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Schellwienella amazonensis (Orthotetida, Brachiopoda): New species of the genus in the Lochkovian of the Amazonas Basin (Manacapuru Formation), northern Brazil

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ABSTRACT

The Devonian was a critical period in the global evolution of brachiopods, during which the phylum reached its maximum diversity in the Emsian and experienced a significant decline during the Frasnian–Famennian, second only to the mass extinction of the Late Permian. The brachiopod fauna of the Manacapuru Formation (Lochkovian) was unknown until 2011, when a significant number of Rhynchonelliformea and Linguliformea samples were recovered during paleontological salvage at the Belo Monte hydroelectric plant in Vitória do Xingu, Pará, Brazil. This study aims to identify the Orthotetida from this salvage. The taxonomic study of the brachiopods from the Manacapuru Formation (Lochkovian) led to the recognition of a new species, *Schellwienella amazonensis* n. sp., Family Pulsiidae Cooper and Grante, 1974. *Schellwienella amazonensis* n. sp. and *Schellwienella marcidula* Amsden, 1958 originally described to the Bois d'Arc Formation (Lochkovian), USA are the oldest records of the genus. The genus *Schellwienella* was present throughout all stages of the Devonian, primarily in the Gondwana siliciclastic marine environments, transiting between temperate and polar latitudes, and disappeared in the Viséan (early Carboniferous) under warmer waters and carbonate platform conditions typical of low-latitude regions.

1. Introduction

Brachiopods are marine macroinvertebrates formed by two asymmetric valves of organophosphate or organocarbonate composition (Williams et al., 2007). During the Devonian, there was a significant increase global in genera diversity, mainly of the Sub-Phylum Rhynchonelliformea, probably caused by favorable environmental conditions, such as the expansion of shallow seas in several regions of northwestern Gondwana and by the increase in temperatures (Williams et al., 2007; Torsvik and Cocks, 2013; Harper et al., 2017).

Climate, tectonic, and evolutionary dynamics marked the paleocontinents Gondwana and Laurussia during the Devonian (Dowding et al., 2021). The distribution of marine invertebrates such as brachiopods, corals, trilobites, and gastropods suggests global patterns of bioregionalizations mainly for the Early – Middle Devonian (Boucot et al., 1969; Penn-Clarke and Harper, 2021). During this period, the Amazonas and Llanos basins were part of the Venezuela-Colombia Province, a biogeographic area of the Eastern Americas Realm (Oliver, 1977); Boucot et al., 2001). Recently, Penn-Clarke and Harper (2021) grouped the Amazonas and Parnaíba basins into the second-order Amazonian (60°S–50°S) biogeographic area located between the bioregions Malvinoxhosan (90°S–70°S) and Colombian-West African (50°S–30°S); in the Amazonas Basin, the brachiopod fauna is predominated by elements from the Eastern Americas while the fauna of the Parnaíba Basin is composed of a mix of Eastern Americas-Malvinokaffric elements.

With the advancement of taxonomic identifications, paleobiogeographical studies of invertebrates have undergone refinement. In the Amazonas Basin, studies of Devonian brachiopods began in the late 19th century, with identifications based on material collected during the "Morgan Expeditions (1870–1871)" and the "Imperial Geological

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Commission of Brazil (1876)". These expeditions primarily focused on the Maecuru (early Eifelian) and Ererê formations (late Eifelian). This fauna were first identified by Derby (1877), Rathbun (1878), Clarke (1899), and Katzer (1897), and later revised by Carvalho (1975), Melo (1985), Fonseca (2004) and Fonseca (2004).

However, the brachiopods of the Manacapuru Formation (Lochkovian) are poorly known, probably due to the lack of significant collections and the few outcrop exposures of this unit. In the northern part of the basin, there are records of sporadic occurrences of Lingulida in an outcrop of the Manacapuru Formation in the municipality of Presidente Figueiredo, state of Amazonas, Brazil (Rocha et al., 2019). On the southern margin of the basin, specimens of Lingula sp. are cited by Grahn and Melo (1990) in a core borehole in the Belo Monte region, municipality of Vitória do Xingu, state of Pará. Recently, around 3,715 samples of paleozoic fossils were recovered, including plant remains, ichnofossils, graptolites, mollusks, arthropods, agnatha, and palynomorphs; Tomassi et al. (2015a) highlighted a significant number of brachiopods found in the Manacapuru Formation, in the Belo Monte region, that is composed of *Lingula* sp., *Orbiculoidea baini*, *Orbiculoidea bondenbenderi*, *Orbiculoidea excentrica*, *Orbiculoidea xinguensis*, *Orbiculoidea katzeri* (Grahn and Melo, 1990; Tomassi et al., 2015a; Corrêa and Ramos, 2023). This is the first record of rhynchonelliformes to the Manacapuru Formation.

Rhynchonelliformeas are record in almost all Devonian units of the Amazonas Basin, except for the Manacapuru, Jatapu, and Curiri formations (Corrêa and Ramos, 2023). To identify the brachiopods from the Manacapuru Formation is fundamental to understanding the evolutionary aspects of this group throughout the Devonian and to helping analyze the paleobiogeographic distribution of these organisms. This research aims to conduct a taxonomic identification of Orthotetida specimens from the Manacapuru Formation, southern margin of the Amazonas Basin, municipality of Vitória do Xingu - Pará, besides discussing the stratigraphic and geographic distribution of the genus *Schellwienella*.

2. Geological settings

The intracratonic Paleozoic Amazonas Basin is located in the northern region of Brazil (Fig. 1A) and covers an area of approximately 500,000 km^2, distributed among the states of Amapá, Amazonas, and Pará (Klemme, 1980; Cunha et al., 1994). It is separated from the Solimões and Marajó basins by the Purus and Gurupá arches, north limited by the Guiana Shield and south by the Brazilian Shield (Cunha et al., 2007). The sedimentary infill consists of two first-order mega-sequences: Paleozoic and Meso-Cenozoic (Matsuda et al., 2010). The Paleozoic mega-sequence includes 3 s-order sequences: Ordovician-Devonian, Devonian-Mississipian, and Pennsylvanian-Permian sequences (Cunha et al., 2007). The Ordovician-Devonian sequence comprises rocks from the Trombetas Group, which registers the early depositional phase in the intracontinental syncline of the Amazonas Basin, characterized by transgressive-regressive pulses. The Trombetas Group comprises the Autás-Mirim, Nhamundá, Pitinga, Manacapuru, and Jatapu formations (Fig. 1B).

