nodules), subsequent reworking will generate layers of phosphate-rich intraclasts (see Li and Schieber, 2015; for a similar Devonian example). The model for the formation of phosphates and phosphatic condensed beds, proposed by Föllmi et al. (1991) and John et al. (2002), fits our example very well. Initially, the first phase of phosphate formation started in an organic-rich, anoxic sediment containing pyrite, bone fragments (e.g., teeth), and organic waste products (e.g., coprolites, peloids) that served as nuclei for phosphatization (see Fig. 6). Subsequently, winnowing processes led to the concentration of the nodules into a distinct layer of phosphate-coated particles. Reworking of phosphatized particles and break-up of cohesive phosphate layers occurred during high-energy events, which were

followed by the transport and redeposition of particles. Next, the reworked phosphatic nodules and clasts (including intraclasts) may have served as new nuclei for renewed phosphate precipitation. The phosphate layer shows evidence that the process above was repeated several times to give rise to a complex, condensed interval (Föllmi et al., 1991; John et al., 2002) (Fig. 6). In fact, repeated reworking of phosphate-rich sediments is suggested by the erosional base with scour and fill structures (Fig. 6B). This led to erosion of the underlying muddy substrate by bottom currents or wave orbitals. Subsequently, the troughs and scours were filled with coarse grains (including pelitic intraclasts and phosphate nodules) during the waning stage of the flow. As predicted in the model of Föllmi et al. (1991) and John et al. (2002), the sedimentary processes discussed above points to powerful tractive flows in distal parts of the basin, which may reflect high energy events, such as storms or tsunamis.

Finally, the features above are all indicative of changes in the base level, with episodic sea level drops under a general transgressive context. In fact, transgressions in the section above is, probably, recorded by condensed, thin beds, such as the phosphatic lag bed. In this context, this may be used as a stratigraphic marker, as it can be laterally traced for over a kilometer in the outcrop area and thus may have had a regional distribution.

## 6. Conclusions

Deposits of the Serra Alta Formation were commonly interpreted as monotonous offshore deposits, generated under anoxic or dysoxic conditions (Mendes, 1954; Sanford and Lange, 1960; Schneider et al., 1974; Sousa, 1985; Milani et al., 2007; Meghioratti, 2006; Holz et al., 2010). However, as discussed above, integration of sedimentological, paleontological (trace and body fossils) and diagenetic information tell us a different so far untold, very dynamic depositional history (see also Bondioli et al., 2015; Warren et al., 2015). In other words, the classic interpretation that these fine-grained, siliciclastic-dominated deposits are a record of relatively stable, long-term oxygen-poor distal conditions is, in part, flawed. From now on the depositional history of the Serra Alta Formation, which records the youngest and last transgression in the Paraná Basin (Milani et al., 2007; Holz et al., 2010), must be viewed from this dynamic perspective.

Background conditions represented by laminated siltstones, were dominated by low rates of sedimentation under anoxic to dysoxic conditions. The sparsely bioturbated (except isolated *Planolites*) deposits embrace two main types of low oxygen-associated bivalve faunas, (a) resident populations (sensu Kauffman and Sageman, 1990) represented by infaunal suspension-feeding bivalves (e.g., *Barbosaia angulata*, *Rioclaroa lefevrei*), which were adapted to low-oxygen (dysaerobic) conditions. Usually, these are minute, and preserved as articulated valves (closed or splayed), dispersed in the matrix, and (b) thin-shelled, large (*Tambaqurya*), morphologically bizarre (*Anhemia*) infaunal bivalves that lived in chemically toxic (extremely dysaerobic) substrates. Commonly, their shells are closed articulated and preserved within carbonate concretions.

Event populations (sensu Kauffman and Sageman, 1990) are associated with some particular layers, invariably generated by high-energy sedimentary processes. Thus, establishment of these short-lived populations was linked to changes in substrate type and oxygen content (from anoxic to dysoxic/oxic), following bottom disruptions. A good example is the densely bioturbated top of the sandstone layer with low angle cross-stratifications.

In summary, two broad paleoenvironmental conditions are recorded within the oxygen-deficient facies of the Serra Alta Formation, which are similar to these identified by Sageman et al.

(1991) in modern oceans. The first is characterized by settings where the uppermost layers of the substrate and much of the overlying water column are both dysoxic. Deposit feeders, such as protobranch bivalves, are absent and faunal diversity is extremely low, but the abundance of a few bivalve species may be high in certain layers. Conversely, in a second setting the anoxic zone abruptly set in at or near the sediment-water interface, but the overlying water masses are better oxygenated. Here, the H<sub>2</sub>S-saturated fine-grained substrates were colonized by well adapted, low diversity bivalve fauna, probably including chemosymbiotic species.

