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Article

TAPHONOMIC SIGNIFICANCE OF GROWTH PATTERNS IN *ORBICULOIDEA BODENBENDERI* (BRACHIOPODA: LINGULATA) FROM THE EMSIAN OF THE PARANÁ BASIN

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ABSTRACT – The Emsian transgression established redox conditions (anoxic to dysoxic) and drastic suppression of bioturbation in the Paraná Basin, recorded in the Jaguariaíva Member (Ponta Grossa Formation). The application of morphometric and sclerochronological analyses in *Orbiculoidea bodenbenderi* Clarke (Brachiopoda, Lingulata) allowed the recognition of three shell associations with high time-averaging. The first group of brachiopods had high relative growth rates in the juvenile phase (13.52% ± 2.11%), followed by a sharp decline until senescence (2.81% ± 0.8%); the second group of brachiopods presented moderate juvenile growth rates (7.44% ± 2.32%) and gradual reduction throughout life; finally, the third group exhibited residual growth since maturation (3.85% ± 1.20%), with stagnation during senescence (2.60% ± 1.08%). The coexistence of these distinct patterns in the same stratum (Maximum Flooding Surface - MFS) is incompatible with a single contemporary population, demonstrating a case of time-averaging, in which organisms from different generations and paleoenvironmental conditions were amalgamated during deposition. Slow sedimentation near the MFS, associated with reduced bioturbation under dysoxic/anoxic conditions, allowed shells to remain in the taphonomically active zone for long periods, facilitating temporal condensation and increasing the time-averaging. The *O. bodenbenderi* assemblage is the result of multigenerational integration, highlighting the importance of integrating ontogenetic and taphonomic data for accurate paleoenvironmental interpretations in transgressive contexts.

Keywords: Gondwana, time-averaging, morphometry, sclerochronology, taphonomic condensation.

INTRODUCTION

Brachiopods (such as *Orbiduloidea*) are excellent archives for paleoenvironmental reconstructions in the Paleozoic due to their long geological history (Cambrian-present), high sensitivity to water physicochemical variations, and resistance to diagenesis (Williams *et al*., 1992, 1994). These characteristics make them ideal indicators for inferring past environmental conditions, favoring morphometric analyses (Lowenstam, 1961; Popp *et al*., 1986; Banner & Kaufman, 1994; Brand *et al*., 2011, 2015). In this context, *Orbiculoidea bodenbenderi* (Class Lingulata) stands out for its distinct ontogenetic growth patterns, shaped by paleoenvironmental conditions, such as changes in salinity, paleoenvironmental toxicity, nutrient availability and climate change (Zhang *et al*., 2018; Ribeiro & Ghilardi, 2025). During the Emsian, the Paraná Basin underwent several paleoenvironmental changes driven by transgressive events associated with global dynamics; these transgressions reconfigured the paleogeography and benthic ecosystems, shifting from energetic conditions favorable to anoxic and restrictive environments (Bosetti *et al*., 2009, 2012; Horodyski *et al*., 2014; Sedorko *et al*., 2018a, b, c, 2019; Ribeiro & Ghilardi, 2025).

Orbiculoidea (Family Discinidae, Class Lingulata) has distinct growth patterns when compared to other brachiopods, shaped by marginal accretion, ontogenetic allometry, environmentally modified growth rates, and reproductive compensations (Rudwick, 1959; Ackerly, 1989). Characterized by an organophosphate shell composition, these sessile benthic organisms display remarkable flexibility and are well adaptable to many paleoenvironmental conditions, with unique growth dynamics and ecological resilience (Holmer, 1989; Freeman, 2001; Carlson, 2016). The main growth mechanism is marginal accretion, where new shell material is deposited along the edges of the valves. This process occurs through the secretion of a compound rich in organic matter and subsequent mineralization with calcium phosphate (Williams *et al*., 1992, 1994).

The morphometric proportions of the valves change unevenly throughout the growth process; juveniles (*e.g.*, *O. bodenbenderi*) have an almost circular outline, optimizing the surface area for attachment, while in adulthood the shell elongates to an elliptical or oval shape (Williams *et al*., 1992, 1994; Freeman & Lundelius, 1999; Freeman, 2001). The ventral valves tend to thicken as they seek stability and anchorage in the substrates, while the dorsal valves remain thin and flat (Rudwick,1959; Noble & Logan, 1981; Mergl, 2010). Fossil specimens reveal that allometry varies among species within the genus *Orbiculoidea*, suggesting adaptive conditions depending on the paleoenvironmental niche (Zhang *et al*., 2018).

Growth lines, concentric ridges on the shell surface, record episodic depositional events and are often correlated with seasonal nutrient availability or paleoenvironmental stresses (Sebens, 1987; Hiller, 1988).

The juvenile phase of *Orbiculoidea* is marked by accelerated radial growth, with rapid growth of the valves to ensure survival and fixation on substrates. At this stage, the growth lines are more spaced, reflecting the speed of development. As individuals advance to the subadult stage (maturation), growth slows down and is directed towards the thickening of the ventral valve, an adaptation that favors stability in soft sediments; this change results in growth lines being closer to each other. After sexual maturity, a critical energetic transition occurs, prioritizing reproduction over shell expansion, further reducing the growth rate. As a consequence, the lines become very close together or even absent, indicating the final deceleration of development (Emig, 1997; Freeman & Lundelius, 1999; Ribeiro *et al*., 2024; Ribeiro & Ghilardi, 2025).

Brachiopods are extremely sensitive to environmental variations and seasonality; its relative growth may reflect changes in temperature, nutrient availability, water oxygenation, and physical/chemical stress that influenced their development, proving to be a fundamental metric for understanding past conditions (Huxley, 1932; Brey *et al*., 1995; Pérez-Huerta *et al*., 2014; Ribeiro & Ghilardi, 2025). The ontogenetic phases of *Orbiculoidea* (and other Discinidae) can be determined from the calculated growth rates. In the juvenile stage, growth is extremely accelerated, prioritizing shell expansion and ensuring survival, with growth rates ranging from 10% to 33%. During maturation, rates drop to 5% to 10%, and growth stabilizes, with energy directed towards reproductive maturation and structural strengthening. In the adult stage, rates drop to 2% to 5%, when energy is focused on reproduction, with growth limited to damage repair or morphological adjustments. Finally, in senescence, growth ceases almost completely, with rates close to 3%, linked to exhaustion or environmental stress accumulated throughout life (Rudwick, 1959; Freeman, 2001; Kelley *et al*., 2003).