The Manacapuru Formation registers the Siluro-Devonian transition

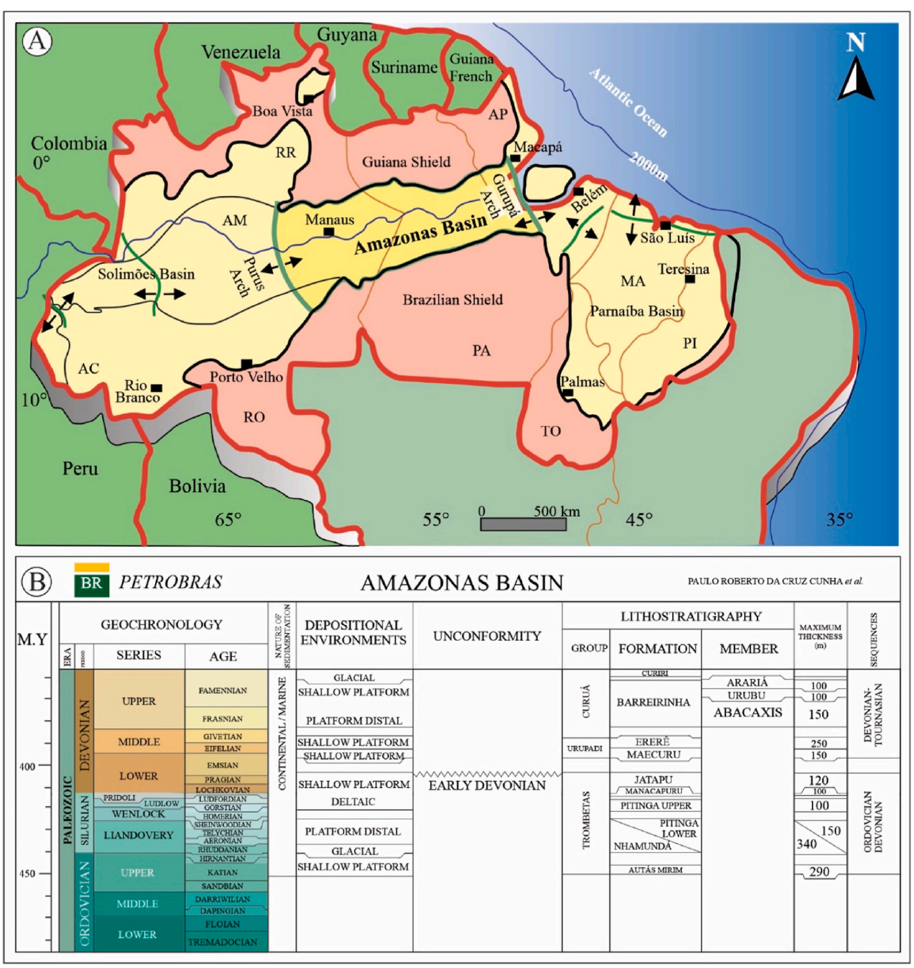

Fig. 1. Location of the Amazonas Basin; b) Cronostratigraphic chart of the Amazonas Basin, highlighting the Trombetas Group. Source: a) Cunha (2000); b) Cunha et al. (2007).

in the Amazonas Basin (Grahn, 2005). It is characterized by fine to medium-grained sandstone, neritic and littoral pelites, shales, and laminated siltstone, deposited in a deltaic and shallow marine environment during the Pridoli–Lochkovian interval (Carozzi et al., 1973; Caputo, 1984; Grahn and Melo, 1990; Cunha et al., 1994, 2007; Grahn, 2005; Souza and Nogueira, 2009). The fossiliferous content includes brachiopods, cnidarians, eurypterid fragments, ichnofossils, palynomorphs, and fish (Quadros, 1985; Janvier and Melo, 1988; Grahn and Melo, 1990; Grahn, 2005; Wanderley Filho et al., 2005; Steemans et al., 2008; Tomassi et al., 2015a, 2015b Rocha et al., 2019; Corrêa and Ramos, 2021, 2023).

Taking into account the lithological, palynological, and fossil content presented by Tomassi et al. (2015a, 2015b), in addition to the sedimentary and biostratigraphic data from well SR-17 (located in the Belo Monte region) studied by Grahn and Melo (1990), the studied outcrops are positioned in the upper portion of the Manacapuru Formation. According to the literature, the lower portion of this unit is attributed to a deltaic environment without occurrence of macrofossils, while the upper portion is associated with a shallow platform environment (Carozzi et al., 1973; Cunha et al., 2007; Rocha et al., 2019). The marine habitat of the studied brachiopods assemblage (Clarkson, 1992; Williams et al., 2007) recorded in the upper portion of the Manacapuru Formations attest this information.

3. Material and methods

The material investigated was collected by the Terragraph Paleontologia team during the paleontological rescue at the Belo Monte Hydroelectric Powerplant in Vitoria do Xingu, state of Pará (Fig. 2), between July 2011 and October 2015. The type material and additional totalizing 162 valves, from 80 fossil samples are housed in the Museu Goeldi Paleontological collection under the cathalog numbers MPEG-3686-I, MPEG-3761-I to MPEG-3838-I, MPEG-4156-I, and MPEG-4157-I. More information about the sampling are described in Tomassi et al. (2015a,b).

The specimens come from three points of the Manacapuru Formation and most of them were collected at the base of the laminated siltstone layer in the C3P1-1 and C13P1-1 sections, with sporadic occurrence in the massive sandstone layer from C14P1-1 (Fig. 3). In addition, four samples of orthotetids (MPEG-0018, MPEG-0026, MPEG-0029, and MPEG-0053) from the Maecuru Formation and three (MPEG-0159, MPEG-0214, and MPEG-0830) from the Ererê Formation, housed in the Museu Goeldi Paleontological Collection, were also examined to comparative studies.

All samples were examined under a stereoscopic microscope, and measurements were taken using a caliper. Photographs were captured using a camera attached to the Stereomicroscope LEICA S8 APO. Latex casts were made to evaluate properly the internal features of some specimens. Systematic classification and morphological terminology mainly follow terms applied by Williams and Brunton in Williams et al. (2000), Stigall Rode (2005), Bassett and Bryant (2006), and Rezende and Isaacson (2021).

4. Results

The most of studied material is represented by molds internal, external, countermolds, and composite molds, all disarticulated, with good preservation; valves generally entire or with a low degree of fragmentation, preserving internal characteristics such as dental plates, median septum, muscular scars, and in some specimens, a second laminar layer with pseudopunctation.

4.1. Systematic paleontology

Class Strophomenata Williams et al., 1996

Order Orthotetida Waagen, 1884

Suborder Orthotetidina Waagen, 1884.

Superfamily Orthotetoidea Waagen, 1884.

Family Pulsiidae Cooper and Grant, 1974

Genus *Schellwienella* Thomas, 1910

Type species. — *Spirifera crenistria* Phillips (1836). Lower Carboniferous (Pendleside Limestone Group, Viséan) of Bowland, Yorkshire, England.

Schellwienella amazonensis new species

Figs. 5–9.

Etymology: Related to the geographic (Amazon) and geological (Amazonas Basin) region from which the species was collected.

Types: Holotype: MPEG-3761-I; Paratypes: MPEG-3774-I, MPEG-3767-I, MPEG-3786-I, and MPEG-3827-I.

Type horizon: Manacapuru Formation (upper unit).

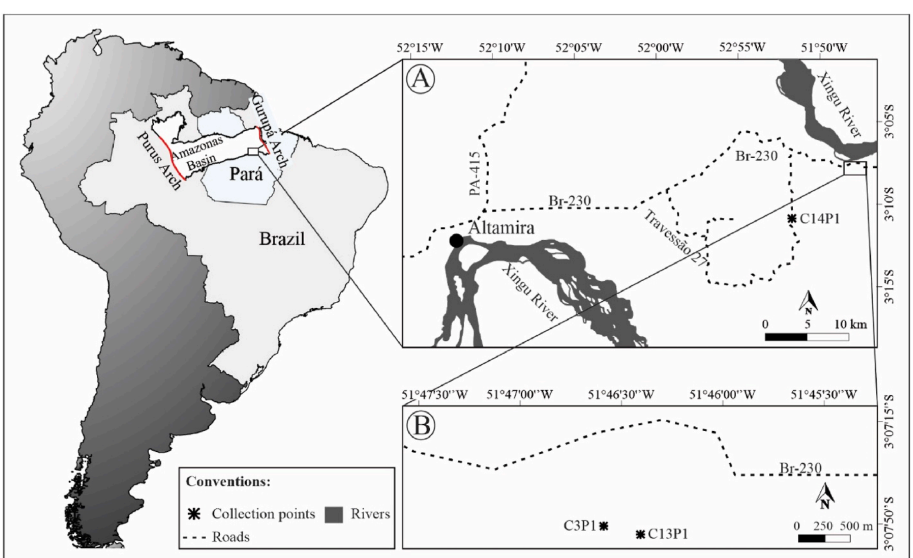

Fig. 2. The study area location. Source: Corrêa and Ramos (2021).