Finally, the level with the phosphate lag bed records a strongly sediment starved interval during major sea level rise following shallowing in the Permian of the Paraná Basin.

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## References

- Alessandretti, L., Warren, L.V., Machado, R., Novelo, V.F., Sayeg, I.J., 2015. Septarian carbonate concretions in the Permian Rio do Rasto Formation: birth, growth and implications for the early diagenetic history of southwestern Gondwana succession. *Sediment. Geol.* 326, 1–15. <http://dx.doi.org/10.1016/j.sedgeo.2015.06.007>.
- Araújo, L.M., 2001. Análise da expressão estratigráfica dos parâmetros de geoquímica orgânica nas Sequências Depositionais Irati (Ph.D. Thesis). Universidade Federal do Rio Grande do Sul.
- Berrococo, A.J., MacLeod, K.G., Calvert, S.E., Elorza, J., 2008. Bottom water anoxia, inoceramid colonization, and benthopelagic coupling during black shale deposition on Demerara Rise (Late Cretaceous western tropical North Atlantic). *Paleoceanography* 23 (3), PA3212. <http://dx.doi.org/10.1029/2007PA001545>.
- Bohacs, K.M., Lazar, O.R., Demko, T.M., 2014. Parasequence types in shelfal mudstone strata—Quantitative observations of lithofacies and stacking patterns, and conceptual link to modern depositional regimes. *Geology* 42, 131–134. <http://dx.doi.org/10.1130/G35089.1>.
- Bondioli, J.G., Matos, S.A., Warren, L.V., Assine, M.L., Riccomini, C., Simões, M.G., 2015. The interplay between event and background sedimentation and the origin of fossil-rich carbonate concretions: a case study in Permian rocks of the Paraná Basin, Brazil. *Lethaia* 48, 522–539. <http://dx.doi.org/10.1111/let.12124>.
- Boyer, D.L., 2010. How dysaerobic is the dysaerobic zone?. In: *The Geological Society of America Annual Meeting, Abstracts with Programs*, 42, p. 192.
- Boyer, D.L., Droser, M.L., 2007. Devonian monospecific assemblages: new insights into the ecology of reduced-oxygen depositional settings. *Lethaia* 40, 321–333. <http://dx.doi.org/10.1111/j.1502-3931.2007.00031.x>.
- Boyer, D.L., Droser, M.L., 2011. A combined trace- and body-fossil approach reveals high resolution record of oxygen fluctuations in Devonian seas. *Palaios* 26, 500–508. <http://dx.doi.org/10.2110/palo.2010.p10-073r>.
- Brenchley, P.J., Harper, D.A.T., 1998. *Palaeoecology: Ecosystems, Environments and Evolution*. Chapman & Hall, New York.
- Brett, C.E., Baird, G.C., 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *Palaios* 1, 207–227. <http://dx.doi.org/10.2307/3514686>.
- Brett, C.E., Zambito IV, J.J., Schindler, E., Becker, T., 2012. Diagenetically-enhanced trilobite obrution deposits in concretionary limestones: the paradox of “rhythmic events beds”. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 367–368, 30–43. <http://dx.doi.org/10.1016/j.palaeo.2011.12.004>.
- Buatois, L.A., Saccavino, L.L., Zavala, C., 2011. Ichnologic signatures of hyperpynal flow deposits in Cretaceous river-dominated deltas, Austral Basin, southern Argentina. In: Slatt, R.M., Zavala, C. (Eds.), *Sediment Transfer from Shelf to Deep Water—Revisiting the Delivery System*. Studies in Geology, 61. AAPG, Tulsa, pp. 153–170. <http://dx.doi.org/10.1306/13271355St611948>.
- CPRM - Serviço Geológico do Brasil, 2006. *Mapa Geológico do Estado de São Paulo—SIG Brasil, scale 1, 750.000*.

