Paleoecology and paleoenvironments of Permian bivalves of the Serra Alta Formation, Brazil: Ordinary suspension feeders or Late Paleozoic Gondwana seep organisms?

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ABSTRACT

This is the first record of a Permian seep deposit and an associated, morphologically bizarre, bivalve-dominated fauna from the Passa Dois Group, Paraná Basin, Brazil. Shales of the outer-shelf facies of the Serra Alta Formation preserve a low-diversity but high-abundant, large-sized bivalve fauna with unusual morphologies inside discoidal carbonate concretions. The bivalves are about ten times larger than tiny bivalves found scattered in laterally equivalent mudstones of the same unit. Intercalated between two concretion-bearing horizons, a cm-thick, sheet-like, disrupted, "brecciated", partially silicified carbonate layer with microbially-induced lamination is recorded. In some areas, the carbonate layer shows vertical structures formed by injections of mud mixed with white limestone clasts and microbial linings. Immediately above this, silicified mudstones preserve small domal structures (= mounds) with a slightly depressed center. Monospecific concentrations of closed articulated shells of *Tambaquyra camargoi* occur at the base of these domes. Carbon-isotope (δ^{13}C) values from the shells, "brecciated" carbonates, and fossil-rich concretions are all depleted (negative values ~ −6.1 to −7.6‰). Combined taphonomic, sedimentological, petrographic, geochemical and paleontological data suggest that the disrupted, "brecciated" carbonate and associated fauna and domes may have formed by an exudation system. Indeed, this interval of the Serra Alta Formation is ~8.7 m above the contact with the underlying, oil-rich Irati Formation. This unit has very high total organic carbon (up to 23%) values and high sulphur contents, supporting the interpretation of the lithological and paleontological features as result of seepage of organic compounds at the seafloor. Where the gases and hydrocarbons escaped, the seabed was colonized by, at least facultatively, chemosymbiotic bivalves. The species above belong to a highly endemic group of pachydomids that were shallow infaunal bivalves (SIB). Hence, they are not related to "classical" bivalves with extant representatives, which are chemosymbionts. This may reflect an extreme adaptive radiation and repopulation of anoxic-dysoxic bottoms of the Paraná Basin by SIB species.

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1. Introduction

Located at the southwestern part of Gondwana (Milani, 1997; Milani and De Wit, 2008; Milani et al., 2007), the Paraná Basin was a vast sedimentation area (1.7 million km^2, Holz et al., 2010), throughout Paleozoic and Mesozoic times. During deposition of the

Gondwana I Supersequence (Milani, 1997) in the Cisuralian and Guadalupian epochs, an epeiric sea of a wide extension developed, covering parts of South America (Brazil, Paraguay and Uruguay), Namibia and South Africa (*e.g.*, Milani and De Wit, 2008). This sea had restricted connections with the Panthalassic Ocean, and widespread anoxic to dysoxic conditions that developed in distal areas (*i.e.*, below storm wave-base). Paralic conditions were occasionally disrupted by high-energy, climatically and tectonically induced events (Bondioli et al., 2015; Warren et al., 2015; Silva, 2016; Simões et al., 2016; Matos et al., 2017). Concomitantly, thick successions of organic-rich black shales were deposited across the craton and are today represented by the preserved records of the oil-rich Irati and Serra formations, Passa Dois Group. Barren shales, carbonates, carbonate concretion-bearing horizons, phosphate-rich layers and clastic dikes typify the latter unit (Warren et al., 2015; Simões et al., 2016), which records the last transgressive event in the basin (Milani et al., 2007; Holz et al., 2010). Hence, during that time, the offshore bottoms of the Paraná epeiric sea were characterized by widespread hypoxia (*i.e.*, dead zones). These conditions are documented by the fossil-poor shales of the Serra Alta Formation (Bondioli et al., 2015; Warren et al., 2015; Simões et al., 2016). However, in a precise stratigraphic interval of the basal part of the Serra Alta Formation, within a restricted geographic region (central region of the State of São Paulo), black shales, ^{13}C-depleted carbonate concretions and disrupted "brecciated" limestones contain abundant, large-sized, highly endemic bivalves: a- *Anhembia froesi* (Mendes, 1949), b- *Tambaquyra camargoi* (Beurlen, 1954a), c- *Maackia contorta* Mendes, 1954; here called the ATM-assemblage (Bondioli et al., 2015; Silva, 2016; Simões et al., 2016). Thus, in this interval the bottoms of the Paraná Basin were teeming with life, contrasting markedly with the background conditions characterized by oxygen-depleted muddy bottoms devoid of macrobenthic invertebrates.

Based on the criteria suggested by Campbell and Bottjer (1995) for recognizing chemosynthetic marine habitats (*e.g.*, cold seeps and mud volcanoes) in the geologic record, the laterally and vertically restricted, fossil-rich shales and mound-bearing limestones of the Serra Alta Formation are interpreted, for the first time, as a Permian seep deposit (see also Silva, 2016). Therefore, we present paleontological, sedimentological, stratigraphic, petrographic and geochemical evidence supporting this interpretation, and discuss its geological, ecological and evolutionary significance.

Cold seeps (Paull et al., 1984) are places where hydrocarbons, such as methane, ethane, propane, and oil are transferred from the lithosphere to the hydrosphere and occasionally to the atmosphere, leaking on the seafloor. Similarly to hydrothermal vents (Lonsdale, 1977; Campbell and Bottjer, 1995; Little, 1997), large vertebrate carcasses (Allison et al., 1991; Dahlgren et al., 2006; Kaim et al., 2008; Danise et al., 2010) and wood-falls (Distel et al., 2002; Kiel and Goedert, 2006), these are often marine oases for microbial and macrofaunal communities, packed with life based on chemosynthesis (Campbell, 2006). As summarized by this author, present-day cold seeps are recorded at water depths varying from a few meters to several kilometers and at various latitudes. The "classical" examples of cold seep habits are recorded along plate boundaries, in back-arc basins, but they are also a product of faulting, diapirism, sediment compaction, organic matter degradation, or undersea leaking of organic-rich pore waters due to landslides (Milkov, 2000; Campbell, 2006).

Extensive literature surveys (see Campbell and Bottjer, 1995; Campbell, 2006) indicate that chemosymbiont-dominated benthic communities were rare during the Permian. Therefore, our example is noteworthy due to its Guadalupian (mid-Permian) age and geotectonic context (*i.e.*, an isolated intraplate basin). In this context, the aims of this contribution are (a) to describe and document the Permian seep deposits and associated structures (disrupted "brecciated" carbonates, muddy mounds and fossil-rich carbonate concretions) of the Serra Alta Formation; (b) to show that members of the ATM-bivalve assemblage were, at least facultatively, chemosymbiotic; (c) to determine the nature and dynamics of the paleoenvironment in which this assemblage thrived, and (d) to discuss the evolutionary implications of our data.

2. Geology of the study area

Massive, dark grey mudstones and black shales, also containing decimeter-thick layers of fine-to medium-grained sandstones and rare layers of limestones, carbonate concretions and clastic dikes characterize the 50−90-m-thick Permian Serra Alta Formation (Guadalupian, Wordian/Capitanian) of the Passa Dois Group, Paraná Basin, Brazil (Fig. 1A) (Sanford and Lange, 1960; Schneider et al., 1974; IPT, 1981; CPRM, 2006; Meglhioratti, 2006; Holz et al., 2010; Teixeira, 2014; Bondioli et al., 2015; Warren et al., 2015; Simões et al., 2016). The unit rests discordantly on the oil-rich Irati Formation and is capped by the Teresina Formation of shallow-water origin (Warren et al., 2015) (Fig. 2). The Serra Alta Formation is interpreted to have been, for the most part, deposited in a low saline epeiric sea (Runnegar and Newell, 1971; Teixeira, 2014), below storm wave-base, and under predominantly anoxic to dysoxic conditions, during the last transgressive event in the geological history of the Paraná Basin (Milani et al., 2007). Therefore, settling of fine-grained siliciclastics from suspension is the dominant depositional sedimentary process in the distal, offshore settings recorded in the Serra Alta Formation (Holz et al., 2010; Bondioli et al., 2015; Warren et al., 2015).

General aspects of the geology of the sedimentary succession of the Serra Alta Formation in the central-eastern part of the State of São Paulo have been discussed in a series of papers and monographs (Sousa, 1985; Sousa et al., 1991; Maranhão and Petri, 1996; Simões et al., 2000a, b; Teixeira, 2014; Bondioli et al., 2015; Warren et al., 2015; Silva, 2016; Simões et al., 2016), and for this reason, will be only briefly described below.

3. Material and methods

The studied interval of the Serra Alta Formation, cropping out near Porangaba City, State of São Paulo, was chosen based on the occurrence of a several-cm-thick bed of tabular, disrupted, "brecciated" marly carbonate that is immediately succeeded by originally(?) micritic to marly domal structures with tens of autochthonous to parautochthonous (*sensu* Kidwell et al., 1986), large-sized bivalve shells at their base (Figs. 1 and 2). This carbonate unit, now partially silicified, is intercalated between two carbonate concretion-bearing horizons, also rich in bivalve shells (Figs. 2 and 3) (Bondioli et al., 2015; Silva, 2016; Simões et al., 2016). These are all recorded in an 11-m-thick interval of dark grey shales, locally situated ~8.7 m above the oil-rich Irati Formation (Figs. 2 and 4). In this mudstone-dominated interval, bivalves belonging to the *Barbosaia angulata-Anhembia froesi* Association Biozone (sensu Rohn, 1994) are recorded (Bondioli et al., 2015), indicating that it correlates with the basal part of the Serra Alta Formation (Holz et al., 2010; Warren et al., 2015).

During the field work, the investigated stratigraphic interval of the Serra Alta Formation was analyzed in detail (sub-cm scale), and the sedimentary facies was recorded for an 11-m-thick succession (Figs. 2 and 3). In addition, several (cm-to m-scale) slabs of disrupted, "brecciated" carbonates as well as dozens of discoidal carbonate concretions (Bondioli et al., 2015) and 116 bivalve shells were collected. Some rock slabs were sectioned and polished with silicon carbide powder of various grain sizes and digitally imaged.
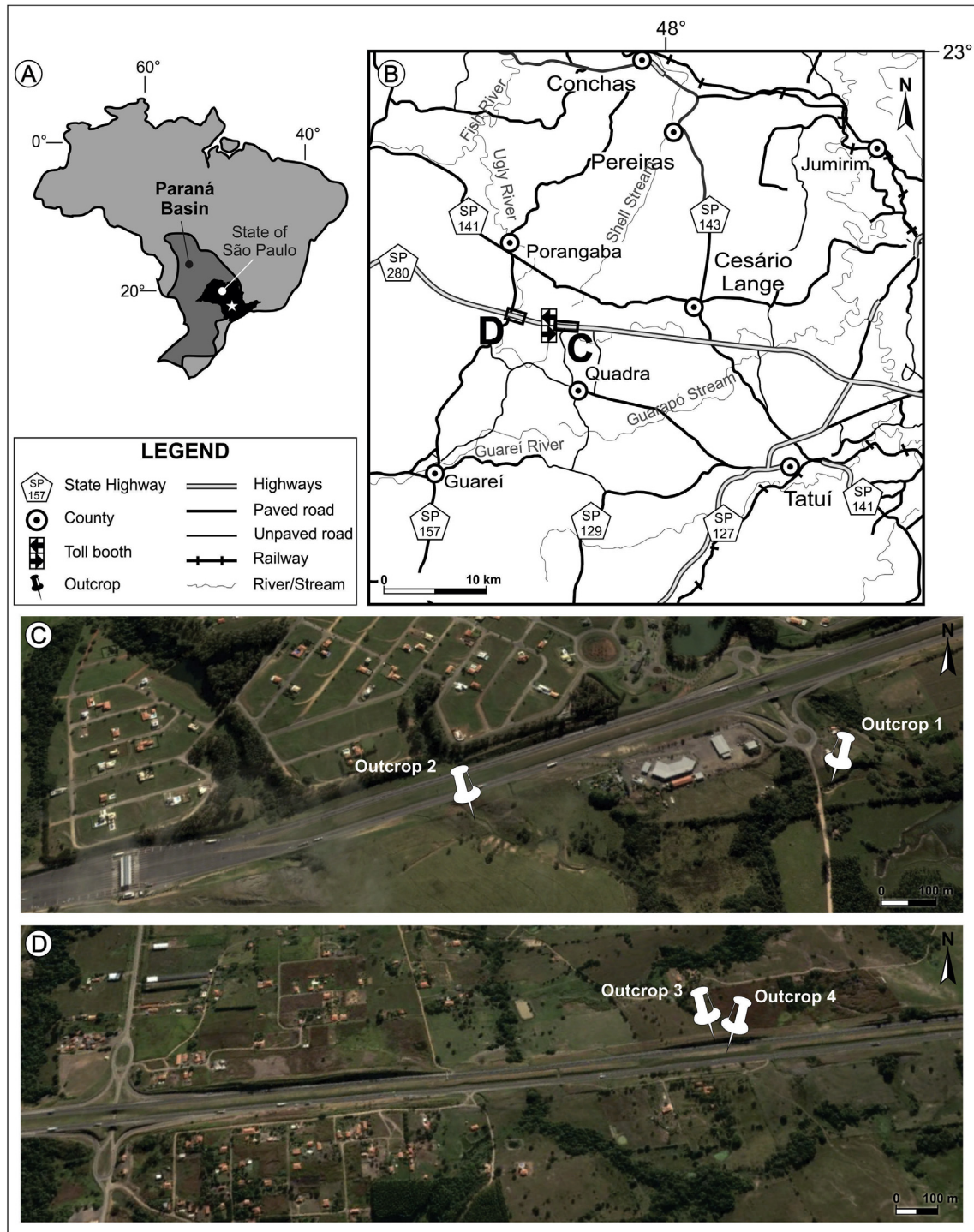
Fig. 1. Location map of the study area, Porangaba County, State of São Paulo. A- Index map showing the Paraná Basin. B- Map presenting the location of the main investigated outcrops of the Serra Alta Formation. C and D- Google Earth images (Date: 15/03/2016; Satellite sensor: Landsat) showing the precise location of the exposures of the Irati and Serra Alta formations at the river margins (outcrop 1) and road cuts (outcrops 2–4) Scales: 100 m.