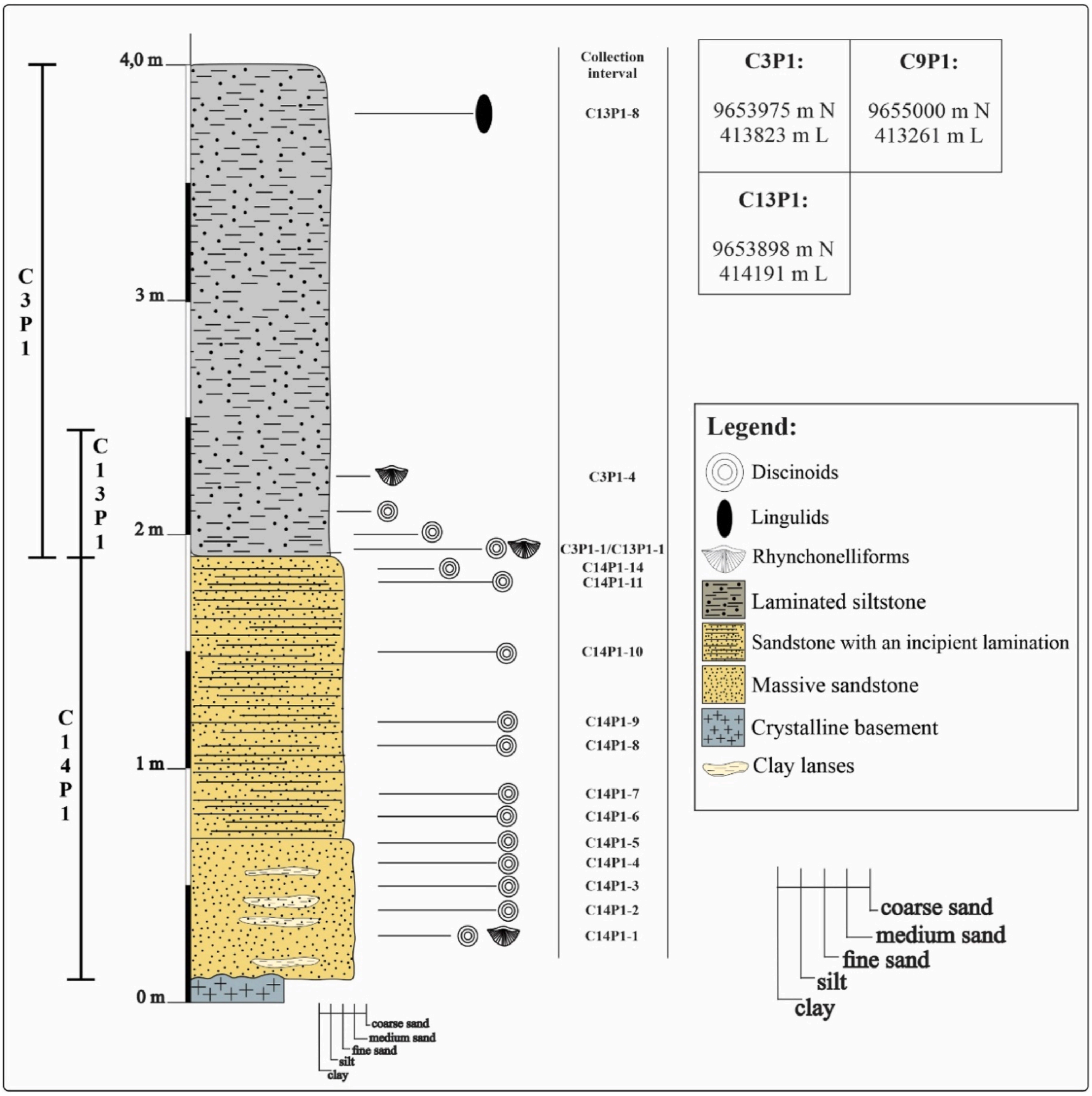

Fig. 3. Composed stratigraphic section, Manacapuru Formation. Source: Corrêa and Ramos (2021).

Type locality: Laminated siltstone in section C13P1, Manacapuru Formation (upper sequence), Amazonas Basin.

Material: 100 ventral valves (44 external and 56 internal); 62 dorsal valves (44 external and 18 internal). More details **in supplementary material 1**.

Dimensions: Holotype: MPEG-3761-I (w: 9.6 mm; l: 7.6 mm); paratypes: MPEG-3774-I (fragmented), MPEG-3767-I (w: 7.5 mm; l: 5.2 mm), MPEG-3786-I (w: 9.7 mm; l: 7.1 mm), and MPEG-3827-I (w: 14.8 mm; l: 10.5 mm). Measurements of ventral and dorsal valves are represented in Fig. 4. Complete measurement data available **in supplementary material 1**.

Diagnosis: Dorsibiconvex shell, short dental plate anteriorly divergent, ventral muscle field triangular separated by a median septum of approximately ½ the length of the valve. Parvicostellate ornamentation, with growth lines irregularly spaced and pseudopunctation in an apparently random pattern.

Occurrence: Sections C3P1, C13P1, and C14P1, located at Sitio Belo Monte, municipality of Vitoria do Xingu, State of Para, Brazil. Manacapuru Formation (Lochkovian), Amazonas Basin.

Description: Shell subcircular to circular in outline, dorsibiconvex. Small to medium size, width (w) varying from 6.9 mm to 24.1 mm and length (l) from 4.7 mm to 20.1 mm. Hinge line straight to weakly triangulate. Shell surface parvicostellate, with costae originating in the apex and costellae by intercalation, with reduced interspace. Growth lines appear irregularly spaced, more frequent as it approaches the anterior rectimarginate commissure. The sectioning by the growth lines causes in some specimens, an ornamentation pattern by multiplication (Fig. 9E). 15 costellae in average per 5 mm^2 in the anterior region. The proportion of length to a width is about 0.68–0.83. Ventral valve (Fig. 5A–O) weakly convex near the umbo, flattening laterally and anteriorly to become flat, while the median portion of the valve presents a sulcus. Umbo low, beak projected only slightly beyond the hinge line. Dorsal valve (Fig. 6A–O) moderately convex, higher than the opposite valve. Greatest height at the umbo. Beak high, projected posteriorly beyond the hinge line. Pseudopunctate shell (Fig. 9C and D).

