

Devonian Tentaculitoids from Brazil: extinction and stratigraphic distribution

Tentaculitoídeos do Devoniano do Brasil: distribuição estratigráfica e extinção

Tentaculitoides del Devónico brasileño: distribución estratigráfica y extinción

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Abstract: The class Tentaculitoidea is an extinct group composed of small carbonatic coniform-shaped invertebrates, distributed from Ordovician to Devonian. This group is more often recorded to the North Hemisphere, being less recorded to South Hemisphere deposits. This study aims (i) analyze the species found in Brazilian Devonian outcrops, in addition (ii) to investigate their paleogeographic and stratigraphic distribution. The analyzed samples, which come from Paraná, Amazonas and Parnaíba basins, are hosted in 9 Brazilian Research Centers. It was diagnosed 12 species of tentaculitoids: *Tentaculites crotalinus*, *Tentaculites jaculus*, *Tentaculites kozlowskii*, *Tentaculites paranaensis*, *Tentaculites eldredgianus*, *Tentaculites trombetensis*, *Tentaculites stubeli*, *Tentaculites oseryi*, *Uniconus ciguelii*, *Homoctenus katzerii*, *Styliolina langenii*, and *Styliolina clavulus*. The species from Paraná Basin are different from those recorded in Amazonas and Parnaíba basins, all present distinct stratigraphic ranges (Pragian to Givetian in Paraná Basin and Eifelian to Givetian in Amazonas and Parnaíba basins).

Keywords: Tentaculitoidea, Paleobiogeography, Devonian, Paraná Basin.

Resumo: A classe Tentaculitoidea é um grupo extinto representado por invertebrados de conchas coniformes carbonáticas, em diminutas dimensões. Representantes desse grupo são encontrados desde o Ordoviciano até o Devoniano, quando se extinguem. Constatou-se que no Hemisfério Norte o registro de tentaculitoideos é amplamente maior se comparado ao Hemisfério Sul. O objetivo deste trabalho foi (i) analisar as espécies encontradas em afloramentos do Devoniano brasileiro, e (ii) verificar a distribuição paleogeográfica e estratigráfica do grupo e as espécies que o compõem. As amostras analisadas são provenientes das bacias do Amazonas, Paraná e Parnaíba e encontram-se depositadas em nove instituições de pesquisa brasileiras. Foram reconhecidas 12 espécies de tentaculitoideos: *Tentaculites crotalinus*, *Tentaculites jaculus*, *Tentaculites kozlowskii*, *Tentaculites paranaensis*, *Tentaculites eldredgianus*, *Tentaculites trombetensis*, *Tentaculites stubeli*, *Tentaculites oseryi*, *Uniconus ciguelii*, *Homoctenus katzerii*, *Styliolina langenii* e *Styliolina clavulus*. Verificou-se que as espécies encontradas na Bacia do Paraná não possuem correspondentes com as encontradas nas bacias do Amazonas e Parnaíba. As espécies da Bacia do Paraná distribuem-se do início do Praguiano até o início do Givetiano, enquanto que as espécies das outras bacias são distribuídas do Eifeliano até o Givetiano.

Palavras-chave: Tentaculitoidea, Paleobiogeografia, Devoniano, Bacia do Paraná.

Resumen: La clase Tentaculitoidea es un grupo extinto compuesto por pequeños invertebrados carbonáticos de forma coniforme, distribuidos desde el Ordovícico hasta el Devónico. Este grupo se registra con mayor frecuencia en el hemisferio norte, y menos en los depósitos del hemisferio sur. Este estudio tiene como objetivo (i) analizar el registro de especies del Devónico de Brasil, además (ii) investigar su distribución paleogeográfica y estratigráfica. Las muestras analizadas, que provienen de las cuencas de Paraná, Amazonas y Parnaíba, se encuentran alojadas en 9 Centros de Investigación brasileños. Se diagnosticaron 12 especies de tentaculitoides: *Tentaculites crotalinus*, *Tentaculites jaculus*, *Tentaculites kozlowskii*, *Tentaculites paranaensis*, *Tentaculites eldredgianus*, *Tentaculites trombetensis*, *Tentaculites stubeli*, *Tentaculites oseryi*, *Uniconus ciguelii*, *Homoctenus katzerii*, *Styliolina langenii* y *Styliolina clavulus*. Las especies de la cuenca del Paraná son diferentes a las registradas en las cuencas de Amazonas y Parnaíba, todas presentan rangos estratigráficos distintos (Pragian a Givetian en la cuenca de Paraná y Eifelian a Givetian en las cuencas de Amazonas y Parnaíba).

Palavras clave: Tentaculitoidea, Paleobiogeografía, Devoniano, Cuenca del Paraná.

