Stalked echinoderms of the Brazilian Devonian and their palaeobiogeographical affinities

Equinodermos pedunculados do Devoniano do Brasil e suas afinidades paleobiogeográficas

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Abstract: The first occurrences of stalked echinoderms in Brazil were from the second half of the nineteenth century. Until the 1950s they were known in five Devonian formations of three major Brazilian intracratonic basins: Paraná, Amazonas, and Parnaíba. However, after the first quotes and identifications, stalked echinoderms remained for many decades without study. Only in the late twentieth century, and especially in this century, have stalked echinoderms been targets of a series of publications that greatly expanded their known morphological diversity. Currently there are almost 70 morphological patterns recognized in the Devonian. Brazilian occurrences reinforce some existing paleobiogeographicals ideas, principally related to marine currents and patterns of connections between the basins within Brazil and other parts of South America and the world. Here is also an extreme endemism in the Paraná Basin (Lower Devonian) and affinities between faunas of North Gondwana and Amazon and Parnaíba basins, in the Middle Devonian.

Keywords: Crinoidea. Blastoidea. Paleobiogeography. Brazil. South America.

Resumo: Os primeiros registros da ocorrência de equinodermos pedunculados no Brasil datam da segunda metade do século XIX. Até a década de 1950, já eram conhecidos em cinco unidades estratigráficas do Devoniano das três grandes bacias intracratônicas do país (bacias do Paraná, do Paranaíba e do Amazonas). No entanto, após as primeiras citações e identificações, este grupo ficou muitas décadas sem estudos. Apenas no final do século XX e, principalmente, neste século que os equinodermos pedunculados foram alvo de uma série de publicações que ampliaram o conhecimento acerca de sua diversidade morfológica. Atualmente, conhecemos quase 70 padrões morfológicos no Devoniano. As ocorrências brasileiras reforçam algumas ideias paleobiogeográficas já existentes, principalmente relacionadas às conexões marinhas e padrões de correntes entre as bacias no país e entre outras regiões da América do Sul e do mundo, mas também apontam para um endemismo extremo para a Bacia do Paraná, no Devoniano Inferior, e afinidades norte-gonduânicas para a fauna das bacias do Parnaíba e do Amazonas, no Devoniano Médio.

Palavras-chave: Crinoidea. Blastoidea. Paleobiogeografia. Brasil. América do Sul.

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INTRODUCTION

The first recorded occurrence of stalked echinoderms in Brazil dates from 1875, when Charles F. Hartt and Richard Rathbun reported the occurrence of "fragments of crinoidal columns" in the Ererê Formation (Hartt & Rathbun, 1875). In 1897, Friedrich Katzer reported the presence of fragments of crinoid stems in the Maecuru Formation (Katzer, 1897). When working at both the Maecuru and Ererê formations, Katzer (1903; published in german, and later translated for portuguese in Katzer, 1933) attributed a part of the crinoid material to the genus *Ctenocrinus*. This is considered the earliest identification of fossil crinoids in Brazil. Subsequent identifications of crinoids were carried out in the basin from the Maecuru Formation and have been published as short communications (Ferreira & Fernandes, 1985, 1989; Fernandes *et al.*, 2000). The same identifications were conducted in the Ererê Formation by Fernandes *et al*. (2008).

Following these initial communications during the 19th Century, stalked echinoderm ossicles attributed to the Devonian were discovered in two other major intracratonic basins in Brazil, the Paraná and Parnaíba basins.

Erichsen (1937 *apud* Petri, 1948) was the first to mention the presence of "*entroclas*" in crinoids from the eastern border of the Paraná Basin, in the Tibagi locality, Paraná State. Lange (1943) was the first to describe the stems and columnals of crinoids discovered in the Paraná Basin as Crinoidea indet. This was done by correlating the shapes of crinoids from the Paraná state with the crinoids obtained from the state of Mato Grosso, investigated by Erichsen & Löfgren (1940). Echinoderm materials discovered on the northwestern border of the Paraná Basin in the Chapada Group of the state of Goiás were first cited by Löfgren (1937) as belonging to the Devonian period. This indicated the presence of "*hastes de crinóides*", which were described as belonging to the state of Mato Grosso from the Devonian (Erichsen & Löfgren, 1940) and was discovered near the city of Rio Bonito. However, this material remained unidentified until the 1980s, when Ferreira & Fernandes (1985, 1989) attributed the material described by Erichsen & Löfgren (1940) to *Laudonomphalus ornatus*. This identification needs to be revised, as it has been discovered that the specimen identified as *Laudonomphalus ornatus* from Mato Grosso is clearly different from the accurately identified specimen obtained from the Maecuru Formation.

The identification of stalked echinoderms from the Devonian commenced during the 1950s in the Parnaíba Basin. The first report on the occurrence of crinoids in the Cabeças Formation was by Kegel (1953). These were discovered in rocky outcrops at the border of the eastern basin in the state of Piauí. Crinoids discovered in this formation were identified almost 60 years later (Scheffler *et al.*, 2010). Ramos (1957) made the initial reference to fossils belonging to this class when he reported their occurrence in association with *Spongiophyton* in the rocky outcrops of the western border in the Pimenteira Formation in the Tocantínia locality, currently known as Palmas – the capital of the Tocantins State. The crinoids from the Pimenteira Formation were comprehensively identified over 50 years after this initial discovery by Gama Jr. & Scheffler (2007), Scheffler (2010), and Scheffler *et al*. (2011).

Throughout the 20th century, with the exception of a few comprehensive identifications carried out in the form of short communications (Lange, 1943; Ferreira & Fernandes, 1985, 1989; Fernandes *et al*., 2000), the Brazilian Devonian pelmatozoans were only mentioned as occurrences in various outcrops within the three afore mentioned Devonian basins (Petri, 1948; Lange, 1954; Almeida, 1954; Sommer & Van Boekel, 1964; Lange & Petri, 1967; Ramos & Barbosa, 1967; Ciguel, 1989; Popp & Barcellos-Pop, 1986; Melo, 1985; Machado *et al.*, 1996).

There have been numerous reports on the presence of stalked echinoderms such as crinoids, in the Brazilian shallow sea communities from the

Devonian. However, they have always been considered elements of minor importance, as they are believed to be negligibly diversified and rare, especially in the Paraná Basin (Boucot, 1971; Cooper, 1977; Boucot & Racheboeuf, 1993). It is clear that this phylum does not match the abundance and diversity of contemporaneous faunas from Europe and North America; however, its diversity has been grossly underestimated. Detailed description, figuration, and identification of the Brazilian Devonian echinoderms material began only in the 21st Century. Today, this has led us to identify almost 70 distinct taxa (included taxa of the formal systematic classification, taxa of the parasystematic classification and indeterminates morphotypes *sensu* Scheffler, 2008) for the pelmatozoans obtained from the three basins, many of which have been identified to a generic and specific level. This includes the identification of the class Blastoidea from the Devonian in the state of Paraná.