Ventral interior (Fig. 7A–O). Delthyrium triangular, closed by a pseudodelthydium (convex in shape), large, triangular-elongated hinge teeth, supported by short dental plates (24–34 percent of the valve length [n = 22]), evident, and anteriorly divergent (Fig. 9A and B), varying between 56.49° to 78.95° [n = 41], with the lowest divergence

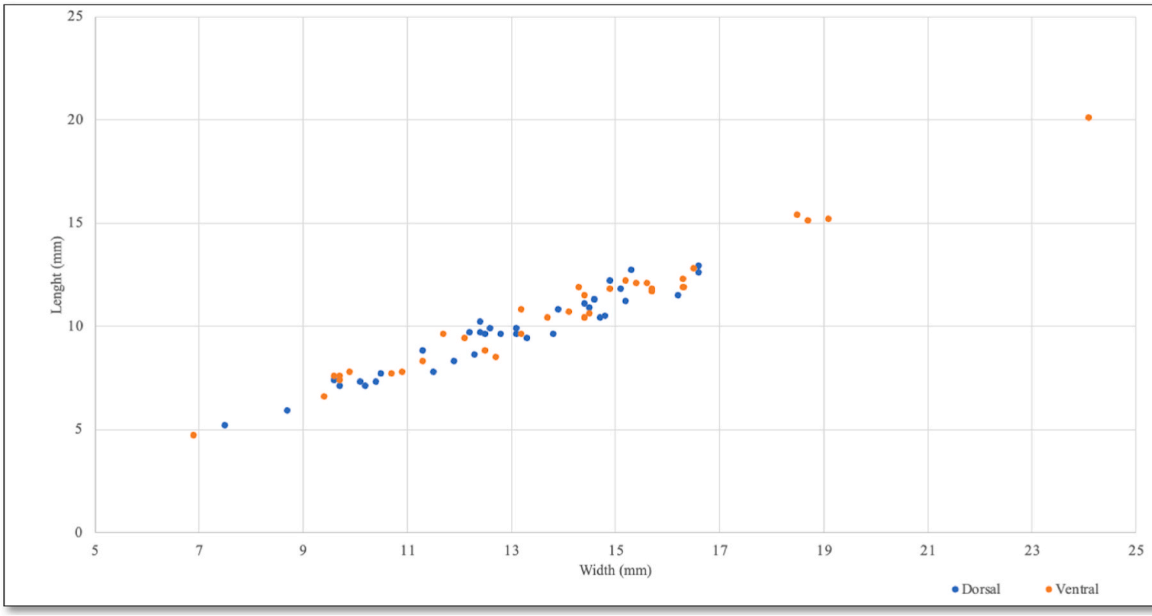

Fig. 4. Scatter diagram plotting length to width of *Schellwienella amazonensis* n. sp. from the Amazonas Basin, Brazil.

values attributed to the smallest specimens (Fig. 7A). The muscle field is triangular, composed of a subcircular to circular, anteriorly striated diductor scars (Fig. 9Aand B), that completely surrounds the lanceolate adductor scars. The field is divided by a median septum (Fig. 9A and B), reaching 40 to 51 percent of the valve's length [n = 17]. Adductor scars between the cardinal margin and mid-length of the dental plates; diductor scars larger, extend anteriorly beyond the limit of the dental plate extensions. Pseudopunctation with no distribution pattern.

Dorsal interior (Fig. 8A–L). Bilobed cardinal process, with elongate lobes (Fig. 8A and B), exposed by posteriorly open notothyrium, covered by a convex chilidium. Dental sockets are short, deep, and divergent; with angles varying between 68.66° and 75.17° [n = 11], supported by short and straight socked plates. Median septum present, splitting lanceolate adductor scars, not as marked as the one in ventral valves, extending approximately one-third the length of the valve.

Remarks: The external and internal morphological characters, such as the rectimarginate commissure, growth lines, parvicostellate ornamentation, short and divergent dental plates, muscle field triangular, and ventral muscular impressions divided by the median septum, refer to the diagnosis proposed for the genus *Schellwienella* Thomas, 1910 and to differentiate it from the other Late Paleozoic Orthotetida genera (*Schuchertella* Girty, 1904; *Floweria* Cooper and Dutro, 1982; *Eoschuchertella* Gratsianova, 1974; *Iridistrophia* Havlíček, 1965; *Schuchertellopsis* Maillieux, 1939; *Streptorhynchus* King, 1850; *Xystostrophia* Havlíček, 1965; *Derbyia* Waagen, 1884).

Similarly to what is observed in other Devonian *Schellwienella* species, intraspecific morphological variations were observed in *Schellwienella amazonensis* n. sp., that presents, in some specimens, parvicostellate ornamentation, with costellae that multiply by bifurcation (Fig. 9F), while others multiply by intercalation, increasing the number of costellae as it gets closer to the commissure, delimited by growth lines (Fig. 9E). Another common variation to *Schellwienella* species is related to the outline, which in *Schellwienella amazonensis* n. sp. varies from subcircular to circular.

Comparison with Devonian Schellwienella species. — In *Schellwienella justinianoi* Rezende et al., (2019), the profile is plano-convex, the median septum occupies 1/3 of the valve length, and the pseudopunctations have a radial distribution. In *Schellwienella clarkei*, the shells are larger (maximum length 27 mm; maximum width 38 mm), the profile ranges from biconvex to plano-convex, the dental plates have a greater divergence angle (120°–70°), and the growth lines are less pronounced. *Schellwienella goldringae* Caster (1939), the profile is convex-plano or convex-concave, the muscle field is circular with flabellate adductor scars, and the dental plates are weakly marked. Caster (1939) did not describe pseudopunctuations or median septum.

Schuchertella sulivani Morris and Sharpe (1846), and *Schuchertella sancticrucis* Morris and Sharpe (1846), were reclassified as *Schellwienella sulivani* and *Schellwienella sancticrucis* by Caster (1939). Although the author did not review the material, Caster (1939) noted that if the illustrations are reliable, all *Schuchertella* species described for the Devonian of South America and South Africa (*Schuchertella agassizi*, *Schuchertella sancticrucis*, *Schuchertella sulivani*) would belong to *Schellwienella*, due to that they all have short dental plates; however, he did not consider the other diagnostic characteristics of the genus. Subsequent works followed Caster's classification (Aldiss and Edwards, 1999; Stone, 2010, 2012, 2016; Stone and Rushton, 2013). Clarke (1913) did not describe pseudopunctations, dental plates, or a median septum, casting doubt on its identification as *Schellwienella sulivani*. The largest specimen analyzed by Clarke (1913) is more than twice the size of the largest specimen of *S. amazonensis* n. sp. In *Schellwienella clarkei,* the dorsal muscular scars are oval, and in the *S. amazonensis* n. sp. are lanceolate.

Rezende and Isaacson (2021) highlighted the similarity between the ornamentation patterns of the external molds of *Schellwienella sulivani* and *Schellwienella clarkei*, differing only in the shape of the dorsal adductor scar, which is oval in the former and lanceolate in the latter. They suggest this difference might be intraspecific variation but emphasize the need to analyze more specimens. For now, they consider it prudent to accept both as distinct species.

Schellwienella sancticrucis (Clarke, 1913) differs from *S. amazonensis* n. sp. due to its circular outline and simple costellae, which lack bifurcation or intercalation. It has a large flabellate adductor scar. Clarke (1913) stated that the limited and poorly preserved material prevents a thorough comparison with other species. Rezende and Isaacson (2021) emphasize the lack of sufficient material and the need for further studies on *Schellwienella sancticrucis*.

