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Macroevolution and adaptive processes of the Leptocoeliidae family (Brachiopoda) throughout the Silurian and Devonian

Macroevolução e processos adaptativos da família Leptocoeliidae (Brachiopoda) ao longo do Siluriano e Devoniano

Macroevolución y procesos adaptativos de la familia Leptocoeliidae (Brachiopoda) a lo largo del Silúrico y Devónico

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Abstract: The Leptocoeliidae family (genera *Anabaia*, *Australocoelia*, *Eocoelia*, *Leptocoelia*, *Leptocoelina* and *Pacificocoelia*) has an important place in the global paleobiogeography, during the Silurian and Devonian. During these periods, global climate changes impacted a lot of invertebrate faunas in the epicontinental seas of Gondwana. In the Silurian, the genus *Eocoelia* reached a cosmopolitan behavior, while *Leptocoelia* emerged by adaptive sympatric processes and *Anabaia* became extinct. After that, during the Devonian, the genus *Australocoelia* emerged and reached cosmopolitan levels while *Leptocoelina* and *Pacificocoelia* emerged by sympatries in the equatorial regions. *Australocoelia*, during the Devonian, occupied the same ecological niches that were previously occupied by *Anabaia* in the Silurian. It can be said that the same occurred with *Pacificocoelia* and *Eocoloelia* in the seas of Laurentia, configuring a process of succession of faunas.
Keywords: succession of faunas, paleobiogeography, Gondwana, climate change

Resumo: A família Leptocoeliidae (gêneros *Anabaia*, *Australocoelia*, *Eocoelia*, *Leptocoelia*, *Leptocoelina* e *Pacificocoelia*) ocupa um lugar importante na paleobiogeografia global, durante o Siluriano e Devoniano. Durante esses períodos, as mudanças climáticas globais impactaram muitas faunas de invertebrados nos mares epicontinentais de Gondwana. No Siluriano, o gênero *Eocoelia* atingiu um comportamento cosmopolita, enquanto *Leptocoelia* emergiu por processos simpátricos adaptativos e *Anabaia* foi extinto. Depois disso, durante o Devoniano, o gênero *Australocoelia* emergiu e atingiu níveis cosmopolitas enquanto *Leptocoelina* e *Pacificocoelia* surgiram por simpatrias nas regiões equatoriais. *Australocoelia*, durante o Devoniano, ocupou os mesmos nichos ecológicos que antes eram ocupados por *Anabaia* no Siluriano. Pode-se dizer que o

mesmo ocorreu com *Pacificocoelia* e *Eocoloelia* nos mares de Laurentia, configurando um processo de sucessão de faunas.
Palavras-chave: sucessão de faunas, paleobiogeografia, Gondwana, mudanças climáticas

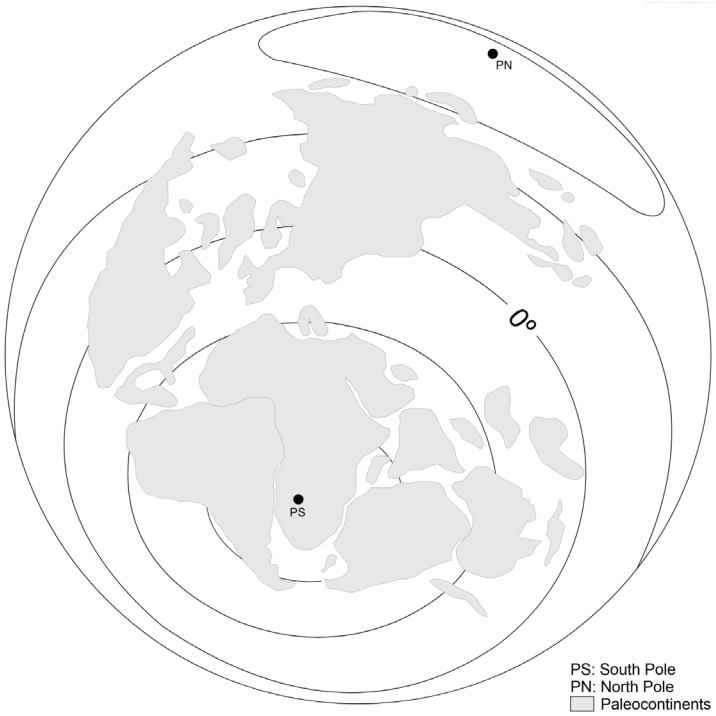
Resumen: La familia Leptocoeliidae (géneros *Anabaia*, *Australocoelia*, *Eocoelia*, *Leptocoelia*, *Leptocoelina* y *Pacificocoelia*) ocupa un lugar importante en la paleobiogeografía mundial, durante el Silúrico y el Devónico. Durante estos períodos, los cambios climáticos globales afectaron a muchas faunas de invertebrados en los mares epicontinentales de Gondwana. En el Silúrico, el género *Eocoelia* alcanzó un comportamiento cosmopolita, mientras que *Leptocoelia* surgió por procesos simpátricos adaptativos y *Anabaia* se extinguió. Posteriormente, durante el Devónico, surgió el género *Australocoelia* y alcanzó niveles cosmopolitas mientras que *Leptocoelina* y *Pacificocoelia* surgieron por simpatrías en las regiones ecuatoriales. *Australocoelia*, durante el Devónico, ocupó los mismos nichos ecológicos que antes ocupaba *Anabaia* en el Silúrico. Puede decirse que lo mismo ocurrió con *Pacificocoelia* y *Eocoloelia* en los mares de Laurentia, configurando un proceso de sucesión de faunas.
Palabras clave: sucesión de faunas, paleobiogeografía, Gondwana, cambio climático