GEOLOGICAL SETTING

The Paraná Basin is one of the largest sedimentary basins in South America, covering an area of approximately 1,500,000 km^2 and accumulating a thick sequence of sediments, which can reach up to 8 km in thickness (Bergamaschi, 1999; Milani, 2004; Milani *et al*., 2007a). In Brazil, the basin covers the states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Minas Gerais, and Mato Grosso, and reaches Uruguay, northwestern Argentina, and southwestern Paraguai (Assine, 1999; Milani *et al*., 2007b) (Figure 1A). During the Devonian (Emsian), southwest Gondwana experienced a widespread marine transgression, resulting from the interaction between global and regional factors. While the 4th and 5th order (high frequency) cycles were controlled by global sea level variations, the 2nd and 3rd order (low frequency) cycles are tectonic reflections (Assine *et al*., 1994; Bergamaschi, 1999; Vargas *et al*., 2020).

The Paraná Basin records one of these cyclical transgressions of Gondwana, which began in the Pragian and triggered an extensive flood in the Emsian, recorded in the Jaguariaíva Member, Ponta Grossa Formation (Assine *et al*., 1994; Bergamaschi, 1999; Sedorko *et al*., 2018a, b, c, 2019; Vargas *et al*., 2020). The second transgression in the basin began at the end of the Emsian, associated with the deposition of the São Domingos Member, representing a subsequent global transgression (Assine *et al*., 1994; Bergamaschi, 1999; Sedorko *et al*., 2018a, 2019). It was during this transgressive event that significant marine connections were established between the South American basins (*e.g.*, the Parnaíba and Amazon Basins), enabling important faunal migrations (Clarke, 1913; Derby, 1878; Melo, 1988; Troth *et al*., 2011; Bosetti *et al*., 2012; Horodyski *et al*., 2014). In sum, the Emsian was a fundamental transition period for the Paraná Basin, when a marine regression initiated in the Pragian ended its depositional cycle, associated with a second transgressive cycle, which led to a new phase in the paleogeography of southwestern Gondwana (Figure 1B).

Previously, sedimentological (*e.g.*, Bergamaschi, 1999; Bergamaschi & Pereira, 2001; Plantz *et al*., 2024), geochemical (*e.g.*, Rocha *et al*., 2023), taphonomic (*e.g.*, Bosetti, 2004; Bosetti *et al*., 2009) and ichnological studies (*e.g.*, Sedorko *et al*., 2018a, b, c, 2019) were made on these areas, however sclerochronological and morphometric approaches have not yet been applied to brachiopods (*Orbiculoidea bodenbenderi*) from these localities. *O. bodenbenderi* exhibits high dimensional stability during the Lower Devonian, reflecting non-restrictive growth conditions. This differs from *O. baini* and *O. excentrica*, which underwent size reduction during subsequent stress events (*e.g.*, the Kačák Biotic Crisis) (Ribeiro & Ghilardi, 2025). Thus, the main objective of this study is to understand the taphonomic processes associated with the Pragian–Emsian transgression in the southern Paraná Basin, using the ontogenetic patterns of *Orbiculoidea bodenbenderi* as paleoenvironmental indicators.

MATERIAL AND METHODS

Considering the main goal of this study, outcrops near the city of Ponta Grossa (Paraná State) were selected (Figure 1C), being them: Rivadávia Farm (25°17’09.00” S - 50°00’47.00” W), Tibagi 1 (24°30’01.98”S - 50°24’55.25”W), Tibagi 2 (24°29’49.55” S - 50°25’01.21”W), Curva 1 (25°03’55.88”S - 50°08’00.06”W), and Curva 2 (25°03’58.97”S - 50°07’39.00”W), where the Maximum Flood Surface (MFS) was identified by Bergamaschi (1999) and Sedorko *et al*. (2018a, c). The shells of *Orbiculoidea bodenbenderi* (four ventral and 18 dorsal valves) are deposited in the Laboratório de Estratigrafia e Paleontologia of the Universidade Estadual de Ponta Grossa (UEPG), in the city of Ponta Grossa (numbers MPI-13978, MPI-3492, MPI-5506, MPI-5895, MPI-5227, MPI-5595, MPI-5557, MPI-5890, MPI-5519, MPI-5499, MPI-13878, MPI-5530, MPI-5161, MPI-13667, MPI-5452, MPI-5538, MPI-5244, MPI-5653, MPI-5241, MPI-5550, MPI-5557 (F1) and MPI-5615) (Figure 2).

The *Orbiculoidea bodenbenderi* shells were morphologically differentiated into dorsal and ventral valves, and only the dorsal valves were used in sclerochronological analyses due to lack of ventral valves. Specimens were photographed using a Nikon D7000 camera equipped with a macro lens to ensure high-resolution imaging, followed by post-processing of the images in CorelDRAW 2021 (64-bit) graphic editing software.