The comparison with *Schellwienella marcidula* Amsden (1958), *Schellwienella pauli* Gallwitz (1932), and *Schellwienella percha* Stainbrook (1947), is primarily limited to external morphology, as the internal valves of these species are scarce and poorly preserved. None of these

Fig. 5. *Schellwienella amazonensis* n. sp., external ventral valves. A) MPEG-3827-I mold; B) MPEG-3814-I mold; C) MPEG-3774-I mold; D) MPEG-3803-I mold; E) MPEG-3802-I countermold; F) MPEG-3793-I mold; G) MPEG-3761-I mold; H) MPEG-3817-I mold; I) MPEG-4157-I mold; J) MPEG-3783-I mold; K) MPEG-3790-I mold; L) MPEG-3824-I mold; M) MPEG-3801-I mold; N) MPEG-3788-I countermold; O) MPEG-3778-I mold. Scale bar: 2 mm.

species exhibit a median septum, cardinal process, or pseudopunctation. *Schellwienella marcidula*, described by Amsden (1958), has a profile ranging from plano-convex to convexo-concave. In some specimens, the width and length are approximately equal; it has fewer costellae per 5 mm^2 (9–10) and shorter dental plates. *Schellwienella pauli* differs from *S. amazonensis* n. sp. in having bigger shells (reaching at least 45 mm in width), an oval outline, and a ventribiconvex profile. Its costellae increase only by intercalation, with relatively fewer costellae per 5 mm^2 (11–13), and the anterior scars are slightly flabellate. *Schellwienella percha* differs from *S. amazonensis* n. sp. in having a subquadrate outline, a plano-convex profile, and costellae that increase only by intercalation.

Orthotetida from the Devonian of the Amazonas Basin. — The first

Fig. 6. *Schellwienella amazonensis* n. sp., external dorsal valves. A) MPEG-3774-I mold; B) MPEG-3806-I mold; C) MPEG-3810-I mold; D) MPEG-3802-I countermold; E) MPEG-3832-I mold; F) MPEG-3832-I mold; G) MPEG-3818-I countermold; H) MPEG-3894-I countermold; I) MPEG-3895-I mold; J) MPEG-3826-I mold; K) MPEG-3814-I countermold; L) MPEG-3828-I countermold; M) MPEG-3767-I countermold; N) MPEG-3834-I countermold; O) MPEG-3816-I mold. Scale bar: 2 mm.

identification of Orthotetida in the Devonian of the Amazonas Basin was carried out by Rathbun (1874) when analyzing specimens from the Ererê Formation. Rathbun (1874) proposed the species *Streptorhynchus agassizi*, describing it with a biconvex profile and a circular to subelliptical outline; the impressions of the dental plates are visible only in the hinge area beside the fissure, appearing as shallow depressions that do not extend into the valve; the cardinal process is small and thin, with two small processes on each side projecting backward; the socket plates are short, thin, and highly divergent, forming an angle of about 135°; the ornamentation of the valves consists of costellae that increase in number by intercalation or bifurcation. Clarke (1913) relocated *Streptorhynchus agassizi* to the genus *Schuchertella* based on the shapes of its costellae and

Fig. 7. *Schellwienella amazonensis* n. sp., internal ventral valves. A) MPEG-3799-I mold; B) MPEG-3778-I mold; C) MPEG-3761-I mold; D) and E) countermold of MPEG-3761-I; F) MPEG-3825-I mold; G) MPEG-3797-I mold; H) MPEG-3809-I mold; I) MPEG-3796-I mold; J) MPEG-3773-I mold; K) MPEG-3823-I mold; L) MPEG-3768-I mold; M) MPEG-3802-I mold; N) MPEG-3803-I mold; O) MPEG-3802-I mold. Scale bar: 2 mm.

size, flabelliform ventral muscular impressions. Carvalho (1972) identified specimens of *Streptorhynchus agassizi* from the Maecuru and Ererê formations when analyzing only ventral valves; the report of short and shallow dental plates complements the description made by Rathbun (1874). Carvalho (1972) compared the material studied only with the work of Rathbun (1874), ignoring the reallocation made by Clarke (1913). Copper (1977) cited the occurrence of *Schellwienella agassizi* in the Devonian of the Amazonas Basin (Maecuru and Ererê formations); however, the author did not provide any description, discussion, or illustration of the material, nor did he justify the criteria used to classify it. Rezende and Isaacson (2021) reviewed specimens of *Schuchertella agassizi* from the Paraná Basin (Ponta Grossa and São Domingos

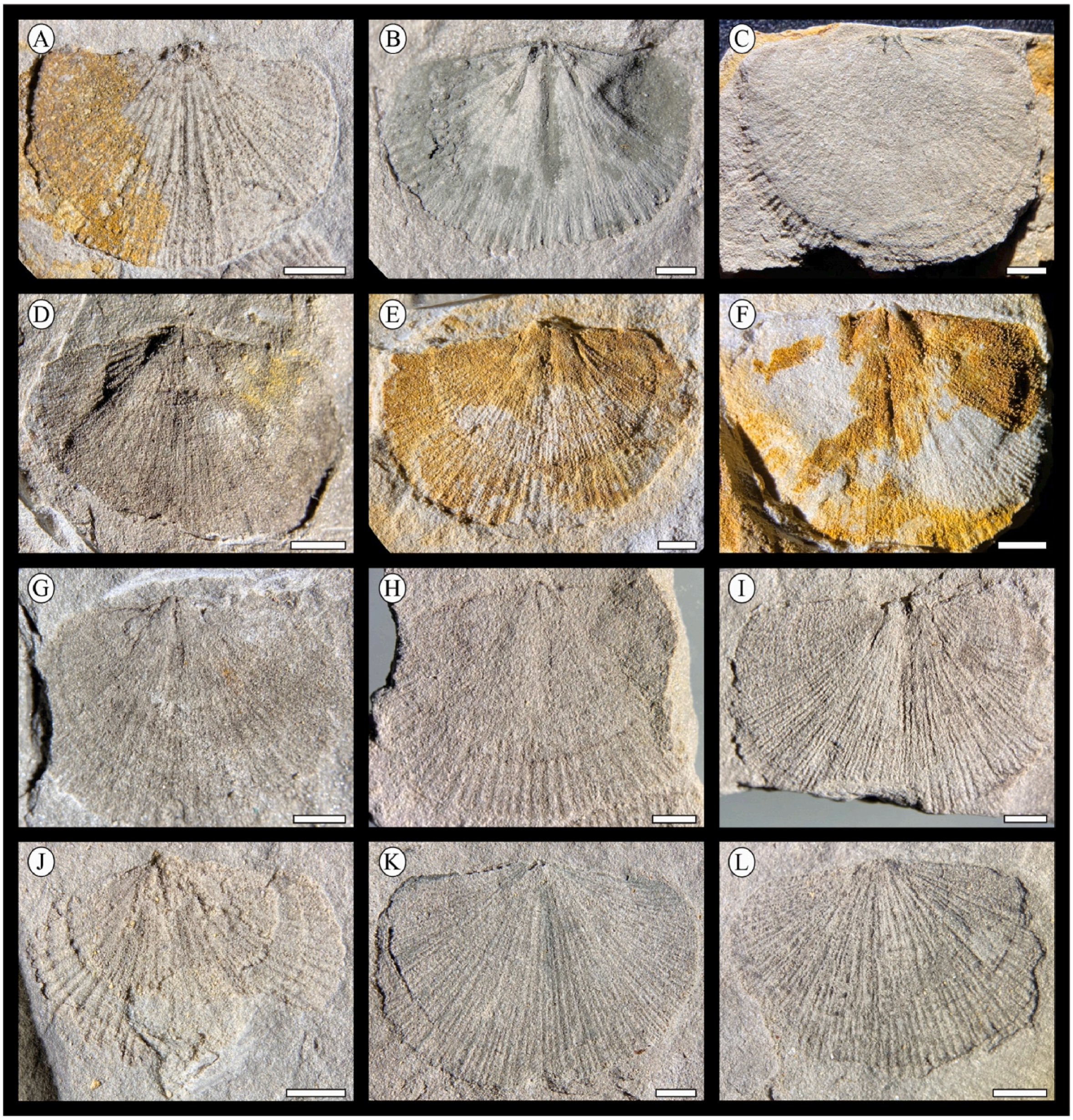

Fig. 8. *Schellwienella amazonensis* n. sp., internal dorsal valves. A) MPEG-3786-I countermold; B) MPEG-3827-I mold; C) MPEG-3767-I countermold; D) MPEG-3767-I mold; E) MPEG-3808-I mold; F) MPEG-3768-I mold; G) MPEG-3767-I mold; H) MPEG-3804-I mold; I) MPEG-3796-I mold; J) MPEG-3786-I countermold; K) MPEG-3819-I countermold; L) MPEG-3832-I countermold. Scale bar: 2 mm.

formations) and Bolivia (Icla, Belén, Gamoneda, and Huamampampa formations) and proposed the species *Schellwienella clarkei*; they report the need to review *Schuchertella agassizi* from the Amazonas Basin.