INTRODUCTION

Tentaculitoids have their first occurrence since the Ordovician, and it is considered a problematic group due to divergent interpretations regarding taxonomic affinities (Fisher & Young, 1955; Fisher, 1962; Farsan, 2005; Wittmer, 2009; Wittmer & Miller, 2011; Schindler, 2012). The abundance of tentaculitoids in some marine deposits is very well described; on the other hand, there is a scarcity of detailed studies about its paleoecologic and definitive diversity (Wittmer, 2009).

The Tentaculitoidea class is worldwide distributed with reports from Australia, Austria, Brazil, Canada, China, Czech Republic, France, Libya, New Zealand, Russia, Spain, South Africa, Ukraine, United Kingdom, Venezuela, and other areas (Lyashenko, 1955, 1957, 1959; Bouček, 1964; Blind, 1969; Lardeux, 1969; Alberti, 1970, 1993, 2000; Hajłasz, 1974, 1976, 1993; Larsson, 1979; Farsan, 1984, 1994, 2005; Lindemann & Yochelson, 1984, 1992; Yochelson & Kirchgasser, 1986; Lindemann & Melycher, 1997; Berkyová, Fryda & Lukes, 2007; Wittmer & Miller, 2011; Schindler, 2012; Wei, Gong & Yang, 2012; Comniskey, Ghilardi & Bosetti, 2015). These fossils are mostly preserved in black shales however, they can occur in gray limestones or other lithologies as well (Wittmer & Miller, 2011).

This group is well described in North Hemisphere with a large amount of genus and species (Lyashenko, 1955, 1957, 1959; Bouček, 1964; Blind, 1969; Lardeux, 1969; Larsson, 1979; Alberti, 1970, 1993, 2000; Hajłasz, 1974, 1976, 1993; Farsan, 1984, 1994, 2005; Yochelson & Kirchgasser, 1986; Lindemann & Yochelson, 1984, 1992; Lindemann & Melycher, 1997; Berkyová, Fryda & Lukes, 2007; Wittmer & Miller, 2011; Schindler, 2012; Wei, Gong & Yang, 2012). However, in the South Hemisphere, taxonomic studies are very rare, with just a few mentions to the group.

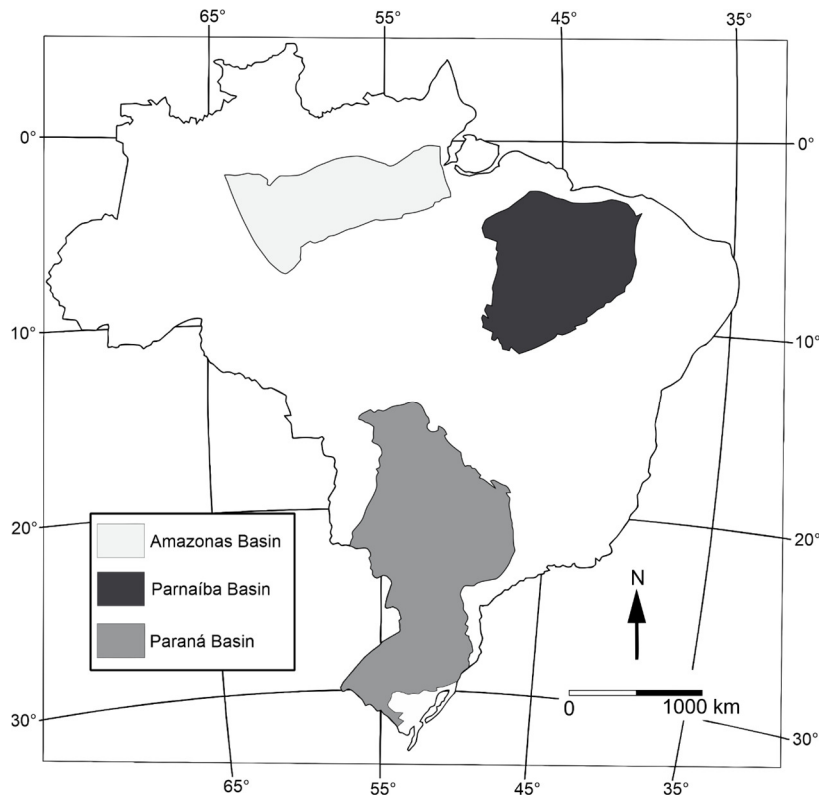
However, many authors mentioned Tentaculitoids in South American deposits (Clarke, 1913; Bosetti, Grahn, Horodyski & Mauller, 2012; Comniskey & Ghilardi, 2013, 2018; Comniskey, Ghilardi & Bosetti, 2015). Although, Wittmer & Miller (2011) suggest that the tentaculitoids of South America are restricted to the Devonian period, and the occurrence would be concentrated in areas of low paleolatitudes, mainly in Laurentia, Baltica, and Avalonia. Indicating that Tentaculitoids might have had a preference for tropical climatic conditions, and it was absent in high paleolatitudes seas (Wei, Gong & Yang, 2012).