- Davies, D.J., Powell, E.N., Stanton Jr., R.J., 1989. Relative rates of shell dissolution and net sediment accumulation - a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor? *Lethaia* 22, 207–212. <http://dx.doi.org/10.1111/j.1502-3931.1989.tb01683.x>.
- Edelman-Furstenberg, Y., Kidwell, S.M., 2015. Chemosymbiont-dominated seafloor communities in modern and Cretaceous upwelling systems support a new, high-productivity variant of standard low-oxygen models. *Geology* 43, 975–978. <http://dx.doi.org/10.1130/G37017.1>.
- Föllmi, K.B., Garrison, R.E., Grimm, K.A., 1991. Stratification in phosphatic sediments: illustration from the neogene of California. In: Einsele, G., Ricken, W., Seilacher, A. (Eds.), *Cycles and Events in Stratigraphy*. Springer Verlag, Berlin-Heidelberg, pp. 493–507.
- Ghilardi, R.P., 1999. Paleoaotocologia dos bivalves do Grupo Passa Dois (Neopermiano), no estado de São Paulo: bivalves fósseis como indicadores da dinâmica sedimentar (Master Thesis). Instituto de Geociências, Universidade de São Paulo.
- Ghilardi, R.P., Simões, M.G., 2000. Permian megadesmids (Bivalvia, Anomalodesmata) as Paleozoic candidates to be chemosymbiotic bivalves. In: Proceedings - XXXI International Geological Congress, CD-room.
- Ghilardi, R.P., Simões, M.G., 2002. Foram os bivalves do Grupo Passa Dois (exclusive Formação Rio do Rasto) moluscos dulcícolas? *Pesq. em Geociências* 29, 91–99.
- Holz, M., França, A.B., Souza, P.A., Iannuzzi, R., Rohn, R., 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. *J. S. Am. Earth Sci.* 29, 381–399. <http://dx.doi.org/10.1016/j.jsames.2009.04.004>.
- IPT - Instituto de Pesquisas Tecnológicas, 1981. Carta Geológica do Estado de São Paulo, scale 1, 500,000.
- John, C.M., Föllmi, K.B., De Kaenel, E., Adatte, T., Steinmann, P., Badertscher, C., 2002. Carbonaceous and phosphate-rich sediments of the miocene monterey formation at El Capitan state beach, California, U.S.A. *J. Sediment. Res.* 72, 252–267. <http://dx.doi.org/10.1306/080701720252>.
- Kauffman, E.G., 1984. Paleobiogeography and evolutionary response dynamic in the Cretaceous western interior seaway of north America. In: Westermann, G.E.G. (Ed.), *Jurassic-cretaceous Biochronology and Paleogeography of North America*. Special Paper, 27. Geological Association of Canada, St. John, pp. 273–306.
- Kauffman, E.G., Sageman, B.B., 1990. Biological sensing of benthic environments in dark shales and related oxygen-restricted facies. In: Ginsburg, R.N., Beaudoin, B. (Eds.), *Cretaceous Resources, Events and Rhythms*. Kluwer Press, Amsterdam, pp. 121–138.
- Kauffman, E.G., Harries, P.J., Meyer, C., Villamil, T., Arango, C., Jaecks, G., 2007. Paleogeology of giant inoceramidae (*Platyceramus*) on a santonian seafloor in Colorado. *J. Paleontology* 81, 64–81. [http://dx.doi.org/10.1666/0022-3360\(2007\)81\[64:POGIPO\]2.0.CO;2](http://dx.doi.org/10.1666/0022-3360(2007)81[64:POGIPO]2.0.CO;2).
- Kidwell, S.M., Holland, S.M., 1991. Field description of coarse bioclastic facies. *Palaios* 6, 426–434. <http://dx.doi.org/10.2307/3514967>.
- Kidwell, S.M., Fürsich, F.T., Aigner, T., 1986. Conceptual framework for the analysis of fossil concentrations. *Palaios* 1, 228–238. <http://dx.doi.org/10.2307/3514687>.
- Li, Y., Schieber, J., 2015. On the origin of a phosphate enriched interval in the Chattanooga Shale (Upper Devonian) of Tennessee—A combined sedimentological, petrographic, and geochemical study. *Sediment. Geol.* 329, 40–61. <http://dx.doi.org/10.1016/j.sedgeo.2015.09.005>.
- Matos, S.A., 2016. Tafonomia e paleoecologia de bivalves permianos em fácies silicilásticas deficientes em oxigênio: o exemplo das formações Irati e Serra Alta, Bacia do Paraná, Brasil (Ph.D. Dissertation). Instituto de Geociências, Universidade de São Paulo.