The specimens of *Schuchertella agassizi* from the Maecuru and Ererê formations, housed in the paleontological collection from the MPEG (Fig. 10A–I), are not well-preserved. Despite being fragmented, the valves of *Schuchertella agassizi* are higher and bigger than those of *S. amazonensis n. sp.* The dorsal valve has a rounded and more convex umbo when compared to the ventral valve. The costellae multiply by bifurcation and intercalation; the growth lines, weakly marked, intercalate the costellae near the anterior margin, occurring less frequently compared to *S. amazonensis* n. sp. The socket plates are short, well-marked, and divergent, with a divergence angle of 137.94°. There are no internal ventral valves in the analyzed material. Though *Schuchertella agassizi* is similar to *Schellwienella clarkei*, the absence of internal morphological characteristics, such as dental plates, median septum, bilobed cardinal process, muscle scars, and pseudo punctations, prevents its reclassification.

***Comparison with carboniferous Schellwienella species.* —** The species *Schellwienella alternata* Weller (1914), *Schellwienella burlingtonensis* Weller (1914), *Schellwienella chouteauensis* Weller (1914), *Schellwienella crenulicostata* Weller (1914), *Schellwienella inaequalis* Hall (1858), *Schellwienella planumbona* Weller (1914), and *Schellwienella rustica* Stainbrook (1950) were described based on solely external morphology, making comparison with *S. amazonensis* n. sp. impractical due to the absence of crucial internal features. In *Schellwienella inflata* White and Whitfield (1862), the profile is concavo-convex, the outline is subelliptical, and the ventral muscle scars are flabellate.

Schellwienella radialiformis Demanet (1934), has larger shells (up to 51 mm width) with a square to sub-square outline. It features fewer costellae per 5 mm^2 (7–11), and the divergence angles of the dental plates are larger than in *S. amazonensis* n. sp. (78°–93°). *Schellwienella crenistria* Phillips (1836) has a profile ranging from plano-convex to gently resupinate, with a semicircular outline. It has fewer costellae per

Fig. 9. Morphological details of *Schellwienella amazonensis n. sp.* A) MPEG-3761-I internal ventral countermold; B) MPEG-3808-I internal ventral mold; C) and D) MPEG-3797-I internal ventral mold; E) MPEG-3793-I external ventral countermold; F) MPEG-3802-I external ventral mold.

5 mm^2 (8–10), which increase only by intercalation, and the diductor are flabellate. Both *Schellwienella radialiformis* and *Schellwienella crenistria* are the only Carboniferous species that exhibit pseudopunctations.

In *Schellwienella umbonata* Easton (1958), the profile is plano-convex, the outline is semicircular, the dental plates are thin and poorly defined, and the median septum is smaller, limited to the muscle field. *Schellwienella ornata* Demanet (1934) has a ventribiconvex profile, a subquadrate outline, and costellae that increase only by intercalation, with fewer costellae per 5 mm^2 (6–7). Its dental plates are thin and diverge at a smaller angle (35°–37°). *Schellwienella cheuma* Bassett and Bryant, 2003 differs from *S. amazonensis* n. sp. by having a subcircular to subquadrate outline, dorsobiconvex profile, and multicostellate ornamentation, with fewer costellae per 5 mm^2 (12). It also has a weaker and shorter median septum, and dental plates with slightly smaller divergence angles compared to *S. amazonensis* n. sp.

5. *Schellwienella* paleobiogeographic remarks

The genus *Schellwienella* has a stratigraphic distribution that ranges from the Lower Devonian to the Lower Carboniferous (Williams et al., 2000). The oldest records include the species *S. marcidula* from the Bois d'Arc Formation (Lochkovian), USA, and now *S. amazonensis* n. sp. from the Manacapuru Formation (Lochkovian), Brazil (Amsden, 1958). During the Devonian, seven other species were present: *S. clarkei*, *S. goldringae*, *S. justinianoi*, *S. pauli*, *S. percha*, *S. sancticrucis*, and *S. sulivani* (geographic and geological location information for each species **in supplementary material 2**) (Morris and Sharpe, 1846; Clarke, 1913; Caster, 1939; Stainbrook, 1947; Sanchez and Benedetto, 1983; Biernat, 1966; Halamski and Baliński, 2009; Rezende et al., 2019; Rezende and Isaacson, 2021).

Despite the genus *Schellwienella* having a wide geographic distribution during the Devonian, a significant portion of its occurrences was

Fig. 10. "*Schuchertella*" *agassizi* from Maecuru and Ererê formations. A) MPEG-0830-I external ventral mold; B) MPEG-0159-I external ventral mold; C) MPEG-0159-II external ventral mold; D) MPEG-029-I external ventral mold; E) MPEG-029-I ornamentation details; F) MPEG-159-III external dorsal mold; G) MPEG-026-I external dorsal countermold; H) MPEG-0214-I internal dorsal countermold; I) MPGE-053-I internal dorsal countermold. Maecuru Formation: MPEG-029-I, MPEG-026-I, and MPGE-053-I; Ererê Formation MPEG-0830-I, MPEG-0159-I, MPEG-0159-II, MPEG-159-III, and MPEG-0214-I. Scale bar: 2 mm.

concentrated in Gondwana (Brazil, Bolivia, Colombia, Falkland Islands, South Africa, and Venezuela), where it inhabited siliciclastic marine environments. During the Lochkovian, the genus emerged in the Amazonas Basin, in the same stage at which it is found in Oklahoma (USA) (Amsden, 1958). It is difficult to determine whether the larvae migrated first from Laurussia (Bois d'Arc Formation) to Gondwana (Manacapuru Formation) or vice versa (Fig. 11). The first hypothesis is most likely, given that during the Ordovician and Silurian, environmental conditions in Gondwana were temperate to cold (Torsvik and Cocks, 2016); the main Paleozoic basins of Gondwana are located between the polar latitudes (60° - 90°S); evidence of the Ordovician-Silurian Glaciation are recorded in the diamictites of the Pitinga (Amazonas Basin), Iapó and Ipu (Parnaíba Basin) formations (Assine et al., 1998; Cunha et al., 2007; Barrera et al., 2020). There are no record of brachiopods from the Amazonas, Parnaíba, Jatobá, and Parecis basins in the Ordovician and Silurian. A low-diversity fauna composed of unidentified Rhynchonelliformeans, *Kosoidea australis*, ?*Palaeoglossa* sp., and Lingulidae? were the only records in the Iapó Formation (Hirnantian), exception to *Kosoidea australis* that extended to the Vila Maria Formation (Hirnantian), Paraná Basin (Zabini et al., 2019; 2021). Based in these factors mentioned above, brachiopods probably preferred warmer marine environments, from low-latitude regions as in Laurentia, as evidenced by *Orbiculoidea* (Finnegan et al., 2011; Zhang et al., 2018; Corrêa and Ramos, 2021).

