



The *Tropidoleptus carinatus* controversy: Did this brachiopod occur in the Devonian of the Paraná Basin, Brazil?

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Non-technical Summary.—*Tropidoleptus* was a genus of brachiopods that had a very peculiar morphology and occurred in the Devonian period (about 419–358 million years ago) throughout the world. Although there have been reports of the presence of this genus in the Paraná Basin (Brazil) since the nineteenth century, its actual occurrence has been the subject of much debate. The objective of this work was to clarify this situation. For that, dozens of specimens from the Brazilian state of Mato Grosso were analyzed. The studied samples have typical characteristics of *Tropidoleptus*, therefore this genus actually also occurred in the Paraná Basin. *Tropidoleptus* possibly arrived in the Paraná Basin 385 million years ago, at the moment when there was a marine connection among the Brazilian Paraná, Parnaíba, and Amazonas basins. The occurrence of *Tropidoleptus* can be used as a marker of shallower marine environments, and in the Paraná Basin in particular, it can indicate that the rocks, where they are present, are less than 390 million years old.

Abstract.—*Tropidoleptus* is a brachiopod genus with a very peculiar morphology that existed throughout the Devonian as a cosmopolitan taxon. Although there have been reports of the presence of this genus in the Paraná Basin since the nineteenth century, its actual occurrence has been the subject of much debate. The objective of this paper was to clarify this situation. For this purpose, dozens of specimens from Monjolo dos Padres and Juscimeira outcrops (São Domingos Formation, possibly Givetian) in the Brazilian state of Mato Grosso were analyzed. The samples studied here exhibit the typical characteristics of *Tropidoleptus*, confirming that this genus also occurred in the Paraná Basin. It is possible that *Tropidoleptus* entered the Paraná Basin during the Eifelian/Givetian from the Amazonas and/or Parnaíba basins (Brazil), during a period of warm-water transgression. When *Tropidoleptus* is found in situ, it can serve as an indicator of a shallower water environment (shoreface to shallower portions of transitional offshore). In the Paraná Basin, its presence can indicate rocks no older than the Eifelian–Givetian transition.

Introduction

The brachiopod *Tropidoleptus* underwent several morphological changes throughout its existence in the Devonian (Isaacson and Perry, 1977) and is considered a cosmopolitan genus (Harper, 2007). This genus has unique characteristics that make its classification into a distinct order challenging. It previously has been assigned to the orders Strophomenida, Terebratulida, and Orthida (see Hall and Clarke, 1894; Schuchert, 1929; Schuchert and Cooper, 1932; Williams and Wright, 1961; Wright, 1965). Jaanusson (1971) included *Tropidoleptus* in the order Telotremata, which would encompass spiriferids and terebratulids. On the other hand, Harper et al. (2003) and Harper (2007) suggested that this genus belong to an undefined order. More recently, Harper et al. (2010) proposed elevating the family Tropidoleptidae to the order Tropidoleptida.

In Brazil, the presence of this taxon in the Amazonas and Parnaíba basins is indisputably recorded (e.g., Rathbun, 1874, 1878; Carvalho, 1972; Fonseca and Melo, 1987; Melo, 1988;

Gama Junior, 2008; Queiroz et al., 2013; Santos et al., 2021). However, its occurrence in the Paraná Basin is still a matter of debate (see Ribeiro, 2020). Although Derby (1895) documented the occurrence of *Tropidoleptus* in the Paraná Basin (Chapada dos Guimarães, Mato Grosso), he relied on a single poorly preserved specimen. Subsequently, Orville Derby himself issued a note in Clarke's (1913) monograph correcting his identification and stating that it was actually *Leptocoelia* sp. (= *Australocoelia* sp.). The specimen studied by Derby (1895) was not illustrated in his work, but Kunzler (2012) found it in the paleoinvertebrate collection of the Museu Nacional/UFRJ (MN 3323-I) and provided the first illustration of it. Upon review, Kunzler (2012) concluded that it was indeed *Tropidoleptus*, but due to the poor state of preservation of the specimen, its identification remains open to discussion (e.g., Ribeiro, 2020). Clarke (1895) reported the occurrence of *Tropidoleptus*? in samples from Jaguariaíva, Paraná state.

Caster (1947) reported the presence of specimens of *Tropidoleptus* in the Paraná Basin, specifically in the state of Mato Grosso, but neither described nor illustrated them. Almeida (1954) mentioned the occurrence of *Tropidoleptus* in the region of Chapada dos Guimarães. Suárez-Riglos (1967) mentioned

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that Caster's material included specimens of *Tropidoleptus*. Additionally, Lange and Petri (1967) noted that *Tropidoleptus carinatus* (Conrad, 1839) was the most common macrofossil of the São Domingos "member", clearly referring to the Middle Devonian layers of Mato Grosso, as evident from the subsequent fossil listing. Finally, Quadros and Melo (1989) claimed to have found *Tropidoleptus* in the locality of Monjolo (dos Padres?) (Chapada dos Guimarães), but they did not provide descriptions or illustrations of the specimens.

As can be seen, the occurrence of *Tropidoleptus* in the Paraná Basin has been supported primarily by citations, with only one poorly preserved specimen illustrated and partially described (Kunzler, 2012). Therefore, the purpose of this paper is to definitively establish the presence of *Tropidoleptus* in the Paraná Basin by analyzing numerous samples from the state of Mato Grosso. Resolving this question is crucial because *Tropidoleptus* is a significant taxon for paleobiogeographic discussions concerning the connections between the main Brazilian intracratonic basins (Amazonas, Parnaíba, and Paraná) and other basins in South America, the Old World, and Laurasia during the Devonian (see Isaacson and Perry, 1977; Harper et al., 2010).

Geological setting

The Paraná Basin, covering an area of about 1,500,000 km², is among the largest intracratonic basins in South America. It extends across parts of Brazil, Argentina, Paraguay, and Uruguay (Melo, 1988; Grahn, 1992; Milani et al., 2007; Fig. 1). Devonian outcrops are found along the borders of this basin, specifically in the Brazilian states of Paraná (eastern border), Mato Grosso, Mato Grosso do Sul, and Goiás (northwestern border) (Melo, 1988). Although there are different proposals to divide the Devonian in the Paraná Basin into various different units (e.g., Bergamaschi, 1999; Milani et al., 2007; Grahn et al., 2010; Sedorko et al., 2018), this paper adopts the lithostratigraphic framework presented by Grahn et al. (2013) for the entire basin. In their classification, Grahn et al. (2013) divided the Devonian strata in the Paraná Basin into the Furnas Formation (Lochkovian), Ponta Grossa Formation (late Pragian–early Emsian), and São Domingos Formation (late Emsian–Frasnian).

São Domingos Formation.—The specimens examined in this formation were collected from the Monjolo dos Padres and Juscimeira outcrops, both located in the state of Mato Grosso (Fig. 1). Due to the friable sandstone lithology of these outcrops, dating them through palynology is not possible. However, based on the macrofaunal content, it is likely that these specimens are of Givetian age (see Quadros and Melo, 1989; Sedorko et al., 2021), suggesting their affiliation with the São Domingos Formation (Figs. 1–3). The São Domingos Formation is stratigraphically situated above the Ponta Grossa Formation and below the Itararé Group (Carboniferous) on the eastern border, and below the Aquidauana Formation (Carboniferous) on the northwest border. It represents a marine deposit that encompasses foreshore to offshore environments, with deltaic facies observed at some localities

(Sedorko et al., 2018; Ribeiro et al., 2019). Lithologically, the São Domingos Formation is composed of poorly sorted conglomeratic sandstones, sporadically bituminous shales, and micaceous siltstones containing abundant plant fragments (Grahn et al., 2013). In the lower part of the São Domingos Formation (late Emsian–Eifelian), elements of the depleted Malvinokaffric fauna (or Malvinoxhosan, sensu Penn-Clarke and Harper, 2021) are present, while after the Givetian, organisms of the typical Malvinokaffric fauna become scarce or disappear (Bosetti et al., 2010, 2012).

Materials and methods

The specimens examined in this study are housed in the paleo-invertebrate collection of the Museu Nacional/Universidade Federal do Rio de Janeiro (MN-I) and the Universidade Federal de Mato Grosso (MP, CD). The Museu Nacional specimens are the same ones previously analyzed by Caster (1947) and are part of the Caster Collection. Initially, these specimens were sent to the University of Cincinnati and later repatriated to the Museu Nacional collection in 2016 (see Scheffler et al., 2021). The specimens that were not affected by the tragic fire in 2018 because they were not inside the palace are MN 12002-I, MN 12003-I, MN 12004-I, MN 12005-I, MN 12006-I, MN 12007-I, MN 12008-I, MN 12009-I, MN 12010-I, MN 12011-I, MN 12012-I, MN 12013-I, MN 12014-I, MN 12015-I, MN 12016-I, MN 12017-I, MN 12018-I, MN 12019-I, MN 12020-I, MN 12021-I, MN 12022-I, MN 12023-I, MN 12024-I, MN 12025-I, MN 12026-I, and MN 12035-I. The specimens that were inside the palace and were later rescued are MN 10674-I, MN 10675-I, MN 10676-I, MN 10680-I, MN 10681-I, MN 10686-I, MN 10687-I, MN 10688, and MN 10690-I. Unfortunately, specimen MN 3323-I, which was previously studied by Derby (1895), was lost in the fire and is no longer available for examination.

The original accession numbers of specimens MN 10674-I, MN 10675-I, MN 10676-I, MN 10680-I, MN 10681-I, MN 10686-I, MN 10687-I, MN 10688-I, and MN 10690-I were inferred based on the positions of specimens in the collection before the fire. However, it is not possible to relate these individual specimens to their individual numbers. Because all of these specimens originated from the Monjolo dos Padres outcrop, we have designated the specimen in Figure 5.6 as MN 10674-I.

The samples deposited in the Universidade Federal de Mato Grosso collection include MP 533, MP 522a, b, MP 506, MP 507, MP 508 (part and counterpart), MP 510, and CD 310a–c.

We conducted a comparison of the material from the Paraná Basin with the hypotypes of *Tropidoleptus carinatus* (Conrad, 1839) studied by Williams (1913) from the Devonian of New York, United States of America. Currently, these samples are housed in the National Museum of Natural History/Smithsonian Institution collection with accession number USNM 59603 (1–88), originating from the Portage Formation. Additionally, Devonian specimens from the Amazonas Basin (Mae-curu and Ererê formations) and Parnaíba Basin (Pimenteira and Cabeças formations) in Brazil were also analyzed. These samples are preserved in the collection of the Museu de Ciências da Terra/CPRM (DGM 2845-Ia–d; DGM 2902-I; DGM