These studies have allowed us to contemplate the great diversity of the existing stalked echinoderms, and understand the vital role this group played in the structuring of benthic communities from the shallow seas from the Devonian strata in Brazil.

STALKED ECHINODERMS IN THE BRAZILIAN DEVONIAN

We have provide here an updated and complete list of stalked echinoderms attributed to the Brazilian Devonian, isolated from the basins of Paraná, Parnaíba, and Amazonas (Tables 1, 2, and 3). This list serves as the basis for the paleobiogeography discussions, which are the main purpose of this article.

Currently 38 taxa of stalked echinoderms have been identified in the Devonian of the Paraná Basin. Among these, ten crinoids were described by parasystematic classification, ten crinoids described by formal systematic classification, and five were identified as blastoids, while the remaining 13 were classified as indeterminate peduncle ossicles of crinoids, or alternately, as belonging to no determined class (morphotypes). Out of the 38 taxa, 14 occur exclusively in the Ponta Grossa Formation (Pragian-early Emsian), and 17 are exclusive to the São Domingos Formation (late Emsian-Givetian), both in the state of Paraná (eastern border of the Paraná Basin). These formations were discovered to display only three taxa in common. In the Chapada Group III, present at the northwestern border of the basin (state of Goiás), only one taxon has been described so far, which has been correlated to the São Domingos Formation from Paraná. Three taxa discovered in the Chapada Group IV (Mato Grosso), related to the specimens found in the middle and upper parts of the São Domingos Formation, have also been described. In total, 24 taxa have been identified in the São Domingos Formation throughout the whole Brazilian basin extension, and 17 in the Ponta Grossa Formation (Table 1).

As previously mentioned, 14 taxa of stalked echinoderms from the Devonian period have been identified in the Cabeças (eastern border) and Pimenteira (western border) formations in the Parnaíba Basin. Of these, two are described by formal systematic classification, eight by parasystematic classification, and four as indeterminate peduncle ossicles of crinoids, or without any determined class. Of these, three morphological patterns have been described in the Cabeças Formation, two of which are probably crinoids, and 11 have been identified in the Pimenteira Formation, two of which occur at the northwestern border of the Paraná Basin (Table 2).

Twenty-one taxa of stalked echinoderms have been discovered in the Maecuru and Ererê formations in the Devonian of the Amazon Basin; four of these were identified by formal systematic, ten by parasystematic classification; seven have been identified as indeterminate peduncle ossicles of crinoids, or as belonging to an undetermined class. Of these, 18 were observed in the Maecuru Formation and the rest in the Ererê Formation (Table 3).

Table 1. List of stalked echinoderms identified from the Devonian in the Paraná Basin (Ponta Grossa and São Domingos formations, including Chapada Group III and IV).

(Continue)

Geological units/Age	Previous identification/Author	Taxa currently valid/Author	Class/Sub-class/ Order
Western border			
Chapada Group IV? (São Domingos Formation?)			
Early Givetian?		*øLaudonomphalus ornatus*/ Ferreira & Fernandes (1985, 1989)	Crinoidea
Givetian?	*øExaesiodiscus* sp./Scheffler *et al*. (2009a) *øExaesiodiscus* sp. A/Scheffler (2010)	*øExaesiodiscus dimerocrinosus*/ Scheffler *et al*. (2011)	Crinoidea
Givetian?		*øLaudonomphalus* sp. B/Scheffler (2010)	Crinoidea
Chapada Group III (São Domingos Formation?)			
Early Emsian-Eifelian		*Costalocrinus*? sp./Francisco *et al*. (2013) (differently than found in Paraná state)	Crinoidea
Eastern border			
São Domingos Formation			
Early Givetian	*øMarettocrinus* sp. C/ Francisco & Scheffler (2013)	*øMarettocrinus katzeri*/ Scheffler *et al*. (2015a)	Crinoidea
Early Givetian		*øSalairocrinus*? sp./ Francisco & Scheffler (2013)	Crinoidea
Late Emsian-early Eifelian?		øPRap/PG-008/Scheffler (2008, 2010)	Crinoidea
Late Emsian-early Eifelian?		øPRap/PG-009/Scheffler (2010)	Crinoidea
Late Emsian-early Eifelian?		*øCrenatames* sp. A/Scheffler (2010)	Crinoidea
Late Emsian		Crinoidea indet. D/Scheffler (2010)	Crinoidea
Late Emsian		*øLaudonomphalus multituberculatus*/ Scheffler & Fernandes (2007a)	Crinoidea
Late Emsian		Pentremetidae indet./ Scheffler & Fernandes (2007b)	Blastoidea/ Spiraculata
Late Emsian	Crinoidea cup/Scheffler *et al*. (2001); Blastoidea theca/Scheffler & Fernandes (2003)	*Pachyblastus*? sp./Scheffler & Fernandes (2007b)	Blastoidea/ Fissiculata
Late Emsian	Crinoidea cup/Scheffler *et al*. (2001); Blastoidea theca/Scheffler & Fernandes (2003)	Fissiculata indet./Scheffler & Fernandes (2007b)	Blastoidea/ Fissiculata
Late Emsian		Blastoidea indet. A/Scheffler (2010)	Blastoidea/ Fissiculata
Late Emsian		Blastoidea indet. B/Scheffler (2010)	Blastoidea/ Fissiculata

Table 1. (Conclusion)

