

# Relationships between brachiopod fauna (Lochkovian–Frasnian) from northwest Gondwana (Amazonas Basin) and environmental changes during the Devonian

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## ABSTRACT

The Devonian marked a significant phase in the evolutionary history of the Brachiopoda. During this period, the Phylum achieved its peak diversity (Emsian) and suffered one of its greatest declines (Frasnian–Famennian), ranking second only to the mass extinction event at the Late Permian period. In Brazil, the Amazonas Basin has a rich record of Devonian brachiopods distributed in four stratigraphic units: i) Manacapuru (Lochkovian), ii) Maecuru (early Eifelian), iii) Ererê (late Eifelian), and iv) Barreirinha (early Frasnian) formations. This article aims to survey the occurrences of brachiopods during the Devonian in the Amazonas Basin and to discuss the possible factors that influenced their diversity. Environmental changes may explain the variation of brachiopod diversity throughout the Devonian in the Amazonas Basin. We noted that the diversity variation of Devonian brachiopods in the Amazonas Basin unfolded in three distinct stages. The peak of brachiopod diversity occurred in the early Eifelian (Maecuru Formation), when the Amazonas Basin was between the subtropical latitudes 30°S and 60°S, under shallow marine and cold conditions, justified by the absence of carbonates, evaporites, and reefs in the region (Stage 1). The first diversity decline is recorded in the Ererê Formation (late Eifelian), attributed to a warmer climate and deeper water than in the Maecuru Formation (Stage 2). During the Frasnian, there was a second diversity decline of brachiopods in the Amazonas Basin (Barreirinha Formation). A major global transgression occurred in the Late Devonian. In this period, the Amazonas basin experienced the deepest marine conditions in its history. The brachiopods of the Barreirinha Formation occur in layers of black shale (offshore), attributed to an anoxic or dysoxic environment of high stress, which explains the low diversity of brachiopods in this unit (Stage 3).

## 1. Introduction

Brachiopods have a complete fossil record, emerging in the Cambrian period and occurring in smaller proportions in modern oceans (Williams et al., 2007; Harper et al., 2017). The apex of their diversity was in the Devonian, with a record of 460 genera during the Emsian. In the same period occurred the second largest faunal decline during the Famennian, with the most significant decline during Permo–Triassic extinction (Williams et al., 2007).

During the Silurian–Devonian transition, with the melting of the polar ice caps that covered part of Africa and South America resulted in marine transgressions that reached a large part of the supercontinent Gondwana. It was in this context that the shallow seas in Northwest

Gondwana appeared in the Early Devonian (Carozzi et al., 1973; Caputo, 1984; Johnson, 2006; Torsvik and Cocks, 2013). The emergence of these seas was one of the main factors for the Phylum to reach the peak of its diversity during this period.

In Brazil, the Amazonas Basin has a rich record of Devonian brachiopods distributed in four formations (Fig. 1): i) Manacapuru Formation (Lochkovian), ii) Maecuru Formation (early Eifelian), iii) Ererê Formation (late Eifelian), and iv) Barreirinha Formation (early Frasnian) (Rathbun, 1874; Clarke, 1913; Fonseca and Ponciano, 2011; Corrêa and Ramos, 2021). Most of these records are from samples of the Maecuru and Ererê formations, coming from expeditions that took place in the 19th century (Morgan Expeditions between 1870 and 1871, and Imperial Geological Commission of Brazil between 1875 and 1877) and 20th

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century (Geological and Mineralogical Service of Brazil in between 1918 and 1929, and Expedition Orville Adalbert Derby in 1986).

Recently, paleontological studies in the Manacapuru Formation have advanced due to the rescue of >3000 fossil samples, of which 1386 were brachiopods, collected during the Program of paleontological salvage at Belo Monte hydroelectric power plant construction in the municipality of Vitória do Xingu, Pará State (Tomassi et al., 2015). Corrêa and Ramos (2021) studied part of this material and identified three species of the family Discinidae from the Manacapuru Formation (Amazonas Basin): *Orbiculoidea baini*, *Orbiculoidea bodenbenderi*, and *Orbiculoidea excentrica*. The authors also proposed two new species, *Orbiculoidea katzeri*, and *Orbiculoidea xinguensis*.

Approximately 150 years have passed since the first publication on the Devonian brachiopods of the Amazonas Basin. Much of the research is concentrated on samples from the Eifelian, which mainly addresses the paleobiogeographical and taxonomic aspects of brachiopods, and a good part of these identifications need to be revised (Derby, 1877; Rathbun, 1874, 1878; Katzer, 1897; Clarke, 1899; Katzer, 1903; Clarke, 1913; Katzer, 1933; Carvalho, 1972, 1975; Melo, 1985; Fonseca, 2004; Fonseca and Ponciano, 2011). Besides, in these studies, the authors do not discuss the factors that influenced the variation in the diversity of genera and species of brachiopods along the Devonian in the Amazonas

Basin.

Since the first paleobiogeographical studies of the Devonian, the affinities between brachiopod species found in the Amazonas Basin and those in other regions have been observed and discussed. Clarke (1913) pointed out that the invertebrate fauna of the Ererê Formation had a boreal affinity, similar to the forms that occurred further north in the Devonian. For Boucot et al. (1969) and Boucot (1971), the invertebrate fauna of the Maecuru and Ererê formations belonged to the Eastern Americas Realm, characterized by temperate waters, and located between the Old World and Malvinokaffric realms (now called Malvinohosian Realm by Penn-Clarke and Harper, 2020), in the middle to low latitudes (30°S–60°S). Recently, Penn-Clarke and Harper (2020) proposed a new bioregionalization for West Gondwana during the Pragian–Eifelian interval based on the distribution of brachiopods. According to the authors, the Amazonas Basin was in a border region between two first-order biogeographical units: “Temperate (30°S–60°S) latitude” and “High (60°S–90°S) latitude” (Penn-Clarke and Harper, 2020).

This article aims to survey of occurrences of brachiopods during the Devonian in the Amazonas Basin and to discuss the factors possibly that influenced their diversity. We adopted the taxonomic classification described by Carvalho (1975), Melo (1985), and Fonseca (2004).