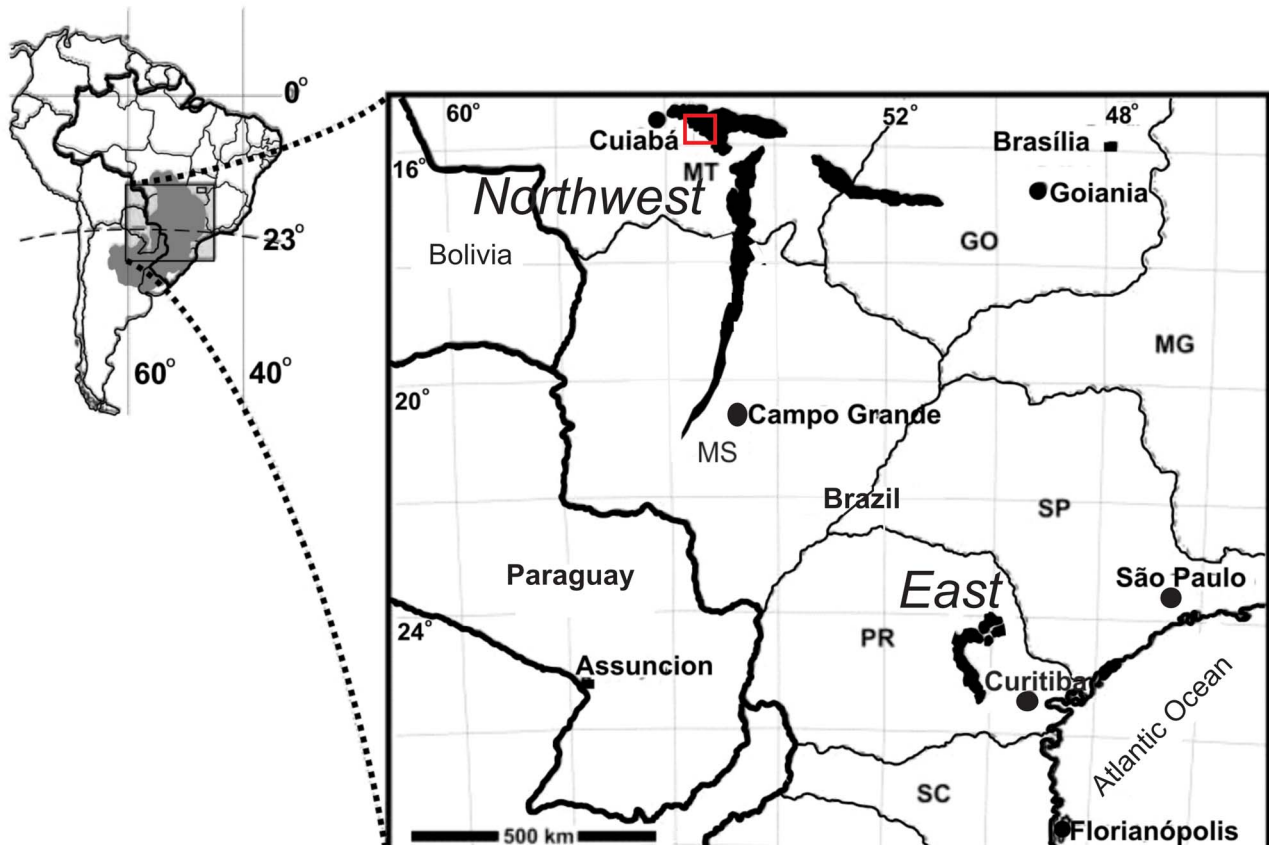


Figure 1. Map of the Paraná Basin highlighting the Devonian outcrops. The red square indicates the region of the Juscemeira and Monjolo dos Padres outcrops, northwest–northwestern border of Paraná Basin, east–eastern border of Paraná Basin. Brazilian states: SC = Santa Catarina, PR = Paraná, SP = São Paulo, MG = Minas Gerais, MS = Mato Grosso do Sul, MT = Mato Grosso, GO = Goiás (adapted from Borghi and Fernandes, 2001; Scheffler et al., 2020).

2903-I), Instituto de Geociências/Universidade Federal do Rio de Janeiro (UFRJ 432-Bq, UFRJ 428-Bq), and Museu Nacional/UFRJ (MN 6379-I, MN 6382-I, MN 6391-I, MN 6398-I, MN 6400-I, MN 6402-I (not recovered after the fire).

For taxonomic identification, we consulted the Treatise on Invertebrate Paleontology (Harper, 2007) and various articles on

Tropidoleptus taxonomy across different Devonian regions worldwide.

Repositories and institutional abbreviations.—MN/UFRJ (MN-I), Museu Nacional of Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; IGEO/UFRJ (UFRJ-Bq),

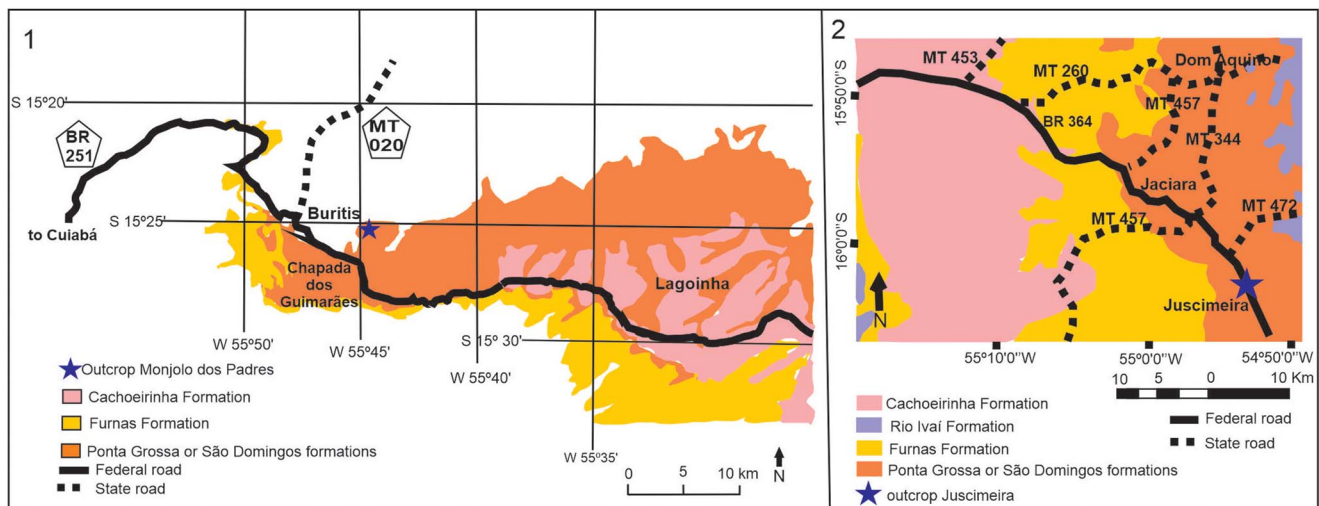


Figure 2. Location of the outcrops: (1) Simplified geological map of the Juscemeira outcrop region (Lacerda Filho, 2004). (2) Simplified geological map of the Monjolo dos Padres outcrop region (Grahn et al., 2010).

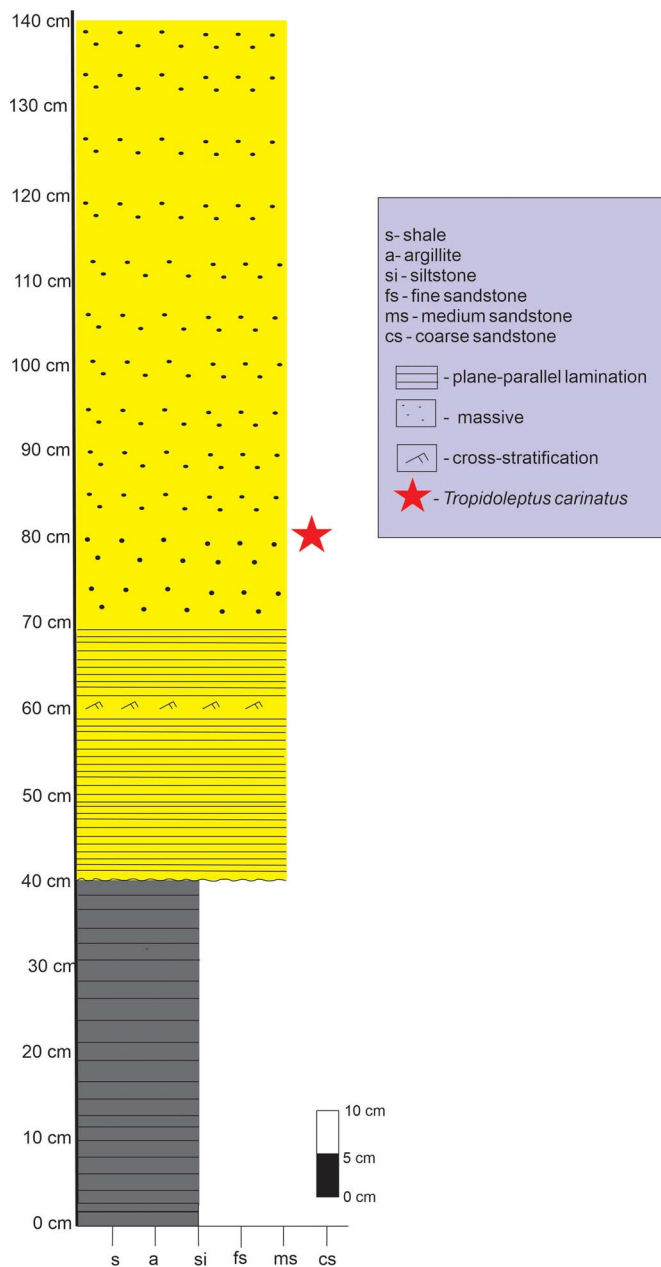


Figure 3. Sedimentological profile of the Juscimeira outcrop (adapted from personal correspondence, Henrique Z. Tomassi, 2021).

Instituto de Geociências of Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; UFMT (MP, CD), Universidade Federal de Mato Grosso, Cuiabá, Brazil; MCT/CPRM (DGM-I), Museu de Ciências da Terra of Serviço Geológico do Brasil, Rio de Janeiro, Brazil; NMNH/SI (USNM), National Museum of Natural History/Smithsonian Institution, Washington D.C., United States of America.

Systematic paleontology

Class Rhynchonellata Williams et al., 1996
 Order Tropidoleptida Schuchert, 1896
 Superfamily Tropidoleptoidea Schuchert, 1896

Family Tropidoleptidae Schuchert, 1896
 Genus *Tropidoleptus* Hall, 1857

Type species.—*Strophomena carinata* Conrad, 1839.

Tropidoleptus carinatus (Conrad, 1839)
 Figures 4, 5

- 1839 *Strophomena carinata* Conrad p. 64.
 1857 *Tropidoleptus carinatus* (Conrad); Hall, p. 151.
 1895 *Tropidoleptus?* sp. Derby, p. 76.
 1897 *Tropidoleptus rhenana* Frech, p. 143, note 1, pl. 23a, fig. 9.
 1902 *Tropidoleptus carinatus* var. *rhenana* (Frech); Drevermann, p. 99, pl. 12, figs. 11, 12.
 1933 *Tropidoleptus carinatus* var. *maecurensis* Katzer; Clarke, p. 181, pl. 10, fig. 7a, b.
 1947 *Tropidoleptus* sp. Caster, p. 126.
 1967 *Tropidoleptus carinatus* (Conrad); Suárez-Riglos, p. 33, pl. 1, figs. 1–11.
 1972 *Tropidoleptus carinatus* (Conrad); Carvalho, p. 25, pl. 2, figs. 1–14, pl. 3, fig. 1–3.
 1977 *Tropidoleptus carinatus* (Conrad); Isaacson, pl. 1, figs. 20–37, pl. 2, figs. 1–3.
 1977 *Tropidoleptus carinatus* (Conrad); Isaacson and Perry, p. 1115.
 1977 *Tropidoleptus carinatus rhenana* (Frech); Isaacson and Perry, pl. 2, figs. 1–17.
 1982 *Tropidoleptus platys* Cooper and Dutro, p. 43, pl. 4, figs. 13–21.
 1987 *Tropidoleptus carinatus* (Conrad); Fonseca and Melo, pl. 1, figs. 1–9, pl. 2, figs. 1–12.
 2004 *Tropidoleptus* sp. Racheboeuf et al., p. 104, fig. 4.10.
 2010 *Tropidoleptus carinatus* (Conrad); Harper et al., figs. 1–6.

Holotype.—Undesignated holotype; type-series likely deposited in the American Museum of Natural History, United States of America (Gama Júnior, 2008; Queiroz et al., 2013).