Research indicates that the Devonian was a period of warm global greenhouse conditions, with latitudinal climatic belts varying between tropical (low latitudes), arid-temperate (intermediate latitudes), and cold (high latitudes) climates. (Boucot, 1988; Scotese and Barrett, 1990; Frakes et al., 1992; Copper, 1994; Sepkoski, 1996; Scotese et al., 1999; Copper and Scotese, 2003; House and Gradstein, 2004; van Geldern et al., 2006; Joachimski et al., 2009; Becker et al., 2012; Boucot et al., 2013). In the Lochkovian, the Amazonas Basin was one of the regions of Gondwana closest to Laurussia (where most of the brachiopod records were concentrated during the periods preceding the Devonian), located in temperate latitudes (60°S–30°S), with favorable shallow marine conditions. Brachiopods of the genus *Schellwienella* first settled in this basin in Gondwana and later migrated to the other basins further south.

Fluctuations in relative sea-level marked the Devonian (Ross and Ross, 1988). *Schellwienella* probably moved between the different regions of Gondwana throughout this period when sea level reached its greatest amplitude, which allowed the connection of basins and the migration of these organisms. In the Pragian, the species of this genus occupied the southwest and south of Gondwana (Bolivia, Paraná Basin, South Africa, and the Falkland Islands) in the paleobiogeographic region known as the Malvinoxhosan bioregion (former Malvinokaffric) (Boucot, 1975; Boucot et al., 2001; Penn-Clarke and Harper, 2021). This realm included subpolar and polar regions (60° S – 90° S) with cold waters (Boucot et al., 2001). Later, during the Emsian-Givetian, the genus spread to a region further from the South Pole, Northwestern Gondwana, specifically the Llanos Basin (Colombia and Venezuela).

In the Frasnian, there is a single record of *Schellwienella* (Paraná Basin), the age when the genus reached its lowest diversity and geographic amplitude. The Kellwasser Bio-Event, attributed to transgressions that caused anoxic conditions, leading to an 86% reduction in

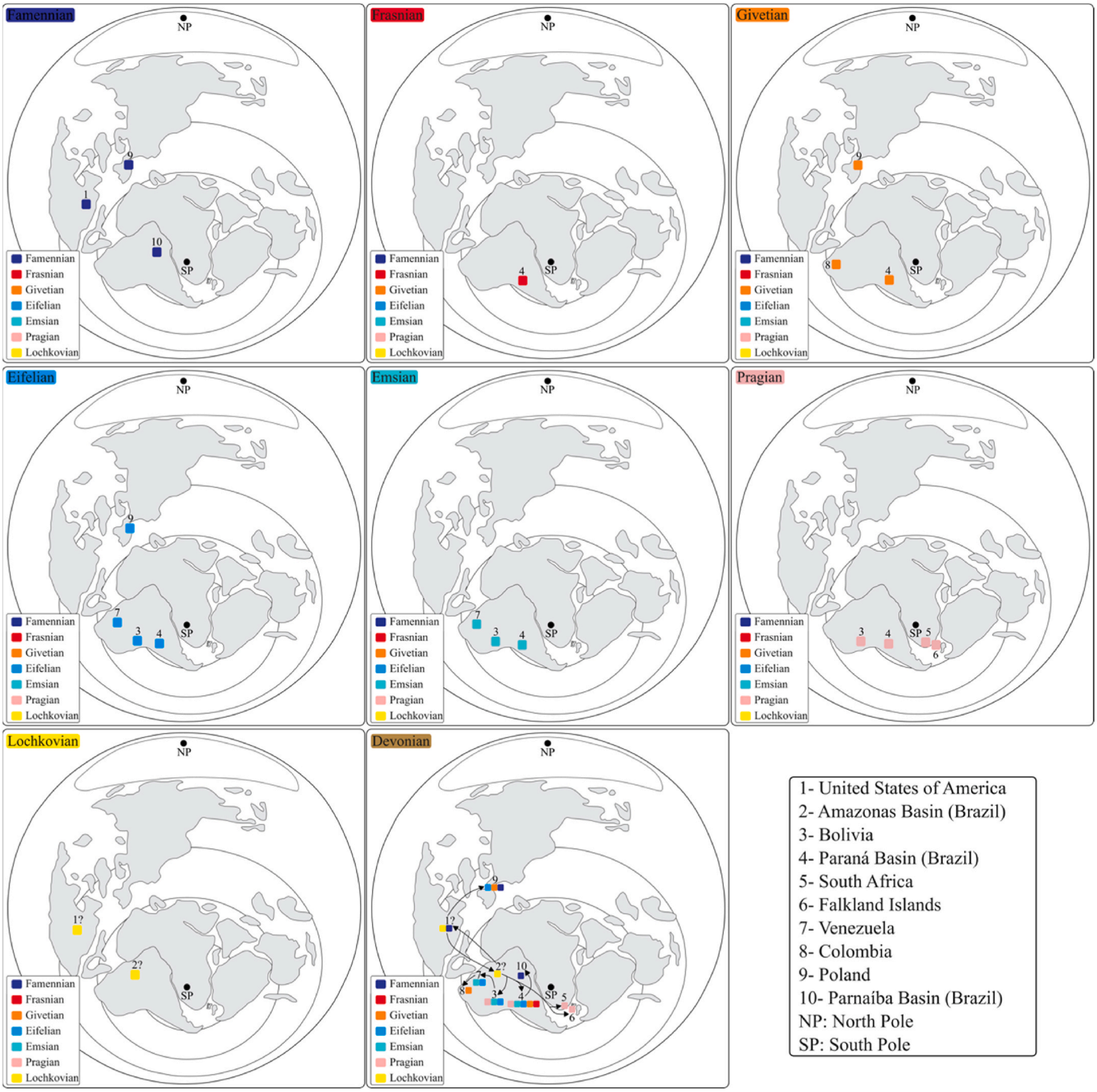

Fig. 11. Distribution of the *Schellwienella* throughout the Devonian. Base map modified from Scotese et al. (1999), Boucot et al. (2013), Ribeiro (2019), Videira-Santos and Scheffler (2024).

brachiopod diversity, occurred in this stage (Johnson, 1971; 1974; Boucot, 1973; McGhee, 1981; Sepkoski, 1996). By the Famennian, the remaining species inhabited regions near low latitudes in the USA, Poland, and Brazil (Parnaíba Basin), similar to what occurred in the Carboniferous (Tournaisian – Visean).