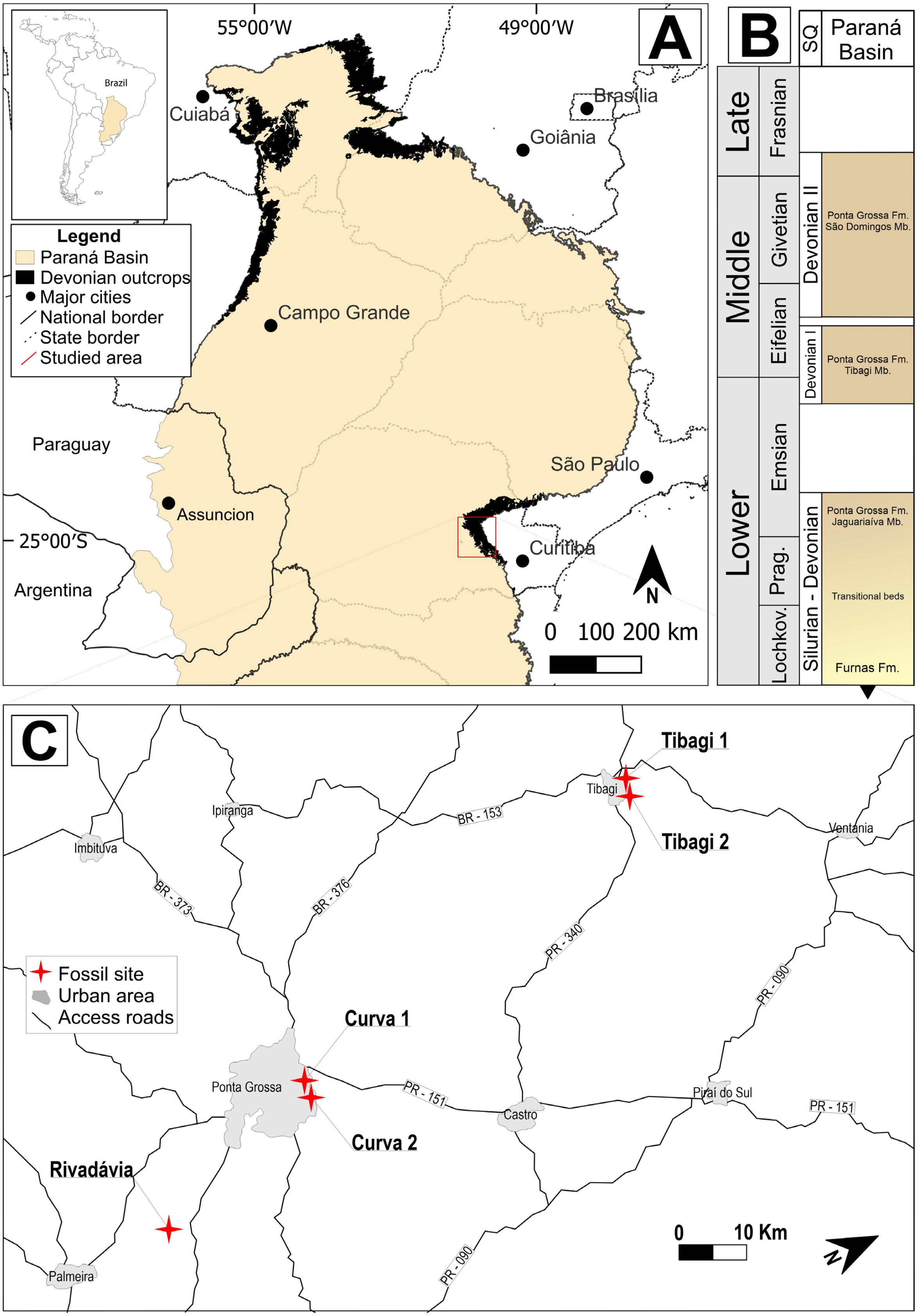

Figure 1. A, Area covered by the Paraná Basin with outcrops of Devonian rocks; **B**, chronostratigraphy of rocks in the southern portion of the basin (adapted from Grahn *et al*., 2013; Sedorko *et al*., 2018a); **C**, locations studied in the State of Paraná.

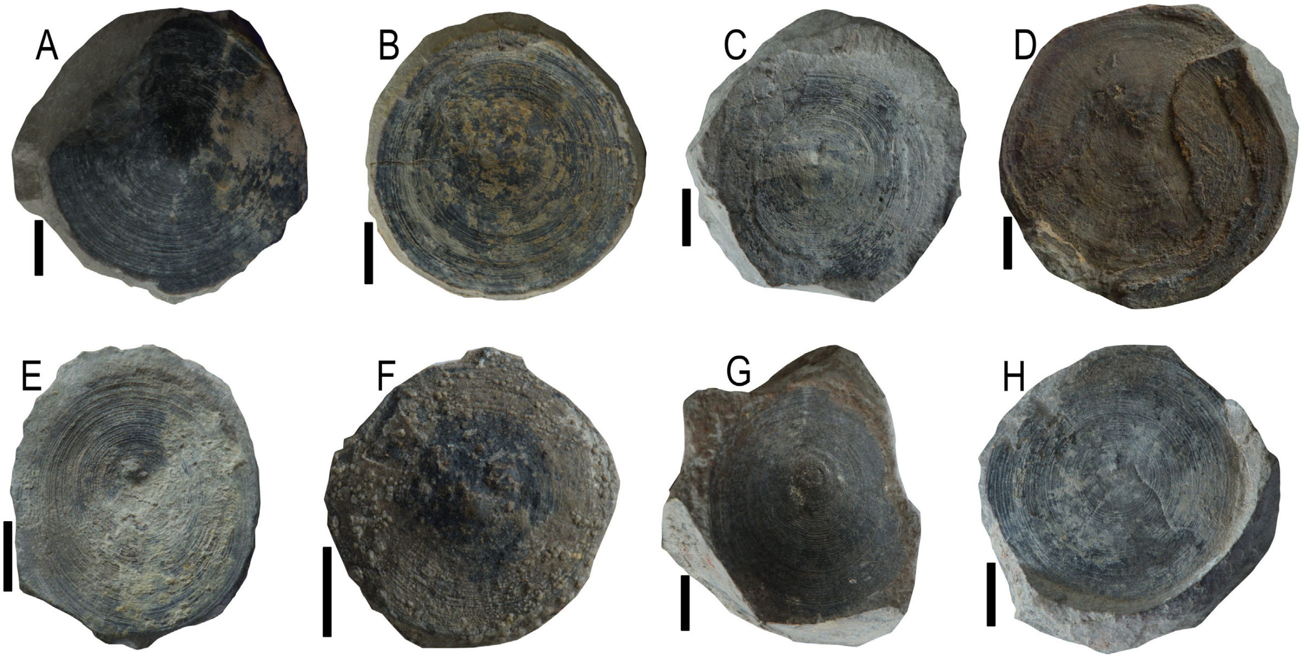

Figure 2. Some of the *Orbiculoidea bodenbenderi* studied in this article, internal mold of the dorsal valve (**A**, MPI-5519; **B**, MPI-5452; **D**, MPI-5557; **E**, MPI-5595; **F**, MPI-5653; **G**, MPI-5890) and ventral valve (**C**, MPI-5506; **H**, MPI-5584). Scale bars = 5 mm.

Measurements were taken with an accuracy of 0.001 mm, using calibrated metric scales. The data were organized in Excel® spreadsheets and analyzed in Past5 software (Paleontological Statistics, version 5.2.1) (Hammer & Harper, 2001). Considering the morphometric analyses, the dimensions (length and width) of the valves were taken and tabulated. These parameters were subsequently subjected to normality assessment using the Shapiro-Wilk test ($\alpha = 0.05$) to check their distributional properties. Since the data deviated significantly from normality ($p \leq 0.05$), nonparametric statistical methods were used to ensure analytical robustness. Thus, the paired t-test was used to identify significant differences between samples (Zar, 2010). The methodological protocol prioritized the standardization of morphometric measurements, mitigating biases towards morphological variability and taphonomic changes.

For the sclerochronological analysis, only valves with intact growth lines were used, where the apex of the shell was defined as the zero point (0) to begin measurements. From this point, a linear transect was drawn to quantify the distances between the growth lines. Transect 'a' is oriented parallel to the median plane of the shell, extending from the apex to the anterior region of the shell (Figure 3).