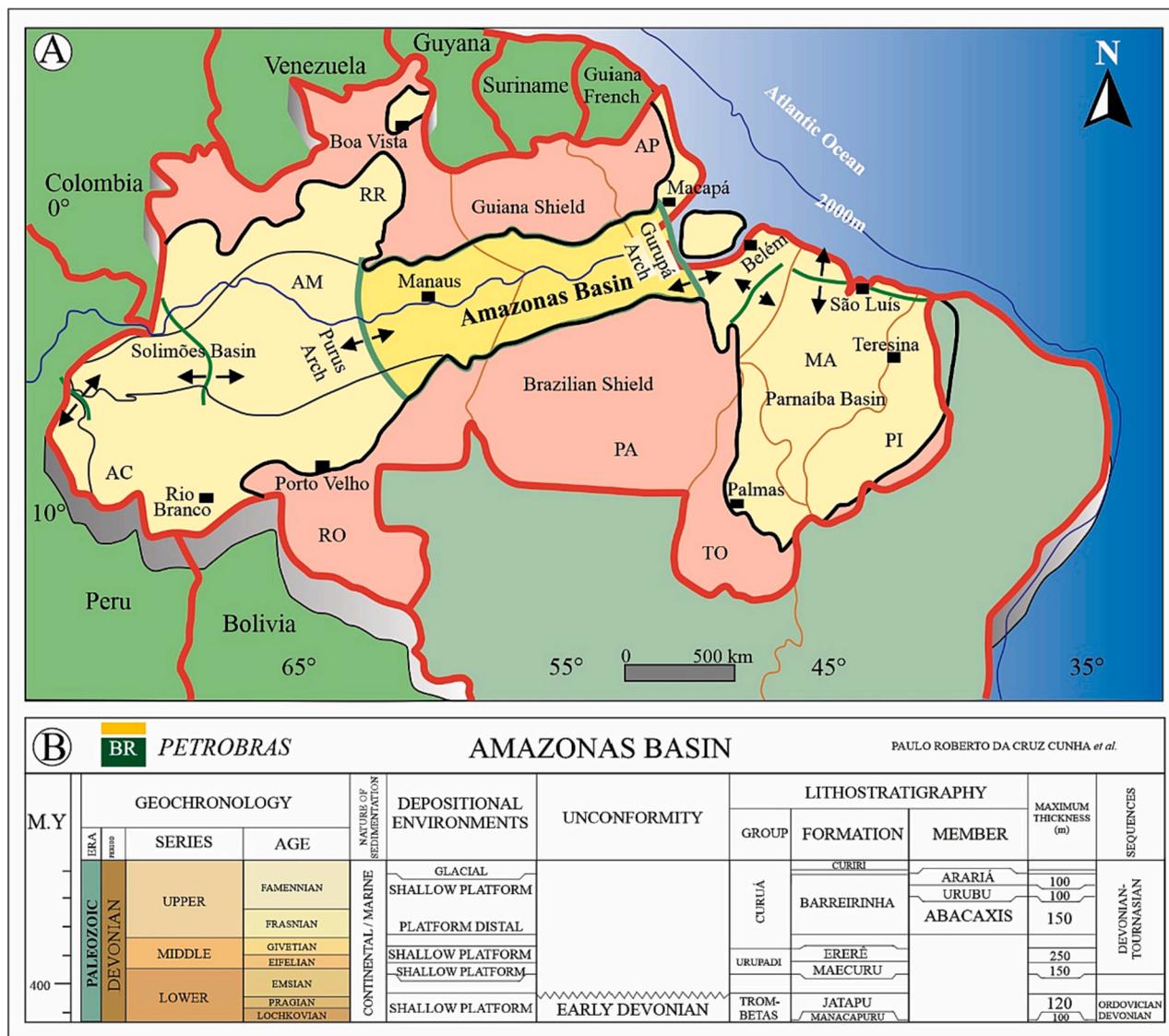


Fig. 1. A) Location of the Amazonas Basin (Cunha, 2000); B) Stratigraphic chart of the Amazonas Basin (Cunha et al., 2007), highlighting the Devonian.

## 2. Data and methods

A database on Devonian brachiopods from the Amazonas Basin was generated from the literature records. Additionally, we consulted online paleontological collections and the curators of the following institutions:

NMNH, National Museum of Natural History of the Smithsonian Institution.

NYSM, New York State Museum, Albany.

MN/UFRJ, Museu Nacional, Universidade Federal do Rio de Janeiro.

MPEG, Museu Paraense Emílio Goeldi.

MCT/DNPM, Museu de Ciências da Terra do Departamento Nacional de Produção Mineral.

The data were organized in an Excel program (see Supplemental Material Table S1) containing the following information: catalog number, taxon, geographic and geological location, collectors, and observations. For the taxonomic information, we followed the information provided by the literature and the curators of each collection. Therefore, we did not conduct a taxonomic review of this material since it is not the objective of this study.

## 3. Major scientific expeditions in the Devonian of the Amazonas Basin

Brachiopod research in the Amazonas Basin (Fig. 2) started in the 19th century, with the Morgan Expeditions (1870 and 1871), led by Charles Frederick Hartt, in the Ererê region (Katzner, 1933). In 1875, Dom Pedro II authorized the creation of the Geological Commission of Brazil (Katzner, 1933). The scientists of that commission visited the Serra de Ererê and discovered new outcrops rich in fossils on the banks of the Maecuru and Curuá rivers, also explored by Katzner in 1897 (Katzner, 1933; Fonseca and Ponciano, 2011). Later, João Coelho (March 1895), carried out an expedition through the Maecuru River and collected invertebrate fossils in sandstone at the Teuapixuna waterfall (Katzner, 1897; Moura, 1938; Fernandes and Schefflerk, 2014).

During the 20th century, there were expeditions by the Geological and Mineralogical Survey of Brazil and the Orville Adalbert Derby Expedition. In 1918, technicians from the Geological and Mineralogical Service of Brazil conducted an expedition in the Amazonas Basin, where they collected fossils of Devonian brachiopods on the banks of the Urubú River, close to the municipality of Iracema, in the state of Amazonas.

One year later, the same team found brachiopod fossils at rivers Erepucuru and Curuá banks (Albuquerque, 1922). In 1928, Anibal Alves Bastos and Pedro de Moura collected invertebrate fossils upstream of the Tenapizuruna Waterfall on the Maecuru River, State of Pará (Bastos and Moura, 1929). In the following year, Mathias G. de O. Roxo and José Moreira Mendonça collected brachiopods in outcrops close to Serra de Ererê and from a core in Serra de Itauajuri (Oliveira, 1930).

Fifty years later, scientific expeditions in the Devonian of the Amazonas Basin returned with the Orville Adalbert Derby Expedition (1986), headed by José Henrique Gonçalves de Melo. This expedition explored the classic outcrops of the Serra de Ererê and the banks of the Maecuru River in the Amazonas Basin, carried out an expressive fossiliferous collection and the first geographic records of these locations (Fig. 3 A and B) (Fonseca and Ponciano, 2011; Fernandes and Schefflerk, 2014). After 35 years of the Orville Adalbert Derby Expedition, a new expressive collect occurred during the Program of paleontological salvage of the Belo Monte hydroelectric power plant construction in the Vitória do Xingu, Pará State, between the years 2011 and 2015 (Fig. 3 C and D), Tomassi et al. (2015) collected approximately 1386 samples of brachiopods from the Manacapuru Formation.

## 4. Devonian brachiopods from the Amazonas Basin deposited in museums and universities

Six institutions store the brachiopod samples collected over the last 150 years in the Amazonas Basin: two in the United States of America (the NMNH and NYSM) and four in Brazil (MN/UFRJ, MPEG, MCT/DNPM, and the Laboratório de Estudos de Comunidades Paleozoicas at the Federal University of the State of Rio de Janeiro) (see Supplemental Material Table S1).

Most of the collected material from the Morgan Expeditions is at the NMNH (Rathbun, 1878). The type and figured specimens published by Katzner (1897, 1903, 1933) are currently deposited at the NYSM, as reported by Fonseca and Ponciano (2011) and Fernandes and Schefflerk (2014).

The MN/UFRJ stores part of the samples collected by the Imperial Geological Commission of Brazil and the Orville Albert Derby Expedition, in addition to the type specimens of brachiopods collected during the Morgan Expeditions, transferred from the NMNH (Fonseca and Ponciano, 2011). The collection of paleoinvertebrates at the MN/UFRJ