The disrupted, "brecciated" carbonate was investigated at the FG Paläoumwelt, GeoZentrum Nordbayern der Friedrich-August-Universität Erlangen-Nürnberg, Germany, using petrographic microscope and Energy-dispersive X-ray spectroscopy (EDS). The element mapping and selected point analysis of elemental compositions have been carried out with an EDS (Oxford Instruments X-Max) attached to a stereo electron microscope (Tescan Vega 2 xmu). All slabs and fossils are housed in the scientific collection of the Department of Zoology, Institute of Biosciences, UNESP, Botucatu campus, under the DZP-code.

Geochemical analyses (δ^{13}C and δ^{18}O analyses) were carried out at Beta Analytic radiocarbon dating laboratory, Miami, FL, USA. The precise positions where samples were taken for analyses are indicated in Figs. 5 and 6. In the laboratory, the pre-treatment included washing the material with deionized water to remove associated organic sediments and debris, if present. The material (2 mg) was
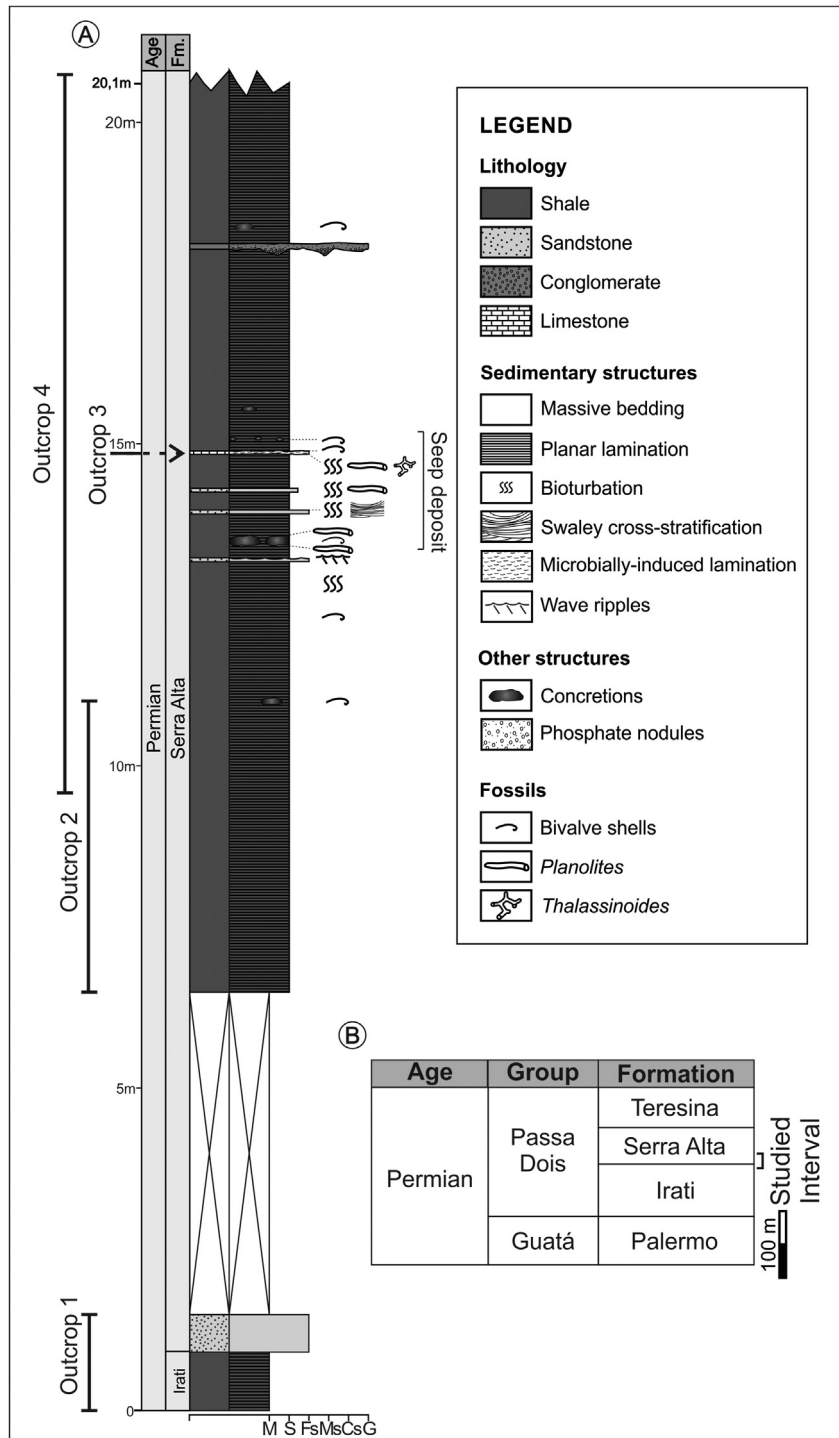
Fig. 2. Sedimentary succession of the Irati and Serra Alta formations. A- Composite section of both units, showing the stratigraphic position of each outcrop (1–4). B- Simplified chart of the Permian succession of the Paraná Basin, in which the examined interval of the Serra Alta Formation is indicated.

then crushed/dispersed and repeatedly subjected to HCl etching baths to eliminate secondary carbonate components. In the case of thick shells, as is the case of *Anhembia froesi*, the surfaces were physically abraded prior to etching. According to Beta Analytic laboratory, acid exposure times, concentrations, and number of repetitions are applied according to the uniqueness of each sample (see http://www.radiocarbon.com). Determination of stable isotope ratios ($\delta^{13}C$ and $\delta^{18}O$) were made by Isotope Ratio Mass Spectrometry (IRMS) with ranges of −100 per mil to 100 per mil,

and detection limits of 0.05 mV mass 13 output (see http://www.radiocarbon.com).

3.1. Localities and stratigraphy

Rocks of the Permian Passa Dois Group are relatively well exposed in the central-eastern part of the State of São Paulo, particularly along road cuts of the SP-280 highway (kms 160–161), and at the margins of rivers and creeks (*i.e.*, Aleluia creek) (Figs. 1, 2,
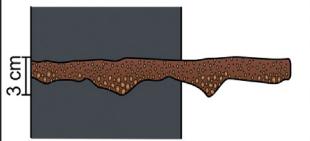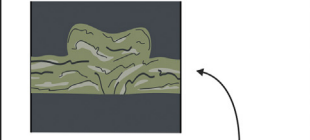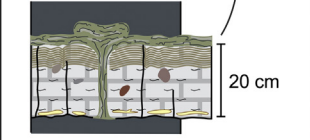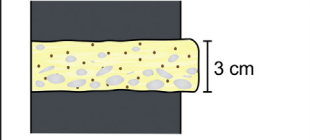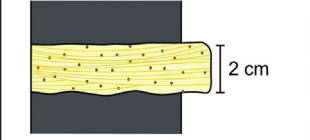
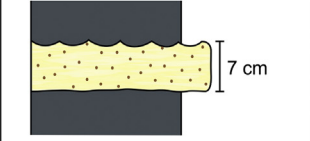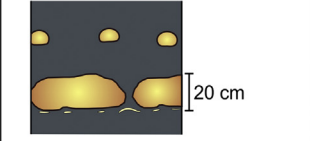| LITHOLOGY M S Fs Ms Cs G	LITHOTYPE	BODY FOSSILS	TRACE FOSSILS	TAPHONOMY	INTERPRETATION
	Conglomerate with rounded, fine sandy to pebble-sized phosphatized particles and intraclasts.	Mainly fish remains (e.g., teeth, scale), plus coprolites and enterospires.	————	Chaotically oriented, densely packed, abraded fish remains.	Abrupt burial of organic-rich sediments, followed by periods of minimal sedimentation and erosion. After the formation of the phosphate-rich sediments, subsequent reworking by high energy flows generate layers of coarse-grained, phosphate-rich particles.
	Highly bioturbated mudstones with domal structures.	Gigantic bivalves: *T. camargoi*.	High levels of bioturbation.	Densely packed pavements of in situ shells of *T. camargoi*.	Mound structure generated by methane exudations, colonized by large populations of endemic large-bodied bivalves.
	Tabular, brecciated limestone with microbial lamination at the top.	————	*Thalassinoides*-like traces and *Planolites* at the base.	————	Carbonate precipitation mediated by chemosynthetic bacterial activity (anaerobic oxidation of methane/sulfate-reduction). Disruption ("brecciation") of the still plastic carbonate mud presumably linked to methane-gas outbreaks.
	Highly bioturbated and silicified silty/muddy sandstone.	————	Highly bioturbated by *Planolites*, which is larger at the base.	————	Event-influenced deposition of fine-grained sandstones, later colonized by burrowing invertebrates, under improved bottom oxic conditions.
	Fine-grained sandstone with gradational top and swaley cross-stratification.	————	*Planolites* at the top of the bed.	————	Event-influenced deposition of fine-grained sandstones, followed by the opportunistic colonization of the bottoms, during brief oxic-dysoxic conditions.
	Current-rippled sandstone.	————	Low levels of bioturbation.	————	Current-generated influx of sediments from more proximal areas to locally distal settings.
	Shales.	————	————	————	Background setting of mud and silt in the distal settings, dysoxic to anoxic bottom conditions.
	Carbonate concretions.	Gigantic bivalves; *T. camargoi*; *A. froesi*; *M. contorta*.	Isolated, horizontal burrows at the top of concretions.	Closed articulated and disarticulated shells inside concretions.	Low-energy, oxygen-depleted bottom colonized by chemosymbiotic (?) bivalves. Concretions formed by a combination of background and event sedimentation, followed by periods of prolonged low sedimentation rates.

Fig. 3. Summary chart showing the lithotypes, and associated sedimentary, paleontological, and taphonomic features of the mound interval of the Serra Alta Formation.

4 and 7). In this area, the Permian succession is mainly represented by three lithostratigraphic units, including the oil-rich Irati, Serra Alta and Teresina formations (Fig. 2). Here we focus on the deposits of the basal Serra Alta Formation, including the contact with the underlying Irati Formation. All studied fossil-rich carbonate concretions, domal structures and associated disrupted, "brecciated" limestones were documented and collected from two outcrops (3 and 4) (see Figs. 1, 2 and 7). These have been described by Sousa
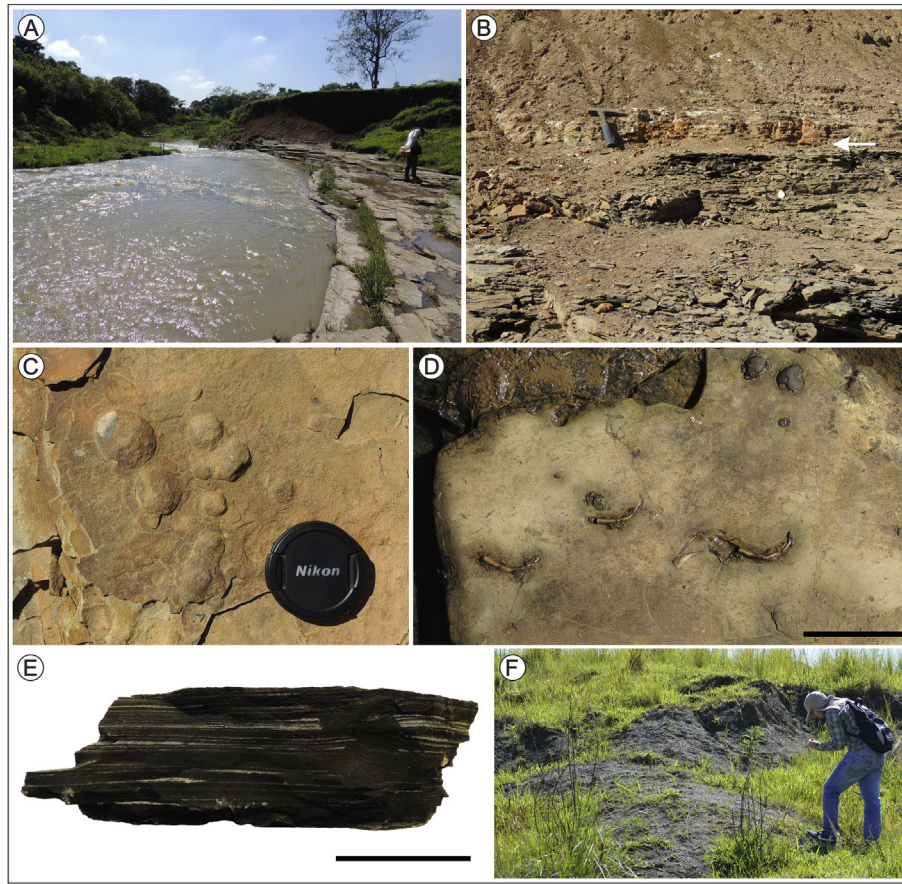
Fig. 4. Exposures of the Irati and Serra Alta formations along the Aleluia creek, Porangaba County, State of São Paulo. A- Black shales with petroleum odor, of the underlying Irati Formation. B- Fine-grained sandstones of the basal Serra Alta Formation. C- Silex chert nodules in shale. D- Small mesosaur ribs in a limestone bed immediately below the black shales in E. E- Close-up of the well-laminated, pyro-bituminous dark shales of the Irati Formation. F- Mudstones of the basal part of the Serra Alta Formation, which locally overlie the black shales of the oil-bearing Irati Formation. Scales in D and E: 5 cm.