- Matos, S.A., Bondioli, J.G., David, J.M., Anelli, L.E., Warren, L.V., Riccomini, C., Simões, M.G., 2013. Paleogeology of 'giant' *Tambaquyra* bivalves on Permian epeiric seafloors in the Paraná Basin, Brazil. In: *Paleontologia em Destaque - Boletim de Resumos do XXIII Congresso Brasileiro de Paleontologia*, pp. 194–195.
- Meghioratti, T., 2006. Estratigrafia de sequencias das formações Serra Alta, Teresina e Rio do Rasto (Permiano da Bacia do Paraná) na porção nordeste do Paraná e centro-sul de São Paulo (Master Thesis). Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista.
- Mendes, J.C.M., 1954. Contribuição à estratigrafia da Série Passa Dois no Estado do Paraná. *Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo*, 175. *Geologia* 10, 1–119.
- Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., França, A.B., 2007. Bacia do Paraná. *Bol. Geociências Petrobras* 15, 265–287.
- Oschmann, W., 1994. Adaptive pathways of marine benthic organisms in oxygen-controlled environments. *Neues Jahrb. für Geol. Paläontologie Abh.* 191, 393–444.
- Rhoads, D.C., Morse, J.W., 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. *Lethaia* 4, 413–428. <http://dx.doi.org/10.1111/j.1502-3931.1971.tb01864.x>.
- Rohn, R., 1994. Evolução ambiental da Bacia do Paraná durante o Neopermiano no leste de Santa Catarina e do Paraná (Ph.D. Dissertation). Instituto de Geociências, Universidade de São Paulo.
- Runnegar, B., Newell, N.D., 1971. Caspian-like relict molluscan fauna in the South America Permian. *Bull. Am. Mus. Nat. Hist.* 146, 1–66.
- Sageman, B.B., Wignall, P.B., Kauffman, E.G., 1991. Biofacies models for organic-rich facies: tool for paleoenvironmental analysis. In: Einsele, G., Seilacher, A., Ricken, W. (Eds.), *Cycles and Events in Stratigraphy*. Springer Verlag, Berlin, pp. 542–564.
- Sanford, R.M., Lange, F.W., 1960. Basin study approach to oil evaluation of Paraná Miogeosyncline south Brasil. *Bull. Am. Assoc. Petrol. Geol.* 44, 1316–1374.
- Savazzi, E., Peiyi, Y., 1992. Some morphological adaptations in freshwater bivalves. *Lethaia* 25, 195–209. <http://dx.doi.org/10.1111/j.1502-3931.1992.tb01384.x>.
- Savrda, C.E., 1992. Trace fossils and benthic oxygenation. In: Maples, C.G., West, R.R. (Eds.), *Trace Fossils. Short Courses in Paleontology*, 5. Palaeontological Society, Knoxville, pp. 172–196.
- Savrda, C.E., Bottjer, D.J., 1986. Trace fossil model for reconstruction of paleo-oxygenation in bottom waters. *Geology* 14, 3–6. [http://dx.doi.org/10.1130/0091-7613\(1986\)14<3:TMFROP>2.0.CO;2](http://dx.doi.org/10.1130/0091-7613(1986)14<3:TMFROP>2.0.CO;2).
- Schneider, R.L., Mühlmann, H., Tommasi, E., Medeiros, R.A., Daemon, R.F., Nogueira, A.A., 1974. Revisão estratigráfica da Bacia do Paraná. In: *Anais do XXVIII Congresso Brasileiro de Geologia*, 1, pp. 41–65.
- Seilacher, A., 1982. General remarks about event deposits. In: Einsele, G., Seilacher, A. (Eds.), *Cyclic and Event Stratification*. Springer, Berlin, pp. 161–174.
- Seilacher, A., Reif, W.E., Westphal, F., 1985. Sedimentological, ecological and temporal patterns of fossil lagerstätten (and discussion). *Philosophical Transactions of the Royal Society of London, Series B. Biol. Sci.* 311, 5–24. <http://dx.doi.org/10.1098/rstb.1985.0134>.
- Sellés-Martínez, J., 1996. Concretion morphology, classification and genesis. *Earth Sci. Rev.* 41, 177–210. [http://dx.doi.org/10.1016/S0012-8252\(96\)00022-0](http://dx.doi.org/10.1016/S0012-8252(96)00022-0).
- Simões, M.G., Rohn, R., 1996. On the significance of a phosphatic concentration of the Serra Alta Formation (Passa Dois Group, Late Permian), Paraná Basin, Brazil. In: *Anais do XXXIX Congresso Brasileiro de Geologia*, 2, pp. 295–297.