Schellwienella persisted after all extinction events that occurred in the Devonian, including two first-order events (Kellwasser and Hangenberg). In the Carboniferous (Tournaisian/Visean), the genus increased the number of species compared to the previous period with twenty species known for this period: *S. alternata*, *S. aspis*, *S. australis*, *S. burlingtonensis*, *S. cheuma*, *S. chouteauensis*, *S. crenistria*, *S. crenulicostata*, *S. inaequalis*, *S. inflata*, *S. izirii*, *S. minilyensis*, *S. ornata*, *S. planumbona*, *S. radialiformis*, *S. radialis*, *S. rustica*, *S. scotica*, *S. umbonata*, and *S. weaberensis* (geographic and geological location information for each species **in supplementary material 2**) (Weller, 1914; Smyth, 1930; Stainbrook, 1950; Minato, 1951; Easton, 1958; Thomas, 1971; Gratsianova, 1974; McIntosh, 1974; Roberts and Oversby, 1974; Yugan and Waterhouse, 1986; Wendt et al., 2002; Bassett and Bryant, 2006; Mottequin and Simon, 2017; Tazawa, 2020). This radiation of the genus that occurred in the Mississippian is probably related to the behavior of these organisms post-events biotic, such as reduced competition, freeing up of niches, and adaptive radiation. Other group also underwent adaptive radiation post-Kellwasser Event as the conodont *Palmatolepis* (Sepkoski, 1996).

During the Carboniferous, *Schellwienella* had a shorter stratigraphic range, confined to the Tournaisian–Viséan interval, with a preference for warm, carbonate environments near low-latitude regions (Fig. 12A). Seven of the eleven occurrence localities (Illinois – USA, New Mexico – USA, England, Wales, Ireland, Belgium, and Russia) are located in the Laurussia supercontinent, near the latitude 0°. Throughout the Mississippian, latitudinal gradients controlled the distribution of marine benthic faunas, which were closely related to local temperatures. These factors account for the geographical distribution of *Schellwienella* during the Tournaisian–Viséan interval (Ross and Ross, 1988; Torsvik and Cocks, 2016).

The genus extinction is likely related to environmental factors such as temperature and oxygen availability. During the Mississippian (late Viesan – early Serpukhovian), the planet experienced prolonged global cooling associated with the late Paleozoic ice age (LPIA), which extended into the early Permian (Stanley and Powell, 2003; Montañez and Poulsen, 2013). In the Serpukhovian, a mass extinction event occurred, resulting in the extinction of approximately 26% of invertebrate genera (Fig. 12B) (Sepkoski, 1996; Stanley and Powell, 2003). The temporal proximity between this extinction event and the LPIA suggests a causal link. One likely hypothesis is that global cooling led to a drastic reduction of carbonate habitats (Stanley and Powell, 2003; Wang et al., 2013; Balseiro and Powell, 2019). Another factor that may have contributed to the reduction of biodiversity during the Early Carboniferous is the expansion of anoxic waters, which has been recorded in several sedimentary basins (Siedenberg et al., 2016; Kabanov et al., 2016; Liu et al., 2019; Hu et al., 2022). The incursions of deep anoxic waters may have led to the instability of oceanic redox conditions and reduced habitable ecospaces on shallow platforms (Hu et al., 2022).

6. Conclusions

The taxonomic study of the Orthotetida from the Manacapuru Formation (Lochkovian) has led to the identification of a new species, *Schellwienella amazonensis* n. sp. This species and *S. marcidula* from the Bois d'Arc Formation (Lochkovian), USA, represent the oldest genus records. The Maecuru and Ererê formations (Amazonas Basin) have records of "*Schuchertella*" *agassizi*. In the Paraná Basin, this species has been reviewed, and a new species, *Schellwienella clarkei*, has been proposed. A revision of "*Schuchertella*" *agassizi* in the Amazonas Basin is needed, involving a thorough analysis of the internal ventral and dorsal valves. Until this review is completed, *S. amazonensis* n. sp. is considered the only *Schellwienella* occurrence in the Amazonas Basin.

In the Devonian, *Schellwienella* is found throughout all stages of the period, with most of its occurrences concentrated in Gondwana, inhabiting siliciclastic marine environments and transitioning between temperate, subpolar, and polar regions. In the Carboniferous, the genus had a shorter stratigraphic range, confined to the Tournaisian – Viséan interval, and showed a preference for warm environments and carbonate platforms near low-latitude regions.

CRediT authorship contribution statement

Luiz Felipe Aquino Corrêa: Conceptualization, Data curation,

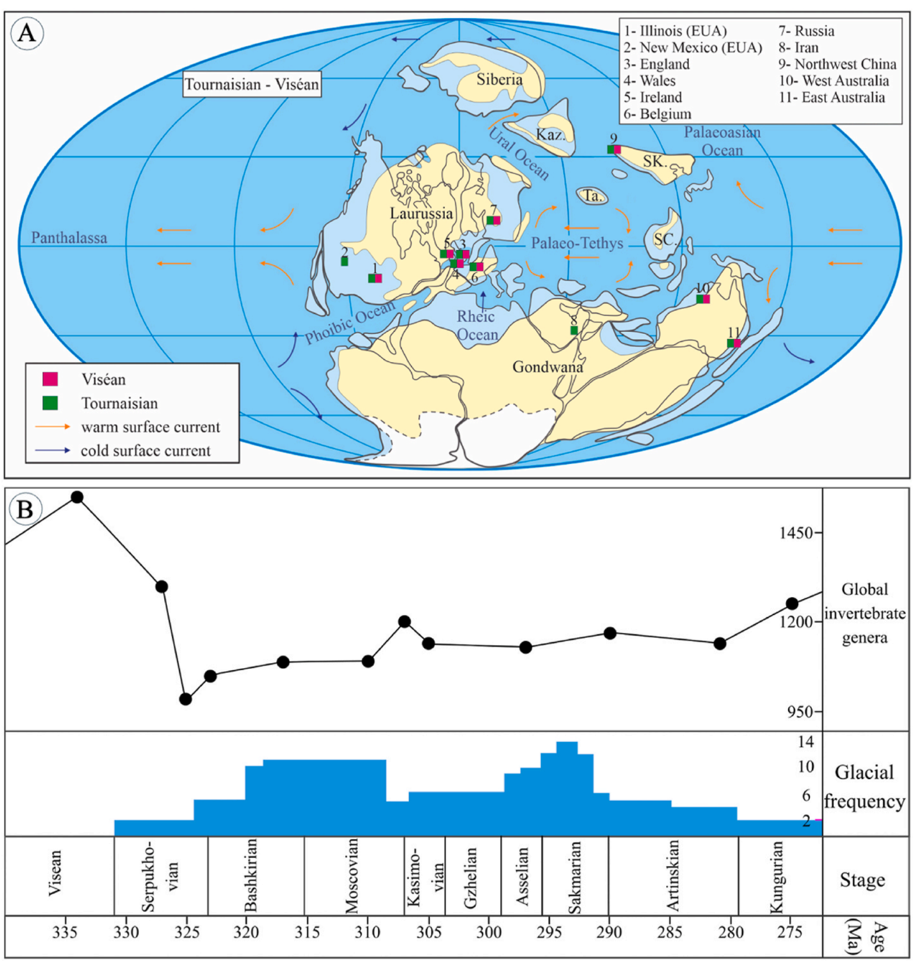

Fig. 12. A) Distribution of the *Schellwienella* throughout the Carboniferous. Base map modified from Scotese (2004), Metcalfe (2011), and Shi et al. (2016). Ocean surface circulation patterns modified from Smith and Read (2000), Hüneke (2006), and Shi et al. (2016). B) Variations in glacial frequency and invertebrate genera. Adapted from Montañez and Poulsen (2013), Stanley and Powell (2003), and Hu et al. (2022).

Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Maria Inês Feijó Ramos:** Conceptualization, Data curation, Methodology, Supervision, Writing – original draft, Writing – review & editing. **João Marcelo Pais de Rezende:** Conceptualization, Data curation, Methodology, Supervision, Writing – original draft, Writing – review & editing.

Declaration of competing 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2024.105253.

Data availability

Data will be made available on request.

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