In South America, the oldest Tentaculitoids can be found in Silurian rocks, specially recorded in countries as Argentina, Bolivia, Brazil, Paraguay, and Peru (Clarke, 1899b; Isaacson, Antelo & Boucot, 1976; Boucot, Isaacson & Laubacher, 1980; Ciguel, 1988, 1989; Grahn, 1992; Heredia, Mestre & Milana, 2007; Malanca, Aris, Boso, Gallardo, Brandán & Fernández, 2010). In relation to Devonian, there are just few records in Argentina, Bolivia, Brazil, Chile, Peru, and Uruguay (Hartt & Rathbun, 1875; Derby, 1890; Ulrich, 1893; Von Ammon, 1893; Katzer, 1897, 1903, 1933; Kayser, 1897, 1900; Siemiradzki, 1898; Clarke, 1899a, 1913; Schuchert, 1906; Knod, 1908; Boucot, Isaacson & Laubacher, 1980; Ciguel, 1988, 1989).

Thus, considering the lack of studies about tentaculitoids in South America, this study aims to (i) analyze the species found in Brazilian Devonian outcrops, and (ii) to

investigate their paleogeographic and stratigraphic distribution in three Devonian basins, Amazonas, Paraná, and Parnaíba (Fig. 1).

Figure 1: Geographic distribution of the three main Paleozoic Intracratonic basins in Brazil.



Source: modified from Melo (1998).

MATERIAL AND METHODS

During 9 visits to Brazilian Research Centers, eight hundred samples of tentaculitoid were analyzed. In addition, fieldwork was realized to increase the number of specimens, totalizing 4,818 studied specimens.

The samples from Paraná Basin come from fieldworks, and they were placed in Laboratório de Estratigrafia e Paleontologia in Universidade Estadual de Ponta Grossa (UEPG). The stratigraphic data considered in this study was based on Grahn et al. (2010), Grahn et al. (2013), and Horodyski et al. (2014).

The samples from Amazonas and Parnaíba basins were lodged in Departamento de Paleoinvertebrados - Museu Nacional (UFRJ), Núcleo de Estudos Paleontológicos e Estratigráficos in Universidade Federal do Rio de Janeiro (UFRJ), Departamento Nacional de Produção Mineral (DNPM), and Laboratório de Estudos de Comunidades Paleozoicas in Universidade Federal do Estado do Rio de Janeiro (UNIRIO). The stratigraphic data used for these basins were proposed by Grahn et al. (2010), and Scheffler (2010).

RESULTS

In general, most samples come from Paraná Basin (757 samples with 4576 specimens), followed by Parnaíba Basin (27 samples with 143 specimens), and finally the Amazonas Basin (13 samples with 99 specimens).

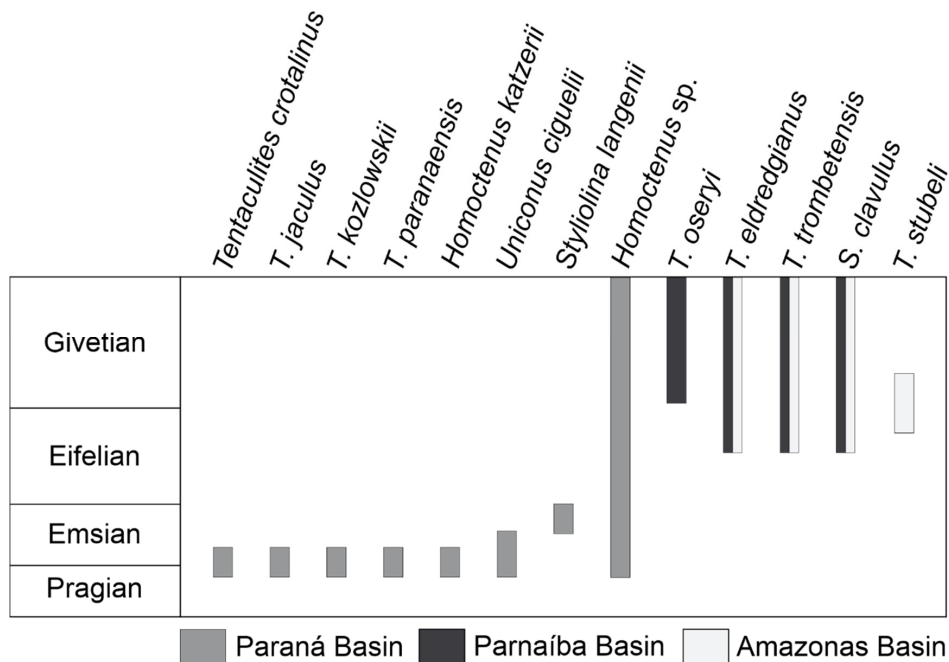
These samples allowed the identification of 12 species from the Devonian beds in Brazil (*sensu* Comniskey & Ghilardi, 2018), distributed as follows: 7 in the Paraná Basin (*T. crotalinus* (Salter, 1856), *T. jaculus* (Clarke, 1899), *T. kozlowskii* (Comniskey & Ghilardi, 2018), *T. paranaensis* (Comniskey & Ghilardi, 2018), *U. ciguelii* (Comniskey & Ghilardi, 2018), *H. katzerii* (Comniskey & Ghilardi, 2018) and *S. langenii* (Comniskey & Ghilardi, 2018)), 4 species in Amazonas Basin (*T. stubeli* (Clarke, 1899), *T. trombetensis* (Clarke, 1899), *T. eldredgianus* (Hartt & Rathbun, 1875) and *S. clavulus*)) and 4 from Parnaíba Basin (*T. oseryi* (Clarke, 1899), *T. trombetensis*, *T. eldredgianus* and *S. clavulus* (Clarke, 1899)).