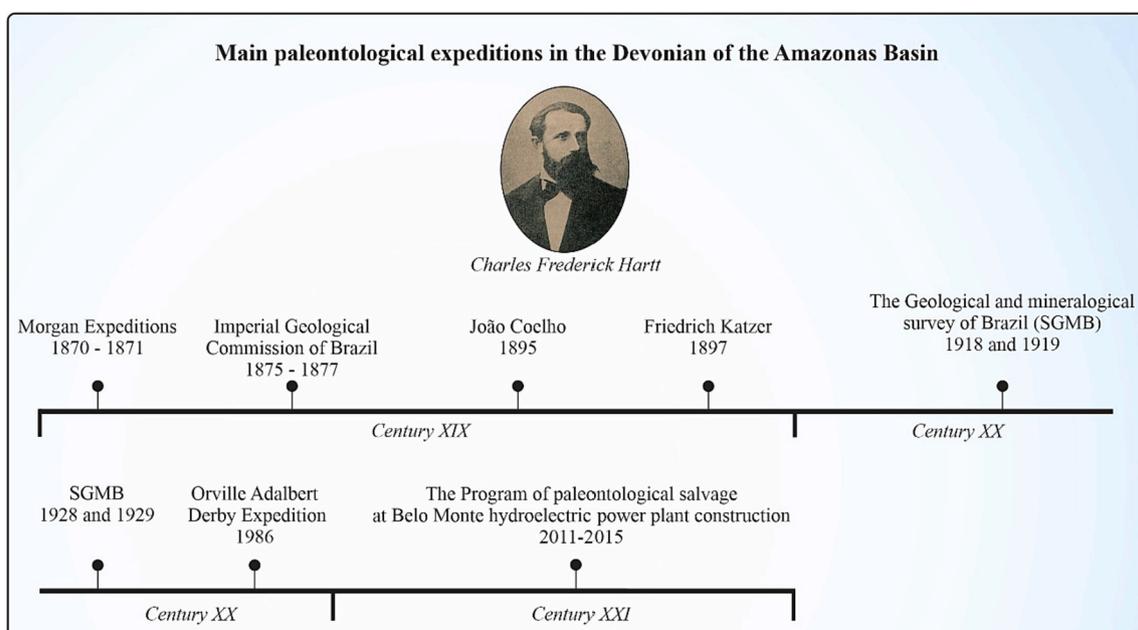
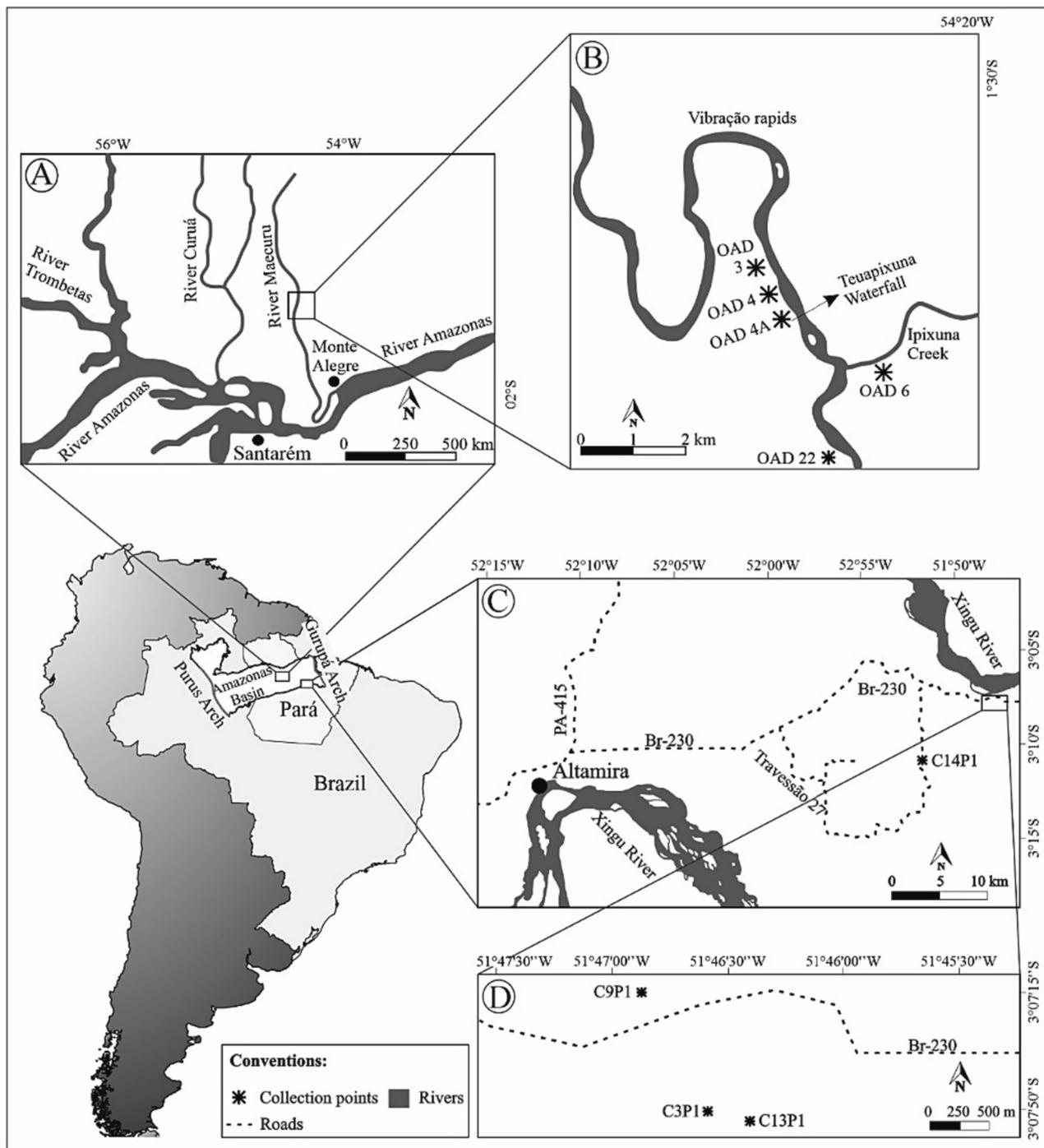


Fig. 2. Expeditions in the Amazonas basin.



**Fig. 3.** A) and B) Sampling sites of the Maeuru (OAD3, OAD4, and OAD4A) and Ererê (OAD6 and OAD22) formations marked during the Orville Adalbert Derby Expedition (Fonseca, 2004). C) and D) Sampling sites of the Manacapurú Formation (Corrêa and Ramos, 2021).

stored 657 samples of Devonian fossils from the Amazonas Basin before the fire in the museum on September 2nd, 2018 (Fernandes and Scheffler, 2014). During the recovery work after the accident, Dr. Sandro Marcelo Scheffler managed to rescue two samples of brachiopods, one bivalve, and one cephalopod collected by the Imperial Geological Commission of Brazil (Silva et al., 2019).

In the Paleontological collection from the MPEG, 64 specimens collected by João Coelho, coming from the Maeuru Formation, 17 samples collected by Friederich Katzer from the Ererê Formation, and 1386 fossils samples of brachiopods collected by Henrique Tomassi (Fig. 4), from the Manacapurú Formation are stored.

The paleoinvertebrate collection of the MCT/DNPM is composed of

samples collected by the Imperial Geological Commission of Brazil, the Geological and Mineralogical Survey of Brazil, and the Orville Albert Derby expeditions. It includes 313 specimens of brachiopods from the Maeuru Formation and 47 from the Ererê Formation. Part of the fossil material from the Orville Albert Derby expedition is at the Laboratório de Estudos de Comunidades Paleozoicas at the Federal University of the State of Rio de Janeiro (Fonseca and Ponciano, 2011; Fernandes and Scheffler, 2014).

## 5. The Devonian brachiopods from the Amazonas Basin

The Devonian strata in the Amazonas Basin document the presence

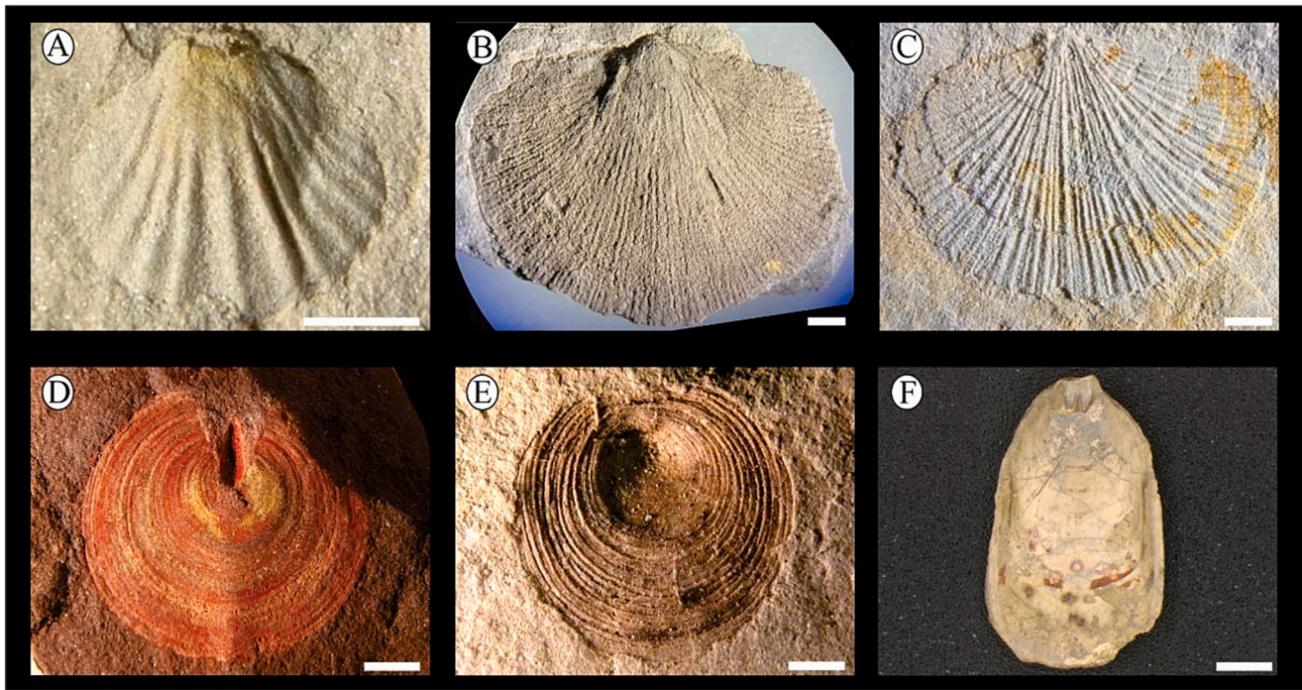


Fig. 4. Brachiopods collected during the Program of paleontological salvage of the Belo Monte hydroelectric power plant construction and stored in the paleontological collection from Museu Paraense Emílio Goeldi. Rhynchonellata: A) MPEG-4155-I, B) MPEG-4156-I and C) MPEG-4157-I; Lingulata: D) MPEG-3660-I, E) MPEG-3686-I and F) MPEG-4154-I. Scale bar: 2 mm. Source: A) – C) and F) author; D) – E) Corrêa and Ramos (2021).

of three classes, nine orders, 31 genera, and 52 species of brachiopods distributed among the Manacapuru, Maecuru, Ererê, and Barreirinha formations (see Supplemental Material Table S2). The Jatapu and Curiri formations do not have any records of Devonian brachiopods.