Geological units/Age	Previous identification/Author	Taxa currently valid/Author	Class/Sub-class/ Order
Late Emsian		øPRap/PG-002/Scheffler (2008)	?
Late Emsian		øPRap/PG-003/Scheffler (2008)	Crinoidea
Late Emsian		øPRap/PG-004/Scheffler (2008)	?
Late Emsian		øPRap/PG-005/Scheffler (2008)	?
Late Emsian		øPRap/PG-006/Scheffler (2008)	Crinodea
Late Emsian		øPRap/PG-007/Scheffler (2008)	?
Late Emsian		øPRap/PG-010/Scheffler (2010)	Crinoidea
Late Emsian		øPRap/PG-011/Scheffler (2010)	?
Ponta Grossa Formation			
Pragian/Emsian? (Ponta Grossa Formation?)	Dimerocrinitidae? indet./Scheffler (2010)	Monobathrida indet./ Scheffler *et al.* (2013)	Camerata/ Monobathrida
Pragian/Emsian? (Ponta Grossa Formation?)	Poteriocrinida indet./ Scheffler & Fernandes (2007a)	*Ctenocrinus* sp./Scheffler *et al*. (2013)	Camerata/ Monobathrida
Pré late Pragian-early Emsian	Crinoidea? indet./Scheffler (2006)	Pisocrinidae indet./Scheffler (2010)	Disparida
Pragian-early Emsian?	Gênero *Crenatames*/Scheffler (2004)	ø*Crenatames amicabilis*/ Scheffler & Fernandes (2007a)	Crinoidea
Pragian/Emsian?		ø*Crenatames* sp. B/Scheffler (2010)	Crinoidea
Pragian	*Ophiucrinus stangeri*/ Scheffler & Fernandes (2007a)	*Ophiocrinus stangeri*/ Scheffler *et al.* (2013)	Camerata/ Diplobathrida
Pragian	ø*Cyclocaudex paranaensis*/ Scheffler & Fernandes (2007a)	*Costalocrinus*? sp./ Scheffler *et al*. (2013)	Cladida
Pragian		Crinoidea indet. C/Scheffler (2010)	Crinoidea
Pragian		Crinoidea indet. E/Scheffler (2010)	Crinoidea
Pragian		øPRap/PG-001/Scheffler (2008)	Crinoidea? (possible stem of *Ophiocrinus stangeri*)
Pragian		øPRap/PG-008/Scheffler (2008, 2010)	Crinoidea
Pragian?		øPRap/PG-012/Scheffler (2010)	Crinoidea
Pragian		øPRap/PG-013/Scheffler (2010)	?
Pré late Pragian		Crinoidea indet. B/Scheffler (2010)	Crinoidea
Pré late Pragian		ø*Crenatames* sp. A/Scheffler (2010)	Crinoidea
Pré late Pragian		ø*Marettocrinus* sp. D/Scheffler (2010)	Crinoidea
Pré late Pragian		øPRap/PG-009/Scheffler (2010)	Crinoidea

Table 2. List of stalked echinoderms identified from the Devonian in the Parnaíba Basin (Pimenteira and Cabeças formations).

Geological units/Age	Previous identification/Author	Taxa currently valid/Author	Class/Sub-class/ Order
Pimenteira Formation			
Late Eifelian	Genus *Monstrocrinus*/Gama Jr. & Scheffler (2007) *Monstrocrinus* sp. B/Scheffler (2010)	*Monstrocrinus incognitus*/ Scheffler *et al*. (2011)	Camerata/ Diplobathrida
Late Eifelian		Crinoidea indet. A/Scheffler (2010)	Crinoidea
Late Eifelian	ø*Exaesiodiscus* sp./Scheffler *et al.* (2009a) ø*Exaesiodiscus* sp. A/Scheffler (2010)	ø*Exaesiodiscus dimerocrinosus*/ Scheffler *et al.* (2011)	Crinoidea
Late Eifelian		ø*Exaesiodiscus*? sp. B/Scheffler (2010)	Crinoidea
Late Eifelian		ø*Laudonomphalus* aff. *L. tuberosus*/ Scheffler *et al.* (2011)	Crinoidea
Late Eifelian		ø*Laudonomphalus* sp. A/Scheffler (2010)	Crinoidea
Late Eifelian		ø*Laudonomphalus* sp. B/Scheffler (2010)	Crinoidea
Late Eifelian		ø*Laudonomphalus* sp. C/Scheffler (2010)	Crinoidea
Late Eifelian		ø*Laudonomphalus* sp. D/Scheffler (2010)	Crinoidea
Late Eifelian		ø*Marettocrinus*? sp. A/Scheffler (2010)	Crinoidea
Late Eifelian		øPB/Pm-01/Scheffler (2010)	Crinoidea
Cabeças Formation			
Givetian		øPB/Cb-01/Scheffler *et al.* (2010)	?
Givetian	*Pentagonostipes*? sp./Silva (2001)	øPB/Cb-02/Scheffler *et al.* (2010)	Crinoidea
Givetian	*Hexacrinites*? sp./Silva (2001)	øPB/Cb-03/Scheffler *et al.* (2010)	Crinoidea

Table 3. List of stalked echinoderms identified from the Devonian of the Amazon Basin (Maecurú and Ererê formations). (Continue)

Geological units/Age	Previous identification/Author	Taxa currently valid/Author	Class/Sub-class/ Order
Maecuru Formation			
Middle Eifelian		*Monstrocrinus securifer*/Scheffler *et al.* (2006)	Camerata/ Diplobathrida
Middle Eifelian		*Monstrocrinus* sp. A/Scheffler (2010)	Camerata/ Diplobathrida
Middle Eifelian	*Thylacocrinus?* sp./Scheffler (2010)	*Thylacocrinus* sp./Scheffler *et al*. (2015a)	Camerata/ Diplobathrida
Middle Eifelian	*Ctenocrinus* sp./Katzer (1903, 1933)	ø*Laudonomphalus regularis*/Scheffler *et al.* (2006)	Crinoidea
Middle Eifelian		ø*Laudonomphalus ornatus*/Scheffler *et al.* (2006)	Crinoidea
Middle Eifelian	ø*Laudonomphalus* sp. E/Scheffler (2010)	ø*Laudonomphalus ferreirai*/Scheffler *et al.* (2015a)	Crinoidea
Middle Eifelian	Crinóide indet./Machado *et al.* (1996) ø*Marettocrinus* sp. B/Scheffler (2010)	ø*Marettocrinuskatzeri*/Scheffler *et al.* (2015a)	Crinoidea

Table 3. (Conclusion)

Geological units/Age	Previous identification/Author	Taxa currently valid/Author	Class/Sub-class/ Order
Middle Eifelian	ø*Marettocrinus* sp. C/Scheffler (2010)	ø*Marettocrinushartti*/Scheffler *et al.* (2015a)	Crinoidea
Middle Eifelian	ø*Exaesiodiscus* aff. *minutus*/ Scheffler *et al.* (2006) ø*Exaesiodiscus* aff. *E.* sp. A/ Scheffler (2010)	ø*Exaesiodiscus* aff. *E. dimerocrinosus*/ Scheffler *et al*. (2015a)	Crinoidea
Middle Eifelian	ø*Exaesiodiscus* sp. C/Scheffler (2010)	ø*Exaesiodiscus derbyi*/Scheffler *et al.* (2015a)	Crinoidea
Middle Eifelian	ø*Eurax* sp./Scheffler *et al.* (2009b) ø*Eurax* cf. *E. opercularis*/Scheffler (2010)	ø*Eurax opercularis*/Scheffler *et al.* (2015a)	Crinoidea
Middle Eifelian	ø*Pentaridica?* sp./Scheffler *et al.* (2009b) ø*Pentaridica* sp. A/Scheffler (2010)	ø*Pentaridica mendesi*/Scheffler *et al.* (2015a)	Crinoidea
Middle Eifelian		øAM/Ma-01/Scheffler (2010)	Indet.
Middle Eifelian		øAM/Ma-02/Scheffler (2010)	Indet.
Middle Eifelian		øAM/Ma-03/Scheffler (2010)	Crinoidea
Middle Eifelian		øAM/Ma-04/Scheffler (2010)	Crinoidea
Middle Eifelian		øAM/Ma-05/Scheffler (2010)	Crinoidea
Middle Eifelian		øAM/Ma-06/Scheffler (2010)	Crinoidea
Ererê Formation			
Early Givetian	*Ctenocrinus* sp./Katzer (1903, 1933); ø*Botryocrinus*? sp./Fernandes *et al*. (2008); ø*Botryocrinus* sp. A/Scheffler (2010)	ø*Botryocrinus melloi*/ Scheffler *et al.* (2014)	Crinoidea/ Cladida
Early Givetian		ø*Tjeecrinus*? sp./Scheffler *et al.* (2014)	Crinoidea
Early Givetian		øAM/Er-01/Scheffler *et al.* (2014)	Crinoidea