Relative growth rate is a mathematical ratio that measures how much the organism has grown relative to its previous size, reflecting the efficiency of growth at each stage (Brey *et al*., 1995; Curry *et al*., 1989). For brachiopods, this method is useful for identifying phases of accelerated growth, stagnation or reduction caused by environmental events or ecological stressors, especially for the *Orbiculoidea* (family Discinidae), whose haloperipheral growth allows the preservation of growth lines due to low ontogenetic deformation (Ackerly, 1989). This rate eliminates dependence on absolute size, allowing comparison of individuals of different ages and sizes, based on the number of growth lines and the growth rates (Brey *et al*., 1995; Curry *et al*., 1989). Similar sclerochronological methods are used in mollusks, where relative rate is critical for modeling nonlinear growth (Schöne & Surge, 2005). Thus, the application of this methodology to taxa exhibiting low ontogenetic/tephonomic deformation is promising (Rudwick, 1959; Ackerly, 1989; Ribeiro *et al*., 2024; Ribeiro & Ghilardi, 2025).

To establish the Relative Growth Rate (%) of brachiopods, the formula was used:

$$\text{Relative Growth Rate}(\%) = (\Delta di \,/\, di - 1) \text{ x } 100 \qquad (1)$$

Where $\Delta d_i = \mathbf{d_i} - \mathbf{d_{i-1}}$ is the absolute increment between two growth lines and $\mathbf{d_{i-1}}$ is going to be the previous size, cumulative distance to line **i-1**, adapted from Rudwick (1959), Parkinson (1969), Alexander (1977), Thayer (1977), Curry *et al*. (1989), Collins (1991), Hoffmann & Poorter (2002) and, Congreve *et al*. (2021). After the determination of ontogenetic stages and their respective relative growth rates, specimens were subjected to classical cluster analysis with 100 bootstrap replicates. The Euclidean distance coefficient was applied as a dissimilarity measure, followed by hierarchical aggregation of pairs using the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) linkage method, allowing fossils to be hierarchically grouped based on their relative growth rate. For differentiation of ontogenetic phases, growth rates greater than 7% between growth lines were assigned to the juvenile phase, 7% – 5% to maturation, 5% – 3% to the adult phase, and less than 3% to senescence.

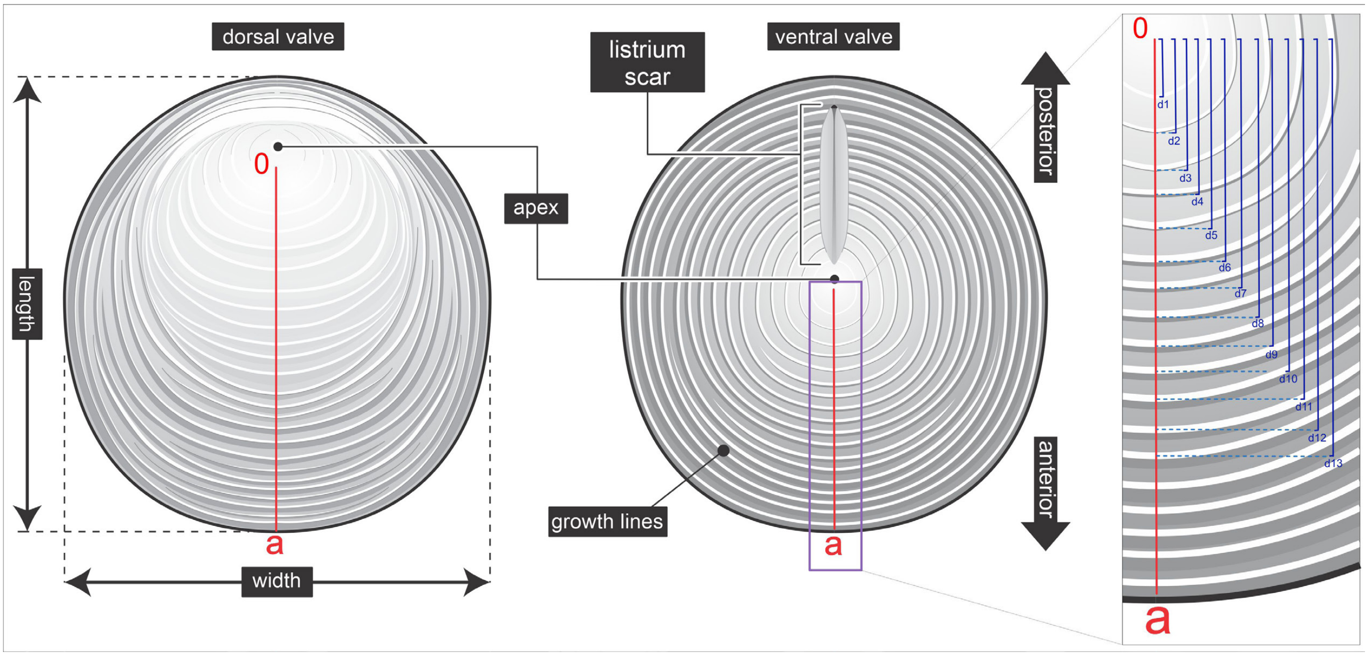

Figure 3. Morphology of *Orbiculoidea* with the measured transect (adapted from Ribeiro *et al*., 2024).

RESULTS

Morphometry

The average size of the dorsal valves is 22.649 mm (length - L) by 21.334 mm (width - W), while the ventral shells average is 20.953 mm (L) by 20.971 mm (W) (Table 1 in the Supplementary Data). In the boxplot graph (Figure 4) it is possible to observe that the dorsal shells have lengths ranging from ~10 mm (minimum) to ~30 mm (maximum) and widths ranging from ~5 mm (minimum) to ~25 mm (maximum), with averages of ~20 mm and ~18 mm (Length and Width) (Figure 4). On the other hand, the ventral valves have lengths ranging from ~10 mm to ~30 mm and widths ranging from ~10 mm to ~22.5 mm, with averages of ~20 mm and ~17.5 mm (Length and Width). The Shapiro-Wilk test values, although relatively low, show significant differences between the two valves. In the dorsal valve, the results were length ($p = 0.3138$) and width ($p = 0.0660$). In the ventral valve, the length value was $p = 0.7022$, more than twice that of the dorsal, while the width value ($p = 0.9973$) was approximately 15 times greater than that of the dorsal valve. In contrast, the t-test results showed similar values for both valves.

Sclerochronology

Considering the low number of ventral valves of *O. bodenbenderi* found in the localities, growth rates (%) were measured only in the dorsal valves, where all the ontogenetic stages were recognized (Table 2 in the Supplementary Data). In the initial phases of development (Juvenile phase) the growth is accelerated, with average growth rates of 8.56% (varying from 4.64% – 15.66%), different from what seen in the maturation phase, when the average growth values are 5.62% (2.76% – 10.59%). In the adult phase, these values continue to decline, varying between 11.64% and 2.52% and average 4.07%, finally, in the senescence phase the growth rate falls to 2.72% (varying from 1.76% – 3.76%).