Occurrence.—?Antarctica, unknown geological unit, Givetian (Harper et al., 2010); South Africa, Witterberg Group, Givetian–Frasnian (Boucot et al., 1983a; Penn-Clarke et al., 2018; Penn-Clarke, 2019); Germany, Lower Dark and Neichnerberg formations, Pragian–Emsian (Fuchs, 1982; Ubelacker et al., 2016); ?Australia, Cocktattoo Formation, Frasnian (Roberts, 1971); Belgium, unknown formation, Pragian–Emsian (Boucot et al., 1995); Bolivia, Huamampampa, Belén, and Sicasica formations, late Eifelian–?Frasnian (Isaacson, 1977, 1993; for age see Blicek et al., 1996; Troth et al., 2011); Brazil, São Domingos, Maecuru, Ererê, Pimenteira, and Cabeças formations, middle/late Eifelian–Givetian (Suárez-Riglos, 1967; Fonseca and Melo, 1987; Melo, 1988; this paper); Canada, Torbrook Formation, Lochkovian (Boucot, 1999); Colombia, Floresta and Gutierrez formations, ?Emsian–Frasnian (Caster, 1939; Morales, 1965; Barrett, 1986); Chile, Zorritas Formation, Eifelian or Givetian (Isaacson et al., 1985; Isaacson, 1993; Boucot et al., 1995, 2008); England, unknown formation, Pragian–Emsian (Boucot et al., 1995); Morocco, unknown

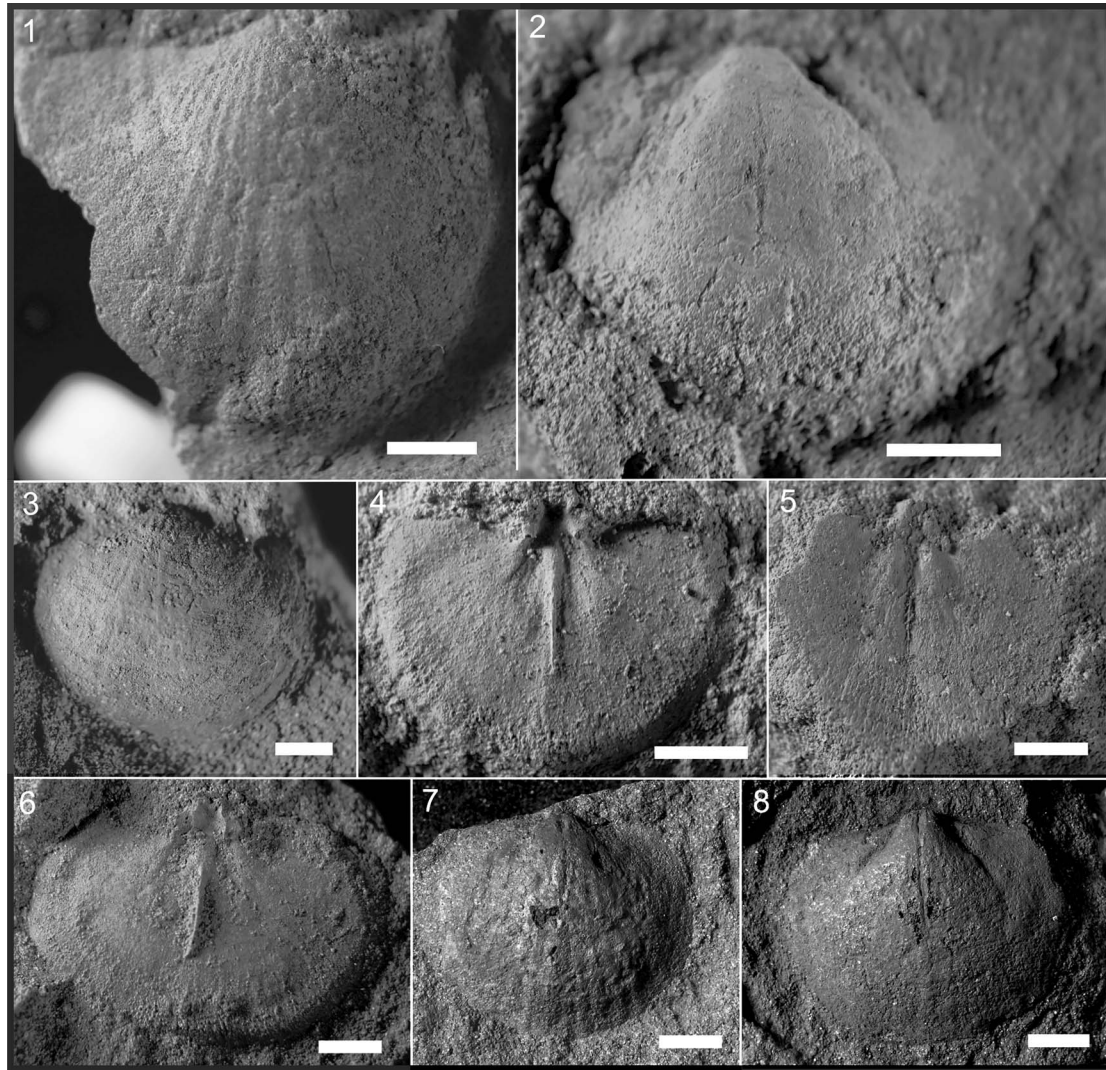


Figure 4. *Tropidoleptus carinatus* (Conrad, 1839): (1) exterior, ventral valve, MN 12003-I; (2) interior, ventral valve, MN 12005-I; (3) exterior, ventral valve, MN 12011-Ia; (4) interior, dorsal valve, MN 12012-I; (5) interior, dorsal valve, MN 12016-I; (6) interior, dorsal valve, MN 12014-I; (7) exterior ventral valve, MN 12015-Ib; (8) interior, ventral valve, MN 12015-Ia. All scale bars represent 5 mm.

formation, Pragian–Givetian (Jansen, 2001; Harper et al., 2010; Halamski and Balinski, 2013); France, unknown formation, Givetian (Rachebouef in Boucot et al., 1995); Central Sahara (Algeria and Niger), Tamesna Basin, Pragian–Givetian (Mergl and Massa, 2004); United States of America, Beechwood Limestone Member, Silica, “Beers Hill”, Portage, Ludlowville and Mahantango formations, Givetian–Frasnian (Williams, 1913; Ellison, 1965; Kesling and Chilman, 1975; McGhee and Sutton, 1985); Spain, Salobral Formation, Givetian (Carls, 1988; Carls and Valenzuela-Ríos, 2002); Libya, Aouinet Ouenine II and Idri formations, ?Pragian–Frasnian (Freulon, 1964; Havlicek and Rohlich, 1987; Mergl and Massa, 1992); Mauritania, Aratane Formation, ?Pragian–Givetian (LeMaître, 1952; Sougy, 1964; Rachebouef et al., 2004); Czech Republic, Drakov Quartzite, Pragian (Isaacson and Chlupac, 1984); Peru, Cabanillas Formation, ?Eifelian (Newell, 1949; for age see Laubacher et al., 1982); Venezuela, Caño Grande and Caño del Oeste formations, ?Early Devonian–Givetian (Sanchez and Benedetto, 1983).

Description.—Length 10.5–25.2 mm, width 12.1–26.3 mm (Table 1, Fig. 6). The width is greater than the length, with the maximum width of valve found in median region; endopunctate; ~20 ribs arising at beak, ribs wider than the interspaces, relatively thick, and sparsely spaced, rarely multiplying by bifurcation; presence of concentric growth lines; contour of valves is subquadrate, semielliptical to semicircular, slightly concavo-convex to plano-convex. The beak is small, extending slightly beyond the hinge line, while the shell margins are rounded. Strophic, with a non-crenulate hinge line. The dorsal valve is almost planar, while the ventral valve is more concave; the median rib on ventral valve is slightly larger than others and extends to the anterior commissure.

Ventral interior.—Open delthyrium with a triangular shape, where height is smaller than the base size, and absence of deltidial plates; prominent teeth are present and diverge anterolaterally; muscular field broad, long, and weakly imprinted, with an inflated umbonal region; presence of delicate myophragm.

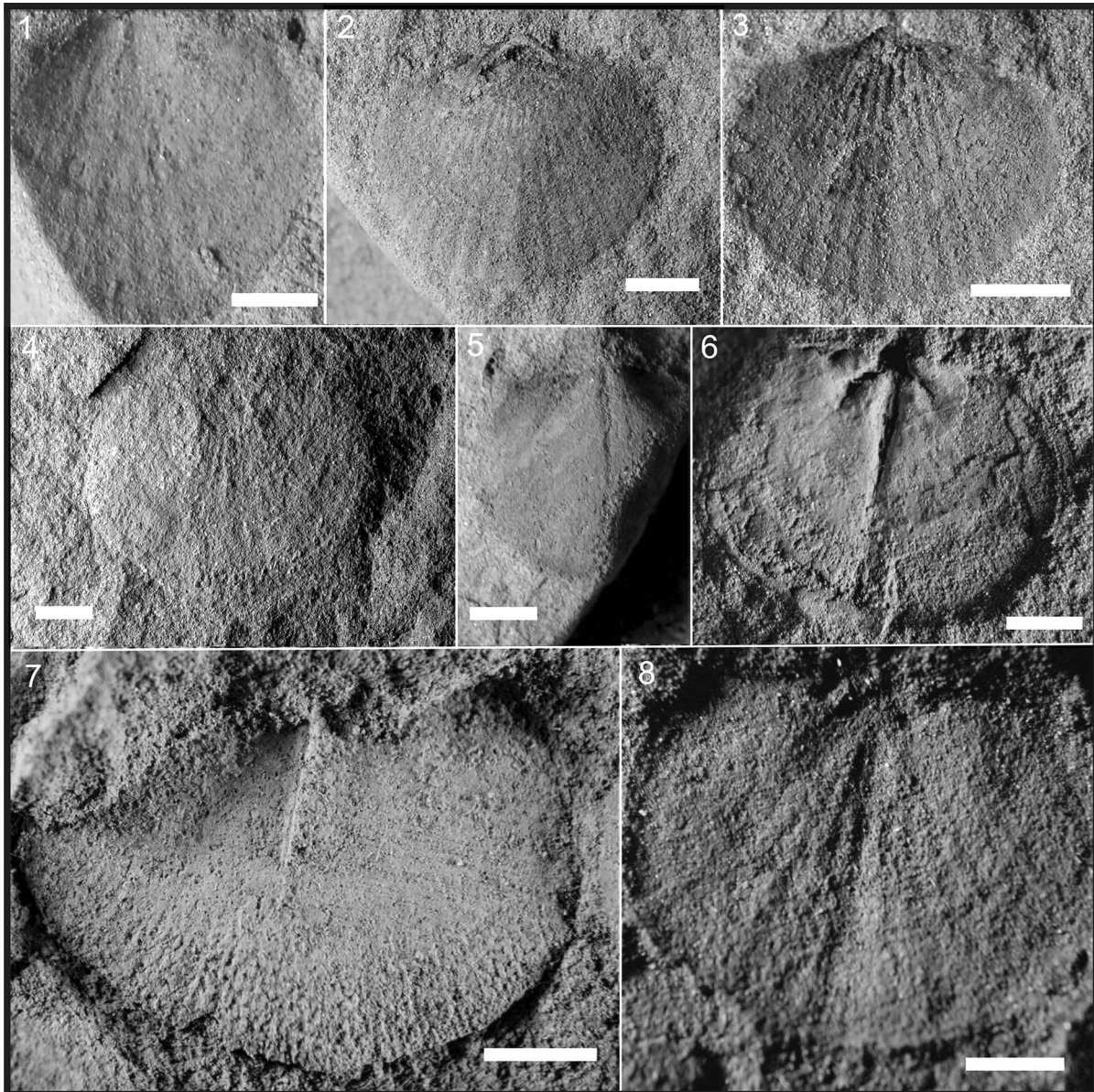


Figure 5. *Tropidoleptus carinatus* (Conrad, 1839): (1) exterior, ventral valve, MP 533; (2) exterior, dorsal valve, MP 522a; (3) exterior, ventral valve, MP 522b; (4) exterior, dorsal valve, CD 310b; (5) interior, ventral valve, MP 507; (6) interior, dorsal valve, MN 12017-I; (7) interior, MN 12004-Ia; (8) interior, dorsal valve, MN 12022-I. All scale bars represent 5 mm.

Dorsal interior.—Well-excavated dental pits are delimited by lateral lobes of the notothyrial platform, poorly preserved cardinal process projects above the hinge line. Crura extend anterolaterally as descending lamellae from the lateral lobes of the notothyrial platform. A thin myophragm starts from the antero-medial region of the notothyrial platform and extends over more than half of the valve, thinning anteriorly.

Material.—MN 10674-I, MN 10675-I, MN 10676-I, MN 10680-I, MN 10681-I, MN 10686-I, MN 10687-I, MN 10688-I, MN 12002-Ia,b, MN 12003-Ia, b, MN 12004-Ia, b, MN 12005-I, MN 12006-I, MN 12007-I, MN 12008-I, MN 12009-I, MN 12010-I, MN 12011-I, MN 12012-I, MN 12013-I, MN 12014-I, MN 12015-Ia, b, MN 12016-I, MN 12017-I, MN 12018-I, MN 12019-I, MN 12020-I, MN 12021-Ia, b, MN 12022-I, MN

12023-Ia, b, MN 12024-I, MN 12025-I, MN 12026-Ia–e, MN 12035-Ia–c, MP 533, MP 522a, b, MP 506, MP 507, MP 508 (part and counterpart), MP 510, CD 310a–c (55 samples).