(1985), Sousa et al. (1991), Simões et al. (2000a), Teixeira (2014), Bondioli et al. (2015), Warren et al. (2015) and Simões et al. (2016), among others. Attention was given to a ~2-m-thick interval of fossil-poor, dark grey shales in the lower part of the Serra Alta Formation, where carbonate concretions are abundant (Bondioli et al., 2015; Warren et al., 2015; Silva, 2016; Simões et al., 2016). Since the concretion-bearing interval (marker bed) is well exposed in the outcrops studied, the precise stratigraphic position of each one can be determined.

Fig. 2 summarizes the compound stratigraphic section of the Serra Alta Formation along road cuts of the SP-280 highway, were a ~19.5-m-thick succession of dark greenish-grey shales is exposed. The studied concretion-bearing interval and the associated disrupted, "brecciated" limestones and other geological structures (domes) is ~12 m above the contact with the underlying Irati Formation. Clastic dikes are also common in this interval of the Serra Alta Formation (Fig. 7) (Sousa, 1985; Silva, 2016). The dikes are filled with monocrystalline very-fine to fine and poorly-sorted quartz grains embedded in a carbonate cement (Sousa, 1985; Alessandretti, 2017). Close to the study area, dikes of a coeval stratigraphic interval are also filled with carbonate veins (Turra, 2009, p. 59).

The studied sedimentary succession starts with a 3.5-m-thick package of non-bioturbated, dark greenish-grey siltstones and subordinate laminated mudstones. Small (mm) dispersed bivalves and isolated, discoidal carbonate concretions are found in this part of the section (Bondioli et al., 2015; Silva, 2016; Simões et al., 2016).

Above this level, a 7-cm-thick layer of fine-grained sandstone with current ripples occurs, which are succeeded by a 60-cm-thick bed of dark grey laminated siltstone with a noticeable horizon with calcite concretions. These concretions were studied in detail by Bondioli et al. (2015), Silva (2016), and Simões et al. (2016) and can be laterally traced for almost a kilometer (Fig. 1). Closed articulated bivalve shells are abundant within the concretions, and are referred to *Anhembia* sp., *T. camargoi,* and *M. contorta*. Above this level, the siltstone is overlain by dm-to cm-thick, fine-grained sandstone beds, showing a sharp and erosional base, normal grading and small-scale hummocky cross-stratification. This sandstone is succeeded by 35-cm-thick, laminated, dark grey siltstones with a 3-cm-thick, highly bioturbated and silicified silty/muddy sandstone layer that is followed by a 47-cm-thick package of dark grey, laminated siltstone. Above this a ~20-cm-thick tabular limestone occurs. This limestone bed, which is described in detail below, is succeeded by a 5.1-m-thick package of siltstone including a well-defined, fossil-rich calcareous concretion horizon similar to that noted at the base of the section. To the top of the section, a 0.7- to 3-cm-thick layer of fine sand-to pebble-sized, rounded phosphatized particles occurs. This layer can be laterally traced for over 1 km. The basal contact of this layer is sharp and erosional with scour and fill structures, and its upper contact is also sharp (Simões et al., 2016) (Figs. 2 and 3). Finally, a monotonous succession of laminated, dark-grey (or reddish when weathered) siltstones forms the uppermost part of the section (Figs. 2 and 3).

The above described succession is representative of an offshore
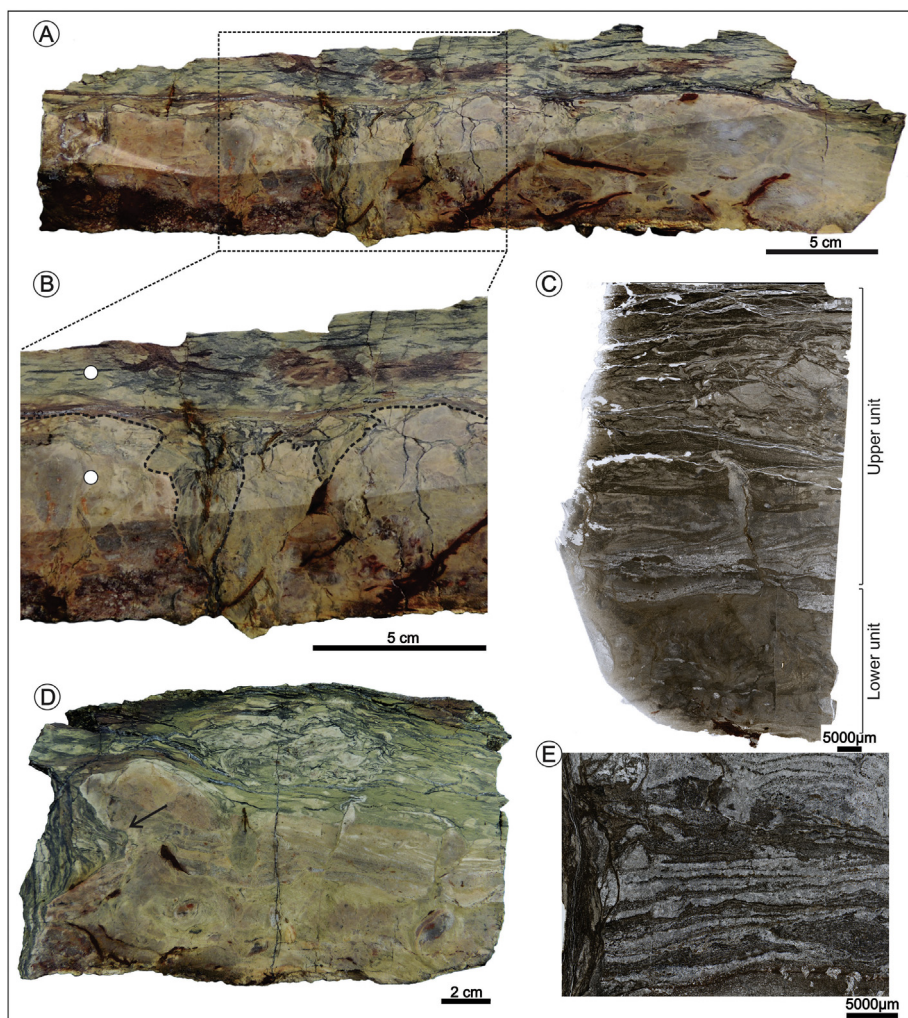
Fig. 5. "Brecciated" carbonate. A- Cross-section of the disrupted, "brecciated" carbonate where the injection structures are visible. B- Detail of an "injection" structure. The circles indicate the position of samples for the geochemical analyses. C-Thin section showing the two units of the "brecciated" carbonate. D- Polished slab showing the upper unit encrusting a vertical fissure (arrowed), thus supporting its microbial origin. E- Upper layer of the "brecciated" limestone with microbial lamination interrupted by thin, sub-vertical fissures. The left margin of the slab is part of a vertical fissure, the wall of which is lined with microbial mudstone.

environment where settling of fine-grained sediment particles was the dominant depositional process (Sousa, 1985; Warren et al., 2015; Simões et al., 2016). In this context, background conditions documented by the shales were dominated by low rates of sedimentation under anoxic to dysoxic conditions. Intercalated hummocky cross-stratified sandstone layers indicate the disturbance of offshore bottoms by episodic high-energy processes. The presence of organic-rich, anoxic bottoms (including scattered pyrite) is indicated by layers of phosphate nodules (Bondioli et al., 2015; Simões et al., 2016). In conclusion, oxygen depletion is the most widespread environmental condition inferred for the deposition of the studied succession (Fig. 2).

4. The mound interval and the associated ATM-bivalve fauna

4.1. Host mudrocks

Fossil-rich carbonate concretions preserving members of the ATM-bivalve assemblage occur in an 11-m-thick interval of barren shales with scattered pyrite crystals and phosphate nodules. This particular stratigraphic interval of the Serra Alta Formation is ~8.7 m above the Irati Formation (Figs. 2 and 4).

At the outcrop scale, the interval is profusely cut by sub-vertical to vertical fractures and clastic dikes (see Sousa, 1985; Sousa et al., 1991; Teixeira, 2014), oriented in both NNW-NW and NNE-NE directions (Teixeira, 2014). In some cases, both the fractures and dikes just terminate at the base of carbonate concretions (= lithologic contact) (Fig. 7). The dikes are irregular, metric scale (up to 3-m high) vertical bodies commonly filled with fine-grained sandstone, discordantly cutting the bedding of the mudstones. Locally, a well-marked bed of fine-grained sandstone occurs at the contact between the Irati and Serra Alta Formation (Teixeira, 2014), which may be the source for the sandstones in the dikes. Above the basal shale interval and high in the local sedimentary succession of the Serra Alta Formation, these structures (particularly the fractures) are less common or are absent (see also Warren et al., 2015).

Finally, the TOC values of the shales of the Serra Alta Formation range between 0.1 and 0.5% (Teixeira, 2014).

4.2. Carbonate concretions

As mentioned above, carbonate concretions are densely developed in the outcrop (Figs. 2 and 7), particularly in a well-defined stratigraphic interval, which is located ~12 m above the top of the
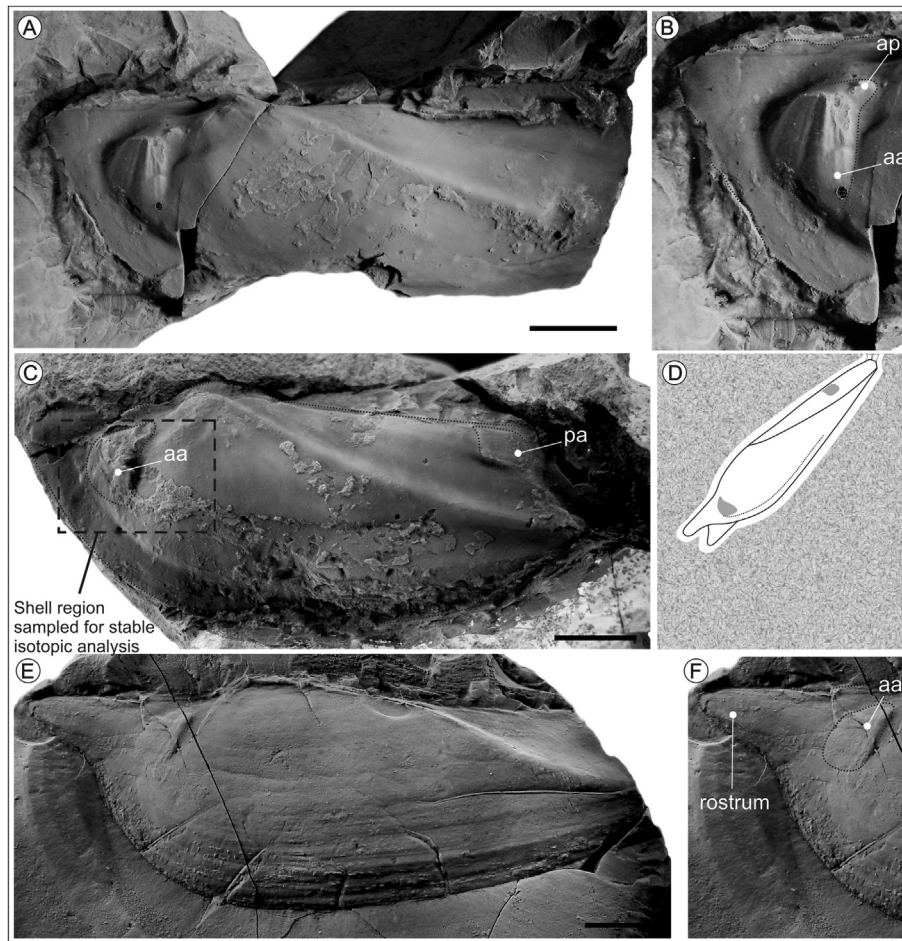
Fig. 6. *Anhembia froesi* A- Lateral view, left valve, showing the large and deeply impressed anterior adductor and retractor muscle scars (DZP-2889). B- Same specimen, detail of the anterior muscle scars. C- Internal mold of the left valve with deeply impressed adductor muscle scars (DZP-2890). D- Inferred mode of life of *A. froesi*. E-F. *Anhembia* sp. E- Internal mold of the left valve, note the well-developed anterior prong (= rostrum). F- Same specimen showing the adductor muscle scar and rostrum. apr-anterior pedal retractor muscle scar; aa-anterior adductor muscle scar, and pa-posterior adductor muscle scar. Scale bar: 1 cm.