Based on these numbers, 68 taxa have been identified as belonging to the Brazilian Devonian, of which 35 were identified to a species or genus level. These are distributed as follows:

1. Pimenteira Formation; 11 taxa; one in common with ø*Exaesiodiscus dimerocrinosus* from the Maecuru Formation and the Chapada Group IV and one (ø*Laudonomphalus* sp. B) in common with the echinoderms of the Chapada Group IV;

2. Cabeças Formation; three taxa of echinoderms, which shared no commonalities with echinoderms from other Brazilian formations;

3. Maecuru Formation; 18 taxa; one in common (ø*Exaesiodiscus dimerocrinosus*) with the echinoderms from the Pimenteira Formation and the Chapada Group IV, another in common (ø*Laudonomphalus ornatus*) only with the Chapada Group IV (this identification needs to be revised), and one (ø*Marettocrinus katzeri*) displaying commonalities with echinoderms from the São Domingos Formation in Paraná State;

4. Ererê Formation; three endemic taxa, none in common with those from other Brazilian formations;

5. Ponta Grossa Formation; 17 morphological types; three (indet. taxa øPRap/PG-008, øPRap/PG-009, and ø*Crenatames* sp. A) in common with echinoderms from the São Domingos Formation;

6. São Domingos Formation (including the Chapada groups III and IV); 24 taxa; three (indet. taxa øPRap/PG-008, øPRap/PG-009 and ø*Crenatames* sp. A) in common with

echinoderms from the Ponta Grossa Formation, one (*øExaesiodiscus dimerocrinosus*) in Chapada Group IV in common with the Maecuru and Pimenteira formations, another (*øLaudonomphalus* sp. B) also present in the Chapada Group IV in common only with echinoderms from the Pimenteira Formation, and two (*øLaudonomphalus ornatus* and *øMarettocrinus katzeri*) sharing commonalities only with echinoderms from the Maecuru Formation.

Until the early 21st century, few taxa and indeterminate peduncle ossicles of stalked echinoderms were identified in Devonian strata in Brazil (see Scheffler, 2007, 2011, for historical work with echinoderms in Ponta Grossa Formation and in the Brazilian Paleozoic). In the Paraná Basin, their occurrence was regarded as being rare and negligibly diversified (Boucot, 1971; Cooper, 1977; Boucot & Racheboeuf, 1993), and were considered to be of little relevance in the structuring of marine benthic communities in Brazil, mainly from Malvinokaffric Realm. Thus, it was surprising that, when confronted with the minor relevance attributed to the group in the past, more than half of all benthic forms currently discovered within the Brazilian Devonian are from the Ponta Grossa and São Domingos formations.

Today, it is possible to affirm that these assertions were incorrect and that the previous lack of knowledge concerning diversity was due to lack of researchers working with the specific phylum, rather than a reflection of the actual structure of communities.

The stalked echinoderms were important components of the Paleozoic communities, of both hard and soft substrates. Around eight classes of stalked echinoderms lived in the lower Paleozoic, inhabiting extensive epicontinental seas. In the Devonian, at least five classes of stalked echinoderms coexisted (Ubaghs, 1967). Despite this abundance in the other parts of the world, only two classes (Crinoidea and Blastoidea) were attributed to the São Domingos Formation (including the Chapada groups III and IV), and one class (Crinoidea) each to the Ponta Grossa, Pimenteira, Cabeças, Maecuru, and Ererê formations.

In addition, a greatest Devonian echinoderm diversity has been described for the Paraná Basin, which should theoretically present a lower diversity than the echinoderms in the Maecuru Formation of the Amazon Basin, and the Pimenteira Formation of the Parnaíba Basin (as is true for other groups of macroinvertebrates; see Melo, 1988), which were both located at lower latitudes during this period, between 30° and 60° latitude south, with temperate climate (Isaacson, 1981, 1996; Cunha, 2005; see Scheffler *et al*., 2015b). This description may also be a reflection of the large research and collection efforts conducted throughout the 20th and 21st centuries. In the Amazon Basin, for example, only sporadic collections were performed by scientific expeditions, mostly in the 19th century. It is expected that, if a study with the Brazilian pelmatozoans is continued, the morphological diversity may easily be doubled, mainly in the aforementioned formations.

PALEOBIOGEOGRAPHIC AFFINITIES

The study of stalked echinoderms in Brazil, almost 140 years after the initial discoveries, is still at an early stage, and much of the material lacks refinement in the taxonomic identification. Due to the few known specimens, which are mostly badly preserved, and the sparse studies on this material, big part of them are still identified in open nomenclature, be it based on formal taxonomy or parataxonomy, or even just as peduncle ossicles with indeterminate class. So, this topic will not be discussed in detail here, and biogeographic methodologies will not be applied to understanding the occurrences. In our current stage of knowledge, we can only make some inferences that might help in the interpretation of the patterns of distribution of Devonian invertebrates in Brazil.

From now on, we will discuss the known occurrences of pelmatozoans in a chronological manner, starting from the Pragian and ending with the Givetian.

Therefore, we will start with the ocurrences of the Pragian-Emsian of the Ponta Grossa Formation, and that of the occurrences of the late Emsian of the São Domingos Formation,

of the Paraná Basin. The fauna of stalked echinoderms, as observed by Scheffler *et al*. (2013), strangely presents insignificant similarities with the remainder of the fauna from the Malvinokaffric Realm. Only four echinoderms from the Ponta Grossa Formation have been identified in other countries in South America or South Africa: *Ophiocrinus stangeri* in South Africa; *Costalocrinus* spp. in Bolivia, North America, and Europe; *Ctenocrinus* spp. in Bolivia, North America, Europe, and Australia; and *Pachyblastus* sp. in Bolivia and South Africa. Of these, only *Ophiocrinus stangeri* and *Pachyblastus* are endemic to the Malvinokaffric Realm, while the others are cosmopolitan.