The Cluster Analysis (CA) showed a clear segregation into three distinct groups (1, 2 and 3), reflecting heterogeneous but structurally coherent development patterns (Figure 5A). This segmentation was corroborated by hierarchical analysis, based on dissimilarity metrics, allowing each group to be associated with specific ontogenetic stages. Cluster 1 is distinguished by specimens with elevated growth rates during the juvenile phase, a key morphometric characteristic differentiating this group from others analyzed, including MPI-3492, MPI-5506, MPI-5895, MPI-5227 and MPI-5595. Quantitatively, mean growth rates demonstrate a progressive decline across life cycle stages: 13.52% (±2.11%) during juvenility, 7.09% (±2.85%) in maturation, 3.94% (±1.09%) in adulthood, and only 2.81% (±0.8%) during senescence (Figure 5B).

The Cluster 2 (MPI-5557, MPI-5890, MPI-5519, MPI-5499) includes specimens with intermediate growth rates throughout all ontogenetic stages and a stabilized growth trajectory with small variability. Quantitative analysis reveals moderate growth rates, gradually declining throughout the development phases: 7.44% (±2.32%) during juvenility, 6.63% (±1.07%) at maturation, 4.06% (±0.5%) at adulthood and 2.83% (±0.84%) during senescence. This attenuated reduction contrasts with the sharp curves of Cluster 1, suggesting different energy optimization strategies (Figure 5B).

Finally, Cluster 3 gathers specimens (MPI-13878, MPI-5530, MPI-5161, MPI-13667, MPI-5452, MPI-5538, MPI-5244, MPI-5653) with considerable growth reduction already in the maturation phase and stagnation in Senescence phase.

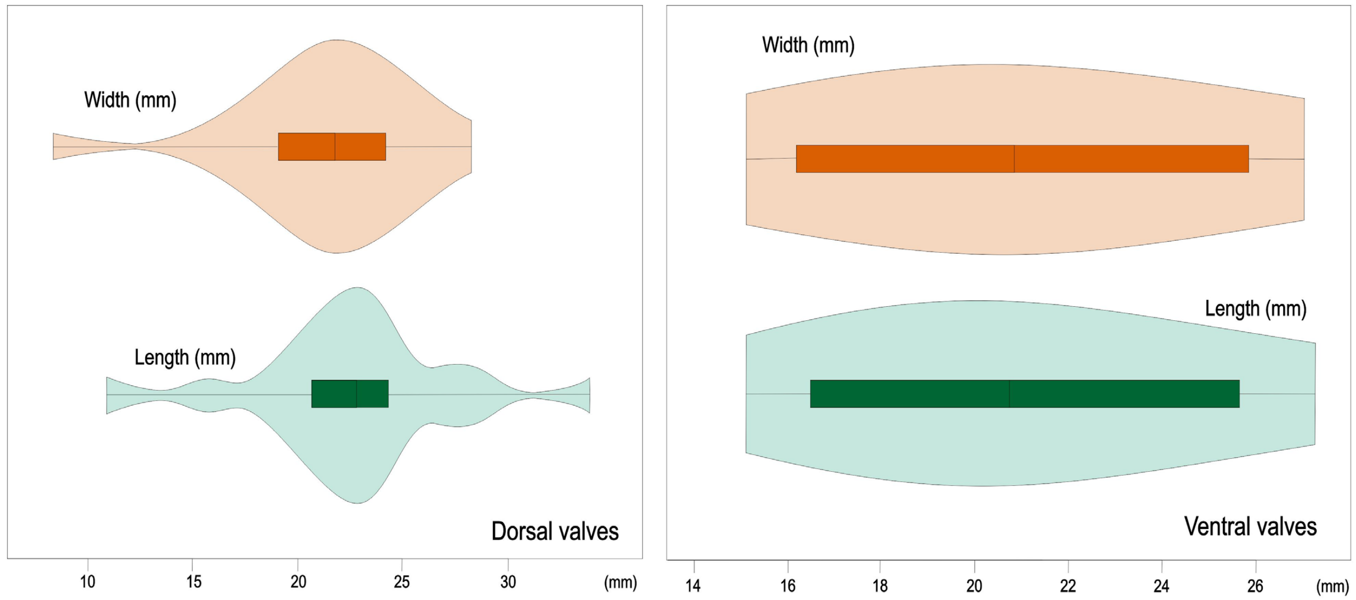

Figure 4. Dimensions of *Orbiculoidea bodenbenderi* studied, variation in length and width (in millimeters) of the dorsal and ventral valves.