Irati Formation (Bondioli et al., 2015; Warren et al., 2015). These are of two types, namely discoidal or sheet-like, and are mainly restricted to three concretion-bearing horizons that can be traced for up to a kilometer (Bondioli et al., 2015). The lowermost concretion-bearing horizon is located 4 m above the base of outcrop 3 (Fig. 2). The carbonate concretions range in size from ~4 cm to almost 100 cm (maximum length) and are lenticular in cross-section (Bondioli et al., 2015). As noted by these authors, the large ones (>40 cm of maximum length) may generate irregular, laterally linked concretions (= 'Laibstein-Bank' *sensu* Seilacher, 2001, p. 45). Smaller (4−22.5 cm of maximum length), spheroidal carbonate concretions are also recorded ~1.5 m above the first interval. In ascending order, these represent the third concretion-bearing horizon.

A detailed geochemical study of these concretions, now conducted by one of us (L. Alessandretti), indicates that the concretions are cemented by micrite with low contents of Na, Fe and Mg, rare very-fine grained monocrystalline quartz grains, pyrite framboids and undifferentiated clay minerals. The carbonate concretions yielded $\delta^{18}O$ values of −7.64 to −6.39‰ (PDB) and $\delta^{13}C$ values of −7.79 to −5.49‰ (PDB).

Intercalated between these concretion-bearing horizons, there is a ~15- to 20-cm-thick, sheet-like disrupted, "brecciated" carbonate with microbially-induced lamination (Figs. 2, 5 and 8). From the top of the carbonate, small domal structures rise (see below)

(Figs. 8 and 9).

4.3. The "breccia" level

The "brecciated" layer (Figs. 5 and 10) consists of two units: a lower, 7- to 12-cm-thick layer and an upper 6- to 8-cm-thick layer. The boundary between the two layers is a discontinuity surface. Apparently, both layers originally were thinly bedded to irregularly laminated, but were subsequently strongly distorted, the lower unit much more so than the upper one (Fig. 5). The matrix is a grey-beige peloidal bio-wackestone, which is now largely silicified. The round to elongated peloids occasionally form a clotted fabric and may be of microbial origin. In the lower unit, the primary lamination has been disrupted by vertical to subvertical structures (Figs. 5 and 10) while the sediment was probably still plastic, resulting in a locally chaotic bedding and in the formation of clasts. Near the top of the lower unit the clasts are more clearly defined, rounded to angular and may indicate that there the lime mud was lithified. The vertical to slightly oblique structures strongly vary in diameter ranging from less than 1 mm to centimeters, are highly irregular, and may end abruptly. Under the binocular microscope, the walls of the fractures locally display a clotted fabric. The fill of the fractures does not vary much from the host sediment, but its orientation is vertical rather than horizontal and corroborates that is has been injected from below. Within the sediment, "unconformities" are
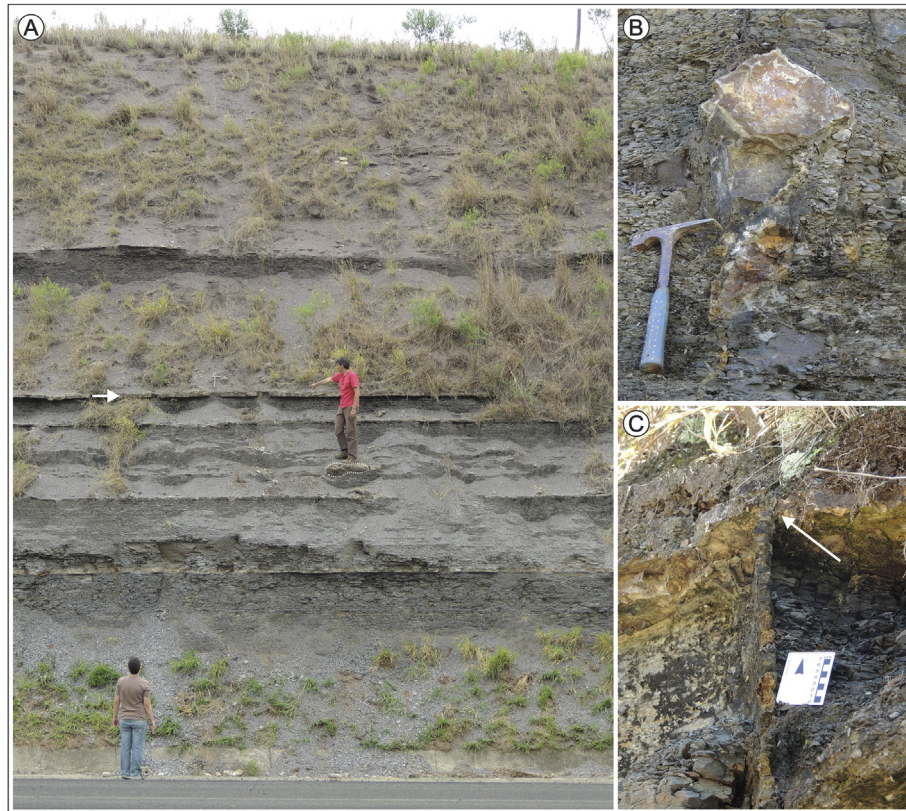
Fig. 7. Carbonate beds and concretions of the Serra Alta Formation. A- Mudstones in the basal part of the Serra Alta Formation showing the main concretion-bearing horizons, and the disrupted, "brecciated" carbonate bed (arrowed). B- Clastic dike ending just at the base of a carbonate concretion. C- Clastic dike just ending at the base of the disrupted, "brecciated" carbonate bed (arrowed).

common as are features resembling centimeter-scale scours and erosional structures but that are more likely the result of internal sediment dislocation. The lamination is caused by irregular, somewhat diffuse, sub-millimetric dark-grey bands that turn brownish in thin-sections, which points to the presence of organic material. Oblique fissures filled with brown ferruginous material are common.

The laminae are more conspicuous in the upper unit where they reach a thickness of up to 3 mm, whereas sub-vertical structures are usually less prominent. Clotted fabric is occasionally present within the laminae. The laminae enclose irregular lenticles ornodules of carbonate mudstone, which appear injected sub-horizontally between some laminae. At some large fissures the lamination extends downward across the lower unit, covering the sub-vertical fissure wall. Long, horizontal to slightly oblique layers of blocky calcite, up to 1 mm-thick, that display remnants of prismatic structures most likely represent shells of the bivalve *T. camargoi* (see below). Short, needle-shaped structures that occur scattered within the sediment probably are most likely calcite prisms derived from the shell of this bivalve. In addition, thin, elongated, curved bioclasts are fragments of small bivalve shells. EDS data of a small 10 × 10 mm large block from the lower 7 cm reveal that much of the carbonate is now silicified. The abundance of Al and Si suggest the presence of clay minerals in the matrix (Fig. 11). The irregular lamination combined with the brownish color of the laminae in thin-sections and the occasional clotted fabric strongly suggest that the "breccia" layer represents a microbial limestone that suffered fracturing and distortion by fluids from below.

4.4. A pavement of small domal structures

Small, dome-like structures are well preserved and exposed on an eroded and weathered surface just at the road lane divide, in outcrop 4 (Figs. 1 and 9). They occur immediately above the sheet-like, disrupted, "brecciated" carbonate layer. The domes are intercalated between the two main concretion-bearing horizons of the Serra Alta Formation (Fig. 2). These structures are known only at this outcrop. Hence, the domes are restricted to the interval were bivalve species of the ATM-assemblage are abundant. In plan-view, at least 34 small, muddy domes were counted (~10 domes/m^2; Fig. 9). Basal diameter (maximum length) of each dome ranges from ~4 to 27 cm, and their height is commonly 4 cm. However, the tallest structure (DZP-Lit/718) has a basal diameter of 31 cm and a height of 9 cm (Fig. 8) The center of the domes is slightly depressed (Figs. 8 and 9). As these structures crop out on a deeply weathered surface these measurements must be viewed as minimum values. The domes may occur isolated or are concentrated forming laterally-linked cones (satellite cones) of slightly similar sizes (Fig. 9). In plan-view, the distance between the isolated domes varies from 27 to 55 cm. At the base of some domes (*e.g.*, DZP-Lit/718), dense, monospecific concentrations of closed articulated bivalve shells are preserved (Fig. 8).

4.5. Stable isotopes

The samples from (a) the disrupted, "brecciated" carbonate layer, (b) shells of *A. froesi* and (c) the carbonate mudstones yielded $\delta^{13}C$ values ranging from −7.6 to −6.1‰ and $\delta^{18}O$ values ranging from −1.6 to −5.7‰ (Table 1).
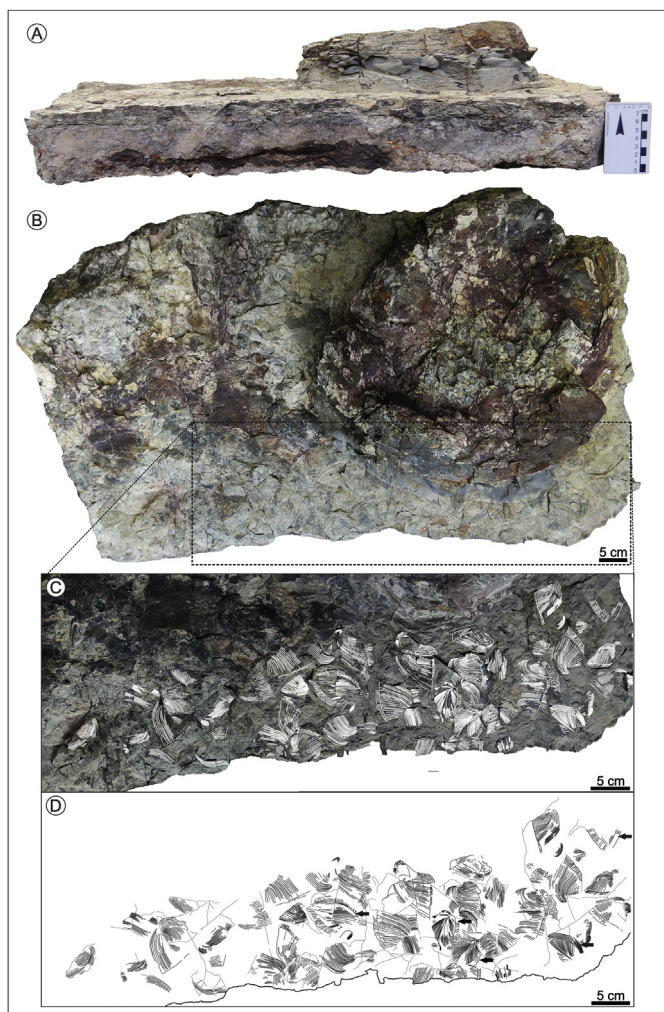
Fig. 8. General taphonomic, paleontological, and sedimentological features of the disrupted, "brecciated" carbonate bed. A- Cross-section of an 86-cm-long slab showing a well preserved low relief mound at right. B- Plan-view of the same slab. C- Mono-specific assemblage of *T. camargoi* at the base of the mound. D- Drawings of the shells in C.

4.6. Unusual permian endemic bivalves

Three bivalve species (Figs. 6, 12 and 13) are mainly associated with the carbonate concretions (Bondioli et al., 2015) and the disrupted, "brecciated" carbonate layer. They are referred to *Anhembia froesi* (Mendes, 1949; Mezzalira et al., 1990), *Tambaquyra camargoi* (Beurlen, 1954a; Simões et al., 2000b), and *Maackia contorta* (Mendes, 1954). Except for *T. camargoi*, these species are only known from the basal part of the Serra Alta Formation. These species were mainly described and their taxonomy reviewed by Beurlen (1954a), Mendes (1954), Runnegar and Newell (1971), Mezzalira et al. (1990), Simões et al. (1997, 2000b) and Mello (1999). Among them, *T. camargoi* is the largest species. Its valves are strongly inflated (maximum convexity in the dorsal/umbonal area), and it lacks siphonal/pedal gapes. The hinge is edentulous, and the anterior muscle scars are large and deeply impressed (Fig. 12). As in the case of other pachydomiid shells (Runnegar, 1967, 1974), the internal molds show fine radial striations. In contrast, shells of *M. contorta* are strongly inequivalved, trapezoidal and posteriorly elongated. The left valve is strongly convex showing two umbonal carinae. The anterior margin is rounded and the posterior

extremity is entirely occupied by the respiratory margin. The anterior adductor scar is deeply impressed, elongated and situated at the anterior extremity of the shell (Fig. 13). The right valve is intensely twisted. Finally, *A. froesi* has an extraordinary shape with an elongated shell that displays a well-developed anterior prong (= rostrum) (Fig. 6). The shell is edentulous having large, deeply impressed adductor muscle scars, and a dotted pallial line (Fig. 6).