A vast majority of the other taxa appear to be endemic to the Apucarana Sub-basin, which may reflect a lack of well-preserved specimens, evidenced by negligible taxonomic refinement of the echinoderms, and the lack of related research in the Alto Garças Sub-basin, and in other countries of South America and South Africa. Some degree of geographical isolation may occur in relation to other South American basins. However, a higher similarity among bivalves, brachiopods, and trilobites, which represent typical malvinokaffric faunas, supports the possibility of this conclusion being derived due to lack of knowledge about pelmatozoans, instead of high endemism of these echinoderms within the Paraná Basin.

Despite this, some biogeographical distribution patterns can be visualized for the Pragian-Emsian age (Figure 1), as previously indicated by Scheffler *et al*. (2013):

1. Several taxa or lineages arose in Europe during the Late Silurian or Pragian-early Emsian, and eventually spread to South America still in the Pragian-Emsian, via Colombia and Bolivia (*Apurocrinus*, *Bogotacrinus*, and *Griphocrinus*). These taxa arrived in Argentina (*Achantocrinus*), the Falkland Islands (*Pterinocrinus australis*), and the Brazilian Paraná Basin (*Costalocrinus* spp.); most appeared only later in North America (during the Middle Devonian);

2. Two taxa (*Ophiocrinus stangeri* and *Pachyblastus* sp.) arose and were recorded only in the Malvinokaffric Realm;

3. One taxon (*Crenatames amicabilis*) arose in the Paraná Basin during the initial Pragian-Emsian, and has dispersed through Armorica and Laurentia during the Middle Devonian.

Nevertheless, the absence of any of these taxa in other Brazilian basins seems to corroborate the lack of direct connection between these basins and the Paraná Basin in the Pragian-Emsian, as traditionally presented in paleogeographic reconstructions for this age (Melo, 1988; Figure 2).

Occurrence of echinoderms in the Middle Devonian are specific to the middle and top of the São Domingos Formation, at the eastern border of the Paraná Basin, to the northwestern border of the Paraná Basin (Chapada groups III and IV, equivalent to São Domingos Formation), to the Pimenteira and Cabeças formations in the Parnaíba Basin, and to the Maecuru and Ererê Formations in the Amazon Basin.

With the exception of those discovered in the Cabeças Formation (taxa with lack of detailed and refined taxonomic studies), the taxa displays some affinities with the taxa identified in the Renish Massif, in the Armorican Massif, in the Iberian Peninsula, and in North Africa. Currently, from the Middle Eifelian, the most characteristic geographical distribution pattern that has been observed is the occurrence of younger taxa in the Brazilian formations when compared to those occurring in Europe and North Africa (Figure 3). We can cite several examples, given by Scheffler *et al*. (2011, 2013, 2014, 2015a) in support of this data: *Monstrocrinus* (from the Emsian of Renish Massif, Armorica, and North Africa, and the middle and late Eifelian in Maecuru and Pimenteira formation); *Thylacocrinus* (Emsian of Armorica, Iberian Peninsula, and North Africa, and middle and late Eifelian in the Maecuru and Pimenteira formations); *Eurax opercularis* (Pragian-Emsian of Armorica and North Africa, and middle and late Eifelian in the Maecuru and Pimenteira formation); dimerocrinitids typical of Gondwana, represented by *Exaesiodiscus dimerocrinosus* (Silurian-Lower Devonian, pre-Emsian in Armorica, the Iberian Peninsula, and North Africa, and middle and late Eifelian in the Maecuru and Pimenteira formations, and possibly late Eifelian or Givetian in the Paraná Basin) (Scheffler *et al*., 2011).

Figure 1. Paleobiogeographic distribution of stalked echinoderm taxa previously identified as belonging to the Lower Devonian (Pragian-Emsian) in South America. Note how the occurrence of taxa is generally older in Europe, when compared to South America (Paraná Basin in Brazil), which is in turn generally older than the taxa identified in North America (entered data on the modified map of Scotese, 2009).