INTRODUCTION

In the Leptocoeliidae family Boucot & Gill 1956 are included the genera *Anabaia* Clarke 1893, *Australocoelia* Boucot & Gill 1956, *Eocoelia* Nikiforova 1961, *Leptocoelia* Hall 1857, *Leptocoelina* Johnson 1970, and *Pacificocoelia* Boucot 1975. The oldest fossil records are in Silurian rocks, but only in the Devonian did the family acquire the capacity to inhabit several localities in Gondwana (Domeier & Torsvik, 2014; Torsvik & Cocks, 2016). During the Silurian and Devonian periods, Gondwana occupied high latitudes. Due to the lack of polar ice caps and the high sea level, several epicontinental seas occupied the interior regions of South America. At the same time, the Euro-American continental block coalesced near the paleo-Equator (Figure 1) (Habicht, 1979; Rowley, Raymond, Parrish, Lottes, Scotese and Ziegler, 1985; Golonka, 1994; Scotese, Boucot and Mckerrow, 1999; Di Pasquo *et al*., 2015).

In northern Australia, northwest Africa, Siberia, Kazakhstan, northwest South America and central Europe the climates were warm and temperate, while in high latitude regions the climates were mostly colder (Habicht, 1979; Rowley *et al*., 1985; Raymond, 1987). These climatic diversities affected directly the brachiopod fauna, causing many processes of ecological dispersion and retraction. Taking into account climate changes in the past and occurrences of the Leptocoeliidae family across the globe, this work aims to discuss the processes of dispersion, retraction, paleobiogeographical migration and extinction that affected these brachiopods during the Silurian and Devonian.

Figure 1: Paleogeography distribution of the continents during the Devonian period.



Source: adapted from Golonka, 1994; Scotese *et al*., 1999; Di Pasquo *et al*., 2015.

The Silurian and Devonian climate changes

With the end of Ordovician glaciation, the planet underwent a gradual global warming throughout the Llandoverian Epoch, resulting in several marine transgressions (Ghienne, Monod, Kozlu and Dean, 2010; Domeier & Torsvik, 2014; Domier, 2015). This climate change interfered directly in the dispersal of marine invertebrates on a global scale, especially brachiopods, giving them a cosmopolitanism characteristic, but the fauna of high latitude in south Gondwana did not reach this attribute (Cocks, 1972; Torsvik & Cocks, 2016). Few dispersal and extinction events happened during the Wenlockian Epoch, and things started to change only in the transition to the Ludlowian Epoch, when climate change caused the disappearance of brachiopod taxa, emergence of the first coral reefs and the biogeographic explosion of tabular corals (Jeppsson, 1987; Boucot 1990).

In the interior basins of Gondwana (Africa, Antarctica, Arabian Peninsula, India, South America, and other areas), the transition from the Silurian to the Devonian was marked by several small extinctions and dispersals. Some taxa of Silurian benthic brachiopods were able to cross this limit, while others became extinct (Chlupác, 1994; Boucot, 1990). In the Lower Devonian, the globe underwent a brief period of cooling, the equatorial seas reached 22ºC and temperatures ranged from 30ºC to 32ºC during the Lochkovian. Sea level changes and climatic variations provided an increase in the diversity of some taxa and the appearance of others (Boucot, 1990; Chlupác, 1994; Sedorko, Bosetti, Ghilardi, Myszynski-Júnior, Silva and Scheffler, 2018).