4.7. Mode of bivalve occurrences

In the studied stratigraphic interval of the Serra Alta Formation, shells of the above mentioned bivalve species are commonly found in the carbonate concretions as well as in laterally equivalent barren mudstones (Bondioli et al., 2015). Their mode of occurrence within carbonate concretions was studied in detail by these authors, who showed that the shells are parautochthonous to autochthonous. Indeed, shells of these species are usually preserved as closed articulated valves in the carbonate concretions or laterally equivalent shales (Bondioli et al., 2015). One of the three species (= *T. camargoi*) forms densely packed shell concentrations at the base of the muddy domes (DZP- Lit/718). Some shells are preserved in life position (Fig. 12). However, since they are preserved as densely packed, compressed molds, it is difficult to count the exact number of specimens preserved *in situ*. Determination of the shell measurements is also precluded, but most of them have shells ranging from 26 to 76 mm in length (Fig. 8).

5. Discussion

The analyzed stratigraphic interval of the Serra Alta Formation (Fig. 2) is unique within this 60-m-thick unit due to the profuse occurrence of large-sized bivalves (*Anhembia*, *Tambaquyra*, *Maackia*). Hence, this occurrence deserves detailed investigation and proper explanation. The shells of *A. froesi* and *M. contorta* have unusual morphologies, characterized by a well-defined anterior rostrum in the first species, and a pronounced torsion of the commissure plane along the hinge axis (*sensu* McGhee, 1978; Savazzi, 1981) in the latter one (Figs. 6 and 13). The shells of *T. camargoi* and *A. froesi* are larger than any other bivalve shell in the Late Paleozoic succession of the Paraná Basin, where the benthic assemblages are dominated by Anomalodesmata and Veneroidea (see also Ghilardi, 1999; and Fig. 14). Their sizes are in extreme contrast with those of almost all coeval shells of the Passa Dois Group, which rarely exceed 48.4 mm and 39.3 mm of length and height, respectively (Fig. 14). Thus, *T. camargoi* is ten times larger than the co-occurring bivalves found in the mudstones of the Serra Alta Formation at the same stratigraphic interval. In contrast, the shells of *T. camargoi* are rare and smaller (i.e., ~40 mm and ~35 mm of maximum length and height, respectively) in fossil assemblages recorded in sandstones generated in proximal, oxygenated facies of the overlying Teresina Formation (Simões and Kowalewski, 1998). In the offshore mudstone facies of the Serra Alta Formation, shells of *Anhembia*, *Tambaquyra* and *Maackia* are usually preserved as articulated valves, indicating that they were autochthonous to parautochthonous (*sensu* Kidwell et al., 1986). This indicates that these bivalves clearly inhabited the exaerobic to dysoxic, muddy substrates of the Serra Alta Formation (Fig. 15). In other words, optimal environmental conditions may have existed in the interval of their profuse occurrence. Therefore, the question is: what were these conditions?

The large shell sizes in *Tambaquyra* and *Anhembia* may simply result from better nutritional conditions for the development of these infaunal suspension feeders. However, there is no micropaleontologic evidence supporting the idea of an improved food supply at that time. Yet, their shells are not only large, but also
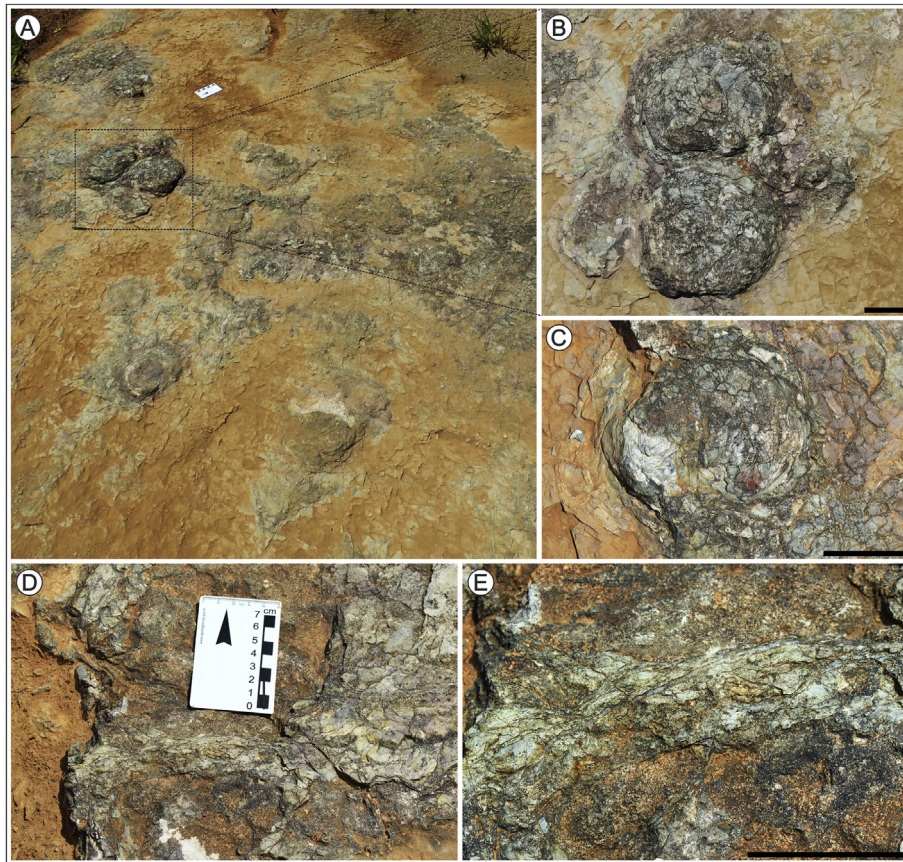
Fig. 9. Plan-views of the small domes and associated structures at the top of the disrupted, "brecciated" carbonate bed, Serra Alta Formation. A- Bedding plane showing various small domes. B- Detail of two low-relief domes in A. C- Isolated dome. D- Bioclastic wackestone intruded (injection structure) in the disrupted, "brecciated" carbonate bed (see also Fig. 5). E- Detail of D. Scale bar in B, C and E: 5 cm.

obese (*sensu* Stanley, 1970, 1972). This anatomical condition is un-expected for suspension feeding bivalves that lived in muddy, organic-rich soupy substrates. In this type of bottom, the mainte-nance of negative buoyancy is an issue faced by all bivalves, particularly suspension feeders (Stanley, 1970, p. 83). The com-monest strategy adopted by most of bivalves inhabiting soupy substrates is to remain small (Stanley, 1970, p. 83). This condition is also noted in the rare, co-occurring shells, such as *Rioclaroa lefevrei*. The large size attained by *Tambaquyra* and *Anhembia* requires a high energy-consuming metabolism, in contrast to the tiny forms that co-occur in the same sedimentary facies. Judging from the sedimentary facies in which these bivalves occur their large sizes may imply an alternative energy source and their unusual morphology could be a response to this.

5.1. Anhembia, Tambaquyra, and Maackia: suspected permian chemosymbiotic bivalves

The taphonomic and sedimentologic evidence provided above indicate that *Anhembia*, *Tambaquyra*, and *Maackia* flourished in nearly anoxic-dysoxic, soupy substrates (see also Simões et al., 1998, 2000a, b, 2016; Bondioli et al., 2015). Based on sedimentary facies association and functional anatomy, Ghilardi (1999) sug-gested that *Anhembia* and *Tambaquyra* were good Permian candi-dates to be chemosymbiotic bivalves. Indeed, the shell of *M. contorta* resembles that of the extant *Trisidos*, the Neogene *Barbatia mytiloides*, the Cretaceous *Pseudopteria*, and the mid-Triassic *Hoernesia*. According to Savazzi (1984, p. 307), the twisted

commissure of these bivalves elevated the posterior region of the valves above the sediment, aligning it roughly horizontally. As *M. contorta*, extant and fossil twisted bivalves are found in fine-grained, H_2S-rich deposits generated under quiet-water condi-tions, and have been interpreted by Seilacher (1990, p. 302) as chemosymbionts. The twisted commissure brings the inhalant or-gans closer to the substrate, allowing them to benefit from the H_2S source available in the sediment (Seilacher, 1990). In contrast, the shell of *A. froesi* with a trunk-like anterior extension (*i.e.*, rostrum) closely resembles that of the unionid *Arconaia lanceolata* (Runnegar and Newell, 1971, p. 146), a living chemosymbiotic bivalve (Savazzi and Yao, 1992). The shell is also similar to that of the Pleistocene *Pleiodon adami* found in anoxic African lakes in which he rostrum may have acted as a H_2S well (Seilacher, 1990). Hence, the unusual shell anatomy of *Anhembia* and *Maackia* may have developed in response to chemosymbiosis. Their sedimentary facies association (anoxic to dysoxic, organic-rich mudstones) favors such an inter-pretation. It is noteworthy that Oschmann (1994), in his study of the Kimmeridgian (Upper Jurassic) black shale fauna of England, interpreted some lucinid and solemyid bivalves as chemo-symbionts. The evidence for this is that *Mesomiltha concinna* and *Solemya* sp. are ten times larger than all co-occurring infaunal taxa (see also Brenchley and Harper, 1998, p. 39). Comparison with extant bivalves indicates that this is probably related to the faster growth rates in chemosymbiotic taxa than in co-occurring non-chemosymbionts (Oschmann, 1994; Brenchley and Harper, 1998).

The above interpretation is also supported by stable isotope data, since the shells of *A. froesi* found inside carbonate concretions
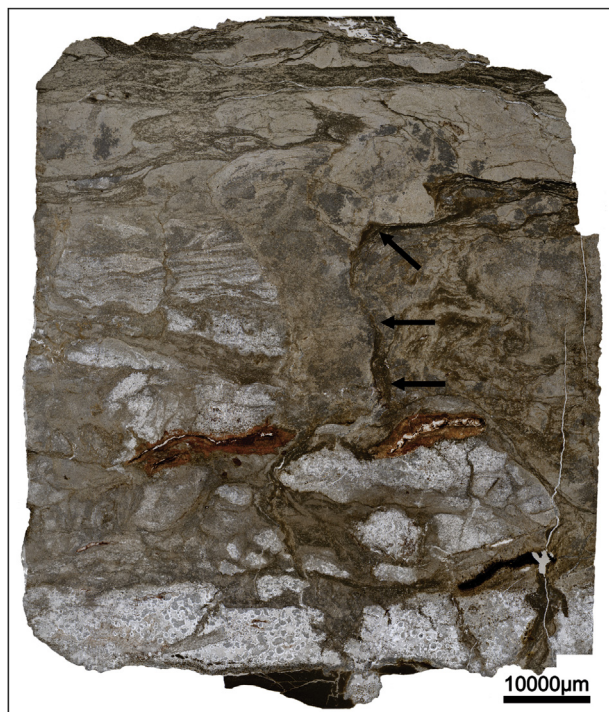
Fig. 10. Thin-section of the "brecciated" carbonate layer. The original bedding is repeatedly interrupted by several irregular sub-vertical cracks and fissures of variable dimensions. The right-central area (arrowed) is part of a large fissure filled with chaotically arranged sediment. The wall of this fissure is partially lined with microbial mudstone.

are ^{13}C-depleted (Table 1). However, one may argue that δ^{13}C values in the range of −6.1 to −7.6‰ are not really depleted compared with those of classical chemosymbiotic bivalves living in seep settings fueled by hydrocarbons. Indeed, this may result from many other sources than hydrocarbons, such as the high organic content and dysoxic conditions at the time of mudstone formation. Nevertheless, these values are also commonly found in seep deposits. Actually, such values may vary from −30 to +24‰, and are thus well within the range of the data from *A. froesi* (*e.g.*, Kauffman et al., 1996; Martens et al., 1999; Stakes et al., 1999; Greinert et al., 2001; Peckmann et al., 2002; Reitner et al., 2005; Wirsig et al., 2012; Cavagna et al., 2015; Lash, 2015; Liang et al., 2016; Loyd et al., 2016).