Provenance.—Outcrops Monjolo dos Padres and Juscimeira, São Domingos Formation (possibly Givetian).

Observation.—*Tropidoleptus* reported by Kayser (1897) from the Los Espejos Formation in Argentina was synonymized as *Castellaroina* (see Boucot in Amos, 1972; Harper and Boucot, 1978; and Benedetto and Montoya, 2015). *Tropidoleptus* cited by Thomas (1905) in Argentina may not belong to the genus either.

Remarks.—The specimens analyzed in this study exhibit the main morphological features of *Tropidoleptus*, as described by

Table 1. Measurements of the analyzed specimens.

Specimen	Length (mm)	Width (mm)	L/W
MN 12003-Ia	18.2	22.3	0.82
MN 12024-I	13.3	—	—
MN 12004-Ia	13.1	18.9	0.69
MN 12004-Ib	12.8	22.3	0.57
MN 12005-I	18.0	24.1	0.75
MN 12006-I	9.2	13.5	0.68
MN 12009-I	25.2	30.0	0.84
MN 12035-Ia	19.0	25.9	0.73
MN 12035-Ib	14.9	19.2	0.78
MN 12010-I	20.5	26.3	0.78
MN 12011-I	15.6	19.6	0.79
MN 12012-I	16.8	24.0	0.7
MN 12013-I	10.5	13.3	0.79
MN 12016-I	16.1	18.4	0.87
MN 12014-I	20.2	29.3	0.69
MN 12019-I	14.4	16.4	0.87
MN 12020-I	21	27.8	0.75
MN 12015-Ia	18.7	22.3	0.81
MN 12015-Ib	14.5	18.6	0.78
MN 12021-Ia	15.7	20.9	0.75
MN 12021-Ib	14.9	19.7	0.76
MN 12022-I	22.6	32.2	0.70
MN 12017-I	21.1	27.6	0.76
MN 12026-Ia	23.9	33.4	0.72
MN 10674-I	13.6	—	—
MP 522a	11.7	15.2	0.77
MP 522b	10.8	13.0	0.83
MP 507	12.5	—	—
MP 508	10.5	—	—
MP 510	10.7	12.1	0.88
MP 533	12.3	—	—
CD 310a	12.8	—	—
CD 310b	18.5	23.0	0.8
Mean	15.9	21.7	0.76
Standard Deviation	4.14	5.75	0.07

Conrad (1839), Isaacson and Perry (1977), Harper (2007), and Harper et al. (2010). These features include: (1) endopunctate shell surface; (2) subquadrate, semielliptical to semicircular

contour of valves, slightly concavo-convex to plano-convex; (3) slightly larger median rib on ventral valve compared to other ribs; (4) ribs originating at the beak, wider than interspaces, relatively thick, and sparsely spaced, rarely multiplying by bifurcation; (5) presence of concentric growth lines; and (6) crura extending anterolaterally as descending lamellae.

Based on these observations, there is no doubt that *Tropidoleptus* was present in the Devonian of the Paraná Basin. We concur with the inclusion of *Tropidoleptus* in the order Tropidoleptida, as discussed by Harper et al. (2010).

Several species have been proposed within the genus *Tropidoleptus*. Other than the type species, at least four additional species can be recognized: *T. occidentis* (Hall, 1860); *T. platys* Cooper and Dutro, 1982; *T. fascifer* Kayser, 1897; and *T. rhenanus* (Frech, 1897).

Tropidoleptus fascifer was proposed by Kayser (1897) from Argentina. However, it was subsequently designated as the type species of the subgenus *Castellaroina* by Boucot in Amos (1972), which was later elevated to genus rank by Harper and Boucot (1978). Benedetto and Montoya (2015) proposed an emended diagnosis for the genus *Castellaroina* and provided a detailed description of the species *Castellaroina fascifer* (Kayser, 1897). As a result, *T. fascifer* is no longer considered a valid species of *Tropidoleptus*.

Tropidoleptus rhenanus (= *rhenana*) was proposed by Frech (1897) based on species from the Devonian of Germany. However, Drevermann (1902) conducted a comprehensive analysis of extensive German, American, and Bolivian material and concluded that *T. rhenana* could not be considered a separate species from *T. carinatus*. The external morphological characteristics (e.g., the number of ribs, length/width ratio, and median rib) are similar among these specimens. Drevermann (1902)

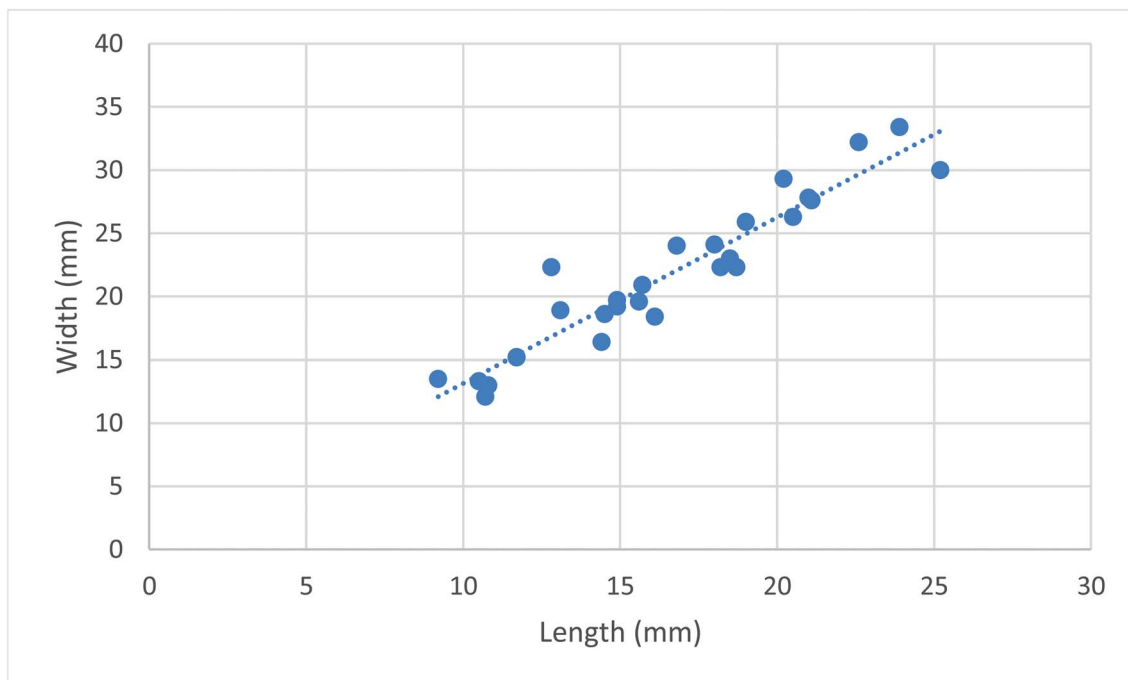


Figure 6. Plots of measurements of length versus width of analyzed *Tropidoleptus carinatus* (Conrad, 1839); $n = 27$.

suggested a possible distinction based on the extent of the muscular field, which extends beyond half of the valve. However, it has been shown in figures by Isaacson and Perry (1977) that *T. carinatus* also can exhibit these features. Upon careful comparison, it is apparent that “*T. rhenanus*” has slightly more angular ribs compared to *T. carinatus* (see Isaacson and Perry, 1977; Harper et al., 2010; Schemm-Gregory and Henriques, 2013). This suggests that “*T. rhenanus*” can be classified as a subspecies (*Tropidoleptus carinatus rhenanus*), rather than a distinct species, which aligns with the findings of Drevermann (1902) and Isaacson and Perry (1977).

Tropidoleptus occidentens was proposed by Hall (1860) for specimens from the Devonian of Iowa, United States of America. However, the limited number of described specimens and their poor preservation make it challenging to conduct a thorough comparison with *T. carinatus*. One notable difference is the presence of two enlarged median ribs on the ventral valve, as described by Hall (1860), which is not a typical characteristic of *Tropidoleptus*. It should be noted that the illustrations by Hall and Clarke (1894) do not provide a clear characterization of these two enlarged median ribs. In contrast, *Tropidoleptus* typically possesses only one enlarged median rib (see Harper, 2007; Harper et al., 2010). Stainbrook (1938) synonymized *T. occidentens* as *Stropheodonta occidentens* (Hall, 1860).

Tropidoleptus platys was proposed by Cooper and Dutro (1982) based on specimens from the Devonian of New Mexico, United States of America. However, the characteristics identified by these authors are not sufficiently robust to designate *T. platys* as a distinct species for the following reasons. (1) The obsolescence of ribs on the anterior margin noted in *T. platys* may be attributed to taphonomic factors rather than being a consistent characteristic across all specimens (some specimens of *T. carinatus* also exhibit this feature, as indicated by Cooper and Dutro, 1982; see also Isaacson and Perry, 1977, for an example. (2) Cooper and Dutro (1982) mentioned that specimens of *T. carinatus* from the Kashong Shale are larger than *T. platys*, while *T. carinatus* specimens from the Tully Limestone are smaller than *T. platys*. Hence, size cannot be considered a diagnostic feature in this case. The samples of *T. carinatus* described by Isaacson and Perry (1977) exhibit lengths of 15–30 mm, while Isaacson (1977) recognized a length range of 3.4–20.4 mm in Bolivian specimens. The specimens described by Cooper and Dutro (1982) have a lengths of 13.9–16.7 mm, which is within the size range expected for *T. carinatus* (3) The supposed smaller concavity and less-pronounced costate in *T. platys* compared to *T. carinatus* are not evident when comparing the illustrations by Cooper and Dutro (1982) with the specimens described by us and in other papers (e.g., Williams, 1913; Isaacson, 1977; Isaacson and Perry, 1977; Fonseca and Melo, 1987; Harper et al., 2010). (4) The more transverse shell of *T. rhenanus* (here considered synonymous with *T. carinatus*) compared to *T. platys* is not a robust diagnostic character because it is highly susceptible to taphonomic influences. Therefore, based on the characteristics presented here, *T. platys* is considered synonymous with *T. carinatus*.

A comparison of *T. carinatus* specimens from the Paraná, Parnaíba, and Amazonas basins, as well as the hypotypes from

New York (hypotypes of Williams, 1913), revealed no significant differences among them. The observed variations were consistent with intraspecific variations, as discussed by Isaacson and Perry (1977), confirming the presence of the same species across these regions (Fig. 7). Nevertheless, two subtle main differences were identified in the analyzed Brazilian specimens compared to those described by Isaacson and Perry (1977): (1) the ventral myophragm appears to be less vigorous, and (2) the median septum (referred to as the myophragm here) is less developed. These differences also were recognized by Fonseca and Melo (1987) in Devonian specimens from the Parnaíba Basin.

Finally, in the existing literature, several subspecies of *Tropidoleptus carinatus* have been proposed, including *T. carinatus freuloni* Boucot, Massa, and Perry, 1983b; *T. carinatus nigeriensis* Boucot, Massa, and Perry, 1983b; and *T. carinatus titanius* Mergl and Massa, 2004. The specimens studied here can be clearly distinguished from *T. carinatus titanius* by their smaller size (with a maximum width of ~33 mm, compared to 56 mm in *T. carinatus titanius*). However, in order to reliably differentiate the *T. carinatus* specimens studied here from *T. carinatus freuloni* and *T. carinatus nigeriensis*, it would be necessary to examine specimens the latter two subspecies. Analysis of the photos presented by Boucot et al. (1983b) was inconclusive for this purpose.