### 5.1. Manacapuru Formation (Lochkovian)

Grahn and Melo (1990) were the first authors to report the occurrence of brachiopods in layers of the Manacapuru Formation (*Lingula* sp.) from the Amazonas Basin, but without providing any taxonomic or taphonomic details. Later, Tomassi et al. (2015) made a preliminary report on the fossiliferous material recovered during the Program of paleontological salvage of the Belo Monte hydroelectric power plant construction. The authors have drawn attention to the large number of Rhynchonellata and Lingulata brachiopods collected from layers corresponding to the upper portion of the Manacapuru Formation, highlighting the need for further taxonomic studies of this material.

The first taxonomic study on brachiopods from the Manacapuru Formation collected in Belo Monte was published by Corrêa and Ramos (2021), focusing on the taxonomic identification of inarticulate brachiopods from the Discinidae Family. The authors recorded the first occurrence of *Orbiculoidea baini*, *Orbiculoidea bodenbenderi*, and *Orbiculoidea excentrica* in the Amazonas Basin and described two new species (*Orbiculoidea xinguensis* and *Orbiculoidea katzeri*). The records of *Orbiculoidea baini*, *Orbiculoidea bodenbenderi*, and *Orbiculoidea excentrica* in the layers of the Manacapuru Formation (Lochkovian) are the oldest in South America. The authors believe that these *Orbiculoidea* occurrences in the Manacapuru Formation may be related to the proximity of the Amazonas Basin (located in northwest Gondwana) with the Laurasia paleocontinent (which concentrated the highest occurrences of brachiopods during the Silurian–Devonian) during the Early Devonian. Another factor was the global sea-level rise during this period, which flooded part of northwest Gondwana, resulting in shallow marine conditions in the Amazonas Basin and consequently expanding ecological niches of marine fauna.

### 5.2. Maecuru Formation (early Eifelian)

In 1876, Orville Adalbert Derby made the first record of brachiopods from the Maecuru Formation in a sandstone layer from the banks of the Maecuru and Curuá rivers (Derby, 1877). Rathbun (1878) conducted further taxonomic studies on this material and identified 21 species, eight of which were new. Subsequently, several researchers, such as Katzer (1897, 1903, 1933), Clarke (1899, 1913), Carvalho (1975), Melo (1985), and Fonseca (2004), revised and studied part of the taxa identified by Rathbun, along with additional material acquired in the following decades.

Carvalho (1975) reviewed the brachiopods of the Orthida, Strophomenida, Spiriferida, and Terebratulida orders from the Maecuru Formation, first studied by Rathbun (1878) and Katzer (1897, 1899, 1903). In his work, of the 11 species identified, only *Tropidoleptus carinatus* and *Amphigenia elongata* remained with their original classification. The other nine species were reclassified as *Discomyorthis hatti*, *Platyorthis nettoana*, *Protoloptostrophia* sp., *Megastrophia hoeferi*, *Acrospirifer duodenaria*, *Acrospirifer buarquiana*, *Mucrospirifer pedroanus*, *Plicoplasia curupira*, *Derbyina jamesiana*, and *Paranaia wardiana*.

Fonseca (2004) studied the superfamily Chonetoidea from the Maecuru and Ererê formations. The author established the diagnosis of *Chonetes freitasi* Rathbun, 1878, designating its lectotypes and paratypes, besides proposing a new species: *Montsenetes carolinae*.

The following taxa listed herein have questionable identifications and require revision: *Podolella rathbuni*, *Mucrospirifer katzeri*, *Australospirifer? laurosodreanus*, *Spirifer derbyi*, *Spirifer hartti*, *Cyrtina? maecuruensis*, *Camarotoechia? aff. C. soppo*, *Leptocoelia? sp.*, *Chonetes? curuaensis*, *Productella maecuruensis*, *Anoplia nucleata*, *Chonostrophia knodi* and *Schuchertella agassizi*. The complete list of brachiopods from the Maecuru Formation is in supplemental material Table S2.

The paleoecological data inferred for the Maecuru Formation come from studies of two associations of benthic marine invertebrates: *Schuchertella agassizi* – *Ptychopteria eschwegegi* and *Mucrospirifer katzeri* – *Ptychopteria eschwegegi* (Ponciano et al., 2007a, 2007b). The first is the only one to have brachiopods, represented by 12 species, which

correspond to 44% of the individuals in the association, followed by 20 species of bivalves, 12 of trilobites, 14 of gastropods, 3 of crinoids, and 3 of tentaculites. The semi-quantitative and morpho-functional analyses indicated a shallow marine paleoenvironment with agitated waters, well-oxygenated, temperate, and normal salinity (Ponciano et al., 2007a).

The material sampled by the Morgan Expeditions, the Imperial Geological Commission of Brazil, and the Orville A. Derby Expedition did not follow standard collection models for taphonomic analysis, which may result in misinterpretations, which makes it unfeasible and justifies the absence of taphonomic studies.

The brachiopods from the Maecuru Formation occur in the upper portion of the unit, dated through myospores and chitinozoans as early Eifelian (Melo and Loboziak, 2003; Grahn and Melo, 2004; Fonseca and Ponciano, 2011).

During the Middle Devonian, the Amazonas Basin was in a paleobiogeographic frontier region, which probably explains the mixture of faunal elements from the Old World, Eastern Americas, and Malvinohosian realms (Melo, 1985; Fonseca and Ponciano, 2011). Among the brachiopods, there is a predominance of the genera with affinities to the Eastern Americas realm (11 genera), as well as elements from the Old World (8 genera) and Malvinohosian (4 genera) realms. The brachiopods of the Maecuru Formation are part of the Amazon-Colombian subprovince (Boucot, 1975; Boucot et al., 2001).

Recently, Penn-Clarke and Harper (2020) proposed a new bioregionalization for West Gondwana during the Pragian–Eifelian interval

based on the distribution of brachiopods (Fig. 5). The authors identified two first-order areas: the “Temperate Latitude” and “High Latitude” bioregions. The High Latitude bioregion comprises two second-order regions: the “Amazonian” and “Malvinohosian” regions (Penn-Clarke and Harper, 2020). The Maecuru and Ererê formations are inserted in the Amazonian unit, restricted to latitudes 50°S–60°S, situated in a region intermediate between the Colombian-West African and Malvinohosian bioregions.

### 5.3. Ererê Formation (late Eifelian)

The brachiopods from the Ererê Formation occur in layers dated to the late Eifelian age (Melo and Loboziak, 2003; Grahn and Melo, 2004; Fonseca and Ponciano, 2011). Carvalho (1975), Melo (1985) and Fonseca (2004) revised most of the taxa from the Ererê Formation. Carvalho (1975) reclassified six species (*Platyorthis nettoana*, *Derbyina jamesiana*, *Paranaia wardiana*, *Podolella derbyana*, *Mucrospirifer pedroanus*, and *Plicoplasia curupira*) that Rathbun (1874) had previously proposed, and only *Tropidoleptus carinatus* maintained its original classification.

The brachiopods of the Chonetidae Family from the Ererê Formation show inconsistencies in their taxonomic classification due to the poor preservation of important diagnostic characteristics. Rathbun (1874) made the first record of this family, which was later revised by Clarke (1899), Katzer (1933), Kegel (1953), and Melo (1985), who did not reach a consensus regarding the classification. Fonseca (2004) reviewed the *Chonetes* from the Ererê Formation and reclassified *Chonetes*