5.2. The Serra Alta seep system as a small oasis on an oxygen-depleted muddy sea floor

The barren nature of the shales of the Serra Alta Formation contrasts markedly with laterally equivalent shallow-water siltstones and sandstones of the Teresina Formation (Figs. 1 and 15), where shell-rich sandstones and shell beds are recorded (Simões et al., 1996, 1998). As discussed above, during the deposition of the fossil-poor shales of this unit, low-oxygen conditions prevailed at the seafloor, probably too low to support a diverse molluscan fauna. Hence, the studied bivalves were abundant in an offshore shale facies where the biotic diversity was extremely low (Bondioli, 2014; Bondioli et al., 2015). Notably, the shells of *T. camargoi* show their greatest abundance around the muddy mounds described above (Fig. 8). In some cases, at least 50 specimens were recorded forming a densely-packed, *in situ* concentration of closed articulated shells around the mounds. The presence of different size classes suggests that several generations (= distinct cohorts) lived

at the base of these structures. Intercalated between the mound interval are two ^{13}C-depleted carbonate concretions horizons, full of bivalve shells of the ATM-assemblage (Simões et al., 2000b; Bondioli et al., 2015).

As argued above, the studied beds (disrupted, "brecciated" carbonate level) and associated structures, including the small mounds and the fossil-rich carbonate concretions, seem to be associated with subsurface seep activity (see also Silva, 2016; Alessandretti, 2017). According to Alessandretti (2017), nucleation and growth of the Serra Alta bivalve-rich carbonate concretions and pyrite precipitation occurred just below the sediment-water interface (see also Bondioli et al., 2015) and were induced by anaerobic oxidation of methane (AOM) coupled with sulfate reduction at the sulfate-methane transition zone (SMTZ), during times of low sedimentation and diminished burial rate (Bondioli et al., 2015).

In the Paleozoic record of the Paraná Basin, two well defined sources of hydrocarbons could account for the seep system of the Serra Alta Formation, namely the Devonian shales of the Ponta Grossa Formation and the Permian oil and gas prone shales and carbonates of the Irati Formation, the latter worldwide known by its high content of TOC (Milani and De Wit, 2008). However, recent geochemical data from drill-cores from the southern part of the Paraná Basin indicate that the rocks of the Irati Formation contain on average less than 1% of organic carbon (Goldberg and Humayun, 2016). This value represents the normal background conditions in the basin with the oil-rich shales restricted to two main horizons in the uppermost part of the unit (Goldberg and Humayun, 2016). The degree of pyritization of iron (^{DOP}T) and the ratio of Fe_T/Al (see Goldberg and Humayun, 2016) indicate that euxinic conditions were reached only at times during the deposition of the Irati Formation and were responsible for the formation of the intervals with the highest C_{org} content. Finally, the Cu and Cu/Mo ratios suggest bottom-water anoxia driven by increased organic flux derived from the high primary productivity in surface waters, probably tied to high riverine nutrient inputs (Goldberg and Humayun, 2016). The black shales of the Irati Formation were deposited within the interval of maximum flooding of a second-order depositional sequence, under low sedimentation rates (Milani et al., 2007; Holz et al., 2010). The immature bitumens of the Irati Formation contain abundant gammacerane, b-carotane and 3b-methylhopanes, and unusually low ^{13}C values (Summons et al., 2008).

As shown in Fig. 2, the mound interval of the Serra Alta Formation is just a few meters above the contact with the oil-rich Irati Formation. In outcrop 1, the shales have even a bitumen odor. Hence, it is highly probable that the oil-rich succession below the analyzed stratigraphic interval may have acted as the source of organic compounds (methane and/or oil), which seeped to the seafloor diffusely or along cracks, fissures, fractures or clastic dikes during Serra Alta times (Fig. 16). Indeed, the relatively low TOC content of the Serra Alta shales (Teixeira, 2014) indicates that the hydrocarbons that fueled the seep system were not generated by near-surface organic-rich sediments of this unit, but in the unit immediately below. Mateus et al. (2014) pointed out that the Permian-Triassic was the main stage of hydrocarbon maturation of the oil-rich succession of the Paraná Basin. According to them, this was triggered by a high geothermal gradient coupled with various hydrothermal manifestations during the Permian.

In the model above, the dikes, which matrix is usually carbonate, may have acted as the possible plumbing system for the organic compounds, conducting the initially diffuse methane seepage onto the sea floor. Indeed, various authors have shown that the dikes may have acted as conduit pipes for seeping (Mazzini et al., 2003a, 2003b; Duranti and Mazzini, 2005; Minisini and Schwartz, 2007; De Boever et al., 2009; Blumberg et al., 2015; Cavagna et al.,
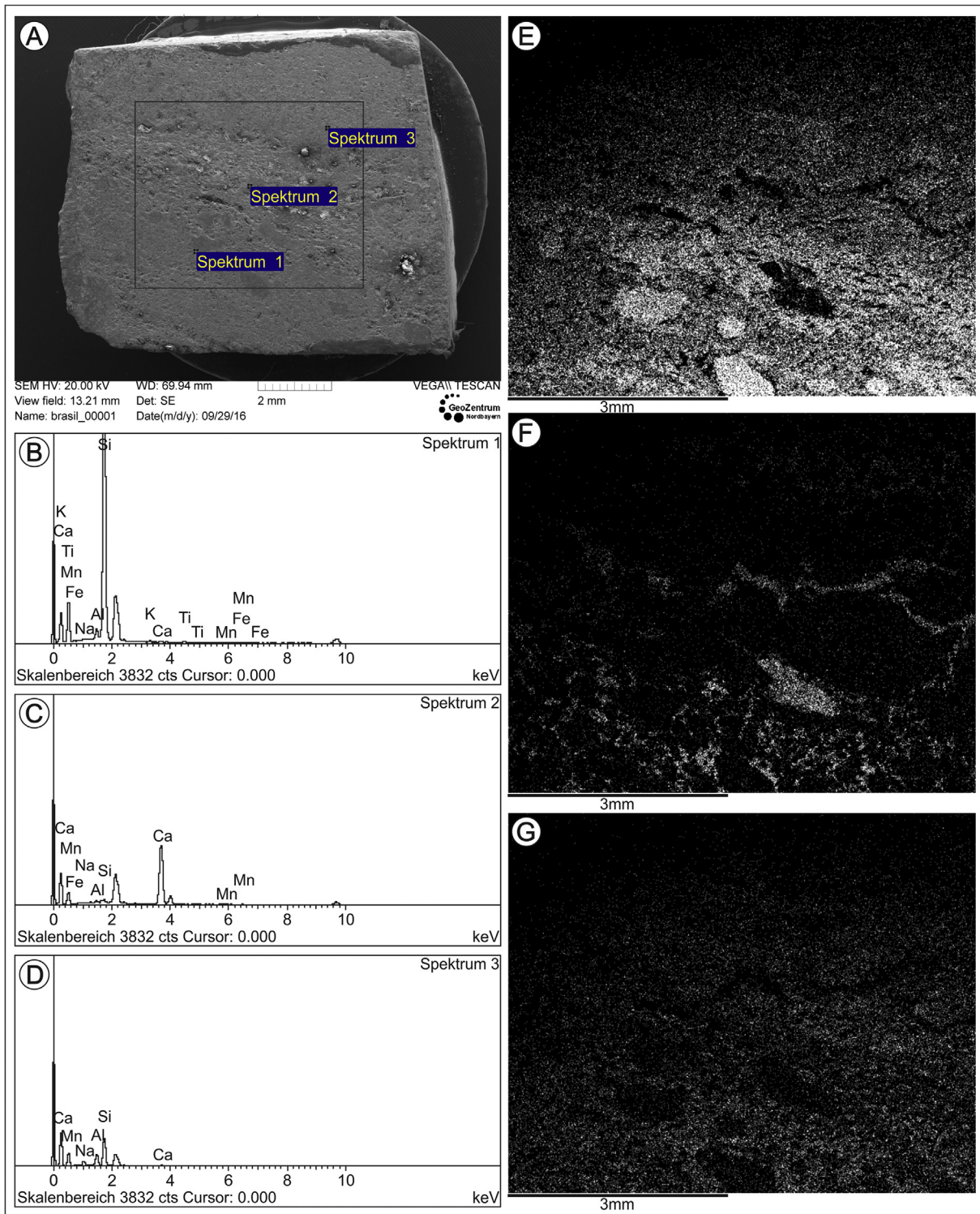
Fig. 11. SEM-EDS analysis of the lower unit of the "brecciate" carbonate. A- SEM image with positions of the three spectral analyses. B- EDS spectrum 1. C- EDS spectrum 2. D- EDS spectrum 3. E-G- Mapping results: E, Silica; F, Calcium; G, Alumina.

2015; Wirsig et al., 2012; Zwicker et al., 2015). Yet, methane seeping could also be associated with sand injections (Cosgrove, 2001; Schwartz et al., 2003; Duranti and Mazzini, 2005; Hurst et al., 2011), faults (Moore et al., 1990; Ogawa et al., 1996), hydraulic fracturing (Mazzini et al., 2003a, 2003b), and sea floor erosion (Mazzini et al., 2003a, 2003b). In our case study, the disrupted, "brecciated" carbonate also shows vertical structures that were probably produced by flows coming from below (Figs. 5, 10 and 16). In this context, initial disruption and "brecciation" of carbonate could be linked to methane outbreaks (Nobuhara, 2003) (Fig. 17), depending on methane availability, temperature and pressure conditions in the organic-rich subsurface sediment package (Irati

Table 1
δ13C and δ18O values of carbonates from the mound interval of the Serra Alta Formation.

| Sample	Code	d^{13}C	d^{18}O
Shell material (*A. froesi*)	Sample 1—435021	−6.1‰	−5.7‰
Disrupted, "brecciated" carbonate bed	Sample 2—435022	−7.6‰	−1.6‰
Mound	Sample 3—435023	−7.3‰	−2.7‰
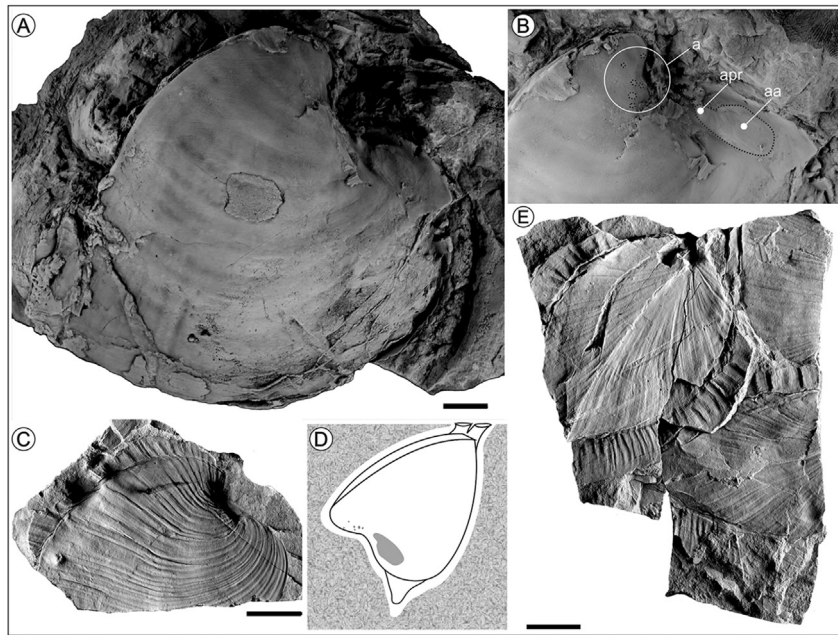
Fig. 12. *Tambaquyra camargoi.* A- Lateral view, internal mold, right valve of a large specimen (DZP-2250). B- Detail of specimen in A, note the large, elongated and deeply impressed anterior adductor muscle scar, as well as other muscle scars. C- Composite mold, right valve, showing the ornamentation. D- Inferred mode of life of *T. camargoi*. E- *In situ* preserved closed valves of *T. camargoi* at the base of a mound. a-accessory muscle scar; apr-anterior pedal retractor muscle scar, and aa-anterior adductor muscle scar. Scale bar: 1 cm.

Formation). This process is known to occur in sedimentary successions generated at passive margins. Finally, the intraplate seismic activity related to the propagation of far-field stress at the southwestern margin of the Gondwana supercontinent, coupled with overpressure in the organic-rich sedimentary succession (Irati shales) and hydrothermal activity (Mateus et al., 2014), is thought to have been the main triggering mechanisms for the seep system in the Irati-Serra Alta formations.