Paleoenvironmental and paleobiogeographic considerations

Paleoenvironment.—*Tropidoleptus carinatus* (Conrad, 1839) is a species commonly associated with shoreface environments worldwide, although it also could occur in shallower areas of the transitional offshore (see Isaacson and Perry, 1977; Boucot et al., 1995; Harper et al., 2010). The Paraná Basin specimens of *Tropidoleptus carinatus* are found in friable, well-sorted sandstones. In the Juscimeira outcrop, the level containing *Tropidoleptus* is characterized by massive medium-grained sandstone (personal correspondence, Henrique Z. Tomassi, 2021). Specimens in the Monjolo dos Padres outcrop were found in sandstones with hummocky cross-stratification (tempestites), interbedded with shales (Quadros and Melo, 1989). Most specimens are disarticulated, and some show signs of abrasion, all of which may be a result of the naturally abrasive nature of the lithology (friable sandstone) and the high-energy paleoenvironment, rather than indicating long-distance transport. *Tropidoleptus carinatus* was not found in thinner facies such as argillite, siltstone, or shale, suggesting that this species was also restricted to shallower environments in the Paraná Basin, likely between the distal shoreface and proximal offshore. Further taphonomic studies are required to provide additional support for this interpretation.

Paleobiogeography.—*Tropidoleptus* is another extra-Malvinokaffric brachiopod genus found in the Devonian deposits of the Paraná Basin, alongside other genera such as *Chonostrophia*?, *Cryptonella*, *Plicoplasia*?, *Pustulatia*?, and *Schellwienella* (Clarke, 1913; Cerri, 2013; Penn-Clarke and Harper, 2021; Rezende and Isaacson, 2021; Sedorko et al., 2021; Videira-Santos et al., 2022).

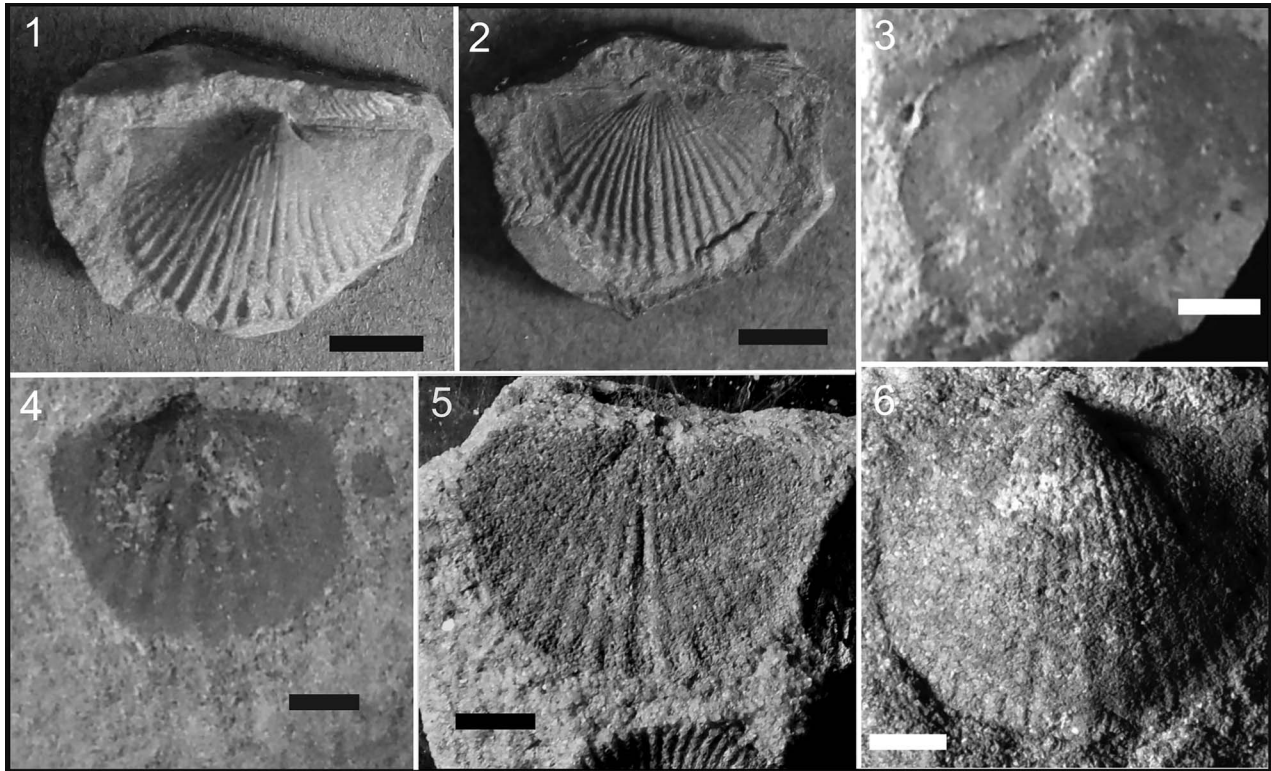


Figure 7. *Tropidoleptus carinatus* (Conrad, 1839). (1) Exterior, ventral valve, Harford Mills, New York, USA, Portage Formation, USNM 59603 (21); (2) exterior, dorsal valve, Harford Mills, New York, USA, Portage Formation, USNM 59603 (88); (3) interior, ventral valve, BR-020, Itainópolis, Piauí, Brazil, Pimenteira Formation, MN 6391-I; (4) exterior, ventral valve, BR-020, Itainópolis, Piauí, Brazil, Pimenteira Formation, MN 6400-I; (5) interior, dorsal valve, Serra de Ererê, Monte Alegre, Pará, Brazil, Ererê Formation, DGM 2845-Ia; (6) exterior, ventral valve, Maecuru River, Monte Alegre, Pará, Brazil, Maecuru Formation, DGM 2902-I. All scale bars represent 5 mm.

The genus *Tropidoleptus* originated in the Lochkovian of Nova Scotia (Canada), part of the ancient Avalonia/Baltica region (see Boucot, 1999; Robardet, 2003), belonging to the “Old World Realm” (Dowding and Ebach, 2018; Dowding et al., 2022). From its origin, *Tropidoleptus* dispersed to different parts of the world, including Europe, North Africa, and South America, the central portion of North America, South Africa, and possibly Antarctica, indicating its cosmopolitan distribution (Isaacson and Perry, 1977; Harper, 2007; Harper et al., 2010) (Fig. 8). However, the genus eventually became extinct during the Late Devonian extinction event, as noted by Harper et al. (2010).

According to paleogeographical reconstructions, Avalonia/Baltica and the rest of Europe were closely positioned during the Early Devonian, with only a narrow Rheic Ocean separating them (Robardet, 2003). Additionally, southeastern Europe, including the Armorican Massif, the Iberian Peninsula, and possibly central Europe (Bohemia) and perhaps the Moesian Terrane, were positioned adjacent to the Gondwana plate, forming its northern border (Plusquellec et al., 1997; Robardet, 2003; Vaida et al., 2005). This paleogeographic context suggests a potential pathway for the rapid migration of *Tropidoleptus* from Avalonia/Baltica to Bohemia and northern Gondwana during the Early Devonian (Fig. 8).

During the Eifelian global transgression (see Haq and Schutter, 2008), the sea advanced into the Amazonas and Parnaíba basins, which are part of the Amazonian sub-region, as defined by Penn-Clarke and Harper (2021). *Tropidoleptus*

along with other brachiopods, echinoderms, trilobites, and various taxa, migrated from regions such as Armorica, Bohemia, and North Africa towards the northern (Amazonas Basin) and northeastern (Parnaíba Basin) parts of Brazil between the Emsian and Eifelian (Fonseca and Melo, 1987; Díaz-Martínez et al., 1993; Scheffler et al., 2011; Carvalho and Ponciano, 2015; Fonseca, 2015; Scheffler, 2015). This migration route highlights the dispersal of organisms during this period of time.

Penn-Clarke and Harper (2021) reached the conclusion, based solely on brachiopods, that the Amazon Basin predominantly hosted taxa from the eastern Americas, including Malvinokaffric elements, while the Parnaíba Basin exhibited a combination of eastern Americas and Malvinokaffric taxa. Nevertheless, as mentioned earlier, it is important to recognize that the faunal composition of these basins also was influenced by elements of the Old World.

During the Eifelian, *Tropidoleptus* also extended its distribution to various other regions of present-day South America (e.g., Bolivia, ?Chile, and ?Peru). The influence of the Northern Gondwana fauna, as noted earlier during the Middle Devonian in South America, has been documented by several studies (e.g., Isaacson and Sablock, 1988; Díaz Martínez et al., 1993; Racheboeuf et al., 1993; Blicke et al., 1996; Tourneur et al., 2000). The evidence presented in this study suggests that the faunal distribution in southwest Gondwana was influenced by sea-level events and facilitated dispersal, which in turn

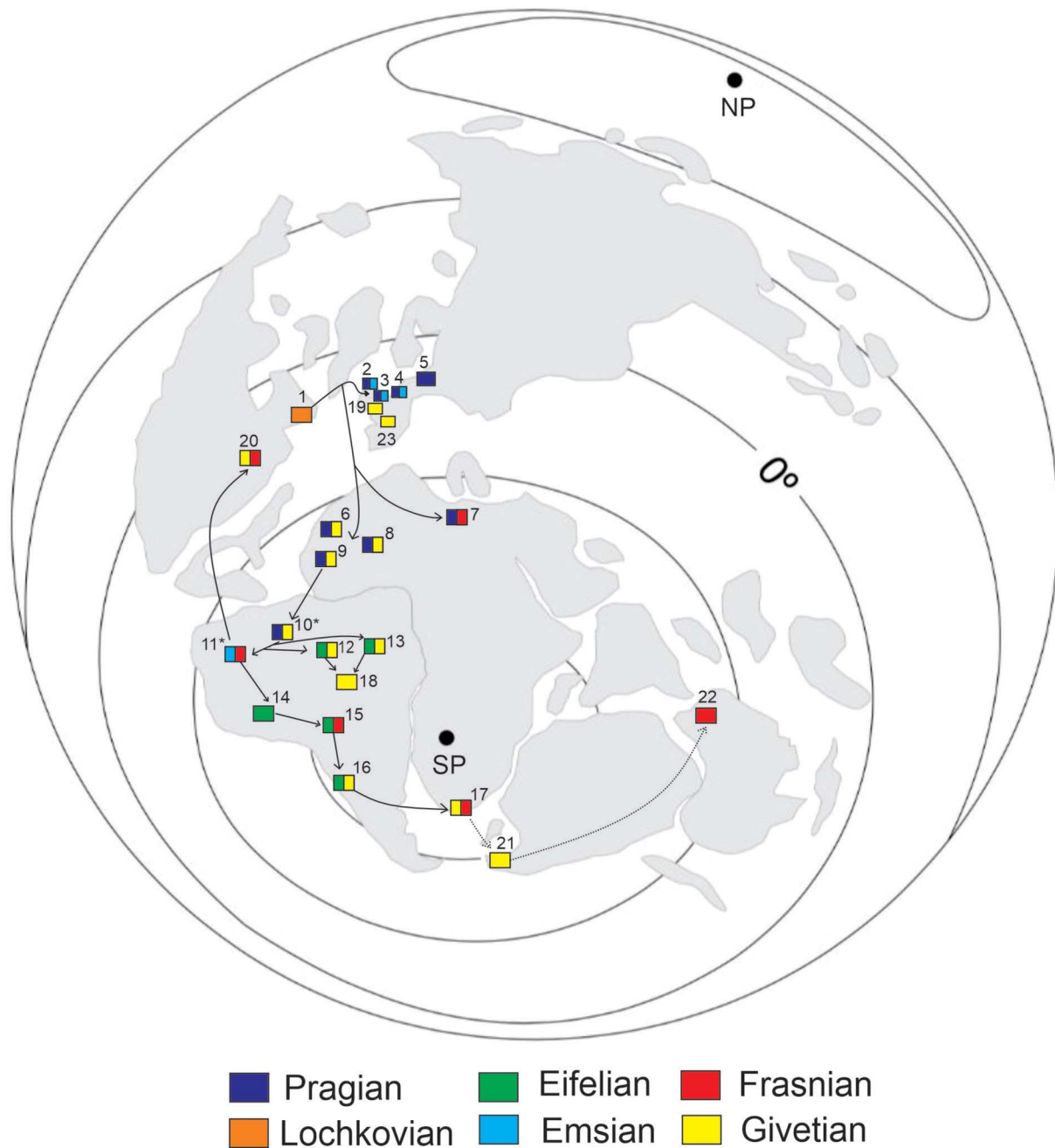


Figure 8. Occurrence of *Tropidoleptus carinatus* (Conrad, 1839) throughout the Devonian. SP = South Pole, NP = North Pole; 1 = Canada, 2 = England, 3 = Belgium, 4 = Germany, 5 = Czech Republic, 6 = Morocco, 7 = Libya, 8 = Central Sahara (Algeria/Niger), 9 = Mauritania, 10 = Venezuela, 11 = Colombia, 12 = Amazonas Basin (Brazil), 13 = Parnaíba Basin (Brazil), 14 = Peru, 15 = Bolivia, 16 = Chile, 17 = South Africa, 18 = Paraná Basin (Brazil), 19 = France, 20 = United States of America, 21 = Antarctica, 22 = Australia, 23 = Spain. Dotted arrow = migration with doubts (adapted from Habicht, 1979; Raymond, 1987; Melo, 1988; Golonka, 1994; Scotese et al., 1999; di Pasquo et al., 2009; Boucot et al., 2013; Ribeiro, 2020). *There are doubts about the Pragian age for Venezuela and the Emsian age for Colombia; *Tropidoleptus carinatus* possibly entered these locations later.

influenced the distribution and mixing patterns between various paleobiogeographic sub-regions, as previously postulated by several authors (e.g., Melo, 1988; Dowding et al., 2022). Additionally, differences in latitudes have an effect on taxonomic distribution and bioregionalization, as supported by the findings of Penn-Clarke and Harper (2021).