The passage from the Lower Devonian to the Middle Devonian was marked by global warming, proved by the formation of several carbonate platforms, coral reefs, increasing occurrence of evaporites, absence of glacial deposits, and cosmopolitanism of marine fauna in low-latitude localities (Elrick, Berkyová, Klapper, Sharp, Joachimski and Fryda, 2009). In addition, this global warming helped the diversification and domination of plants in the continents (Walliser, 1996). Land plants were able to develop roots, which extract nutrients from the soil and increase available biomass in the ecosystems. This intensification of pedogenic weathering may have contributed to the extinction of several benthic taxa, done by a generalized anoxia in the waters in the Middle Devonian (Algeo & Scheckler, 1998; Retallack & Huang, 2011; Di Pasquo *et al.*, 2015).

Another Middle Devonian extinction event of extreme importance for the marine faunas of southern Gondwana was the KAČÁK Event. Originally identified in Europe through taxonomic inconsistencies, the cause is still difficult to define. In Brazil, the only record of this event can be found in the central portion of the Paraná Basin, in the state of Paraná (Bosetti *et al.*, 2011; Bosetti *et al.*, 2012).

The relatively rapid increase in the climate gradient on a global scale, large regressive-transgressive events and global eustatic variations probably caused the extinction of several marine taxa in Gondwana, parallel to selective extinctions in the equatorial regions (Boucot, 1990; Chlupác, 1994; Penn-Clarke, Rubidge and Jinnah, 2018; Penn-Clarke, 2019).

Finally, in the Late Devonian extinctions continued gradually, high rates of organic carbon burial, associated with isostatic sea level changes resulted in global cooling. Massive glaciations occurred in southern Gondwana, recorded in Bolivia, Brazil, Peru, Antarctica and Africa, leading to the final extinctions of brachiopods (McGhee, 1990; Thompson & Newton, 1988; Elrick *et al.*, 2009; Ghilardi, Scheffler, Horodyski and Bosetti, 2011; Dowding & Ebach, 2019).

The Leptocoeliidae family and the Malvinoxhosan fauna

The Leptocoeliidae family plays an important role in understanding the Devonian brachiopods in Gondwana, because *Australocoelia* is a key genus that makes up Malvinokaffric fauna, recently renamed as Malvinoxhosan (Penn-Clarke, 2019). This biota occurred in the epicontinental seas that today are Argentina (Tarija Basin, Central and West), Brazil (Paraná Basin), Bolivia (Tarija and Madre de Dios Basin), Uruguay (Chaco), South Africa (Cape Basin) and Falkland Islands (Habicht, 1979; Rowley *et al.*, 1985; Raymond, 1987; Walliser, 1996; Scotese *et al.*, 1999; Penn-Clarke *et al.*, 2018; Dowding & Ebach, 2019).

For the Devonian, the Malvinoxhosan fauna was a set of high latitude marine taxa, with a high degree of endemicity and low specific diversity. In addition to *Australocoelia*, the brachiopods *Australospirifer*, *Australostrophia*, *Iridistrophia*, *Meristelloides*, *Derbyina*, Linguliids and *Orbiculoidea* are included (Carvalho, 1976; Melo, 1988; Quadros, 1979). The fauna provincialism began in the Pragian (Lower Devonian) and reached its peak in the Lower Eifelian (Middle Devonian) after geographic and reproductive isolation (Clarke, 1913; Boucot, 1975; Melo, 1988; Penn-Clarke, 2019). The endemism decreased throughout

the Middle Devonian, leading to the disappearance of most taxa of brachiopods (Boucot, Rowell, Racheboeuf, Pereira, Melo and Siqueira, 1971; Andrade & Camarço, 1980; Melo, 1988; Grahn, Mauller, Pereira and Loboziak, 2010; Bosetti, Grahn, Horodyski, Mauller, Breuer and Zabini, 2011).

According to Boucot (1975) the Malvinoxhosan fauna can be reported during the Silurian in several locations, as the genera *Anabaia*, *Eocoelia* and *Leptocoelia* already inhabited the seas of Gondwana. Both in the Devonian and in the Silurian, the brachiopod fauna had a limited general diversity, related to the presence of cold waters (Boucot & Johnson, 1967). In addition to the genus *Anabaia, Amosina* Muir-Wood 1962, *Australina* Twenhofel 1914, *Castellaroina* Caster 1939, *Clarkeia* Schmidt 1965 and *Heterorthella* Schuchert & Cooper 1931 comprise the index species of the Silurian Malvinokaffric fauna. Most of the Silurian brachiopods were not able to break the Siluro-Devonian climate barrier, but the genera *Anabaia*, *Eocoelia* and *Leptocoelia* are exceptions, as they can be found in the Lower Devonian, strengthening the importance of understanding the Leptocoeliidae family (Figure 2) in space and time (Berry & Boucot, 1972; Boucot & Johnson, 1967).