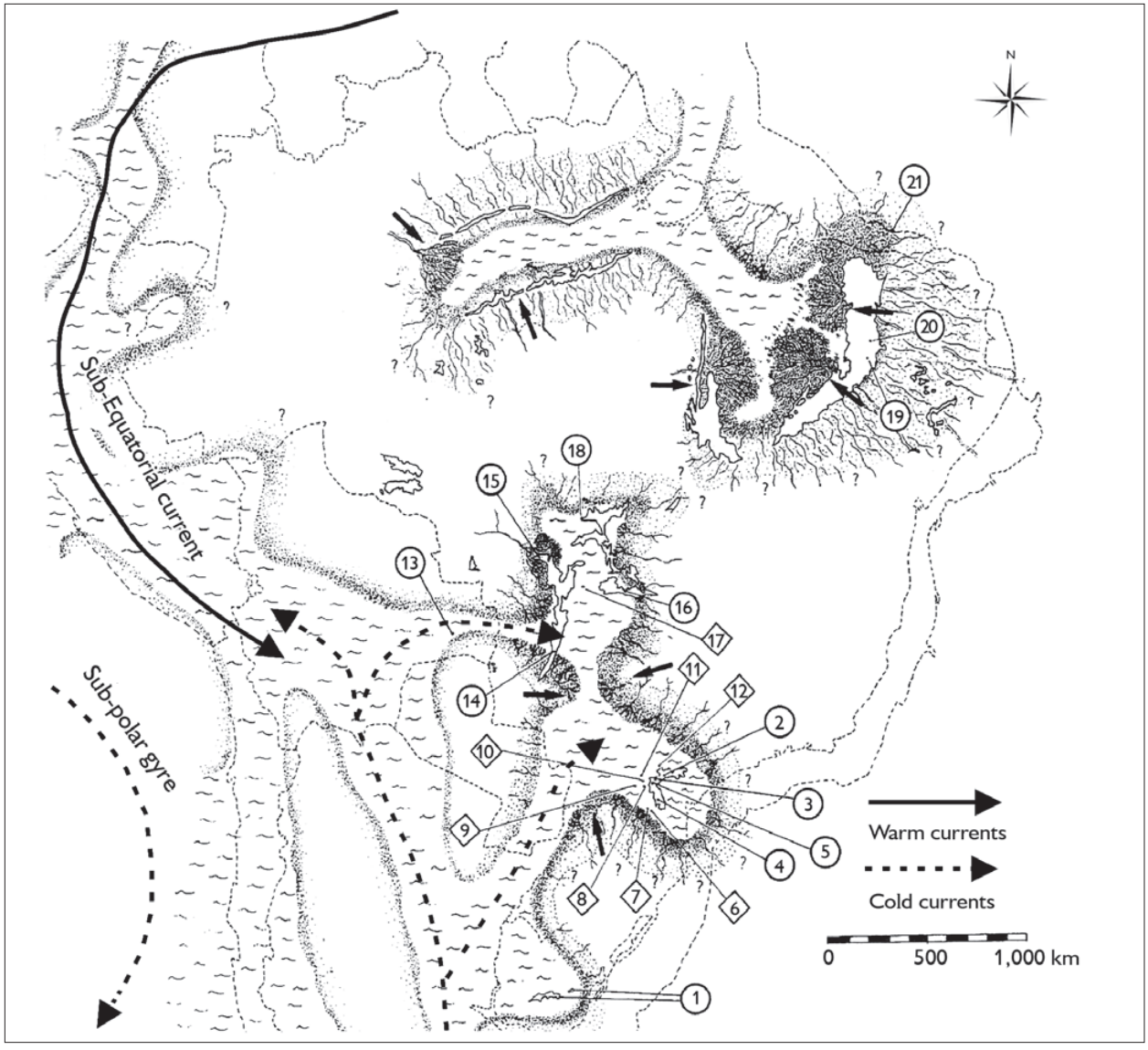

Figure 2. Paleogeography inferred herein for the Pragian-Emsian in Brazil and neighboring regions in South America. Black arrows indicate the main direction of sediment supply; dotted pattern shows the transition to continental environments; solid line highlights the current Devonian sediment outcropping areas; numbers inside circles for outcrops, and enclosed in lozenges for boreholes. Modified from Emsian Paleogeographic Map of Melo (1988, figure 5). Marine currents based on information derived from Isaacson (1981, 1996), with modifications suggested by the occurrence of stalked echinoderms. Legends: information of figure 5 of Melo (1988): 1 - Uruguayan outcrop belt; 2- Municipality of Jaguariaíva (Paraná, Brazil); 3 - Municipality of Lambedor (Paraná, Brazil); 4 - Municipality of Ponta Grossa (Paraná, Brazil); 5 - Municipality of Tibagi (Paraná, Brazil); 6 - Well 10-RC-1-PR, core 13 (Paraná, Brazil); 7 - Well 1-M-1A-PR, core 24 (Paraná, Brazil); 8 - Well 1-R-1-PR, core 21 (Paraná, Brazil); 9 - Well 1-CA-1-PR, deepth interval 2,427-2,604 m (Paraná, Brazil); 10 - Well 1-MO-2-PR, core 19 (Paraná, Brazil); 11 - Well 2-O-1-PR, core 18 (Paraná, Brazil); 12 - Well São José do Paranapanema, deepth interval 515-552 (Paraná, Brazil); 13 - Outcrops in the Santiago area (Chiquitos Province, Bolivia); 14 - Boa Sentença Ridge (Mato Grosso do Sul, Brazil); 15 - Chapada dos Guimarães (Mato Grosso, Brazil); 16 - Toco Preto Ridge (Goiás, Brazil); 17 - Well 2-AG-1-MT (Mato Grosso, Brazil); 17a - Core 17; 17b - Core 18; 18 - Chicórea Norte creek, Roncador Ridge (Mato Grosso, Brazil); 19 - Region of the municipality of Picos (Piauí, Brazil); 20 - South of the municipality of Pimenteiras (Piauí, Brazil); 21 - Accra (Ghana). Note: the age of some localities need to be revised. Many outcrops, for example in the Paraná Basin, are currently considered to be older than interpreted 30 years ago (*e.g.* Grahn *et al*., 2000, 2013; Scheffler & Fernandes, 2007a; Bosetti *et al*., 2012).

Figure 3. Paleobiogeographic distribution of stalked echinoderm taxa previously identified from the Middle Devonian (Eifelian-Givetian) in South America. Note how the taxa occurring in Europe are older than those in South America (Amazon and Parnaíba basins in Brazil) (entered data on the modified map of Scotese, 2009).

Similarly, *Botryocrinus melloi*, a species occurring in the late Eifelian or early Givetian, although endemic to the Ererê Formation (Scheffler *et al*., 2014), is very similar to *Botryocrinus montguyonensis* from Armorica, which occurs during the Lower Devonian.

Therefore, we can identify some apparent migration patterns in the Brazilian Eifelian and Givetian:

1. Stalked echinoderms, which were part of the Ibarmaghian domain (Plusquellec *et al*., 1997) in Europe (Spain and France) and North Africa (Algeria, Morocco, Libya) during the late Silurian, Lochkovian, Pragian, and Emsian, reached the Amazon and Parnaíba basins during the mid to late Eifelian, possibly accompanying the rise in sea level and the subsequent entry of warmer waters connecting the North Africa and Amazon basins (see above examples). Due to the continuous rise in sea level, some representatives (*Exaesiodiscus dimerocrinosus* and *Laudonomphalus* sp. B) of the Amazon and Parnaíba basins also entered the northwest borders of the Paraná Basin and reached the Apucarana Sub-basin (*Marettocrinus katzeri*) during the initial Givetian;

2. Some taxa arose initially in Brazil and South America, during the Lower Devonian or Eifelian, and apparently migrated to other parts of the world, North America in particular, during the Givetian. I can quote: *L. ornatus*, which occurs in the Emsian of the Bolivia and Eifelian of the Maecuru, and Givetian of the Europe and; *L. regularis*, in Eifelian of the Maecuru and Givetian of Europe and United States; *Pentaridica*, in Eifelian of the Maecuru and Fammenian and Carboniferous of Russia, Poland and; *Eleutherocrinus cassedayi*, in Eifelian of Bolivia and Givetian of North America. Following the same pattern in the rest of South America, Scheffler *et al*. (2013) identified crinoids, such as *Ophiocrinus*, *Pyrenocrinus*, *Maragnicrinus*, *Bridgerocrinus*, and the blastoid *Brachyschisma*;

3. A few taxa or lineages occurred during the same time in South America and North America (*Ancyrocrinus*), and Europe (*Tjeecrinus*), or at an earlier age (the youngest representative of the Patelliocrinidae - *Boliviacrinus isaacsoni*) in South America.

Therefore, the crinoid fauna appears to corroborate the theory defended by most paleontologists based on fossils and paleoclimatic indicators (Plusquellec *et al*., 1997; Robardet, 2003), that the Armorican microplate does not actually exist, and that South Eastern Europe (which is composed of the Armorican Massif and Iberian Peninsula) and, possibly, central Europe (Bohemia) were positioned against the Gondwana plate, forming its northern border. This could be corroborated by a discovery indicating that the eastern border of Avalonia (Germany and Belgium) was located close to Northern Gondwana in the Emsian. During this time, the Rheic Ocean would not have possessed huge dimensions, and would therefore not represent a great geographical barrier. Similar observations have been made by Le Menn (1997), who studied the crinoids of North Africa, whose strong affinity with the crinoids from the Iberian Peninsula and Armorica, and continued affinity with the Rhenish Massif crinoids, reinforce the sustainability of this hypothesis