DISCUSSION

Temporal and Spatial distribution of Tentaculitoids from Brazil

Considering the ages of the lithostratigraphic units from Paraná Basin, the tentaculitoids are distributed from upper Pragian to Eifelian; however, fragments of *Homoctenus* sp. were found in Givetian beds too. A decrease in the diversity and quantity of tentaculitoids species occurs after the end of Emsian (Fig. 2).

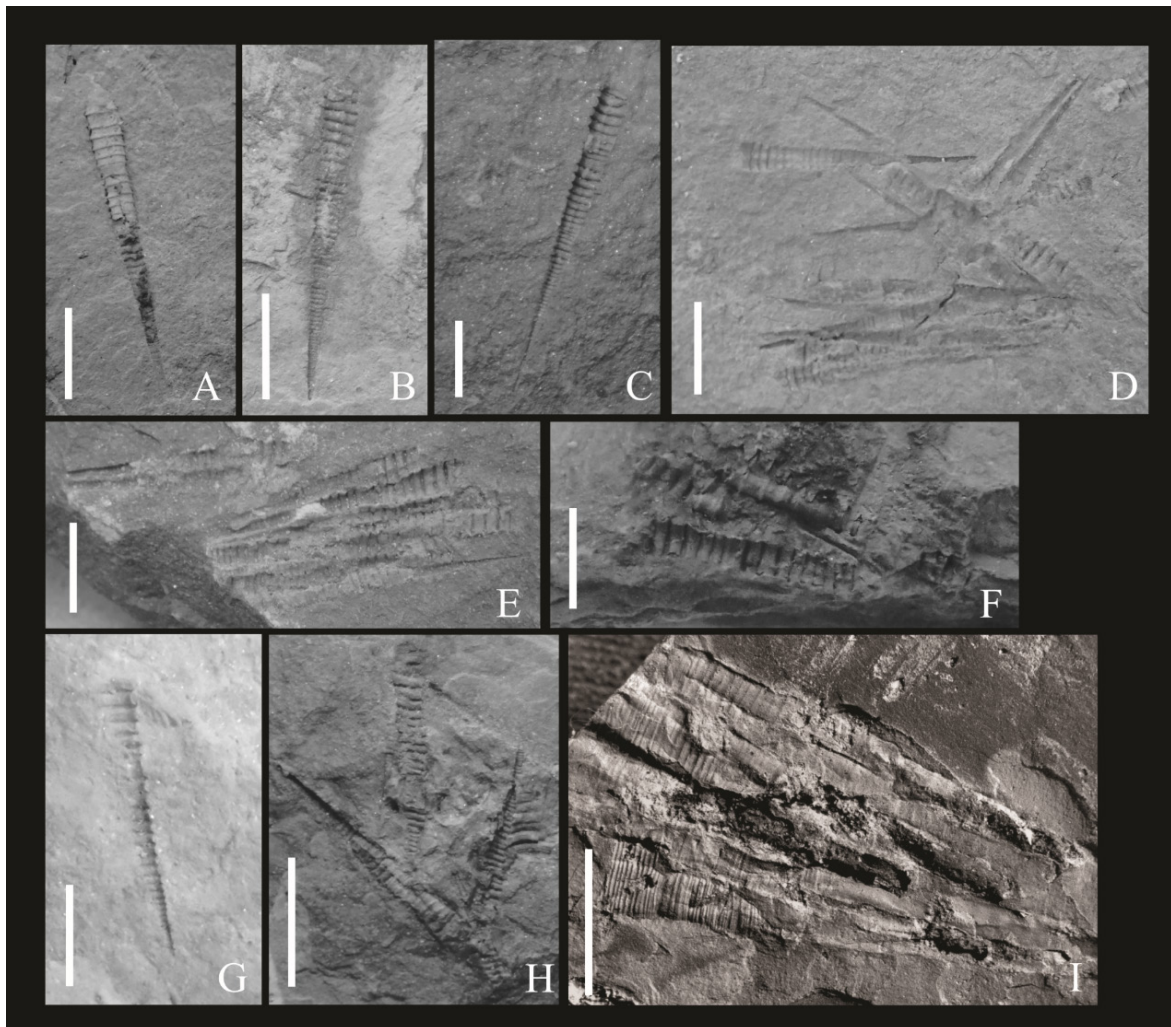
Figure 2: Biostratigraphic distribution of tentaculitoids species of the Brazilian Devonian.