MATERIAL AND METHODS

An extensive bibliographical survey was carried out to reach the goal of this paper. More than 120 fossiliferous occurrences were considered, with around 1200 brachiopods from the Leptocoeliidae family. The fossils are deposited in many countries, such as Argentina (Universidad Nacional de Córdoba), Brazil (Museu Nacional, Departamento Nacional da Produção Mineral and Universidade Estadual de Ponta Grossa), Canada (Quebec Department of Natural Resources, Geological Survey of Canada, University of Western Ontario and University of Montreal), Chile (Museo Humberto Fuenzalida), England (Oxford University Museum of Natural History and Sedgwick Museum), South Africa (Oosthuizen Personal Museum), United States (National Museum of Natural History, California Institute of Technology, Oregon State University and Museum of Natural and Cultural History at the University of Oregon) and Wales (National Museum of Wales).

All the occurrences of Leptocoeliidae family, including the genera *Anabaia*, *Australocoelia*, *Eocoelia*, *Leptocoelia*, *Leptocoelina* and *Pacificocoelia*, were considered. The occurrences in duplicate were taken into account, but discarding one of them. Not only fossils dated to the Devonian were considered, with records of *Anabaia* and *Eocoelia* in the Silurian. As a support, the databases available online in the FossilWorks and Paleobiology Database were used, both having updated data, including information on systematics, taxonomy, provenance.

RESULTS

The genus *Anabaia* occurs in the Silurian rocks of Argentina (from the Llandovery to the Pridoli), the Amazon Basin (Llandovery), Guinea (Ludlow), Paraguay (Llandovery)

and Peru (from the Llandovery to the Ludlow) (Benedetto, 1995; Benedetto & Cocks, 2009; Benedetto & Franciosi, 1998; Grahn, 1992; Harrington, 1972; Lehnert, Bergstroem, Benedetto and Vaccari, 1999; Racheboeuf & Villeneuve, 1992).