- Simões, M.G., Marques, A.C., Mello, L.H.C., Anelli, L.E., 1997. Phylogenetic analysis of the genera of the extinct family Megadesmidae (Pelecypoda, Anomalodesmata), with remarks on its paleoecology and taxonomy. *J. Comp. Biol.* 2, 75–90.
- Simões, M.G., Rocha-Campos, A.C., Anelli, L.E., 1998. Paleoecology and evolution of Permian bivalve faunas (Paraná Basin) in Brazil. In: Johnston, P.A., Haggart, J.W. (Eds.), *Bivalves - an Eon of Evolution - Paleobiological Studies Honoring Norman D. Newell*. University of Calgary Press, Canada, pp. 443–452.
- Simões, M.G., Mello, L.H., Torello, F.F., Ghilardi, R.P., 2000a. *Tambaquyra* gen.n. (Bivalvia, Anomalodesmata), Formação Serra Alta (Neopermiano), Grupo Passa Dois, Bacia do Paraná, Brasil. *Revista da Universidade de Guarulhos. Série Geociências* 6, 11–19.
- Simões, M.G., Torello, F.F., Mello, L.H., Ghilardi, R.P., 2000b. O conteúdo fossilífero de novos afloramentos do Grupo Passa Dois (Neopermiano), nas porções centro sul e nordeste do Estado de São Paulo: implicações bioestratigráficas e paleoecológicas. *Acta Geol. Leopoldensia* 23, 61–90.
- Sousa, S.H.M., 1985. Fácies sedimentares das Formações Estrada Nova e Corumbataí no Estado de São Paulo. Master Thesis. Instituto de Geociências, Universidade de São Paulo.
- Tang, C.M., 2000. Ugly fossil syndrome. *Palaios* 15, 175–176. [http://dx.doi.org/10.1669/0883-1351\(2000\)015<0175:UFS>2.0.CO;2](http://dx.doi.org/10.1669/0883-1351(2000)015<0175:UFS>2.0.CO;2).
- Taylor, A.M., Goldring, R., 1993. Description and analysis of bioturbation and ichnofabric. *J. Geol. Soc.* 150, 141–148. <http://dx.doi.org/10.1144/gsjgs.150.1.0141>.
- Taylor, J.D., Glover, E.A., 2000. Functional anatomy, chemosymbiosis and evolution of the Lucinidae. In: Harper, E.M., Taylor, J.D., Crame, J.A. (Eds.), *The Evolutionary Biology of the Bivalvia*. Special Publication, 177. Geological Society of London, London, pp. 207–225. <http://dx.doi.org/10.1144/GSL.SP.2000.177.01.12>.
- Taylor, J.D., Glover, E.A., 2005. Cryptic diversity of chemosymbiotic bivalves: a systematic revision of worldwide *Anodontia* (Mollusca: Bivalvia: Lucinidae). *Syst. Biodivers.* 3, 281–338. <http://dx.doi.org/10.1017/S1472200005001672>.
- Taylor, J.D., Glover, E.A., 2010. Chemosymbiotic bivalves. In: Kiel, S. (Ed.), *The Vent and Seep Biota - Aspects from Microbes to Ecosystems*. Topics in Geobiology, 33. Springer, Dordrecht, pp. 107–135. [http://dx.doi.org/10.1007/978-90-481-9572-5\\_5](http://dx.doi.org/10.1007/978-90-481-9572-5_5).
- Taylor, J.D., Glover, E.A., Williams, S.T., 2014. Diversification of chemosymbiotic bivalves: origins and relationships of deeper water Lucinidae. *Biol. J. Linn. Soc.* 111, 401–420. <http://dx.doi.org/10.1111/bj.12208>.
- Tyson, R.V., Pearson, T.H., 1991. Modern and ancient continental shelf anoxia: an overview. In: Tyson, R.V., Pearson, T.H. (Eds.), *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication, London, 58, pp. 1–24. <http://dx.doi.org/10.1144/GSL.SP.1991.058.01.01>.
- Warren, L.V., Assine, M.L., Simões, M.G., Riccomini, C., Anelli, L.E., 2015. A Formação Serra Alta, Permiano, no Centro-Leste do Estado de São Paulo, Bacia do Paraná, Brasil. *Braz. J. Geol.* 45, 127–142. <http://dx.doi.org/10.1590/23174889201500010008>.
- Wesseling, F.P., 2007. Long-lived lake molluscs as island faunas: a bivalve perspective. In: Renema, W. (Ed.), *Biogeography, Time and Place: Distributions, Barriers and Islands*. Springer, Dordrecht, pp. 275–314. [http://dx.doi.org/10.1007/978-1-4020-6374-9\\_9](http://dx.doi.org/10.1007/978-1-4020-6374-9_9).
- Wignall, P.B., 1994. *Black Shales*. Oxford Monographs on Geology and Geophysics. Oxford University Press, New York.