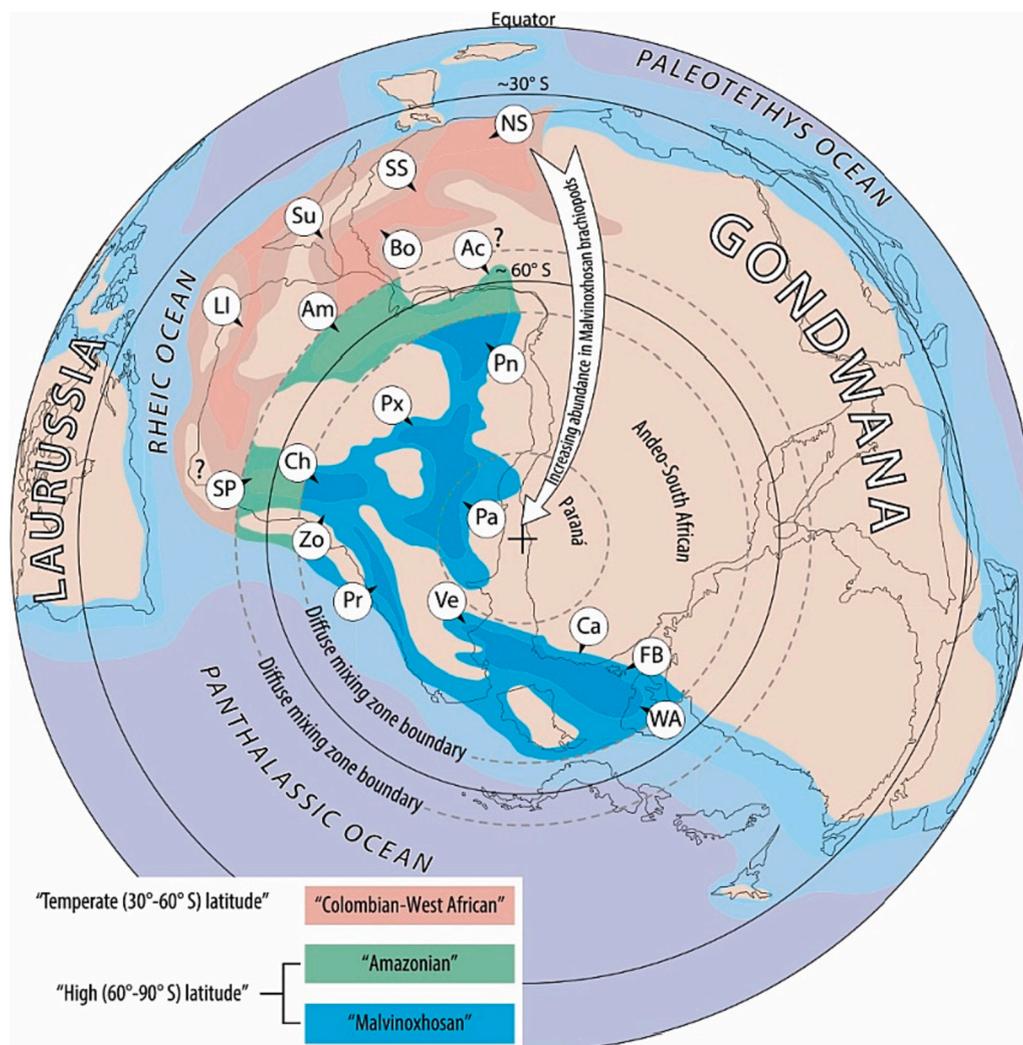


Fig. 5. Brachiopod-based bioregions of West Gondwana during the Pragian–Eifelian (Penn-Clarke and Harper, 2020). Abbreviations: Ac—Accraian (Ghana), Am—Amazonas (Brazil), Bo—Bové (Guinea, Guinea-Bissau, Senegal), Ca—Cape (South Africa), Ch—Chaco (Bolivia), FB—Fox Bay (Falkland Islands), LI—Llanos (Colombia and Venezuela), NS—North Saharan (Tindouf, Ghadamis, Polignac, Murzuq basins), Pa—Paraná (Brazil, Paraguay, Uruguay), Px—Parecis (Brazil), Pr—Precordillera (western Argentina), Pn—Parnaíba (Brazil), SP—southern Peru, SS—“South Saharan” (Tamesna and Taoudeni basins and Adrar, Hodh regions), Su—Suwannee (Florida, Georgia, United States), Ve—Ventana (eastern Argentina), WA—West Antarctica (“Ellsworth-Whitmore Mountains”), Zo—Zorritas (northern Chile).

*comstockii* as *Pleurochonetes comstocki*. The species that Rathbun (1874) classified as *Chonetes freitasi*, *Chonetes herbertsmithi*, and *Chonetes onetianus* do not present a good state of preservation, which does not allow for a detailed description of the material, putting even their classification at the genus level in doubt (Fonseca and Ponciano, 2011).

Considering this taxonomic review, the brachiopod fauna of the Ererê Formation includes *Schuchertella agassizi*, *Camarotoechia?* aff. *C. dotis*, *Rhynchonella ererensis*, *Orbiculoidea* sp., *Lingula ererensis*, and *Lingula spatulata*.

#### 5.4. Barreirinha Formation (early Frasnian)

The brachiopods of the Barreirinha Formation occur in a layer of black shale dated as early Frasnian (Melo, 1985; Melo and Loboziak, 2003). Rathbun (1874) described the species *Lingula gracana*, *Lingula stauntoniana*, *Lingula rodriguezii*, *Orbiculoidea lodensis*, and *Vitulina pustulosa* from black shale layers of the Barreirinha Formation and observed that the fauna of the Ererê region is similar to the fauna recorded in the Hamilton Group from New York.

Dr. Israel Charles White, head of the Coal Commission, provided material collected from the black shale of the Ererê region to Clarke (1913), who analyzed it and identified *Schizobolus truncatus*. This author was one of the pioneers to consider the possibility of this layer being the first record of the Upper Devonian in South America. Later, Macambira

et al. (1977) mentioned the occurrence of *Orthotetes agassizi* and *Spirifer* sp. in a black shale layer attributed to the old Barreirinha Member in the Altamira region, Pará State. The fauna of the Barreirinha Formation has no element of the Devonian paleobiogeographic province or domain.

## 6. Results and discussions

Unlike the Devonian, there is no record of brachiopods during the Ordovician in the Amazonas Basin. For the Silurian, only Clarke (1899) registered a brachiopod fauna collected on the banks of the Trombetas River, referring to the lower portion of the Pitinga Formation, dated through biostratigraphic analysis with chitinozoans as Llandovery – early Wenlock (Grah, 2005).

We observed that the variation in diversity of Devonian brachiopods in the Amazonas Basin occurred in three distinct stages (Fig. 6 A). In Stage 1, there was an increase in classes and genera of brachiopods during the Lochkovian–early Eifelian. The number of genera increased from one to twenty-five, representing the peak of brachiopod diversity during the Devonian in the Amazonas Basin.

In stage 2, the Amazonas Basin experienced its first decline in brachiopod diversity. Approximately 50% of the brachiopod genera went extinct between the early–late Eifelian. Subsequently, a second decline occurred between the late Eifelian–early Frasnian, characterizing stage 3. Additionally, it is possible to observe that the distribution

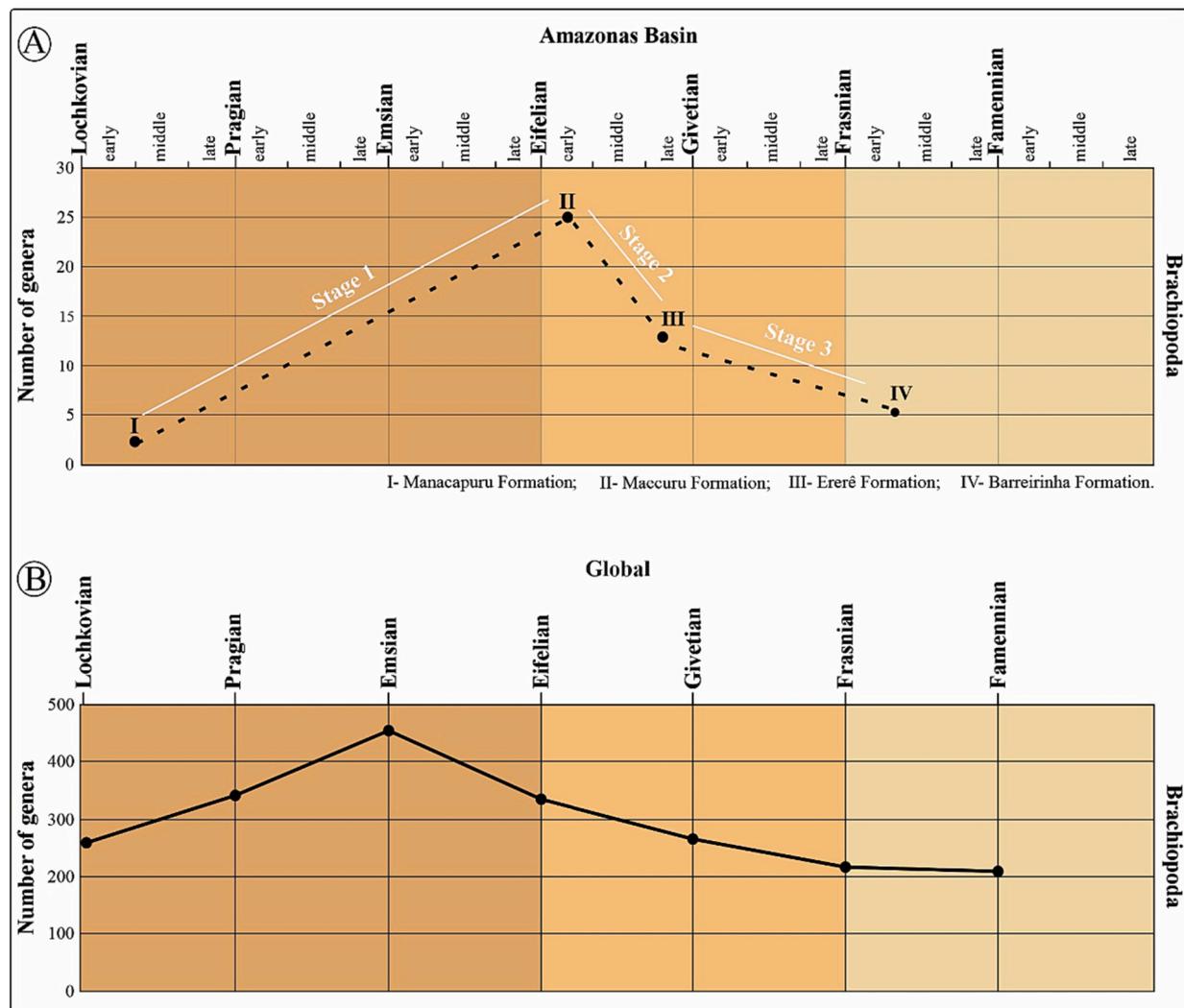


Fig. 6. A) Distribution of the number of brachiopod genera in the Devonian of the Amazonas Basin. B) Global distribution of the number of brachiopod genera in the Devonian (Williams et al., 2007).

of brachiopods in the Devonian of the Amazonas Basin, recorded until now, follows the global trend evolution of the Phylum during this period (Fig. 6 B).