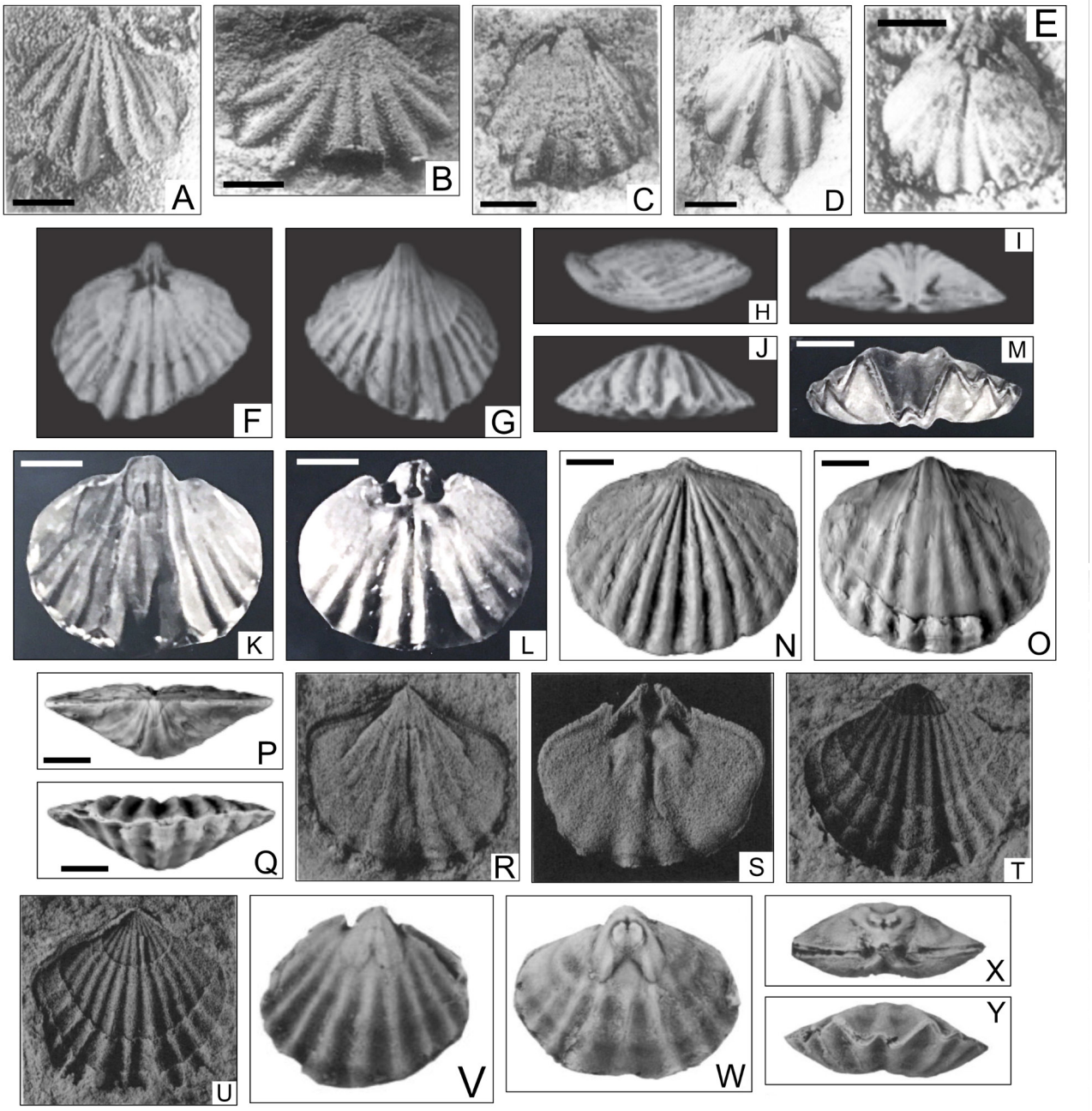
It is important to say that, *Harringtonina* was synonymized to *Anabaia* and was also considered in this survey. There are evidences of *Harringtonina acutiplicata* in Argentina, Los Espejos (Ludlow) and Lipeon (Wenlock to Ludlow) formations (Sanches, Waisfeld and Benedetto, 1991). And in Peru, Laubacher, Boucot and Orstom (1982) described *H. acutiplicata* in the Cerro Monteiro, Taya-Taya and Cerro Japune formations and *H. paraguayensis* in the Cerro Monteiro formation, Llandovery to Ludlow (Figure 3).

The genus *Eocoelia* occurs mostly in the northern regions. In the Canadian Llandovery there is a significant diversity of species, among them *Eocoelia akimiskii*, *E. curtisi*, *E. hemisphaerica* and *E. intermedia*, besides *E. sulcata* in Wenlock (Copper, 1981; Dewing, 1999; Jin & Copper, 1999; Jin, 2003; Gushulak, 2016). On the North American east coast, there are reports of *Eocoelia* (*E. hemisphaerica* and *E. sulcata*) from Llandovery to Ludlow (Woodwar, 1941; Eckert & Brett, 1989; Boucot, 1990).

On the European continent, *Eocoelia* (*E.* sp., *E. curtisi* and *E. hemisphaerica*) can be found in the Llandovery rocks of England (Jones, Brooks, Bassett, Austin and Aldridge, 1969; Curtis, 1972; Williams & Wright, 1981), Ireland (Aldridge, Turner, Jones and Harper, 1996), Czech Republic (Havlíček & Štorch, 1990) and Russia (Sokolov, 1985). During the Wenlockian Epoch, the usual localities for this taxon are the Czech Republic, Norway (Gudveig Baarli, Keilen and Johnson, 1999), Sweden (Bassett & Cocks, 1974) and Estonia. *Eocoelia angelini* can also be found in the rocks of Ludlow in Estonia (Rubel, 1977). Finally, in Paraguay, the genus can be found in rocks from Llandovery to Wenlock, while in Venezuela, occurrences are restricted to Llandovery (Harrington, 1972; Boucot, Benedetto, Grahn and Melo, 1999) (Figure 3).

According to Benedetto & Franciosi (1998), the oldest record of *Leptocoelia* (*L. nunezi*) is in the Wenlock of Argentina. In the Lower Devonian, this taxon can be found in the east and west of the United States (Boucot, Lal Gauri and Southard, 1970; Bartlett & Webb, 1971; Johnson, 1974), in Canada (Kindle, 1938; Lesperance & Sheehan, 1975), Australia (Savage, 1974; Neil, 1982), Venezuela (Sanchez & Benedetto, 1983) and in Mato Grosso do Sul, in the Paraná Basin (Melo, 1988) (Figure 3).