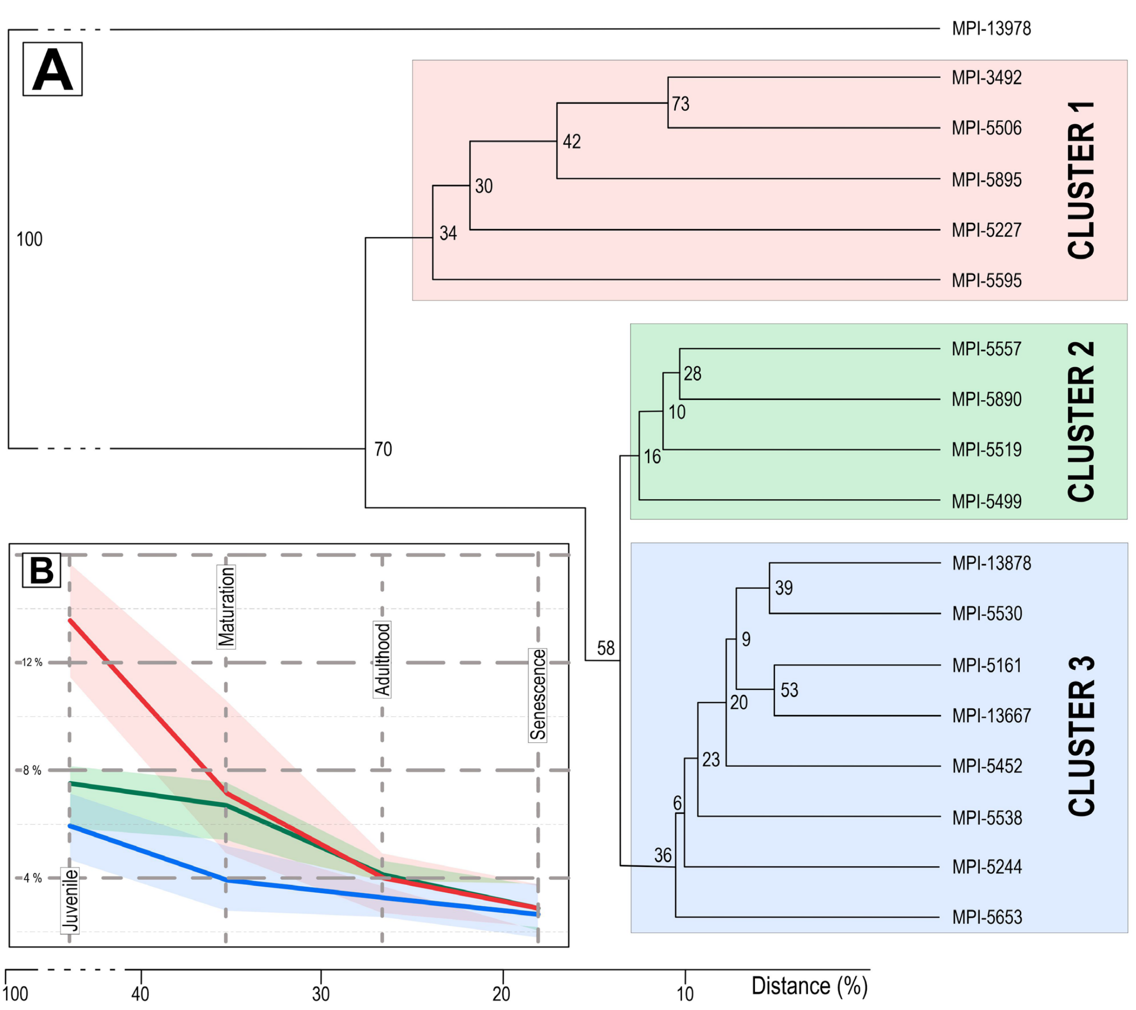

Figure 5. A, Clusters generated from the growth rates of *Orbiculoidea bodenbenderi* from the Paraná Basin. **B**, average growth (in %) in the different ontogenetic phases (juvenile, maturation, adult and senescence) with minimum and maximum amplitude per cluster.

The average growth rates in the juvenile phase are 5.87% (±1.24%), 3.85% (±1.20%) in maturation, 3.21% (±0.68%) in adulthood and 2.60% (±1.08%) in senescence, indicating a trajectory of early decline (Figure 5B). Sample MPI-13978 was isolated from the others, as it was the only one that presented an anomalous growth peak in the adult phase (average of 11.64%), contrasting with the expected ontogenetic patterns.

DISCUSSION

During the Emsian, southwestern Gondwana experienced a significant change in the oxygenation in epicontinental waters, which can be recorded in the Paraná Basin. This event was driven by an extensive marine transgression, initially documented by the deposition of the upper unit of the Furnas Formation, characterized by conglomeratic sandstones that represent the progressive flooding of the continental shelf (Sedorko *et al*., 2018a, 2019; Vargas *et al*., 2020; Rocha *et al*., 2023). The apex of this transgression, marked by the Maximum Flooding Surface (MFS), is identified in the Jaguariaíva Member (Ponta Grossa Formation) by thick layers of laminated black shales, siltstones, and mudstones (Assine *et al*., 1994; Assine, 2001; Bergamaschi, 1999; Vargas *et al*., 2020). These sediments reflect a deep shelf environment with reduced hydrodynamic energy below the storm wave base. The combination of high total organic carbon (TOC, reaching up to 2.28%) and drastically suppressed bioturbation (Bioturbation Index around zero to two) confirms the dysoxic to anoxic conditions (Bergamaschi, 1999; Horodyski *et al*., 2014; Vargas *et al*., 2020; Rocha *et al*., 2023) (Figure 6). The Emsian transgression in the Paraná Basin correlates with global events, such as the Zlichov event, characterized by high biological productivity in marine environments under reducing geochemical conditions (Peters *et al*., 2005; Haq & Schutter, 2008; Sedorko *et al*., 2018a, 2019).

Although this transgression established a domain of fine-grained pelagic sedimentation, the Emsian was not monotonous in the Paraná Basin. Short-term eustatic fluctuations, superimposed on the long-term transgressive trend, generated cyclicity and allowed for occasional transgressive moments (Bergamaschi, 1999; Vargas *et al*., 2020). These regressions are marked in the storm sandstones, indicating the influence of storms in zones between the fair-weather and storm-weather wave bases. Ichnologically, these regressions are evidenced by the alternation of intensely bioturbated proximal ichnofacies and slightly bioturbated distal ichnofacies (Sedorko *et al*., 2018a, 2019). In Transgressive System Tracts (TST), episodic storms are fundamental because they act as dynamic agents in the preservation of fossils, reworking sediments and bioclasts in the most diverse environments, from the upper coast to the transitional coast (Zabini *et al*., 2010; Sedorko *et al*., 2018b). For *Orbiculoidea*, that dominated silty habitats on the coast, this transport was fundamental for preservation, transporting their valves to distal zones, generating fragmented and disjointed parautochthonous accumulations, oriented parallel to stratification, without hydraulic selection (Zabini *et al*., 2010).

The vertical distribution of fossils in the Rivadávia Farm Section, where Bergamaschi (1999) defined the Maximum Flooding Surface (MFS) of the basin from the Praguian-Emsian, reveals a taphonomic and paleoecological pattern related to transgressive depositional variations. At the base, there is a diverse assemblage composed of brachiopods (*Australocoelia tourtelloti*, *Australostrophia mesembria*, *Australospirifer* sp., *Derbyina whitiorum*, *Coelospira* sp.), mollusks (cricoconarids, *Tentaculites crotalinus*, *T. jaculus*, bivalves *Nuculites* sp. and *Palaeoneilo* sp., gastropods *Plectonotus* sp. and *Belerophon* sp.) and trilobites (*Phacopida*). In this interval, the bioclasts are highly fragmented and disarticulated as a result of the energetic action of the lower shoreface.

At the top of the section, there is the domain of *Orbiculoidea* (95%) with sparse occurrences of lingulids, where the bioclasts are preserved intact and articulated, indicating low-energy conditions and the absence of post-depositional reworking (Bosetti, 2004). The large number of *Orbiculoidea* in anoxic conditions may be associated with post-mortem transport, with morphometric evidence indicating preferential selection by size, but with little or no fragmentation. The dorsal and ventral valves of *O. bodenbenderi* studied in this work have similar dimensional proportions between them. The dorsal valves average 22.96 mm (length) by 21.240 mm (width), while the ventral valves measure 20.953 mm (L) by 20.971 mm (W). Statistical tests (Shapiro-Wilk and t-test) confirm the absence of significant differences in dimensions between valves, suggesting that post-mortem transport acted as a selective mechanism in bioclasts. In addition to size selection, it can also be emphasized that all valves were disarticulated without any sign of fragmentation or abrasion.