In Paraná Basin, the species *T. crotalinus*, *T. jaculus*, *T. kozlowskii*, *T. paranaensis*, and *H. katzerii* are restricted to upper Pragian to lower Emsian, while *U. ciguelii* is restricted to upper Pragian to middle Emsian. Finally, *Styliolina langenii* occurs between the Middle and upper Emsian (Figure 3).

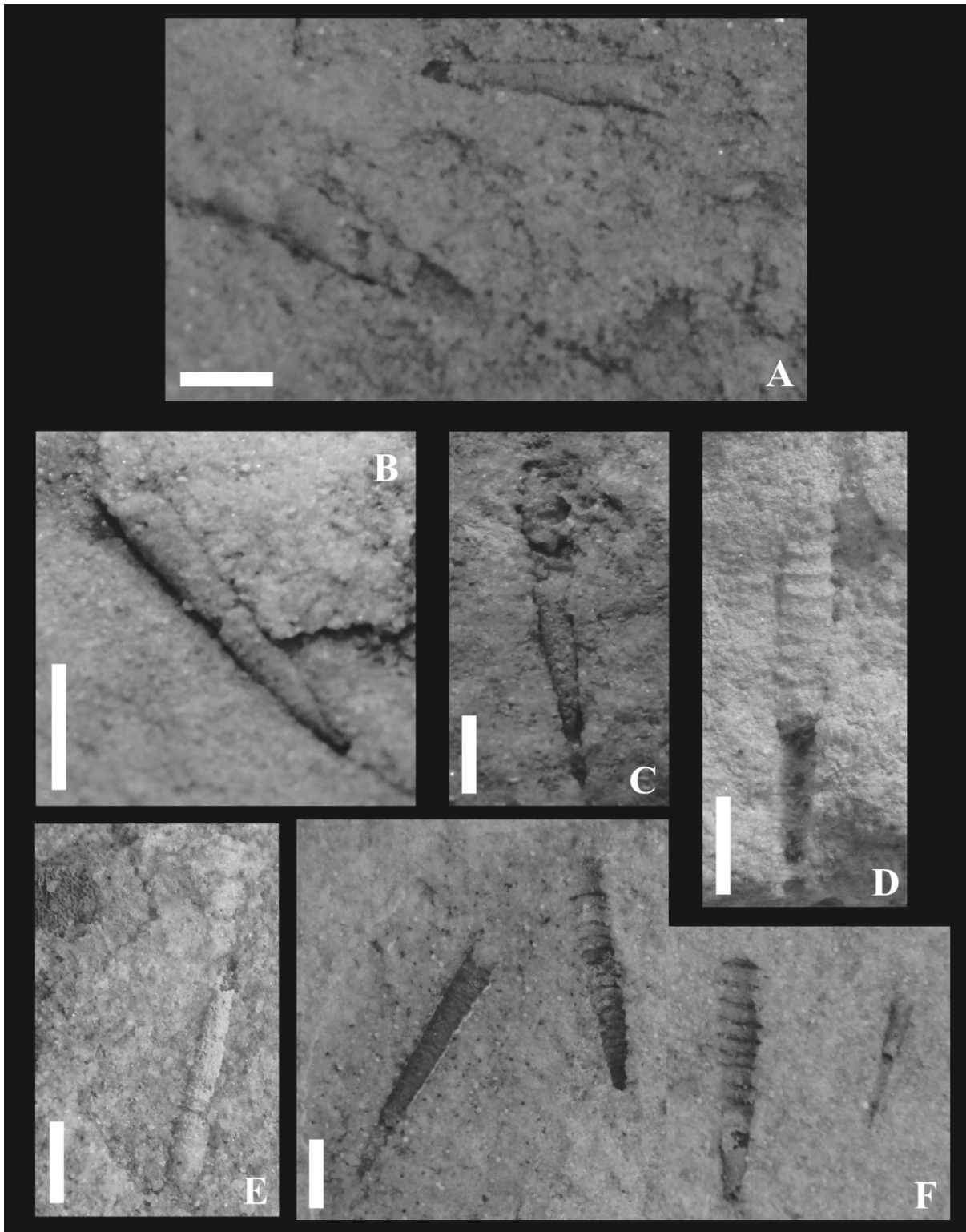
In Amazonas Basin, the stratigraphic distribution of the group is mostly from Middle Eifelian (*T. eldredgianus*, *T. Trombetensis*, and *S. clavulus*) to Givetian. One exception is *T. stubeli* that ranges from upper Eifelian to lower Givetian. In Parnaíba Basin was diagnosed a similar pattern, with most of the species restricted to middle Eifelian (*T. eldredgianus*, *T. trombetensis*, and *S. clavulus*) to Givetian, and only one species occurring during Givetian (*T. oseryi*) (Fig. 4 and 5).