Figure 2: Some specimens of the family Leptocoeliidae. *Anabaia* sp.from northwestern Argentina; scale bar 5 mm (A-E). *Australocoleia palmata* from Morro Vermelho, Brazil (F-J). *Australocoelia tourteloti* from Chapada dos Guimarães, Brazil; scale bar 5 mm (K-M). *Eocoelia akimiskii* from Houston Point, Canada; scale bar 2 mm (N-Q). *Leptocoelia flabelites* (R-U) and *Pacificocoelia acutiplicata* from New York, United States (U-Y).



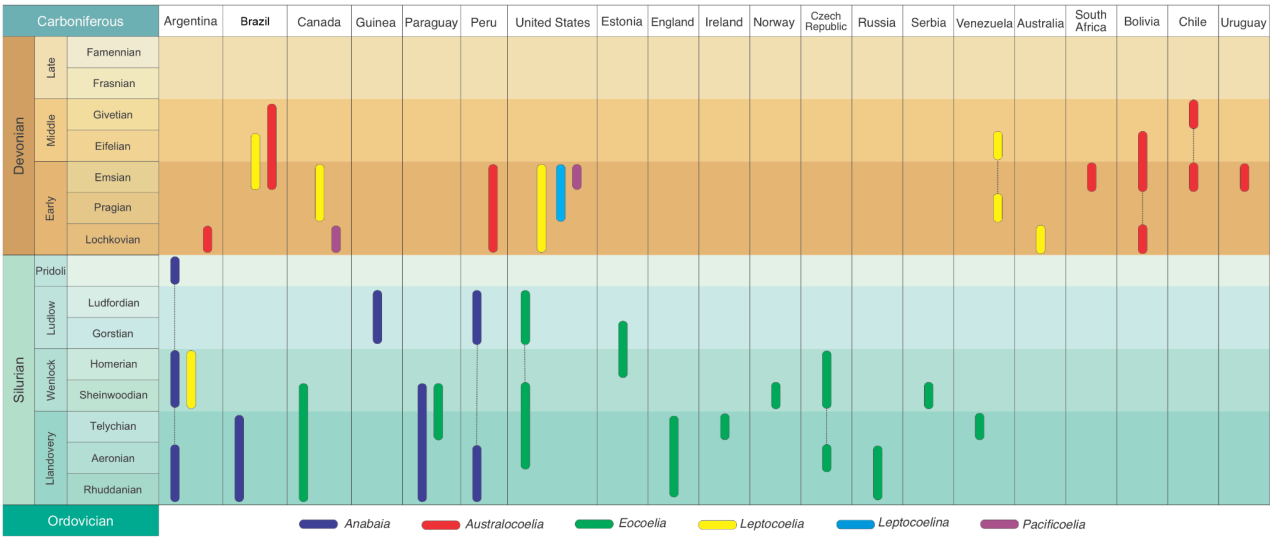
Source: adapted from Boucot, 1959; Boucot & Rehmer, 1977; Quadros, 1979; Benedetto, 1995; Boucot *et al.*, 2001 and Jin, 2003.

Continuing in the Lower Devonian, *Australocoelia* occurs in Argentina (Benedetto, Racheboeuf, Herrera, Brussa and Toro, 1992), Bolivia (Wolfart, 1968; Isaacson, 1977) Uruguay (Mendez-Alzola, 1938; Melo, 1988), Peru (Laubacher *et al.*, 1982), Chile (Boucot, Bahlburg, Breitkreuz, Isaacson, Niemeyer and Urzua, 1995), South Africa (Oosthuizen,

1984). In Brazil, in the northern and northeastern portions of the Paraná basin (Quadros, 1979; Melo, 1988; Ribeiro, Ghilardi and Caminha, 2019), and Parecis (Boucot, Rowell, Racheboeuf, Pereira, Melo and Siqueira, 2001) and Parnaíba basins (Queiroz, Gama-Junior and Pires, 2013; Ribeiro, Sousa, Gaia, Carbonaro, Scheffler and Ghilardi, 2021). During the Middle Devonian, *Australocoelia* was restricted to southern Gondwana, and could be found in the rocks of South Africa (Oosthuizen, 1984), in Brazil (Parnaíba and Paraná Basins) (Carvalho, 1976; Melo, 1988; Bosetti *et al.*, 2011), Bolivia (Isaacson, 1977) and Chile (Boucot *et al.*, 1995) (Figure 3).