The sample MPI-13978, found at the same stratigraphic level as the others, exhibits a significant discrepancy in the growth rates, characterized by exceptional adult phase (11.64%). This pattern contrasts sharply with expected ontogenetic models, in which high rates are biologically plausible only in juvenile stages. This anomaly can be attributed to post-traumatic shell regeneration processes, where physical damage (*e.g.*, predation, abrasion, or bioerosion) triggers compensatory growth mechanisms. Alternatively, diagenetic factors, such as sedimentary compaction, can generate physical deformations capable of simulating atypical growth patterns. The specimen (MPI-13978) requires a thorough approach, even with a high distance (100%) from the other valves. However, its isolation does not impact the reliability of the other clusters (1, 2 and 3), precisely because this specimen belongs to an outgroup.

Growth rates and cluster analysis of brachiopods (*Orbiculoidea bodenbenderi*) indicate the occurrence of generational mixing, with apparently homogeneous individuals presenting distinct rates. Cluster 1 contains individuals with high metabolic investment in the juvenile phase, reflected in the high rates of the first growth lines. In this initial phase, accelerated shell expansion and biomass acquisition are essential to fortify structures, resist environmental pressures, and enable survival in paleoenvironments (Banerjee

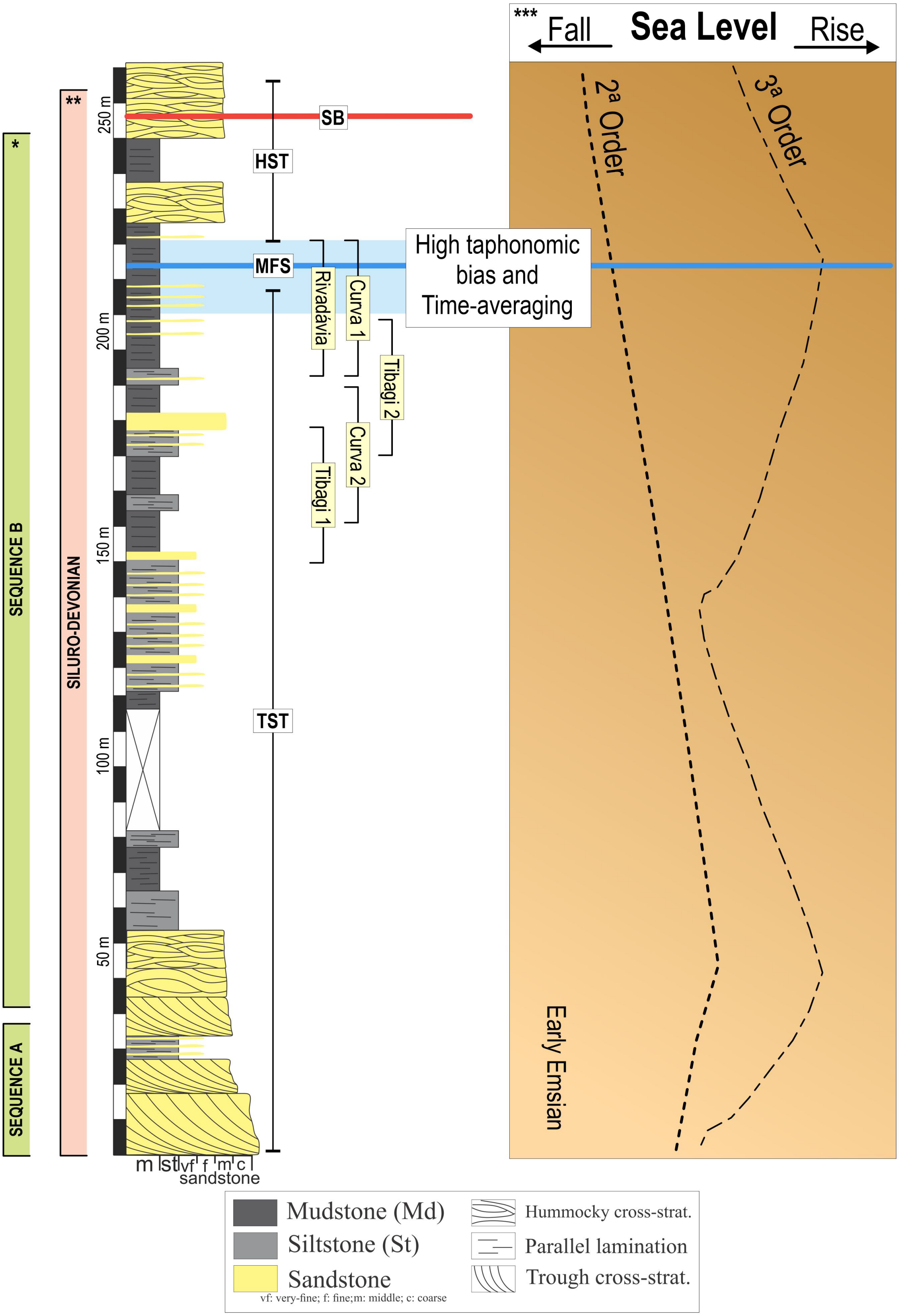

Figure 6. Composite section of the Emsian Transgressive System Tract (**TST**) of the Paraná Basin with the studied localities, associated with the eustatic sea level curves. **Abbreviations: MFS**, Maximum Flooding Surface. **HST**, High System Tract. **SB**, Sequence Boundary. (*Bergamaschi, 1999; **Sedorko *et al*., 2018a; *** Vargas *et al*., 2020).

& Kidwell, 1991). On the other hand, Cluster 2 contains specimens with a progressive deceleration in growth trajectory, with a gradual transition to metabolic stabilization. This pattern may have been a response to paleoenvironmental changes that occurred during the Emsian sea level rise. In the final stage of the TST, close to the Maximum Flooding Surface (MFS), nutrient dilution and the absence of oxygen tend to cause a metabolic reduction, prioritizing longevity (Kidwell, 1991a, b; Ritter & Erthal, 2016). Finally, Cluster 3 includes those fossils with residual or absent growth rates, whose development was minimal or nonexistent. The absence of significant increases suggests a metabolic impairment associated with energy reallocation for maintenance rather than development. This configuration positions Cluster 3 as an individual group, associated with restrictive niches or limiting conditions, differently from the accelerated (Cluster 1) and intermediate (Cluster 2) growth profiles previously described. This tripartition (clusters 1, 2, and 3) and coexistence of individuals that underwent different ontogenetic processes suggest the occurrence of time-averaging, or generational mixing, of brachiopods in the Rivadávia Section (Walker & Bambach, 1971; Ritter & Erthal, 2016).