During the Ordovician (Fig. 7) and Silurian, northwest of Gondwana was located at high latitudes (between 60°S–90°S) (Torsvik and Cocks, 2013). In the Ordovician–Silurian transition, the Hirnantian glaciation occurred, lasting approximately 35 million years (Finnegan et al., 2011). Climatic conditions were extreme in northwest Gondwana when only a low diversity fauna composed of brachiopods Rhynchonelliformea and Linguliformea from the Iapó and Vila Maria formations (Paraná Basin) is recorded in Brazil (Zabini et al., 2019, 2021).

Brachiopods had a preference for areas of low latitude (15°N and 35°S) with relatively warm to temperate conditions during the Ordovician and Silurian periods, as seen in the case of brachiopods of the genus *Orbiculoidea*, which occurred only in the following locations during the Ordovician–Silurian: west of Laurentia (North America), Baltica (Germany) and the east bank of Gondwana (China) (Torsvik and Cocks, 2013; Zhang et al., 2018).

In the Silurian, parts of the North African and South American polar ice caps melted, raising the sea level and consequently causing marine transgressions that extended to several cratonic areas in the Gondwana (Caputo, 1984; Torsvik and Cocks, 2013). As a result, shallow seas emerged in the northwest of Gondwana during the Early Devonian, leading to the expansion of new ecological niches that contributed to the proliferation of brachiopods during the Devonian (Ludwig, 1964; Caputo, 1984; Caputo and Crowell, 1985; Grahn and Caputo, 1992; Cunha et al., 1994).

Environmental changes and the geographic position of paleocontinents may explain the variation in brachiopod diversity throughout the Devonian in the Amazonas Basin, as discussed below.

**Stage 1:** After a low sea level near the Silurian–Devonian boundary, global eustatic sea levels increased considerably in the Early Devonian (Fig. 8 A) (Torsvik and Cocks, 2016). Geographically, the Amazonas Basin was between the latitudes of 30°S and 60°S, the Gondwana was closer to Laurussia (Fig. 10 A), and the global temperature of the oceans increased (Fig. 8 B) (Wallmann, 2004; Torsvik and Cocks, 2013). In this context, the brachiopods of the Manacapuru Formation emerged (Corrêa and Ramos, 2021).

Among the Brazilian sedimentary basins, the Amazonas Basin is the only one to have brachiopod occurrences in the Lochkovian. This suggests a possible relationship with favorable environmental conditions since it is the only basin with a depositional environment related to a shallow marine platform. Another relevant factor is associated with the position of the paleocontinents. The Amazonas Basin was closer to Laurussia compared with the other Brazilian basins. Besides, the same transgression that enabled the emergence of a sea in the Amazonas Basin in the Lochkovian may have transported the cosmopolitan larvae of the *Orbiculoidea* brachiopods to this basin (Corrêa and Ramos, 2021).

During the Early Devonian (Lochkovian), there was a predominance of brachiopods belonging to the Lingulata class, represented by the genus *Orbiculoidea* and other Linguliformes, in rocks of the Manacapuru Formation (Grahn and Melo, 1990; Corrêa and Ramos, 2021). Subsequently, at the early Eifelian, there was a significant increase in Rhynchonellata and Strophomenata found in strata of the Maecuru Formation

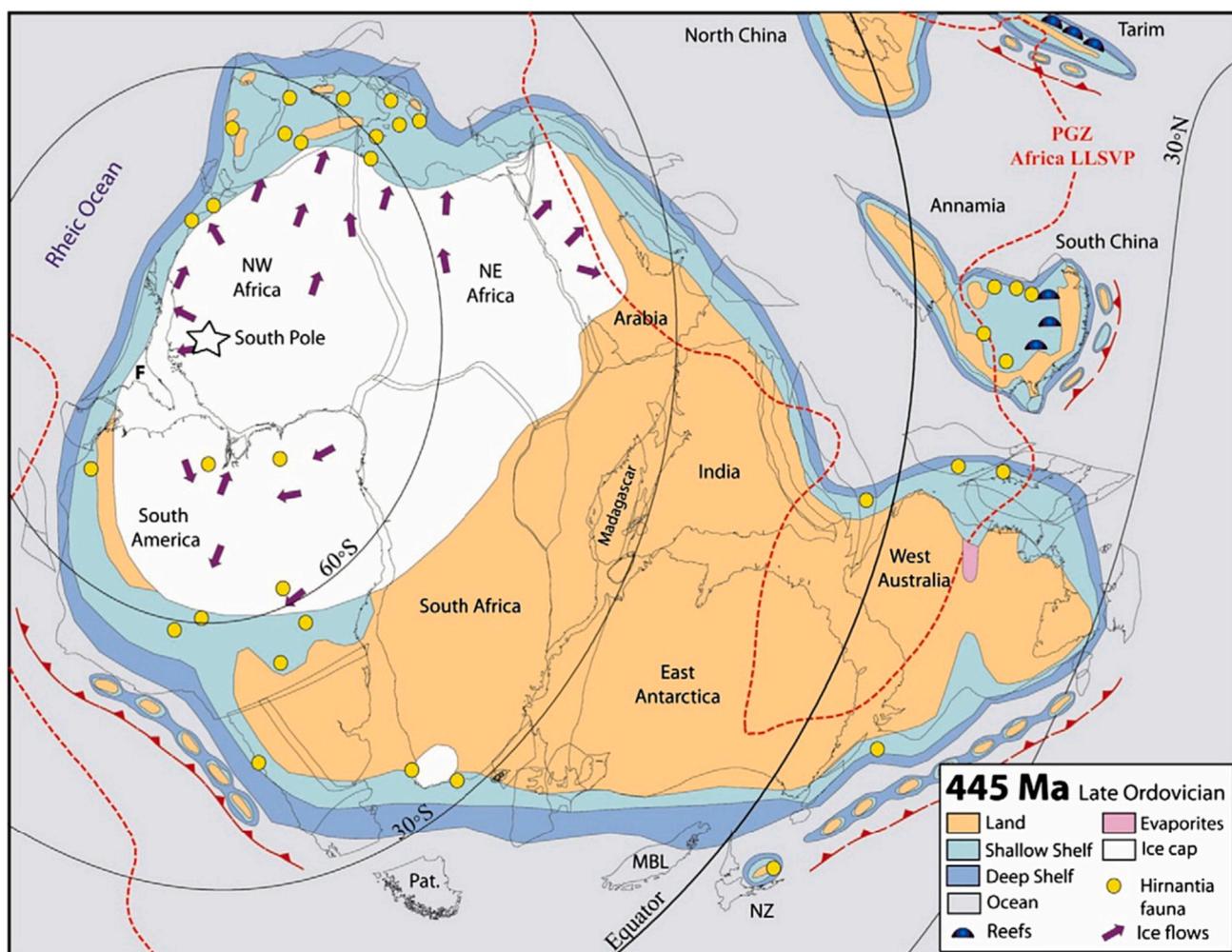


Fig. 7. Paleobiogeographic arrangement of Gondwana 445 Ma. (Torsvik and Cocks, 2013).