The occurrences of *Leptocoelina* and *Pacificocoelia* are restricted to the North American continent, both during the Lower Devonian. According to Johnson (1986) *Leptocoelina* can be found in the state of Nevada, United States. On the other hand, *Pacificocoelia* can be found in the North American Midwest and in the Canadian state of Quebec (Boucot, 1990) (Figure 3).

Figure 3: Occurrences of the Leptocoeliidae family across the globe during the Silurian and Devonian.



Source: the authors

DISCUSSION

The Silurian and Devonian were considerably warm periods, when compared to the underlying Ordovician and the overlying Carboniferous, resulting in an isostatic sea level higher than today. These changes in sea level caused several epicontinental seas to arise in the interior regions of Gondwana, Baltica and Laurentia. The seas that occupied the southern regions (South America, Africa, Australia, Antarctica, etc.) hosted a brachiopod fauna distinct from those regions near the paleo-Equator.

The Leptocoeliidae family (*Anabaia*, *Australocoelia*, *Eocoelia*, *Leptocoelia*, *Leptocoelina* and *Pacificocoelia*) underwent several adaptive processes, including dispersion, speciation and extinctions throughout the Silurian and Devonian, as verified from fossil occurrences.

Following the Morrone and Crisci (1995) purpose, the center of dispersion for the Leptocoeliidae family can be established in the Llandovery (Rhuddanian), however the records are random around the globe. Additionally, there is not only one basal genus, both *Anabaia* and *Eocoelia* coexist temporally, but they have some paleogeographical differences.

The oldest occurrences of *Anabaia* are in the west Gondwana (Argentina, Brazil, Paraguay and Peru), while *Eocoelia* occurs in Laurentia and Baltica (England, Russia and Canada). Considering the climatic differences during the Llandoverian Epoch in the different localities, it can be said that these taxa inhabited distinct paleoecological niches. While *Anabaia* thrived in the southern seas, *Eocoelia* dominated the low-latitude equatorial and temperate oceans. Thus, the dispersal center of the Leptocoeliidae family can be allocated at the beginning of the Rhuddanian, or at the end of the Ordovician, in a warming paleoclimatic context, providing dispersion and diversification of the species.

The passage from Llandovery to Wenlock was a period of extreme importance for the Leptocoeliidae family. The genus *Eocoelia* obtained its maximum dispersion, in addition to the original boreal region (Canada, Estonia, Ireland, Norway, Czech Republic and Serbia), beginning to inhabit the seas of Gondwana, and becoming a cosmopolitan taxon. This fact is justified by the fossils found in Paraguay and Venezuela. The maximum dispersal of *Eocoelia* occurred at the beginning of the Wenlock (Sheinwoodian), and later went through the reverse process, becoming completely extinct at the end of Ludlow, as a result of paleoenvironmental changes in a second-order global event (Barnes *et al.*, 1996).

At the same time, during Wenlock there is the first record of the genus *Leptocoelia* in Argentina. The appearance of this taxon in the epicontinental seas of Gondwana may be associated with a process of sympatric speciation of the genus *Anabaia*, also recurrent in this area. Kohn (1959) and Boucot (1975) point out that this speciation process can occur in geographically limited regions. It is noteworthy that temperatures during this period tended towards warming, which could have helped the speciation process (Berry *et al.*, 1988).

The Silurian-Devonian boundary was crucial for the Leptocoeliidae family, as it was where the extinction of the genus *Anabaia* occurred, its last occurrence being reported in the Argentine rocks of Pridoli. *Leptocoelia* was the only genus capable of breaking through the climatic barrier of the transition to the Devonian.

During the Lower Devonian, the genetic diversity of the Family Leptocoeliidae remained high when compared to the variety in the Silurian. Boucot (1975) already pointed out that in the Devonian the Family Leptocoeliidae had a much greater diversity when compared to what can be seen in the Silurian, since in this period the dispersions and occurrences were concentrated in the equatorial continental blocks. It is also at this time that the genera *Pacificocoelia* and *Leptocoelina* appear and become extinct. Both taxa occur exclusively in regions that were located at low latitudes (Canada and the United States), strengthening the idea that they had a vital behaviour associated with warmer environments. Warm environments are good propellers for sympatric speciation (Kohn, 1959; Smith, 1966; Boucot, 1975), a case that could have resulted in the emergence of the genera *Pacificocoelia* and *Leptocoelina*.