In conclusion, we propose that the echinoderms from the Lower and Middle Devonian corroborate the existence of warm water currents entering South America from the Northern Gondwana region (Armorica, Iberian Peninsula, North Africa, and possibly Bohemia) and Eastern Avalonia (Rhenish Region), which allowed migration of echinoderms from the Old World Realm (mainly from the Ibarmaghian Domain) into the Malvinokaffric Realm (Figures 2 and 4). The influence of taxa from the Rhenish-Bohemia region in the Malvinokaffric Realm has been highlighted in echinoderms by Witzke *et al*. (1979). This is in spite of the proposed paleocurrent models dating to that time, not foreseeing a westward current into South America (Heckel & Witzke, 1979; Eldredge & Ormiston, 1979). Heckel & Witzke (1979) proposed a current to the west of the Rhenish-Bohemia region towards North Africa, and Isaacson (1981, 1996) suggested that this current extended

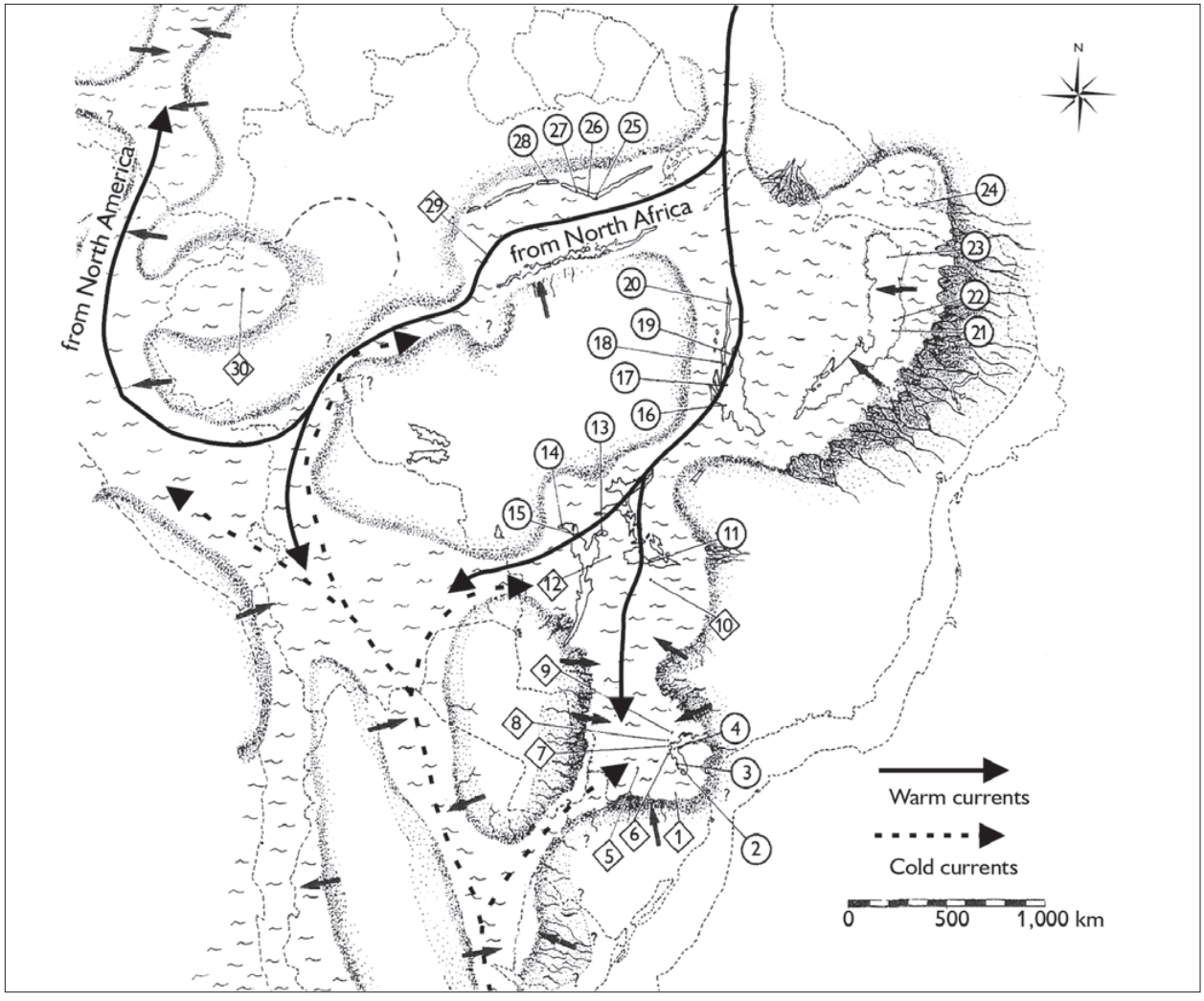

Figure 4. Paleogeography inferred herein for the Brazilian Eifelian-early Givetian, and the neighboring regions in South America. Modified Eifelian/Givetian Paleogeographic map of Melo (1988, figure 7). Additional explanations as provided in the caption of Figure 2. Legends: information of figure 7 of Melo (1988): 1 - Boreholes at municipality of Canoinhas (Santa Catarina, Brazil); 1a - Well 1-CN-2-SC; 1b - Well 2-CN-1-SC; 2 - Region of the municipality of Palmeira (Paraná, Brazil); 2a - Piedade; 2b - Rio Caniú; 2c - Santa Cruz; 3 - Region of the municipality of Ponta Grossa (Paraná, Brazil); 4 - Region of the municipality of Tibagi (Paraná, Brazil); 5 - Well 2-LS-1-PR, deepth 3,600 m and core 32 (Paraná, Brazil); 6 - Well 1-R-1-PR (Paraná, Brazil); 6a - Core 13; 6b - Core 14; 6c - Core 16; 7 - Well 1-MO-2-PR, cores 13-15 (Paraná, Brazil); 8 - Well 2-O-1-PR, core 17 (Paraná, Brazil); 9 - Well 1-SJ-1-PR, core 25 (Paraná, Brazil); 10 - Well 2-JA-1-GO (Goiás, Brazil); 10a - Core 27; 10b - Core 28; 11 - Monte creek (Goiás, Brazil); 12 - Well 2-AG-1-MT, cores 14 and 15 (Mato Grosso, Brazil); 13 - Alminhas creek (Mato Grosso, Brazil); 14 - Chapada dos Guimarães (Mato Grosso, Brazil); 15 - Region of the municipality of Dom Aquino (Mato Grosso, Brazil); 16 - Mangues River (Goiás, Brazil); 17 - Region of the municipality of Palmas (Tocantins, Brazil); 17a - Tabacas creek; 17b - Palmas; 17c - Xerentes Indian Reserv; 18 - Region of the municipality of Guaraí (Tocantins, Brazil); 18a - Pé de Buriti Farm; 18b – Lajedo; 19 - Tupiratins, formerly Panela de Ferro (Tocantins, Brazil); 20 - Santo Antoninho (Tocantins, Brazil); 21 - Region of the municipality of Picos (Piauí, Brazil); 22 - Region of the municipalities of Oitis and Ponta da Serra (Piauí, Brazil); 23 - Pedro Segundo Ridge, eastern slope (Piauí, Brazil); 24 - Accra (Ghana); 25 - Region of the municipality of Monte Alegre (Pará, Brazil); 25a - Ererê fields; 25b - Serviço Geológico e Mineralógico do Brasil, SGMB borehole nº. 84 at municipality of Itauajuri (1929); 26 - Maecuru river and Ipixuna creek (Pará, Brazil); 27 - Curuá river, between Cachoeirinha and Lontra rapids (Pará, Brazil); 28 - Erepecuru river at Barracão de Pedra (or Casa de Pedra, or Salão, Pará, Brazil); 29 - Well 1-UA-1-AM, core 35 (Amazonas, Brazil); 30 - Well 1-JD-1-AM, core 4 (Amazonas, Brazil). Note: The age of some localities need to be revised. Many outcrops, for example in the Paraná Basin, are currently considered to be older than interpreted 30 years ago (*e.g.* Grahn *et al*., 2000, 2013; Scheffler & Fernandes, 2007a; Bosetti *et al*., 2012).