According to Penn-Clarke and Harper (2021) and Dowding et al. (2022), further biogeographic studies are necessary to

reassess the status of sub-regions within the Malvinokaffric Realm. However, these studies should not rely solely on one phylum of organisms. In the case of southwest Gondwana, the similarity between taxa from different Malvinokaffric basins appears to vary depending on the phylum being considered. For instance, the work of Scheffler et al. (2013) highlights the lack of similarity between crinoids from the Paraná Basin and those from other basins in South America and South Africa,

illustrating the need for a comprehensive examination across multiple phyla.

Tropidoleptus, known for inhabiting warmer waters, traditionally has been regarded as an end marker of the typical endemic fauna of certain Devonian paleobiogeographic realms (Dowding et al., 2022). However, its presence has been documented in these areas even prior to the collapse of the aforementioned paleobiogeographic realms (Isaacson, 1977; Penn-Clarke et al., 2018; Penn-Clarke, 2019). For instance, the Malvinokaffric Realm is thought to have ceased to exist by the Givetian (Boucot, 1988; Li, 2010; Dowding and Ebach, 2018; Penn-Clarke and Harper, 2021; Rezende et al., 2021). Nonetheless, there are records of *Tropidoleptus* in Malvinokaffric regions (Bolivia and South Africa) in older deposits (e.g., Isaacson, 1977; Harper et al., 2010; Troth et al., 2011; Penn-Clarke et al., 2018; Penn-Clarke, 2019).

The arrival of *Tropidoleptus* in the Paraná Basin during the Givetian coincides with the decline of the typical Malvinokaffric fauna that had previously inhabited the basin, as well as with the occurrence of a “Lilliput effect” in the relict fauna (Bosetti et al., 2010; Grahn et al., 2016). The occurrence of *T. carinatus* in strata of presumed Givetian age in the Paraná Basin supports the idea that the Parnaíba, Amazonas, and Paraná basins had been interconnected since the early Givetian, and that warm waters entered the Paraná Basin, which was located near the south pole at that time (Grahn et al., 2016). This coincided with the Acadian orogeny and the circulation of warm water counterclockwise currents associated with a transgression and the northward movement of western Gondwana, facilitating the influx of these warm currents (Isaacson and Sablock, 1990; Grahn et al., 2016).

It is likely that *Tropidoleptus* migrated to the Paraná Basin from the Parnaíba and/or Amazonas basins during this transgression episode, supporting the idea that elements of the boreal fauna could colonize southern environments during the Devonian. This migration of invertebrates from the Parnaíba and Amazonas basins to the Paraná Basin in the Eifelian/Givetian transition, associated with the transgression of warmer waters, also is observed in echinoderms (e.g., Scheffler et al., 2011, 2017; Scheffler, 2015).

Conclusions

In this study, we have provided confirmation of the presence of *Tropidoleptus carinatus* (Conrad, 1839) in Devonian strata of the Paraná Basin. The morphological characteristics of the specimens analyzed align with the accepted variations for this species that have been described in the literature. The migration of *T. carinatus* is thought to have occurred during a late Eifelian/early Givetian marine transgression, which facilitated the influx of warmer waters from the Amazonas and Parnaíba basins into the Paraná Basin.

The presence of *T. carinatus* can serve as an indicator of shoreface and shallower portions of the transitional offshore environments, when found in situ. In the context of the Paraná Basin, its occurrence can be used to suggest that the associated strata are not older than the late Eifelian. However, in order to provide further support to these interpretations, it is essential to

conduct a taphonomic study and utilize dating methods other than fossil composition to accurately determine the age of the outcrop where *T. carinatus* is found. Such comprehensive investigations can provide valuable insights into the paleoenvironmental context and temporal distribution of this species within the basin.

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Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

- Almeida, F.F.M., 1954, Geologia do centro-leste mato-grossense: Boletim da Divisão de Geologia e Mineralogia, v. 150, p. 1–97.
- Amos, A.J., 1972, Silurian of Argentina, in Berry, W.B.N., and Boucot, A.J., eds., Correlation of the South American Silurian Rocks: Geological Society of America Special Paper 133, p. 5–19.
- Barrett, S.F., 1986, *Paleoecology and stratigraphy of Devonian sediments in the northern Andes, Colombia: paleogeographic implications* [Ph.D. thesis]: Chicago, University of Chicago, 329 p.
- Benedetto, J.L., and Montoya, E., 2015, The Afro–South American brachiopod *Castellaroina* Boucot from the Silurian of the Argentine Precordillera: its origin and phylogenetic relationships: *Paläontologische Zeitschrift*, v. 89, p. 1–24.
- Bergamaschi, S., 1999, *Análise estratigráfica do Siluro–Devoniano (Formações Furnas e Ponta Grossa) da sub-bacia do Apucarana, bacia do Paraná, Brasil* [Ph.D. thesis]: São Paulo, Universidade de São Paulo, 167 p.
- Blieck, A., Gagnier, P.Y., Bigey, F.P., Edgecombe, G.D., Janvier, P., Loboziak, S., Racheboeuf, P.R., Sempere, T., and Steemans P., 1996, New Devonian fossil localities in Bolivia: *Journal of South American Earth Sciences*, v. 9, p. 295–308. [https://doi.org/10.1016/S0895-9811\(96\)00015-6](https://doi.org/10.1016/S0895-9811(96)00015-6).
- Borghini, L., and Fernandes, A.C.S., 2001, A new trace fossil from the Devonian of the Paraná State (Paraná Basin), Brazil: *Boletim do Museu Nacional, Nova Série, Geologia*, n. 58, p. 1–12.
- Bosetti, E.P., Grahn, Y., Horodyski, R.S., Mauller, P.M., Breuer, P., and Zabini, C., 2010, An earliest Givetian “Lilliput Effect” in the Paraná Basin, and the collapse of the Malvinokaffric shelly fauna: *Paläontologische Zeitschrift*, v. 85, p. 49–65.
- Bosetti, E.P., Grahn, Y., Horodyski, R.S., and Mauller, P.M., 2012, The first recorded decline of the Malvinokaffric Devonian fauna in the Paraná