Figure 3: Analyzed samples from Paraná Basin. A, B, and C (NR 4784, NR 6115, and NR 7137, respectively): *Tentaculites paranaensis*; D and E (NR 7246, NR 5786, respectively): *Homoctenus* sp.; F (NR 7395): *Tentaculites crotalinus*; G (22 TEN): *Uniconus* sp; H (Unirio 15): *Homoctenus katzerii*; I (mpi 9847): *Tentaculites jaculus*. Scale = 0.5cm.



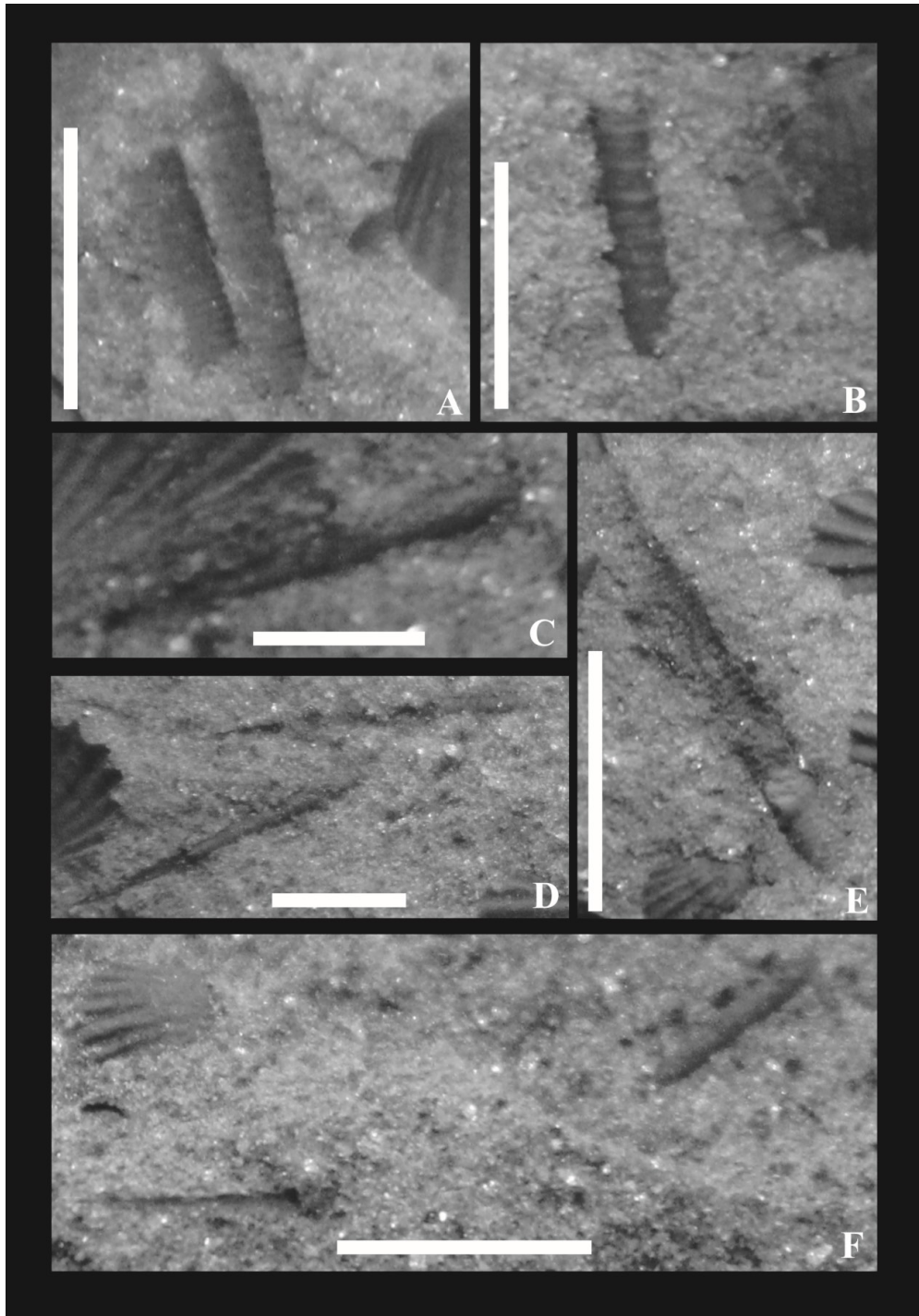
The available data suggests that *Homoctenus* is a genus restricted to Paraná Basin in Brazil. In this sense, during the lower Devonian only species from Paraná Basin were preserved in Brazil.