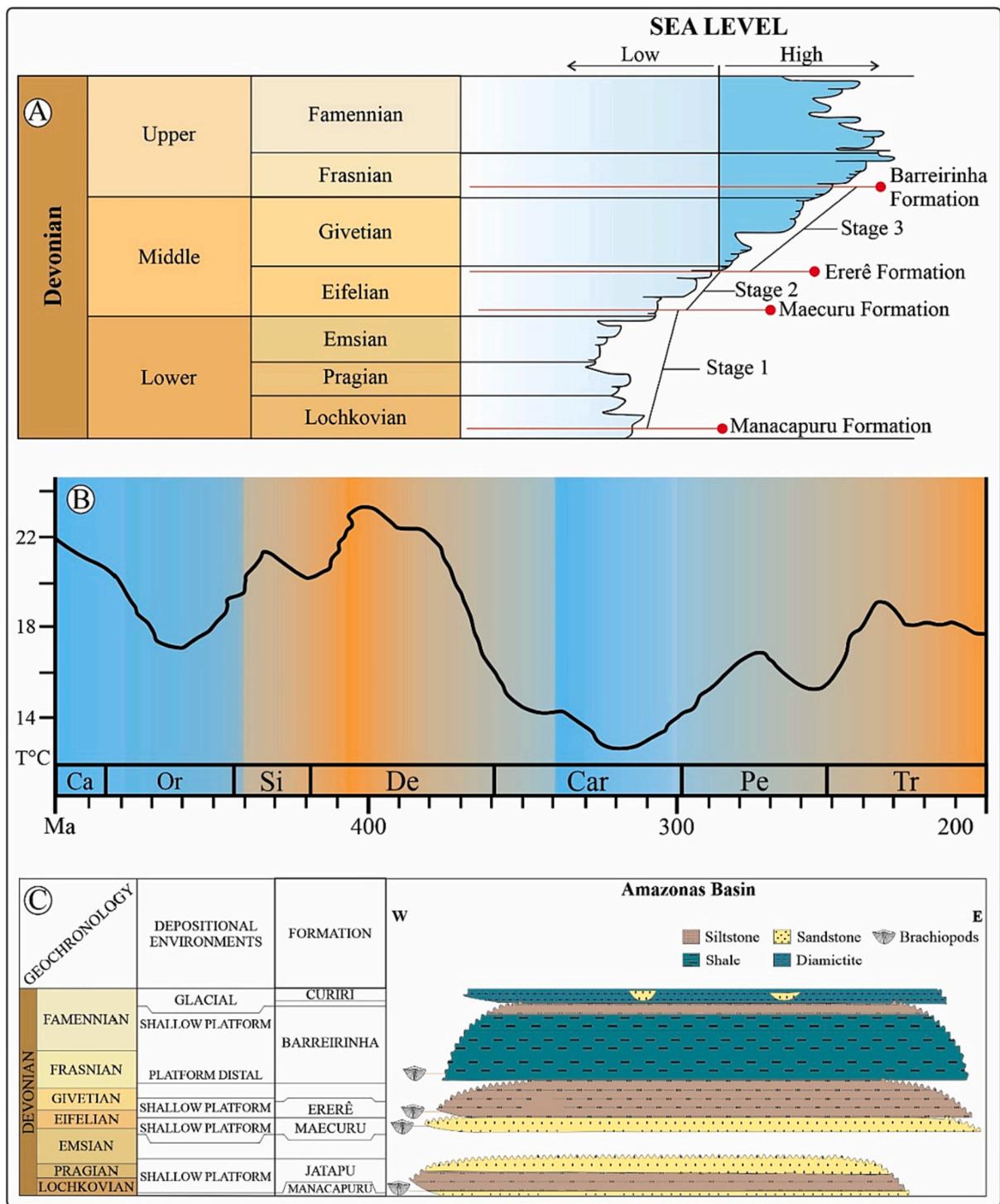


Fig. 8. A) Global eustatic sea level variation in the Devonian (Ross and Ross, 1988); B) global ocean average temperature from 500 to 200 Ma. (Wallmann, 2004); C) Stratigraphy of the Devonian period in the Amazonas Basin (Cunha et al., 2007).

(Fig. 9).

In the Early Devonian, there was a clear differentiation between equatorial and polar temperatures, which led to a notable increase in the provinciality of shallow marine benthic faunas (Boucot and Blodgett, 2001; Penn-Clarke and Harper, 2020). Paleobiogeographic provinces peaked in the Emsian, the same age at which brachiopods reached maximum stratigraphic diversity at the genus level (Williams et al., 2007).

During the Eifelian (Fig. 10 B), the climatic conditions in the Amazonas Basin were still cold, justified by the absence of carbonates,

evaporites, and reefs in the region (Caputo, 1984). In the Amazonas Basin, the brachiopods had the apex of their diversity with twenty-five genera and twenty-eight species, occurring in shallow marine conditions (Caputo, 1984).

In addition to the great diversity of Rhynchonellata and Strophomenata, the Maecuru Formation is the only studied unit that does not show the occurrence of Lingulata (Fig. 9). The absence of this class may be related to environmental factors. In the Manacapuru, Ererê, and Barreirinha formations, the Lingulatas are found in layers of siltstones, fine sandstones, and shales, respectively, associated with more distal

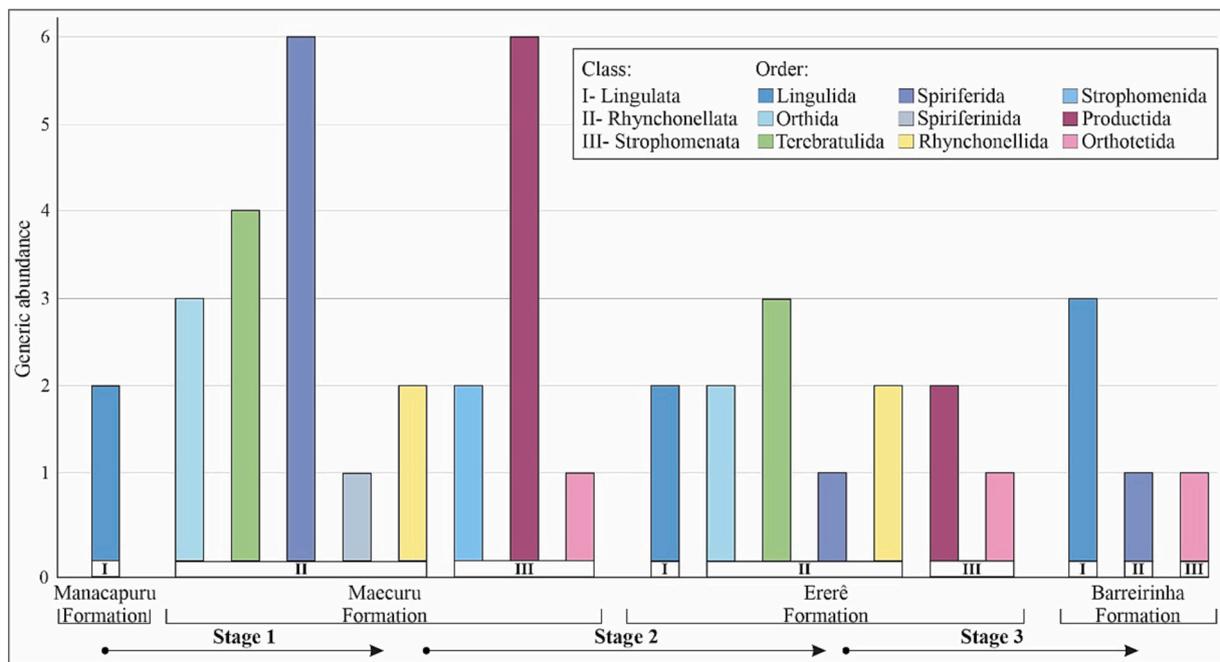


Fig. 9. Brachiopod diversity (class, order, and genus) recorded in the Devonian units from the Amazonas Basin.

environments (Caputo, 1984; Melo, 1985; Fonseca and Ponciano, 2011). On the other hand, the brachiopods of the Maecuru Formation occur in layers of fine to coarse sandstone, attributed to more proximal environments (Caputo, 1984; Melo, 1985; Fonseca and Ponciano, 2011).

**Stage 2:** Thirteen genera and sixteen species of brachiopods occurred in offshore deposits of the Ererê Formation (Fig. 8 C), representing a decline of approximately 50% in the diversity of genera compared to the brachiopods of the Maecuru Formation. Although we observed a considerable decrease in the Ererê Formation, representatives from almost all orders previously documented in the Maecuru Formation remain, except for Spiriferinida and Strophomenida (Fig. 9). The fauna of the Ererê Formation is attributed to deeper water conditions than the Maecuru Formation (Fig. 8A), related to a transgression, in addition to warmer climatic conditions, suggested by the presence of thin dolomitic beds and some calcitic cementations (Caputo, 1984).

Most Devonian extinction events are related to rapid regressive–transgressive pulses. The Choteč and Kačak events are examples of these global extinctions (House, 2002; Becker et al., 2012).