- Basin (southern Brazil) and its cause; taphonomic and fossil evidences: *Journal of South American Earth Sciences*, v. 37, p. 228–241.
- Boucot, A.J., 1988, Devonian biogeography: an update, in McMillan, N.J., Embry, A.F., and Glass, D.J., eds., *Devonian of the World: Proceedings of the Second International Symposium on the Devonian System: Volume III: Paleontology, Paleogeology and Biostratigraphy*: Canadian Society of Petroleum Geologists, Memoir, v. 14, p. 211–227.
- Boucot, A.J., 1999, Some Wenlockian–Gedinnian, chiefly brachiopod dominated communities of North America, in Boucot, A.J., and Lawson, L.D., eds., *Paleocommunities – a case study from the Silurian and Lower Devonian*: Cambridge, Cambridge University Press, p. 549–591.
- Boucot, A.J., Brunton, C.H.C., and Theron, J.N., 1983a, Implications for the age of South African Devonian rocks in which *Tropidoleptus* (Brachiopoda) has been found: *Geological Magazine*, v. 120, p. 51–58.
- Boucot, A.J., Massa, D., and Perry, D.G., 1983b, Stratigraphy, biogeography and taxonomy of some Lower and Middle Devonian brachiopod-bearing beds of Libya and Northern Niger: *Palaeontographica Abt. A*, v. 180, p. 91–125.
- Boucot, A.J., Bahlburg, H., Bretkreuz, C., Isaacson, P.E., Niemeyer, H., and Urzúa, F., 1995, Devonian brachiopods from northern Chile: *Journal of Paleontology*, v. 69, p. 257–263.
- Boucot, A.J., Racheboeuf, P.R., and Niemeyer, H., 2008, Sierra de Almeida Zorritas Formation, northern Chile, Devonian brachiopods: more is better: *Fossils and Strata*, v. 54, p. 69–74.
- Boucot, A.J., Xu, C., Scotese, C.R., and Morley, R.J., 2013, Phanerozoic Paleoclimate: An Atlas of Lithologic Indicators of Climate, Volume 11: Society for Sedimentary Geology, Tulsa. <https://doi.org/10.2110/sepmcsp.11>.
- Carls, P., 1988, The Devonian of Celtiberia (Spain) and Devonian paleogeography of SW Europe, in McMillan, N.J., Embry, A.F., and Glass D.J., eds., *Devonian of the World: Proceedings of the Second International Symposium on the Devonian System: Volume I: Regional Syntheses*: Canadian Society of Petroleum Geologists, Memoir, v. 14, p. 421–466.
- Carls, P., and Valenzuela-Rios, J.I., 2002, Devonian–Carboniferous rocks from the Iberian Cordillera: *Cuadernos del Museo Geominero*, v. 1, p. 299–314.
- Carvalho, M.D.G.P., and Ponciano, L.C.M.O., 2015, The Devonian trilobites of Brazil: a summary: *Journal of South American Earth Sciences*, v. 64, p. 217–228.
- Carvalho, R.G., 1972, *Braquiópodes Devonianos da Bacia do Amazonas* [Ph.D. thesis]: São Paulo, Universidade de São Paulo, 140 p.
- Caster, K.E., 1939, A Devonian fauna from Colombia: *Bulletins of American Paleontology*, v. 24, n. 83, p. 1–218.
- Caster, K.E., 1947, Expedição geológica em Goiaz e Mato Grosso: *Mineração e Metalurgia*, v. 12, n. 69, p. 126–127.
- Cerri, C.A.D., 2013, *Revisão sistemática dos Brachiopoda (Calcicata), da Formação Ponta Grossa, Devoniano, Bacia do Paraná, Brasil* [M.Sc. dissertation]: São Paulo, Universidade de São Paulo, 126 p.
- Clarke, J.M., 1895, As trilobitas do grez de Ereré e Maecurú: *Revista do Museu Nacional*, v. 9, p. 1–58.
- Clarke, J.M., 1913, Fósseis Devonianos do Paraná: Rio de Janeiro, Serviço Geológico e Mineralógico do Brasil, 353p.
- Conrad, T.A., 1839, Descriptions of new species of organic remains: *New York State Geological Survey, Annual Report*, v. 3, p. 57–66.
- Cooper, G.A., and Dutro, J.T., Jr., 1982, Devonian brachiopods of New Mexico: *Bulletins of American Paleontology*, v. 82–83, n. 315, p. 1–215.
- Derby, O.A., 1895, Nota sobre a geologia e paleontologia de Matto Grosso: *Revista do Museu Nacional*, v. 9, p. 59–88.
- di Pasquo, M., Amenabar, C.R., and Noetinger, S., 2009, Middle Devonian microfloras and megaflores from western Argentina and southern Bolivia: their importance in the palaeobiogeographical and palaeoclimatical evolution of western Gondwana, in Königshof, P., ed., *Devonian Change: Case Studies in Palaeogeography and Palaeoecology*: The Geological Society, London, Special Publications 314, p. 191–211.
- Díaz-Martínez, E., Isaacson, P.E., and Sablock, P.E., 1993, Late Paleozoic latitudinal shift of Gondwana: stratigraphic/sedimentologic and biogeographic evidence from Bolivia: *Travaux et Documents des Laboratoires de Géologie de Lyon*, v. 125, n. 1, p. 119–138.
- Dowling, E.M., and Ebach, M.C., 2018, An interim global bioregionalisation of Devonian areas: *Paleobiodiversity and Paleoenvironments*, v. 98, p. 527–547.
- Dowling, E.M., Ebach, M.C., and Mavrodiev, E.V., 2022, Validating marine Devonian biogeography: a study in bioregionalization: *Palaeontology*, v. 65, e12578, <https://doi.org/10.1111/pala.12578>.
- Drevermann, F., 1902, Die Fauna der Unter-koblenzschichten von Oberstadt-feld bei Daun in der Eifel: *Palaeontographica*, v. 49, p. 75–119.
- Ellison, R.L., 1965, Stratigraphy and paleontology of the Mahantango Formation in south central Pennsylvania: *Pennsylvania Geological Survey Bulletin* G48, p. 1–298.
- Fonseca, V.M.M., 2015, Considerações paleobiogeográficas baseadas em braquiópodes Devonianos (Delthyridoidea, Strophodontoidea e Chonetoidea) das bacias do Amazonas e Parnaíba: *Boletim do Museu Paraense Emílio Goeldi-Ciências Naturais*, v. 10, p. 91–101.
- Fonseca, V.M.M., and Melo, J.H.G., 1987, Ocorrência de *Tropidoleptus carinatus* (Conrad) (Brachiopoda, Orthida) na Formação Pimenteira e sua importância paleobiogeográfica: 10º Congresso Brasileiro de Paleontologia, Rio de Janeiro, Brazil, 1987, *Anais. Sociedade Brasileira de Paleontologia*, p. 505–537.
- Frech F., 1897, *Lethaea Geognostica. Lethaea Palaeozoica*, 2. Band, 1, Lieferung: Stuttgart, E., Schweizerbart'sche Verlagshandlung, 256 p.
- Freulon, J.M., 1964, Etude Géologique des Séries Primaires du Sahara Central (Tassili n' Ajjer et Fezzan), *Série Géologie 3*: Paris, Publications du Centre de Recherche sur les Zones Arides, Centre National de la Recherche Scientifique, 198 p.
- Fuchs, G., 1982, Upper Siegenian and lower Emsian in the Eifel Hills: *Courier Forschungsinstitut Senckenberg*, v. 55, p. 229–255.
- Gama Junior, J.M., 2008, *Braquiópodes da Formação Pimenteira (Devoniano Médio/Superior), na região sudoeste da Bacia do Parnaíba, Município de Palmas, Estado do Tocantins, Brasil* [M.Sc. dissertation]: Brasília, Universidade de Brasília, 74 p.
- Golonka, J., Ross, M.I., and Scotese C.R., 1994, Phanerozoic paleogeographic and paleoclimatic modeling maps, in Embry, A.F., Beauchamp, B., Glass, D.J., eds., *Pangea: Global Environments and Resources*: Canadian Society of Petroleum Geologists, Memoir 17, p. 1–47.
- Grahn, Y., 1992, Revision of Silurian and Devonian strata of Brazil: *Palynology*, v. 16, p. 35–61.
- Grahn, Y., Mauller, P.M., Pereira, E., and Loboziak S. 2010, Palynostratigraphy of the Chapada Group and its significance in the Devonian stratigraphy of the Paraná Basin, south Brazil: *Journal of South American Earth Sciences*, v. 29, p. 354–370.
- Grahn, Y., Mauller, P.M., Bergamaschi, S., and Bosetti, E.P. 2013, Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Subbasin (Paraná Basin, south Brazil): additional data and correlation: *Review of Palaeobotany and Palynology*, v. 198, p. 27–44.
- Grahn, Y., Horodyski, R.S., Mauller, P.M., Bosetti, E.P., Ghilardi, R.P., and Carbonaro, F.A., 2016, A marine connection between Parnaíba and Paraná basins during the Eifelian/Givetian transition: review and new data: *Revista Brasileira de Paleontologia*, v. 19, p. 357–366.
- Habicht, J.K.A., 1979, Paleoclimate, paleomagnetism, and continental drift: American Association of Petroleum Geologists, *Studies in Geology*, v. 9, p. 1–29.
- Halamski, A.T., and Balinski, A., 2013, Middle Devonian brachiopods from the southern Maider (eastern Anti-Atlas, Morocco): *Annales Societatis Geologorum Poloniae*, v. 83, p. 243–307.
- Hall, J., 1857, Descriptions of Paleozoic fossils, chiefly from those constituting the third volume of the Paleontology of New York: 10th Annual Report of the Regents of the University, State Cabinet of Natural History, p. 41–186.
- Hall, J., 1860, Descriptions of new species of fossils from the Hamilton Group of western New York, with notices of others from the same horizon in Iowa and Indiana: *New York State Cabinet, 13th Annual Report*, p. 76–94.
- Hall, J., and Clarke, J.M., 1894, An introduction to the study of the genera of Palaeozoic Brachiopoda, v. 8, pt. 2: Albany, Charles van Benthuysen & Sons, 394 p.
- Haq, B.U., and Schutter, S.R., 2008, A chronology of Paleozoic sea-level changes: *Science*, v. 322, p. 64–68.
- Harper, C.W., and Boucot, A.J., 1978, The Stropheodontacea, part I: Leptostrophidae, Eostropheodontidae and Strophonellidae: *Palaeontographica*, A, v. 161, p. 1–118.
- Harper, D.A.T., 2007, Uncertain, in Selden, P.A., ed., *Treatise on Invertebrate Paleontology, Part H, Brachiopoda Revised, Volume 6, Supplement*: Boulder, Colorado and Lawrence, Kansas, The Geological Society of America and The University of Kansas, p. 2820–2821.
- Harper, D.A.T., Alvarez, F., Boucot, A.J., Gourvenec, R., Williams, A., and Wright, A.D., 2003, The genealogy of the aberrant Devonian brachiopod *Tropidoleptus*: resolving morphological and ultrastructural data: *Palaeontological Association Newsletter*, v. 54, p. 133.
- Harper, D.A.T., Alvarez, F., Boucot, A.J., Williams, A., Wright, A.D., and Schemm-Gregory, M., 2010, Tripidoleptida (Brachiopoda): Devonian hopeful monsters or misplaced orphans: *Special Papers in Paleontology*, v. 84, p. 119–136.
- Havlicek, V., and Rohlich, P., 1987, Devonian and Carboniferous brachiopods from the northern flank of the Murzug Basin (Libya): *Sbornik Geologických Ved: Paleontologie*, v. 28, p. 117–177.
- Isaacson, P.E. 1977, Devonian Stratigraphy and brachiopod paleontology of Bolivia, part B Spiriferida and Terebratulida: *Palaeontographica Abt. A*, v. 156, p. 68–217.
- Isaacson, P.E., 1993, Devonian Brachiopoda of Bolivia, in Suárez-Soruco, R., ed., *Fósiles y Facies de Bolivia—Invertebrados y Paleobotánica*: Santa Cruz de la Sierra, Revista Técnica de YPF, vol. 2, n. 13–14 (1–4), p. 5–33.