Figure 4: A, B, and C (44 Ten, Unirio 44 and Unirio 36, respectively): *Styliolina* sp; D and F (DGM 2912 and Unirio 5, respectively): *Tentaculites stubeli*; .E (DGM 2865): *Tentaculites trombetensis*. Scale = 0.5cm.



On the other hand, during Middle Devonian, the species diversity of tentaculitoids from Brazil increases in Parnaíba and Amazonas basins, but in Paraná Basin the diversity decreases, presenting only fragments of *Homoctenus* sp.

Figure 5: A, B, and E. (Unirio 59). C, D, and F. (Unirio 101): *Tentaculites oseryi*. Scale = 0.5cm.



Records of the species (originally described for Brazilian Devonian strata) were recognized in other South American countries, such as *Tentaculites crotalinus* and *Tentaculites trombetensis* in Bolivia and Paraguay (Davila & Rodriguez, 1967; Presser et al., 2004), *Tentaculites jaculus* in Paraguay and Peru (Boucot, Isaacson & Laubacher, 1980; Presser et al., 2004), *Tentaculites stubeli* only in Paraguay (Presser et al., 2004) and *Tentaculites eldredgianus* in Colombia (Forero, 1983).

Tentaculites jaculus has been found in Paraguay and Peru, while *Tentaculites stubeli* is recorded only in the Paraguayan Devonian. *Tentaculites eldredgianus* has also been recognized in the Devonian of Colombia (Boucot, Isaacson & Laubacher, 1980; Forero, 1983; Presser et al., 2004).

Although the genera *Tentaculites* and *Styliolina* were found in the three sedimentary basins, it was verified that there was no migration of genera or species, and different species were found in the three basins. Greater diversification of species of *Tentaculites* of the Paraná Basin is observed. The species of the Paraná Basin are larger than those found in the Amazonas and Parnaíba Basins, remembering that this is not a case of ontogeny, since the morphological characteristics are widely different (see Comniskey, Ghilardi & Bosetti, 2015; Comniskey & Ghilardi, 2018).

Extinction of Tentaculitoids

The extinction of tentaculitoids is a controversial issue in the literature (Bond, 2006; Berkyová, Fryda, & Lukes, 2007; Wittmer & Miller, 2011; Schindler, 2012; Wei, Gong & Yang, 2012). Most authors considered that the final extinction occurred in the Frasnian-Famennian boundary, but the causes are not clear. Lyashenko (1957) pointed out that the genus *Homoctenus* is present in Lower Famennian rocks, being the last representative of the group to go extinct.

Bond (2006) postulated that the homoctenids had at the height of their diversity during the Middle Devonian, being also extinct in the F-F boundary. To Schindler (1990, 1993, 2012), Bond (2006), and Wittmer & Miller (2011) this extinction is associated to the “Kellwasser crisis” (Schindler, 1990, 1993; May, 1995; Schindler & Königshof, 1996; Walliser, 1996; Weddige, 1996; Mcghee, 2001). This crisis was not geologically instantaneous, being the result of successive events.

Roemer (1850) identified the Kellwasser limestone in Germany, which had been associated with extinction events in France and Morocco (Schindler, 1990; Walliser, 1996). The Kellwasser crisis was divided in two horizons: the Lower Kellwasser and Upper Kellwasser Event (Schindler 1990, 1993; May, 1995; Schindler & Königshof, 1996; Walliser, 1996).