The δ ^{13}C values of bivalve shells, the disrupted, "brecciated" carbonate level and the concretions (Table 1) suggest that the seep system was fueled by methane and/or other hydrocarbons (see Peckmann and Thiel, 2004; Kiel and Peckmann, 2007 for a similar example). As is well known today, thermogenic methane shows δ^{13}C values ranging from −50 to −30‰ (Sackett, 1978 in Kiel and Peckmann, 2007), while biogenic methane is more ^{13}C-depleted, normally exhibiting values between −110 and −50‰ (Whiticar, 1999; Kiel and Peckmann, 2007). However, there are also several examples in the literature indicating that these values may vary between −30‰ and +6‰ (Kauffman et al., 1996; Stakes et al., 1999; Peckmann et al., 2002; Reitner et al., 2005; Wirsig et al., 2012; Cavagna et al., 2015; Lash, 2015; Liang et al., 2016). Hence, the lowest δ ^{13}C values around - 7.0‰ of the studied carbonates reveal that some carbon must have been derived from organic matter. In the Gulf of Mexico, modern carbonates forming at oil seeps with high seepage rates have values ranging from −25 to −15‰ (Joye et al., 2004; Kiel and Peckmann, 2007). However, under low
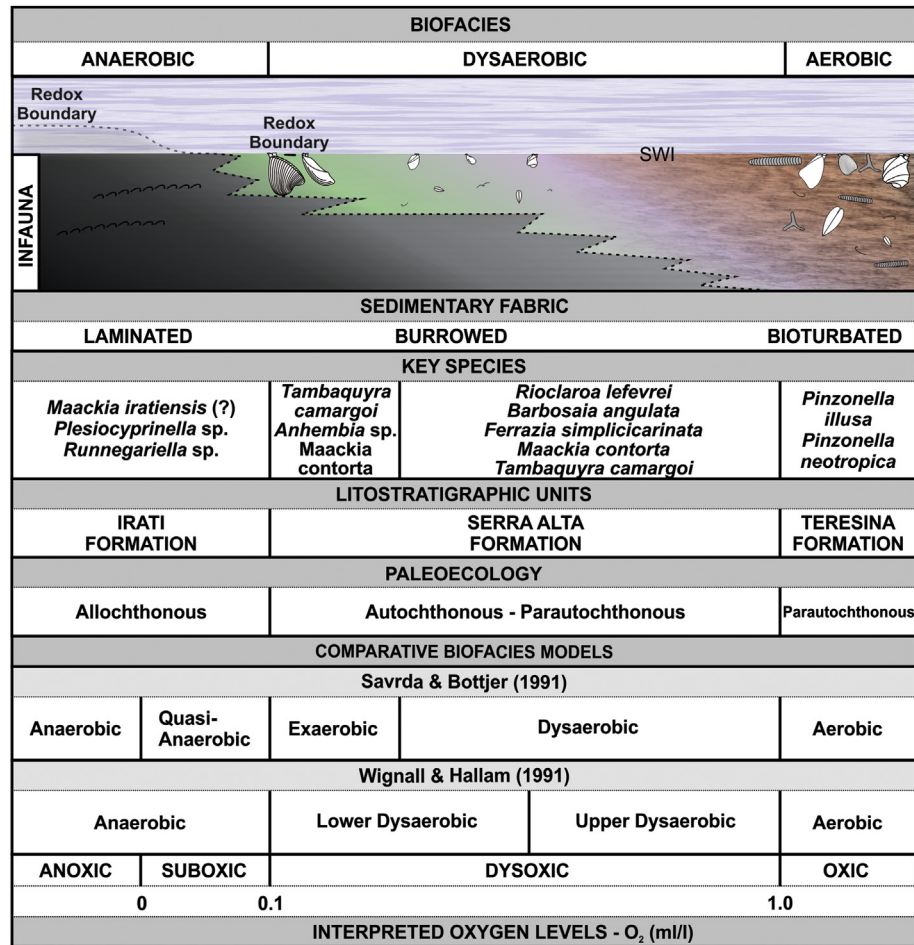
seepage rates, high values around −10‰ are recorded (Joye et al., 2004). In the Wagonwheel Mountains, California, Cenozoic carbonates generated in a hydrocarbon seep system yielded δ^{13}C values ranging from −12.2 to −5.0‰, "indicating oil rather than methane seepage" (Kiel and Peckmann, 2007). The values recorded for the carbonates of the mound interval of the Serra Alta Formation are within the range of those observed by Kiel and Peckmann (2007), suggesting a diffusive (methane/oil) process of seepage. However, based on the available data it is difficult to decide whether seepage fluids contained mostly methane or other types of hydrocarbons. The elevated TOC values (see Milani and De Wit, 2008) and the presence of abundant coccoidal cyanobacteria in chert beds of the oil-rich Irati Formation (Calça and Fairchild, 2012) are, however, strong evidence that the degradation of organic matter in the sedimentary pile below was an important factor of the seep system in the Serra Alta Formation. Indeed, the oil-rich shales of the Irati Formation have TOC values up to 23%, with an average ~2% derived from algal, lipidic-rich, and oil-prone organic matter sources (Zalán et al., 1990). Finally, a similar example of oil seepage was also described by Peckmann et al. (2007), including a very abundant, but low diversity assemblage of Late Devonian dimerelloid brachiopods found in δ ^{13}C-depleted limestones ranging from −12‰ to −1‰ (Peckmann et al., 2007, p. 119). The isotopic and paleoecological features are similar to those noted in the bivalve assemblages of the mound interval of the Serra Alta Formation.
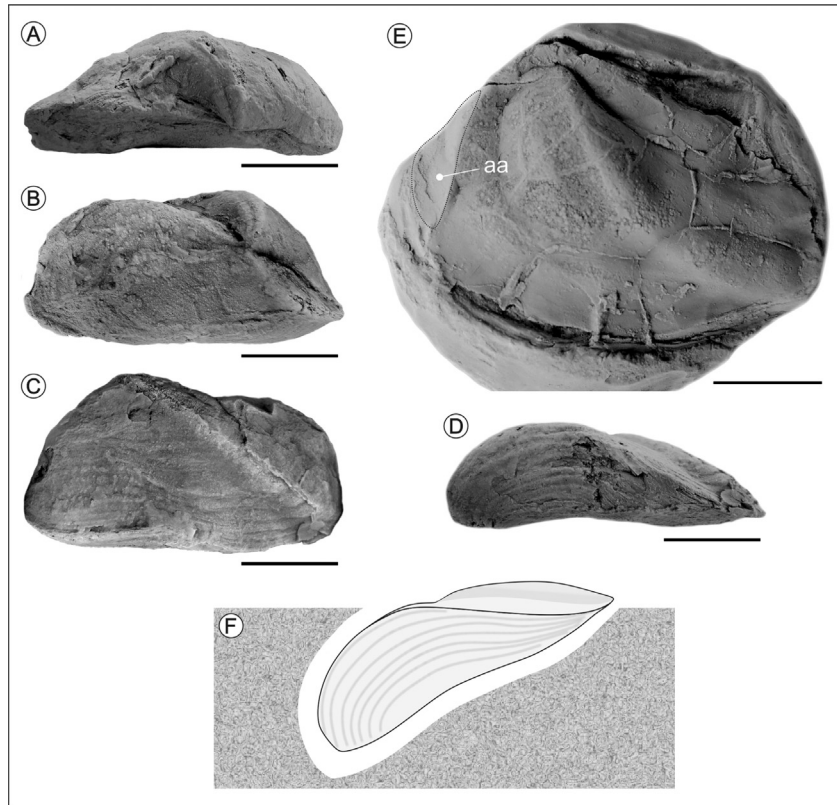
Fig. 13. A-F *Maackia contorta*. A-D Specimen DZP-18996 showing the articulated valves. A- Dorsal view, showing the highly convex left valve, and the flat right one. B- Lateral view of the flat right valve. C- Lateral view of the left valve with a well-developed posterior umbonal carina. D- Ventral view showing the twisted commissure. E- Internal mold of the left valve, showing the large, elongated anterior muscle scar (DZP-18997). F- Inferred mode of life of *M. contorta*. Note the flat right valve and the lifted posterior end of the shell. aa-anterior adductor muscle scar. Scale bar: 1 cm.
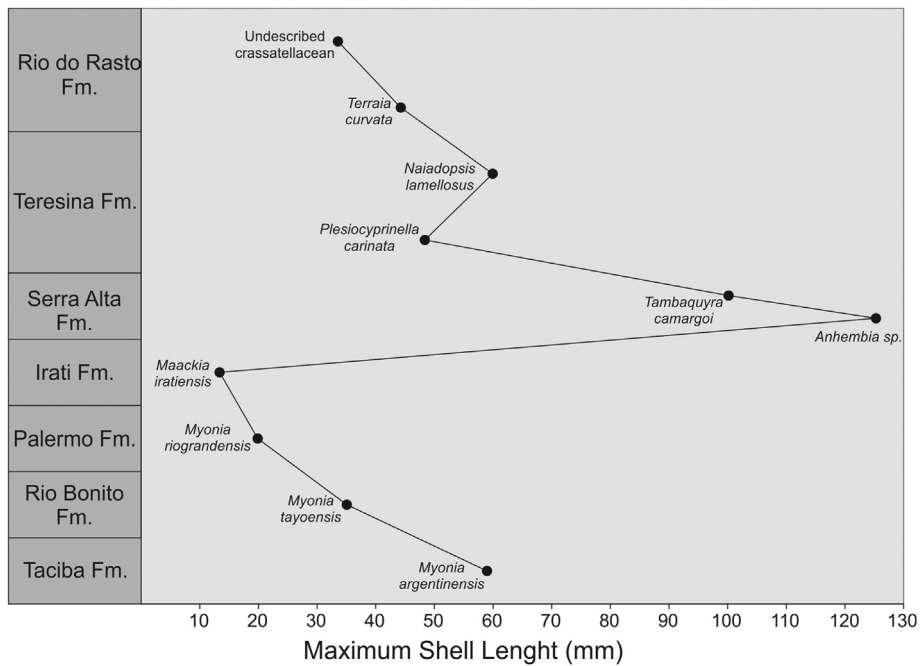
Fig. 14. Maximum length of the largest individuals recorded in assemblages of the Permian Passa Dois Group. Undescribed crassatelacean (35 mm), *Terraia curvata* (42.4 mm), *Naiadopsis lamellosus* (59.9 mm), *Plesiocyprinella carinata* (48.4 mm), *Tambaquyra camargoi* (104.5 mm), *Anhembia* sp. (125 mm), *Maackia iratiensis* (13.5 mm), *Myonia riograndensis* (20 mm), *Myonia tayoensis* (35 mm), and *Myonia argentinensis* (59 mm). Source of data: 2434 specimens from the scientific collection of the Department of Zoology, Institute of Biosciences, UNESP, Botucatu campus (DZP-code) and literature data in Beurlen (1957), Rocha-Campos (1970), Simões (1992), Neves et al. (2014), Simões et al. (2015). Modified from Ghilardi (1999).

BIOFACIES			
ANAEROBIC	DYSAEROBIC		AEROBIC

SEDIMENTARY FABRIC		
LAMINATED	BURROWED	BIOTURBATED

KEY SPECIES			
Maackia iratiensis (?) *Plesiocyprinella* sp. *Runnegariella* sp.	*Tambaquyra camargoi* *Anhembia* sp. *Maackia contorta*	*Rioclaroa lefevrei* *Barbosaia angulata* *Ferrazia simplicicarinata* *Maackia contorta* *Tambaquyra camargoi*	*Pinzonella illusa* *Pinzonella neotropica*

LITOSTRATIGRAPHIC UNITS		
IRATI FORMATION	SERRA ALTA FORMATION	TERESINA FORMATION

PALEOECOLOGY		
Allochthonous	Autochthonous - Parautochthonous	Parautochthonous

COMPARATIVE BIOFACIES MODELS				
Savrda & Bottjer (1991)				
Anaerobic	Quasi-Anaerobic	Exaerobic	Dysaerobic	Aerobic
Wignall & Hallam (1991)				
Anaerobic		Lower Dysaerobic	Upper Dysaerobic	Aerobic
ANOXIC	SUBOXIC	DYSOXIC		OXIC
0	0.1		1.0	
INTERPRETED OXYGEN LEVELS - O_2 (ml/l)				

Fig. 15. Idealized biofacies model for the Late Paleozoic units of the Passa Dois Group, showing the lateral variation in bivalve assemblages and amounts of dissolved bottom oxygen. The Teresina and Irati formations are end members of this model. The chemosymbiotic bivalves of the Serra Alta Formation are found in the exaerobic or lower dysaerobic biofacies of the standard low-oxygen biofacies model of Savrda and Bottjer (1991) and Wignall and Hallam (1991), respectively.

5.3. Other seep examples in the Permian Passa Dois Group, Paraná Basin, Brazil

In the Permian succession of the Passa Dois Group, particularly in the interval represented by the uppermost part of the Irati Formation and in the Teresina Formation (Fig. 2), there are various lines of evidence that methane seeping was indeed a remarkable phenomenon during that time in the Paraná Basin. For example, well-preserved geyserites have been recorded in the Irati Formation (Mateus et al., 2014) and an overall enrichment of black-shales of this unit in Mg-(saponite) and Fe-smectites (nontronite), coupled with silica or microcrystalline quartz, among other authigenic and neoformed minerals has also been noted (Mateus et al., 2014). Genesis of these siliceous chemogenic minerals is related to tectonic activity (faulting), leading to episodic discharges of silica-saturated fluids, which channelized flow into crustal discontinuities throughout the tectonic instability in the Paraná Basin during Permian-Triassic times (Mateus et al., 2014). Tohver et al. (2013) also documented massive methane release due to impactogenic seismicity, during Irati-Serra times, as a consequence of the Araguainha impact event (the second-largest known impact crater in South America, dated 254.7 ± 2.5 million years ago, Tohver et al., 2012).