Time-averaging (or generational mixing) consists of the accumulation of non-contemporary biological remains in the same sedimentary layer, producing fossil associations with distinct temporal intervals, related to imbalances between sedimentation rates and bioclastic input (Kidwell, 1991a, b; Kidwell & Bosence, 1991; Kowalewski, 1996; Olszewski, 1999). When sedimentation is slow, as is the case in the Rivadávia Section, the bioclasts remain exposed at the sediment-water interface, the taphonomically active zone (TAZ), and biological and physical processes act for prolonged periods (Kidwell, 1985, 1986, 1989). This mixing can be positive, increasing species richness and eliminating seasonal variations, or negative, decreasing morphological variations and reducing temporal resolution (Fürslch & Aberhan, 1990; Kidwell & Flessa, 1995; Kowalewski, 1996; Tomašových & Kidwell, 2009).

The Pragian–Emsian Transgression in the Paraná Basin, a high-level event controlled predominantly by global eustasy, recorded its Transgressive Maximum in the black and gray shales. This deposition of organic-rich sediments occurred in a distal offshore environment under calm waters, favoring reducing conditions (anoxic to dysoxic) in the marine substrate, with oxygenation restricted to the water-sediment interface during the period of maximum flooding (Bergamaschi, 1999; Bergamaschi & Pereira, 2001; Vargas *et al*., 2020; Rocha *et al*., 2023). The low sedimentation rate (order of cm/ka) during the TST, associated with anoxic conditions and low bioturbation, favored fossil preservation, although with limited diversity (Sedorko *et al*., 2018c). This sedimentary scenario resulted in a condensed deposit (Kidwell, 1985, 1986; Kidwell, 1991b), characterized by extremely low sedimentation rates near the MFS, where the layers accumulate thousands of years of paleontological information with high time-averaging and environmental condensation (Flessa & Kowalewski, 1994; Kidwell, 2002).

According to Carroll *et al*. (2003), brachiopod shells can accumulate over millennia in the marine substrate, over approximately 3,200 years. Prolonged preservation is facilitated by shallow burial in sediments, which minimizes exposure to destructive processes, allowing postmortem persistence for millennia. Spatial heterogeneity is striking while shallow sites exhibit limited time-averaging, deeper areas record extensive mixing (*e.g.*, Ritter *et al*., 2023). Time-averaging acts as a positive bias, increasing the number of species and creating an artificial diversity number at the top of the outcrop, as reported by Bosetti (2004). However, after the cluster analyses, it is possible to infer that brachiopods (*Orbiculoidea bodenbenderi*) underwent distinct ontogenetic processes, some with accelerated growth in the juvenile phase (Cluster 1), others with slowing growth throughout their lives (Cluster 2), and a third group where growth was minimal or nonexistent (Cluster 3). The coexistence of these animals in the same fossil layer would only be possible if there was temporal mixing, since their distinct growth refers to distinct ontogenetic pasts.

CONCLUSIONS

The deposition of laminated black shales at the transgressive apex (Maximum Flooding Surface - MFS), under dysoxic to anoxic conditions and below storm wave base, promoted the preservation of bioclasts. This is evidenced by the dominance of *Orbiculoidea bodenbenderi* with articulated and intact valves, contrasting sharply with the high fragmentation and disarticulation observed at the basal levels deposited on the lower shoreface. The postmortem transport of *O. bodenbenderi* from silty coastal habitats to distal zones is morphometrically evidenced, as there is significant selectivity in the dimensions between dorsal and ventral valves, resulting from size selection during transport.

The low sedimentation rate during the TST, especially near the MFS, associated with reduced bioturbation, resulted in highly condensed deposits, allowing time-averaging, agglutinating non-contemporary organisms in the same sedimentary context, and staying in the TAZ for long periods. Analysis of growth rates and clusters of *Orbiculoidea bodenbenderi* provides robust evidence for this phenomenon. The coexistence of individuals that underwent distinct ontogenetic processes (Clusters 1, 2, and 3) in the same sedimentary context is incompatible for a single population. These divergent patterns are responses to distinct paleoenvironmental conditions over a significant temporal interval, possibly millennia, that were taphonomically mixed. Time-averaging acted as a positive bias at the end of the Emsian, increasing species richness by amalgamating individuals from different generations and microhabitats.

The taphonomic processes recorded in the Jaguariaíva Member are intrinsic to the sedimentary dynamics of a transgressive system that culminates in deep-sea conditions. Time-averaging, demonstrated by the coexistence of *Orbiculoidea bodenbenderi* with distinct ontogenetic histories within the same temporal window, constitutes an important taphonomic implication.

A fossil assemblage does not represent an ecological snapshot, but rather an amalgamated record of multiple generations of individuals, uniting hundreds to thousands of years of paleobiological and paleoenvironmental information. This emphasizes the importance of detailed taphonomic analysis, integrating sedimentological, paleoecological, and ontogenetic data, for an accurate paleoenvironmental interpretation.

In summary, the fossil association of *Orbiculoidea bodenbenderi* at Rivadávia Farm is the result of distinct taphonomic processes associated with the sedimentary dynamics of the top of the Emsian transgressive system tract of the Paraná Basin. The brachiopods (*O. bodenbenderi*) from the Paraná Basin, were subjected to distinct ontogenetic and paleoenvironmental conditions, revealing three divergent growth strategies. Some organisms exhibit high juvenile growth rates with a sharp decline until senescence (Cluster 1), reflecting intense initial energy allocation. Others exhibit a conservative pattern (Cluster 2), with gradual reduction in rates and low intrastage variability, while a third group demonstrates early decline (Cluster 3), moderate rates during juvenility, and pronounced stagnation after maturation. The coexistence of these distinct individuals at the same sedimentary level is the result of time-averaging, measured from growth rates.

DATA AVAILABILITY STATEMENT

Supplementary data (Tables 1 and 2) are available.

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AUTHOR CONTRIBUTIONS

Victor Rodrigues Ribeiro: conceptualization, methodology, formal analysis, investigation, resources, writing - original draft, visualization. Renato Pirani Ghilardi: resources, writing - review and editing, visualization, project administration, funding acquisition. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

Supplementary material accompanies this paper.

SupplementaryData 1 – Table 1.

SupplementaryData 2 – Table 2.

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