The genus *Australocoelia* became dominant in most Devonian seas, especially in Gondwana (South Africa, Argentina, Bolivia, Brazil, Chile, Peru and Uruguay). Its dispersion center can be allocated in the southern sedimentary basins of the modern South American eastern coast, precisely because it is a region where can be found the oldest report (Lochkovian) of this genus in the fossil record, linked to the favourable paleoclimatic conditions of that time. Later, during the Emsian in particular, *Australocoelia* undergoes an accelerated dispersal process, becoming an extremely cosmopolitan brachiopod during the Devonian.

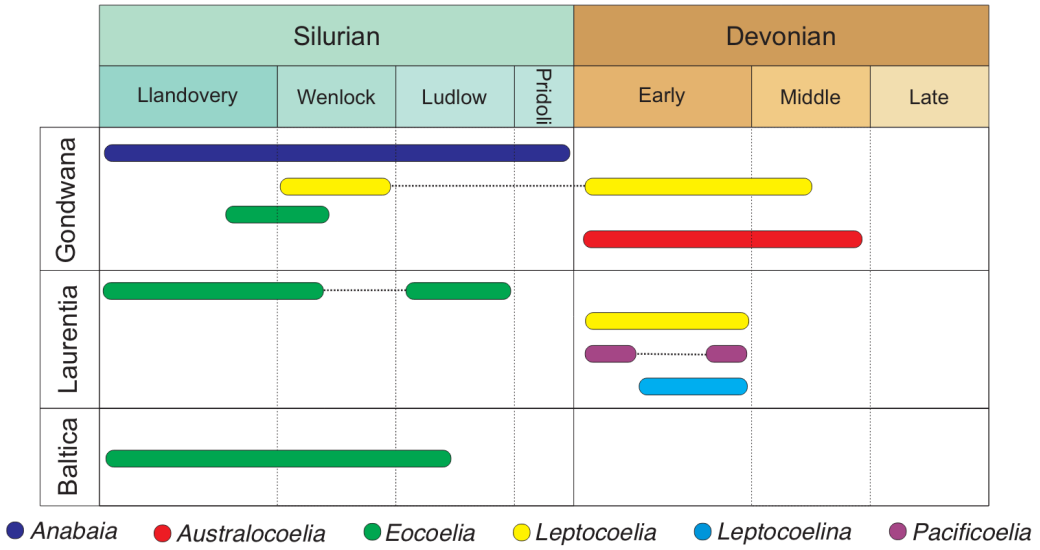
The passage from the Givetian to the Frasnian was marked by a high sea rise, an event that led to the extinction of several taxa of invertebrates across the globe (Barnes *et al.*, 1996). The same happened with the genus *Australocoelia*, which did not support the paleoenvironmental changes and became extinct there, with the most recent fossil records (Late Givetian) located in Chile and Brazil (Paraná Basin).

The cosmopolitanism of the genus *Eocoelia* in the Silurian followed by the cosmopolitanism of *Australocoelia* in the Devonian can be characterized as a process of ecological guild change in the paleoenvironment. Boucot (1975) says that over geological time, fossil communities, when subjected to ecological barriers, can differentiate from one another and occupy ecological niches formerly occupied by their predecessor taxa. Associated with the cosmopolitanism of *Eocoelia* and *Australocoelia* and considering the paleoclimatic oscillations in the transition from the Silurian to the Devonian, we can infer that these taxa went through this process. However, in totally different ecological niches. While *Eocoelia* occupied the equatorial seas, *Australocoelia* thrived in the polar seas of Gondwana (Figure 4).

CONCLUSION

The genus *Eocoelia* achieved a global cosmopolitan behaviour throughout the Silurian, recorded in the most diverse localities of Gondwana, Laurentia and Baltica. On the other hand, *Anabaia* did not manage to transgress the equatorial regions of that time, even with cosmopolitan behaviour in Gondwana. During the Wenlock, the Leptocoellidae family underwent a sympatric process, resulting in the emergence of the genus *Leptocoelia*.

Figure 4: Temporal and regional distribution of the Family Leptocoeliidae in the Silurian and Devonian.



Source: the authors

During the Devonian, cosmopolitanism was borne by the newly emerged genus *Australocoelia* in the Gondwana region, while *Leptocoelia* can be found in the most diverse locations around the globe, both in Gondwana, Laurentia and Baltica. Additionally, the equatorial and tropical regions were regions of extreme phylogenetic importance, this is because during the Lower Devonian sympatric processes resulted in the emergence of the genera *Leptocoelina* and *Pacificocoelia*, and their extinction in the transition to the Middle Devonian. The most recent records of the Leptocoeliidae Family are in charge of the genus *Australocoelia*, which can be found at the end of the Middle Devonian in the seas of Gondwana.

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