Geyserites (Yamamoto et al., 2005) or hydrocarbon seep domes (Amaral, 2016) are also spectacularly preserved in the Teresina Formation, close to the study area (Anhembi region, State of São Paulo). In this case, the internal walls of the domes are filled with globular silica minerals. Recent RAMAN spectrometry of these minerals detected the presence of ethane and methane (Amaral, 2016). The AOM led to an increase in pH and supersaturation of silica, which caused the dissolution and subsequent precipitation of the silica minerals (see Kuechler et al., 2012; Miyajima et al., 2016). Since the domes are preferred aligned in the direction of regional tectonic structures it is reasonable to infer that the silica was migrated through regional faults (Amaral, 2016). When the pH was lowered again the silica re-precipitated (Kuechler et al., 2012) and was responsible for the preservation of the domes (Amaral, 2016). These lines of evidence indicate unequivocally that a hydrocarbon seep system existed in the Paraná Basin during the time of deposition of the Passa Dois Group. The system was fueled by upward migration of organic-rich fluids from the underlying oil-bearing shales of the Assistência Member of the Irati Formation (Mateus et al., 2014; Amaral, 2016; Silva, 2016). If this is true, this has important implications for our knowledge on the main period of hydrocarbon maturation in the Irati Formation, since the early Cretaceous is usually accepted as the main period for this process, due to the high-thermal regimes associated with the extensive magmatism at that time.
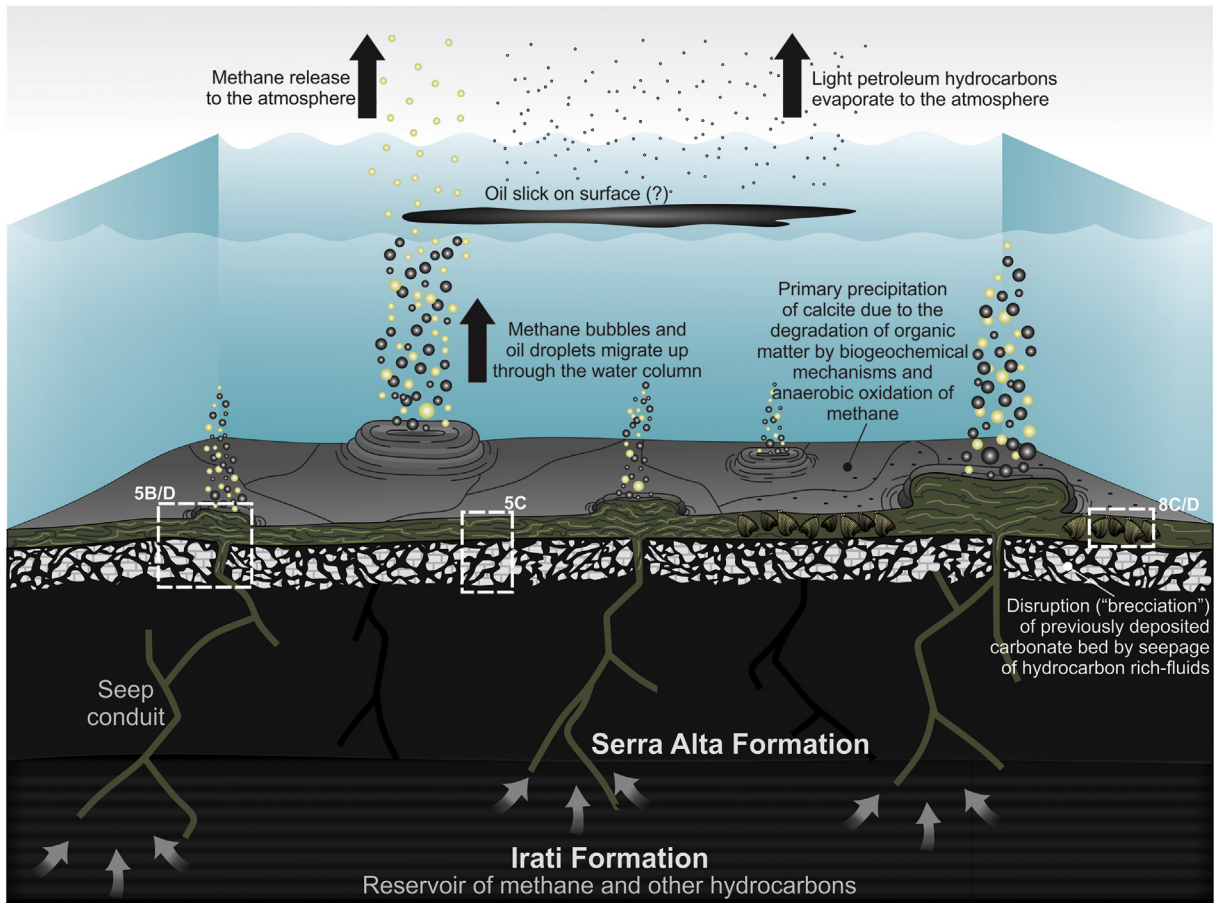
Fig. 16. Speculative, schematic diagram of the carbonate mounds, associated methane/oil seep system and fauna of the Permian Irati and Serra Alta formations, Paraná Basin, Brazil. White letters as in Figs. 5 and 8.

5.4. Evolutionary implications

The data presented above have also important implications for the evolutionary history of chemosymbiosis within a clade of bivalve mollusks (Anomalodesmata). Chemosymbiosis within the Bivalvia is known to occur mainly in the families Lucinidae, Montacutidae, Mytilidae, Nucinellidae, Saxicavellinae, Solemyidae, Teredinidae, Thyasiridae and Vesicomyidae (Distel, 1998; Taylor and Glover, 2010; Duperron et al., 2012; Roeselers and Newton, 2012; Oliver and Taylor, 2012; Oliver, 2013; Oliver et al., 2013). These bivalves house sulfur-oxidizing bacteria (tiotrophic Gammaproteobacteria and Epsilonproteobacteria) and/or methanotrophic Gammaproteobacteria in their tissues (Dubilier et al., 2008; Vrijenhoek, 2010; Anderson, 2014). As argued by the last author, the evolutionary history and relationships of these bivalve groups (hosts) and the bacteria they house indicate that chemosymbiosis evolved repeatedly within members of this molluscan class (Anderson, 2014, p. 50; see also Lorion et al., 2013). The same seems to be true for the endemic bivalves of the Permian Serra Alta Formation. Despite the uncertainties about the systematic affinity of Anhembia and Maackia within the Anomalodesmata, species of these genera are usually assigned to an endemic clade of extinct bivalves (Pachydomiidae, formerly Megadesmidae, see Runnegar and Newell, 1971; Simões et al., 1997; Mello, 1999). The complex evolutionary history and extreme adaptive radiation of this group in the Paraná Basin was documented in detail by Beurlen (1954b), Runnegar and Newell (1971), and Simões et al. (1998). After the Irati anoxic-event this group of shallow burrowing, suspension-feeding bivalves radiated and colonized various subenvironments of the basin from shallow (oxic) to deep (mainly dysoxic) siliciclastic/carbonate, organic-rich bottoms (Simões et al., 1998). Eventually, a rapid adaptive radiation allowed a group of endemic bivalves inhabiting organic-rich substrates (Matos et al., 2017) to thrive in extremely dysoxic (exaerobic) to dysoxic offshore bottoms where organic compounds were released and were used (at least facultatively) as an energy source.

6. Final comments and future prospects

The mound-bearing interval of the Serra Alta Formation and associated carbonate concretions and disrupted, "brecciated" limestone bed are interpreted here as an exceptional Permian seep deposit developed in a siliciclastic-dominated succession within a large intraplate basin. Confirmation of this paleoenvironmental interpretation is based on taphonomic, paleoecological, sedimentological, petrographic and some geochemical evidence. Yet, in the studied stratigraphical interval other seep-derived structures and deposits are also recorded, some with the presence of biomarkers indicative of ethane and methane. Despite the extensive work done documenting distinct features of fossil seep systems (i.e., petrography, stable isotopes, element analysis), and associated carbonates and their faunas (e.g., Kiel, 2010; Kiel et al., 2012; Lorion et al., 2013; and references therein), Permian occurrences are generally poorly known. Thus, together with the Late Carboniferous hydrocarbon-seep carbonates from the glaciomarine Dwyka Group, southern Namibia (Himmler et al., 2008), our bivalves are one of the oldest
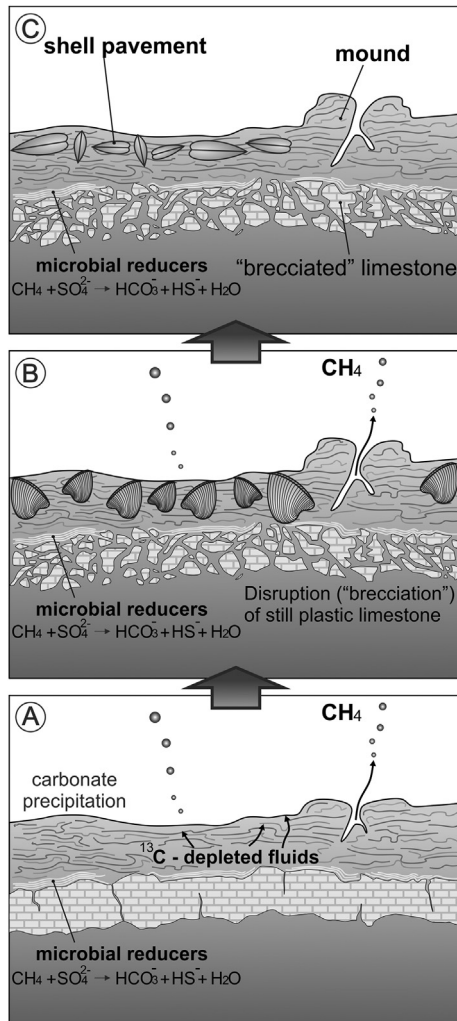
Fig. 17. Diagrams illustrating the formation of the brecciated carbonate and associated autochthonous bivalve shell concentration. A- Carbonate precipitation mediated by microbial activity. Initial disruption and "brecciation" of carbonate, possibly triggered by gas outbreaks. The "brecciated" carbonate allows the passage of the hydrocarbon-rich waters. Seeping and associated microbial activity may account for mound construction; B- Colonization of the basal portions of the mounds by several generations of *Tambaquyra camargoi*; C-Interruption of the seepage or establishment of anoxic conditions cause the death of the bivalves, which in some cases, are preserved in life position. A, B and C in stratigraphical order. Based on Nobuhara (2003).

documented members of Gondwana seep faunas.

The data presented above are unique amongst documented Late Paleozoic seep deposits as they record a 3D-relief of the mounds, which extended above the ancient seafloor, as well as the associated monotypic, endemic and abundant bivalve *T. camargoi*. This taxon and two other bivalve species (*A. froesi* and *M. contorta*) are also common in ^{13}C-depleted carbonate concretions occurring at the same stratigraphic interval. Their shells are also depleted in ^{13}C, and the three species are therefore interpreted as specialized, at least facultatively chemosymbiotic Permian bivalves.

Detailed cm-by-cm investigations of the mudstone below and above the disrupted, "brecciated" carbonates (Silva, 2016; Simões et al., 2016) indicate that infaunal benthic invertebrates were the first occupants of the muddy sea floor. Dense concentrations of shells of *T. camargoi* around the base of the mounds strongly suggest colonization of the bottoms where exudations were common. This suggests that this hydrothermal activity lasted long enough for the area to be populated by several generations of *T. camargoi*

(indicated by different size classes of shells). When the seepage ceased or the bottom became completely depleted in oxygen, the bivalves at the base of the mounds died, as suggested by the unfossiliferous, dark grey shales with scattered pyrite that cap the domes.

The studied Permian bivalves are not related to the "traditional" taxa (*e.g.*, thyasirids, lucinids, and vesicomyids) found in present-day seep deposits. They were endemic anomalodesmatans (= Pachydomiidae) that colonized the Paraná Basin during and immediately after the paleogeographic restriction of the basin in the Permian. They derived from shallow-water species (Runnegar and Newell, 1971; Mello, 1999), showing that chemosymbiosis may have evolved quickly and repeatedly (*e.g.*, Anderson, 2014) in distinct bivalve groups, probably by bursts of adaptive radiation, as already suggested by Campbell (2006; p. 392).

Finally, the paleontological, taphonomic, sedimentological and stratigraphic information gathered, coupled with petrographic, some stable isotope and literature data indicate that a complex seepage system existed in the Paraná Basin, during deposition of the basal interval of the Permian Serra Alta Formation. Obviously, alternative interpretations based on individual features are possible, but the large number of observations from various fields favour a seep origin for the studied deposits and their associated fauna. In this context, future research must focus on improving the geochemical data set, particularly by searching for biomarkers typical of AOM. In this context, a good starting point is the search for globular silica minerals and their subsequent RAMAN spectroscopy in the conduits (*i.e.*, dikes) directly associated with the domes and in brecciated carbonate bed.

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