It is estimated that 60 to 75% of marine groups disappeared or declined in diversity after the Upper Kellwasser Event, mainly corals, ostracods, tentaculitoids, conodonts, and brachiopods (Schindler, 1990; May, 1995). The main agent of extinction was probably a general anoxic in the oceans that dramatically affect benthic communities, and reduced the distribution of pelagic organisms (Wittmer & Miller, 2011). To Schindler (1990) the tentaculitoids were gradually extinct, with dacryoconarids disappearing in the Lower Kellwasser Event and the homoctenids in the Upper Kellwasser Event.

Besides general anoxia, another hypothesis has been raised to explain the F-F extinction, such as asteroids impact, climate changes (glaciation), and transgressive-regressive cycles (Schindler 1990, 1993; May, 1995; Schindler & Königshof, 1996; Walliser, 1996).

During the Devonian drastic changes happened in the world, resulting in disturbances in the groups of planktonic organisms. The dacroconarids were the most common group between the zooplankton, with the first appearance during Lochkovian and dominating the seas during Pragian, with a cosmopolitan distribution. This group was an important source of food in the pelagic realm, and that change in the evolutive dynamic is related to the specialization of some gastropods, possible predators of this group (Berkyová, Fryda & Lukes, 2007).

Wei, Gong & Yang (2012) hypothesized that asteroids were not the cause of tentaculitoids extinctions, because the diversity was not affected in impacts during Emsian and Givetian. The authors also argued that the cooling reported to the climate during the F-F boundary was probably regional rather than global, precluding the attribution of climate causes. The authors also discard the explanation by T-R cycles and anoxic conditions, considering that the diagnosed decrease in the diversity was not enough to cause extinction. The main argument was that homocotenids would support anoxic conditions (characteristic cited by Fisher, 1962). In general, Wei, Gong & Yang (2012) attributed the cause of extinction to competition during Upper Devonian, favored by seaways as a consequence of high sea level.

In the Paraná Basin, tentaculitoids suffered a decrease during the Emsian as reported by Bosetti et al. (2012), but this group was not extinct during this time as recorded to most Malvinokaffric fauna (probably related to the Basal Zlíčov Event; Sedorko, Bosetti & Netto, 2018). Ghilardi et al. (2015) considered the tentaculitoids a resistance group, allowing the inference of general opportunistic behavior, or characteristics of a disaster taxon.

The Upper Pragian to Lower Emsian range coincides with orogenic processes in the Paraná Basin, which may have affected the stability of the ecosystems at that time. In fact, the Devonian sedimentary record in Paraná Basin is marked by different T-R cycles, which can be the cause of stressed paleoenvironments (Melo, 1988; Bosetti et al., 2012). This time interval in Lower Devonian coincides with extinction in other groups and also with the expansion of tentaculitoids worldwide. The tentaculitoids can be one of the most adaptable groups to Ordovician-Devonian interval, with great ecological plasticity to support paleoecologic changes (Schindler, 2012; Wei, Gong & Yang, 2012; Wittmer & Miller, 2011).

Other studies extended the distribution of tentaculitoids to Upper Famennian (Li, 2000), and Niko (2000) described a new genus in the Carboniferous-Permian boundary; but for Schindler (2012), none of the above hypotheses would be valid. Wittmer & Miller (2011) and Schindler (2012) indicated that the post-Devonian occurrences are not persuasive and that the most accepted data is extinction during the F-F boundary. The hypothesis and causes of extinctions are still under discussion; more research is needed about the group, especially in the Southern Hemisphere.

Frasnian and Famennian outcrops are not found on the surface of Paraná Basin, so it is not possible to find this group in these layers. The stratigraphic distribution defined here is according to the studied material and material already described for these localities. The tentaculitoids from Paraná, Amazonas, and Parnaíba basins range from Pragian to

Givetian, being absent in Famennian strata, which corroborates the idea of extinction in the F-F boundary.

CONCLUSIONS

The stratigraphic distribution of tentaculitids in Brazil ranges from Pragian to Givetian. In the Paraná Basin 7 species are identified: *Tentaculites crotalinus*, *Tentaculites jaculus*, *Tentaculites kozlowskii*, *Tentaculites paranaensis*, *Homoctenus katzerii* (from Upper Pragian to Upper Emsian), *Uniconus ciguelii* (from Upper Pragian to Lower Emsian), and *Styliolina langenii* (restrict to Middle Emsian).

In Amazonas Basin occur *Tentaculites eldredgianus*, *Tentaculites trombetensis*, *Styliolina clavulus* (Eifelian to Givetian), and *Tentaculites stubeli* (from Upper Eifelian to Lower Givetian). Finally, in the Parnaíba Basin occur *Tentaculites eldredgianus*, *Tentaculites trombetensis*, *Styliolina clavulus* (Middle Eifelian), and *Tentaculites oseryi* (Givetian).

The absence of tentaculitids in Famennian beds to Brazil corroborates the widespread idea of extinction during the F-F boundary.

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