- Isaacson, P.E., and Chlupac, I., 1984. Significance of a *Tropidoleptus* assemblage from the Devonian of the Moravo–Silesian region, Czechoslovakia: *Casopis pro Mineralogii a Geologii*, v. 29, 141–153.
- Isaacson, P.E., and Perry, D.G., 1977. Biogeography and morphological conservatism of *Tropidoleptus* (Brachiopoda, Orthida) during the Devonian: *Journal of Paleontology*, p. 1108–1122.
- Isaacson, P.E., and Sablock, P.E., 1988. Devonian System in Bolivia, Peru and Northern Chile, in McMillan, N.J., Embry, A.F., and Glass, D.J., eds., *Devonian of the World: Second International Symposium on the Devonian System*: Calgary, Proceedings, p. 719–728.
- Isaacson, P.E., and Sablock, P.E., 1990. Devonian paleogeography and palaeobiogeography of the Central Andes: *Memoir Geological Society of London*, v. 12, p. 431–435.
- Isaacson, P.E., Fisher, L.L., and Davidson, J., 1985. Devonian and Carboniferous stratigraphy of Sierra de Almeida, northern Chile, preliminary results: *Revista Geológica de Chile*, v. 25–26, p. 113–121.
- Jaanusso, V., 1971. Evolution of the brachiopod hinge, in Dutro, J.T., Jr., ed., *Paleozoic perspectives: a paleontological tribute to G. Arthur Cooper*: Washington D.C., Smithsonian Contributions to Paleobiology, v. 3, p. 33–46.
- Jansen, U., 2001. Morphologie, Taxonomie und Phylogenie unter-devonischer Brachiopoden aus der Dra-Ebene (Marokko, Pra-Sahara) und dem Rheinischen Schiefergebirge (Deutschland): *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, v. 554, p. 1–389.
- Katzer, F., 1933. Geologia do estado do Pará, (Brasil): *Boletim do Museu Paraense Emílio Goeldi de História Natural e Etnografia*, v. 9, p. 1–219 (Translation by Friar Hugo Mense) (Reviews and notes by engineers Avelino Inacio de Oliveira and Pedro de Moura, the first, chief assistant at the Instituto Geologico e Mineralogico do Brasil and the second, technical assistant at the same Institute), <http://repositorio.museu-goeldi.br/handle/mgoeldi/1171>.
- Kayser, E., 1897. Beiträge zur Kenntnis einiger paläozoischer Faunen Süd-Amerikas: *Zeitschrift der Deutschen Geologischen Gesellschaft*, v. 49, p. 274–317.
- Kesling, R.V., and Chilman, R.B., 1975. Strata and megafossils of the Middle Devonian Silica Formation: *University of Michigan Papers on Paleontology*, v. 8, p. 1–408.
- Kunzler, J., 2012. *Resgate histórico e taxonomia dos braquiópodes Devonianos do estado de Mato Grosso depositados no Museu Nacional/UFRJ* [M.Sc. dissertation]: Rio de Janeiro, Universidade Federal do Rio de Janeiro, 118 p.
- Lacerda Filho, J.V.d., Abreu Filho, W., Valente, C.R., Oliveira, C.C.d., and Albuquerque, M.C.d., 2004. Geologia e Recursos Minerais do Estado de Mato Grosso: CPRM; Secretaria de Estado de Indústria, Comércio, Minas e Energia do Estado de Mato Grosso (SICME-MT), 252 p., <https://rigeo.sgb.gov.br/handle/doc/4871>.
- Lange, F.W., and Petri, S., 1967. The Devonian of the Paraná Basin: *Boletim Paranaense de Geociências*, v. 21, n. 22, p. 5–55.
- Laubacher, G., Boucot, A.J., and Gray, J., 1982. Additions to Silurian stratigraphy, lithofacies, biogeography and paleontology of Bolivia and Southern Peru: *Journal of Paleontology*, v. 56, p. 1138–1170.
- LeMaître, D., 1952. Contribution à l'Etude des Faunes Paléozoïques de l'Adrar Mauritanien (Sahara Occidental): *Bulletin de la Direction des Mines 15, Gouvernement Général l'Afrique Occidentale Française*, 652 p.
- Li, R.Y., 2010. Middle Devonian brachiopods from Arctic Canada and some preliminary results of North American biogeography based on quantitative assessment: *Journal of Earth Sciences*, v. 21, p. 36–39.
- McGhee, G.R., and Sutton, R.G., 1985. Late Devonian marine ecosystems of the lower West Falls Group in New York, in Woodrow, D.L., and Sevon, W.D., eds., *The Catskill Delta*: Geological Society of America Special Paper, v. 201, p. 199–209.
- Melo, J.H.G., 1988. The Malvinokaffric Realm in the Devonian of Brazil, in McMillan, N.J., Embry, A.F., and Glass, D.J., eds., *Devonian of the World: Second International Symposium on the Devonian System*: Proceedings: Calgary, Canada, Canadian Society of Petroleum Geologists, p. 669–703.
- Mergl, M., and Massa, D., 1992. Devonian and Lower Carboniferous brachiopods and bivalves from western Libya: *Biostratigraphie du Paleozoique*, v. 12, p. 1–115.
- Mergl, M., and Massa, D., 2004. Devonian brachiopods of the Tamesna Basin (Central Sahara, Algeria and North Niger). Part 1: *Acta Musei Nationalis Pragae*, ser. B, *Natural History*, v. 60, p. 61–112.
- Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., and França, A.B., 2007. Bacia do Paraná: *Boletim de Geociências da Petrobras*, v. 15, p. 265–287.
- Morales, P.A., 1965. A contribution to the knowledge of the Devonian faunas of Colombia: *Boletim de Geologia*, v. 19, p. 51–111.
- Newell, N.D., 1949. Geology of the Lake Titicaca region, Peru and Bolivia: Geological Society of America, *Memoir*, v. 36, p. 1–124.
- Penn-Clarke, C.R., 2019. The Malvinokaffric realm in the Early–Middle Devonian of South Africa: *Journal of African Earth Sciences*, v. 158, 103549, <https://doi.org/10.1016/j.jafrearsci.2019.103549>.
- Penn-Clarke, C.R., and Harper, D.A.T., 2021. Early–Middle Devonian brachiopod provincialism and bioregionalization at high latitude: a case study from southwestern Gondwana: *GSA Bulletin*, v. 133, p. 819–836.
- Penn-Clarke, C.R., Rubidge, B.S., and Jinnah Z.A., 2018. Two hundred years of palaeontological discovery: review of research on the Early to Middle Devonian Bokkeveld Group (Cape Supergroup) of South Africa: *Journal of African Earth Sciences*, v. 137, p. 157–178.
- Plusquellec, Y., Boumendjel, K., Morzadec, P., and Paris, F., 1997. Les faunes Dévoniennes d'Ougarta dans la paléogéographie des régions Maghrébo–Européennes: *Annales de Société Géologique du Nord*, v. 5, p. 123–128.
- Quadros, R., and Melo, J.H.G., 1989. Occurrence of *Tropidoleptus carinatus* (Conrad) (Brachiopoda, Orthida) in the northwestern Paraná Basin, Brazil: 11° Congresso Brasileiro de Paleontologia. Curitiba, Brazil, *Resumo de Comunicações*, p. 21–22 (abstract).
- Queiroz, J.P., Gama Júnior, J.M., and Pires, E.F., 2013. Ocorrência de braquiópodes fósseis no entorno do Rio Balsas, Município de Santa Teresa, Estado do Tocantins, em estratos da Formação Pimenteira, Devoniano da bacia do Parnaíba: *Brazilian Geographical Journal*, v. 1, p. 191–212.
- Racheboeuf, P.R., Le Hérisse, A., Paris, F., Babin, C., Guillocheau, F., and Truyols-Massoni M., 1993. El Devónico de Bolivia: bio y cronoestratigrafía: *Bulletin de l'Institut Français d'études Andines*, v. 22, p. 645–655.
- Racheboeuf, P.R., Gourvenec, R., Deynoux, M., and Brice, D., 2004. The Devonian of the Hodh area (Islamic Republic of Mauritania): paleontology and stratigraphy: *Journal of Paleontology*, v. 78, p. 98–110.
- Rathbun, R., 1874. On the Devonian Brachiopoda of Ererê, Province of Para, Brazil: *Buffalo Society of Natural Sciences, Bulletin*, v. 1, p. 236–261.
- Rathbun, R., 1878. The Devonian Brachiopoda of the Province of Para, Brazil: *Boston Society of Natural History, Proceedings*, v. 20, p. 14–39.
- Raymond, A., 1987. Paleogeographic distribution of Early Devonian plant traits: *Palaïos*, v. 2, p. 113–132.
- Rezende, J.M.P., and Isaacson, P.E., 2021. *Schellwienella clarkei* (Orthotetida, Brachiopoda): a new species from the Devonian of the Paraná Basin, Brazil: *Journal of Paleontology*, v. 95, p. 733–747.
- Rezende, J.M.P., Figueroa, R.T., Ponciano, L.C.M.O., and Gallo, V., 2021. A new Late Devonian fish fauna from Northeast Brazil: *Historical Biology*, v. 33, p. 3444–3453, doi.org/10.1080/08912963.2020.1868452.
- Ribeiro, V.R., 2020. *Rotas Migratórias de Braquiópodes (Família Leptocoelidae & Família Tropidoleptidae) das bordas Devonianas das bacias do Paraná e Parnaíba* [M.Sc. dissertation]: Assis, Brasil, Universidade Estadual Paulista “Júlio de Mesquita Filho”, 92 p.
- Ribeiro, V.R., Ghilardi, R.P., and Caminha, S.A.F.S., 2019. Fácies deltaicas Devonianas de Jaciara-Mato Grosso: o indício de uma nova proposta estratigráfica para a sub-bacia de Alto Garças: *Revista de Geociências*, v. 38, p. 687–698.
- Robardet, M., 2003. The Armorica ‘microplate’: fact or fiction? Critical review of the concept and contradictory palaeobiogeographical data: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 195, p. 125–148.
- Roberts, J., 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, Northwestern Australia: Department of National Development, Bureau of Mineral Resources, Geology and Geophysics, *Bulletin No. 122*, v. 1, p. 1–319.
- Sanchez, T.M., and Benedetto, J.L., 1983. Paleoeología, comunidades bentónicas y sucesión paleoambiental en el Grupo Rio Cachiri, Devonico, Sierra de Perija, Venezuela: *Ameghiniana*, v. 20, p. 163–198.
- Santos, C., Rezende, J., and Ponciano, L., 2021. *Catálogo de Macrofósseis da Formação Pimenteira*: Rio de Janeiro, Ed. da Autora, 285 p.
- Scheffler, S.M., 2015. Stalked echinoderms of the Brazilian Devonian and their palaeobiogeographical affinities: *Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais*, v. 10, p. 63–81.
- Scheffler, S.M., Dias-da-Silva, S., Gama, J.M., Jr., Fonseca, V.M.M., and Fernandes, A.C.S., 2011. Middle Devonian crinoids from the Parnaíba Basin (Pimenteira Formation, Tocantins State, Brazil): *Journal of Paleontology*, v. 85, p. 1188–1198.
- Scheffler, S.M., Fernandes, A.C.S., and Fonseca, V.M.M., 2013. Alguns crinoides da Formação Ponta Grossa e suas afinidades paleobiogeográficas (Devoniano Inferior, Bacia do Paraná, Brasil): *Terr@Plural, Ponta Grossa*, v. 7, Número Especial, p. 85–115.
- Scheffler, S.M., Francisco, A.P.S., and Bosetti, E.P., 2017. About echinoderms of the Devonian of the Paraná Basin: faunal turnovers and implications for biostratigraphic utility: *Anuário do Instituto de Geociências (UFRJ)*, v. 40, p. 102–116.
- Scheffler, S.M., Silva, R.C., and Sedorko, D., 2020. O Devoniano do estado de Mato Grosso do Sul, Brasil: nova área de distribuição e presença de típica fauna Malvinocáfrica: *Estudos Geológicos*, v. 30, n. 2, p. 38–76.
- Scheffler, S.M., Fernandes, A.C.S., Silva, M.B., Videira-Santos, R., and Sousa, L.B.G., 2021. Repatriamento, incorporação e destruição: o destino da Coleção Caster no Museu Nacional/UFRJ: *Terr@Plural, Ponta Grossa*, v. 15, p. 1–21, e2117747, <https://doi.org/10.5212/TerraPlural.v.15.2117747.026>.

- Schemm-Gregory, M., and Henriques, M.H., 2013, A Coleção Krantz: Os Brachiópodes da Coleção Krantz do Museu da Ciência da Universidade de Coimbra: Lisboa, Imprensa da Universidade de Coimbra, 262 p.
- Schuchert, C., 1896, Class 2. Brachiopoda, in Zittel K.A. von, ed., Text-book of Palaeontology (Eastman, C.R., Ed. and Trans.): Londres, MacMillan, Co., Ltd., first ed., v. 1, p. 291–343.
- Schuchert, C., 1929, Classification of brachiopod genera, fossil and recent, in Pompeckj J.F., ed., Fossilium Catalogus 1: Animalia, pars 42, Brachiopoda: Berlin, W. Junk, p. 1–140.
- Schuchert, C., and Cooper, G.A., 1932, Brachiopod genera of the suborders Orthoidea and Pentamerioidea: Memoirs of the Peabody Museum of Natural History, v. 4, p. 1–270.
- Scotese, C.R., Boucot, A.J., and McKerrow, W.S., 1999, Gondwanan palaeogeography and palaeoclimatology: Journal of African Earth Sciences, v. 28, p. 99–114.
- Sedorko, D., Netto, R.G., and Savrda, C.E., 2018, Ichnology applied to sequence stratigraphic analysis of Siluro–Devonian mud-dominated shelf deposits, Paraná Basin, Brazil: Journal of South American Earth Sciences, v. 83, p. 81–95.
- Sedorko, D., Netto, R.G., Scheffler, S.M., Horodyski, R.S., Bosetti, E.P., et al., 2021, Paleoeologic trends of Devonian Malvinokaffric fauna from the Paraná Basin as evidenced by trace fossils: Journal of South American Earth Sciences, v. 109, 103200, <https://doi.org/10.1016/j.jsames.2021.103200>.
- Sougy, J., 1964, Les formations Paléozoïques du Zemmour Noir (Mauritanie Septentrionale): Université de Dakar, Annales de la Faculté des Sciences, Série Sciences de la Terre, v. 15, p. 1–695.
- Stainbrook, M.A., 1938, *Atrypa* and *Stropheodonta* from the Cedar Valley Beds of Iowa: Journal of Paleontology, v. 12, p. 229–256.
- Suárez-Riglos, M., 1967, *Some Devonian fossils from the State of Piauí, Brazil* [M.Sc. dissertation]: Cincinnati, Ohio, University of Cincinnati, 121 p.
- Thomas, I., 1905, Neue Beiträge zur Kenntnis der Devonischen fauna Argentinens: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 57, p. 233–290.
- Tourneur, F., Plusquellec, Y., Fernández-Martínez, E.M., and Martínez, E.D., 2000, Revision of *Parastriatopora gigantea* (Knod 1908) (Anthozoa, Tabulata) from the Devonian of Bolivia: Geobios, v. 33, p. 709–724.
- Troth, I., Marshall, J.E.A., Racey, A., and Becker, R.T., 2011, Devonian sea-level change in Bolivia: a high palaeolatitude biostratigraphical calibration of the global sea-level curve: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 304, p. 3–20.
- Ubelacker, C., Jansen, U., and De Baets, K., 2016, First record of the Early Devonian ammonoid *Teicherticeras* from the Eifel (Germany): biogeographic and biostratigraphic importance: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 282, p. 201–208.
- Vaida, M., Seghedi, A., and Verniers, J., 2005, Northern Gondwanan affinity of the East Moesian Terrane based on chitinozoans: Tectonophysics, v. 410, p. 379–387.
- Videira-Santos, R., Scheffler, S.M., and Fernandes, A.C.S., 2022, New occurrences of Malvinokaffric Chonetoida (Brachiopoda) in the Paraná Basin, Devonian, Brazil: Revista Brasileira de Paleontologia, v. 25, p. 3–23.
- Williams, A., and Wright, A.D., 1961, The origin of the loop in articulate brachiopods: Palaeontology, v. 4, p. 149–176.
- Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E., and Popov, L., 1996, A supra ordinal classification of the Brachiopoda: Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, v. 351, p. 1171–1193.
- Williams, H.S., 1913, Recurrent *Tropidoleptus* zones of the Upper Devonian in New York: United States Geological Survey Professional Paper, v. 79, p. 1–108.
- Wright, A.D., 1965, Superfamily Enteletacea, in Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Volume 1. New York and Lawrence, Kansas, Geological Society of America and University of Kansas Press, 521 p.

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