to South America, using as an argument the distribution pattern of *Tropidoleptus carinatus*.

For some authors, the Amazon Basin would be connected to the seas of northern Africa (Melo, 1988; Isaacson, 1996) and of Bolivia (Isaacson, 1996) during the Emsian. The results support the existence of this marine warm water current. However, during the Lower Devonian, the entrance of this current into South America should be at the northwestern border, passing through the north of the Guiana Shield via Venezuela and Colombia, until the seas of Peru, Bolivia, Argentina, the Falkland Islands, and the Brazilian Ponta Grossa Formation, as suggested by the occurrence of stalked echinoderms taxa (Figure 2). This corroborated the existence of a sub-equatorial current, as proposed by Isaacson (1996). However, the absence of echinoderms in the Amazon and Parnaíba basins during the Lower Devonian, either due to intrinsic taphonomic processes in the basins, or non-adequate collection efforts, may have led to important data to be easily hidden. This can result in some biased conclusions.

Clement & Brett (2015), studying the fauna of crinoids and other echinoderms of the upper Silurian and Lower Devonian (Lochkovian-Pragian) of the Tennessee (USA), ruled out the interpretation of the existence of a westward ocean current presented in Heckel & Witzke (1979) and Isaacson (1996). Clement & Brett (2015) give support the reconstitution of Barret (1985), of the existence of an eastward current, running, at that time, from the south of Laurasia to the north of Gondwana. This interpretation was based in the great similarity in fauna of the echinoderms that occur in the upper Silurian and Lochkovian in Tennessee and Pragian of Armorica (seven genera) and Bohemia (11 genera). Examples of this occurrence of crinoids of older age in the United States, and the subsequent appearance in Europe during the Lower Devonian was cited by Witzke *et al*. (1979; *Icthyocrinus* genus and Symbathocrinidae family), which commented that the faunal interchange between Europe and North America must have taken place sometime in the Siegenian (Pragian) or early Emsian. These data on the echinoderms geographic and stratigraphic distribution demonstrate that (1) the current reconstructions of the oceanic currents or continents distribution may be not reliable, (2) the echinoderms fauna is not well known, especially in South America, or (3) both justifications are true (which is more likely). One hypothesis that can be drawn from these contradictory interpretations is that there were two oceanic currents acting on Reico ocean during the Lower Devonian (Pragian-early Emsian): an eastward current moving further north of Reico ocean, of the east of the United States heading to Europe, which would support the data of Witzke *et al*. (1979) and Clement & Brett (2015); and a westward current, moving farther south of Reico Ocean, off the northern Gondwana and entering the northwestern of South America, which would support the results presented in this article and in Isaacson (1996).

During the Eifelian, the constant rise in sea levels, and migration from South America to lower latitudes, led to an evident connection between the Northern Gondwana region and the Brazilian basins, via the Amazon Basin (Fonseca & Melo, 1987; Melo, 1988; Isaacson & Diaz Martinez, 1994). This became a shelter for stalked echinoderms taxa from the Ibarmaghian Domain. The continuous rise in sea levels led to a connection between the Amazon and Parnaíba basins during the Eifelian. A marine connection between the Parnaíba and Paraná basins (see Lange & Petri, 1967; Melo, 1988) occurred at least during the Eifelian-Givetian transition, as demonstrated by the presence of *Marettocrinus katzeri* in the Givetian in the Apucarana Sub-basin. It is more likely, however, that this connection already existed during the late Eifelian, as indicated by the presence of *Exaesiodiscus dimerocrinosus* and *Laudonomphalus* sp. B in the Alto Garças Sub-basin (Scheffler *et al*., 2011) and the presence of *Australocoelia palmata* and several chitinozoans from Paraná (e.g. *Ramochitina ramosi*) at the base of the Pimenteira Formation (Gama Jr., 2008; Lange, 1967) in the western border of the Parnaíba Basin (Figure 4).

It is important to mention that most echinoderm occurrences attributed to the early Devonian or Eifelian in South America, only occur in North America at much younger ages, during the middle and late Devonian or even in the Carboniferous, as evidenced by the distribution pattern of *Tropidoleptus carinatus* (Isaacson & Perry, 1977; Fonseca & Melo, 1987). Therefore, the affinity of the crinoid fauna in the Malvinokaffric Realm to the crinoid fauna of the Eastern America Realm (Laurentia; Webster, 2000) may be due to a migration of elements from the former to the later realm.

The occurrence in the Middle Devonian of the United States of echinoderm taxa characteristic of the Lower Devonian of Europe and North Africa (Rhenish-Bohemia Region; Boucot *et al.*, 1969; Boucot, 1975), has been noted by other researchers (Breimer & Macurda Jr., 1973; Witzke *et al.*, 1979; Le Menn, 1997). During the Givetian, the blastoid fauna from North America was composed of endemic genera or genera migrated from Europe (Spain) by skirting the southern Appalachian lands and South America itself (Waters, 1990). The dispersal pattern of echinoderms in Brazil and the rest of South America seems to demonstrate the existence of marine currents favoring its dispersion from Europe and North Africa towards North America, by passing through the northwestern and/or central-southern of South America (Northern and Central-Western Brazil and Bolivia), eventually entering the Eastern Americas Realm, as already proposed by Isaacson (1981, 1996) based on the occurrence pattern of brachiopods, specifically *Tropidoleptus carinatus*.

Observing the occurrence patterns of echinoderm taxa during later periods in North America when compared to South America, we suggest that this northward current must have intensified only during the Eifelian, as proposed by Isaacson (1996), and corroborated herein by the distribution of echinoderms. The intensification of this current can be related to the change in the patterns of oceanic currents, with the entry of warm waters from the Amazon and Parnaíba basins into the Paraná and Bolivian basins being allied to the movement towards north of the Western Gondwana.

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