In the Paraná Basin, studies recognize two faunistic declines of marine invertebrates related to regressions and transgressions. The first occurred between late Pragian – early Emsian, with the extinction of eight brachiopod species (Bosetti et al., 2012). This decline would be related with the late Pragian – early Emsian regression and the transgression in the early late Emsian (Bosetti et al., 2012). The second decline was identified by Horodyski et al. (2013) in layers from the São Domingos Formation, with a reduction of 57 genera of marine invertebrates, this being the possible record of the global Kačak extinction event in the Paraná Basin. The authors relate this decline with the transgression in the Eifelian–Givetian (Horodyski et al., 2013).

Of the sixteen brachiopod species from the Ererê Formation, seven are remnants from the Maecuru Formation, and nine are new species. This first decline is likely related to the relative sea-level rise, which caused environmental disruptions and a drastic ecological shift responsible for the disappearance of twenty-one brachiopod species. These changes enabled new species to occupy the affected area through speciation or immigration (Krebs, 2014; Bosetti et al., 2011), justifying the emergence of the six new species in the Ererê Formation.

**Stage 3:** In the Frasnian (Fig. 10 C), there was a second diversity decline of Devonian brachiopods in the Amazonas Basin, as recorded in

the Barreirinha Formation when the Phylum was almost extinct, with only records of Lingulida, Spiriferida, and Orthothetida (Fig. 9).

The dark sedimentary facies (indicative of dysoxia or anoxia), with a benthic fauna that is poor in diversity or non-existent, generally characterize the twenty Paleozoic extinctions (House, 2002).

A major global transgression started in the Late Devonian (Caputo, 1984). The brachiopods from the Barreirinha Formation occur in layers of black shale with anoxic or dysoxic (oxygen-deprived) conditions of high stress attributed to an offshore environment. Caputo (1984) believes that in this period, the Amazonas basin experienced the deepest marine conditions in its history. Such conditions do not favor the proliferation of benthic fauna rich in diversity (Copper, 1977; Melo, 1985). Only a few organisms adapted, which explains the second diversity decline.

The subdivisions of the Famennian, as formally established by the Devonian Stratigraphy Subcommittee (SDS) into four substages (Lower, Middle, Upper, and Uppermost), are not recognized in the Amazonas Basin (Becker et al., 2012; Cunha et al., 2007). In the Famennian, the Amazonas Basin experienced a glacial period characterized by the diamictites from the Curiri Formation (Caputo, 1984). Brachiopods are absent in this unit. It is possible that the extreme glacial conditions were an obstacle to the survival of the Phylum.

## 7. Conclusions

The Amazonas Basin has a higher diversity of Devonian brachiopod genera among Brazilian sedimentary basins (Paraná, Parnaíba, Parecis, and Jatobá basins). In quantitative analysis, the number of the genera recorded in the Manacapuru, Maecuru, Ererê, and Barreirinha formations follows the global trend of the Phylum in the Devonian in terms of diversity. There was a significant increase in the variety of genera during the Lochkovian – early Eifelian representing the apex of brachiopod diversity of the Devonian in the Amazonas Basin. The first decline occurred between early Eifelian – late Eifelian when about 50% of brachiopod genera became extinct in the Amazonas Basin. Subsequently, a second decline occurred between the late Eifelian – early Frasnian. The variation in diversity of brachiopod genera throughout the Devonian in the Amazonas Basin is related to factors such as the geographic position of the paleocontinents (Gondwana and Laurussia),

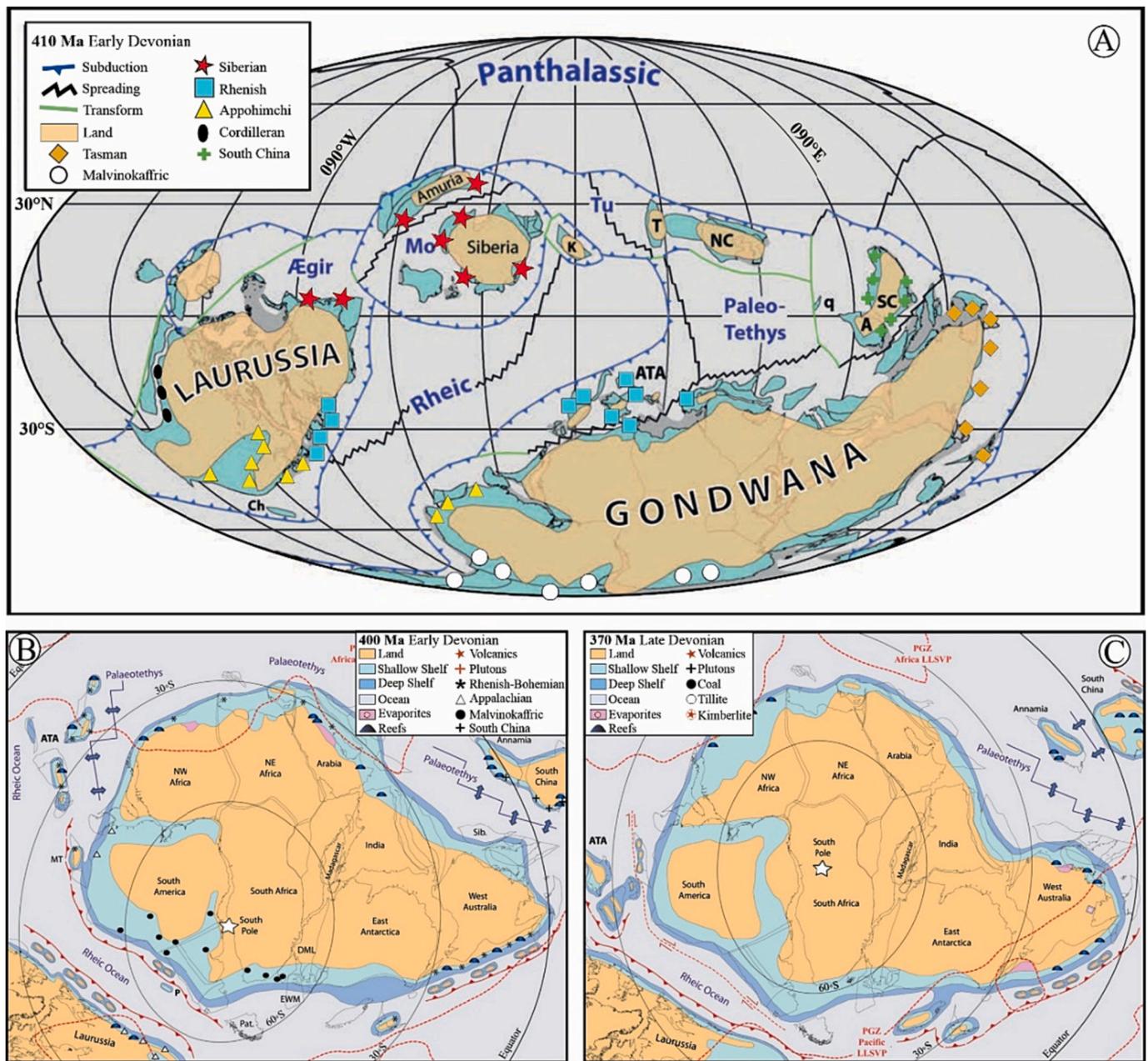


Fig. 10. A) paleogeography at 410 Ma. (Torsvik and Cocks, 2016); B) Gondwana at 400 Ma. and C) Gondwana at 370 Ma. (Torsvik and Cocks, 2013).

ocean temperatures, oxygen availability, and variations in global relative sea levels.

During the Lochkovian, the Amazonas Basin was closer to Laurasia, the environmental conditions were marine, the climate was not as severe as at the beginning of the Silurian, and these conditions probably enabled the migration of cosmopolitan larvae of *Orbiculoidea* from Laurasia to the Amazonas Basin first, as shown by the records of *O. baini*, *O. bodenbenderi*, and *O. excentrica* from the Manacapuru Formation. The peak of brachiopod diversity is recorded in the Maecuru Formation (early Eifelian) in a proximal marine environment, where global ocean temperatures were increasing, and the Amazonas Basin was between subtropical latitudes 30°S and 60°S. The first decline is related to deeper environmental conditions (resulting from a transgression) and higher temperatures than those in the early Eifelian (Maecuru Formation). The Barreirinha Formation registers the second decline (early Frasnian). A major global transgression occurred in the Late Devonian. In this period, the Amazonas basin experienced the deepest marine conditions in its

history. The brachiopods from the Barreirinha Formation occur in layers of black shale with anoxic or dysoxic (oxygen-deprived) conditions of high stress attributed to an offshore environment, which explains the low diversity of brachiopod fauna in this formation. In the Famennian, the Amazonas Basin experienced a glacial period (Curiri Formation). Brachiopods are absent in this unit. It is possible that the extreme glacial conditions were an obstacle to the survival of the Phylum.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2023.111803>.

**Declaration of Competing Interest**

None.

**Data availability**

Data will be made available on request.

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