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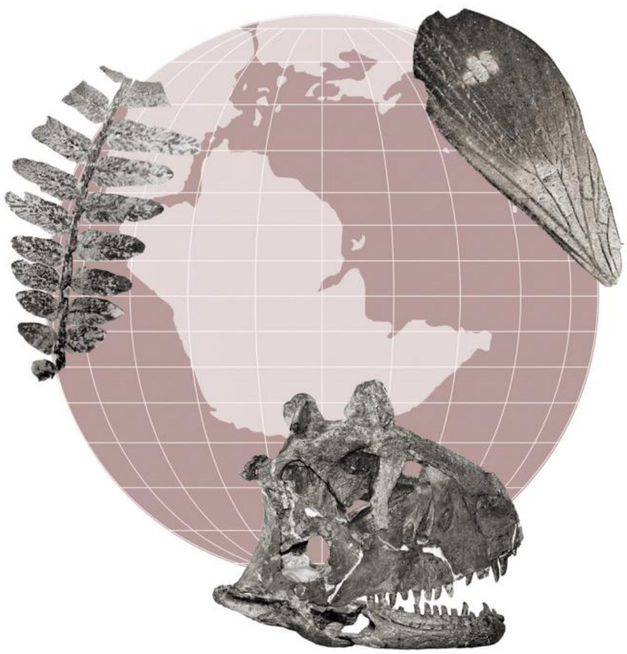

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Brachiopoda (Strophomenata and Rhynchonellata) from the Devonian of the Paraná Basin, Brazil

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Running Header: Devonian Brachiopoda from the Paraná Basin

Short Description: Taxonomic review of Devonian brachiopods from the Paraná Basin, with emphasis on *Chonostrophia raquelae* nov. sp.

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Abstract. Rhynchonelliformea brachiopods from the Devonian of the Paraná Basin have been known and studied since the 19th century. Since then, several brachiopod taxa have been proposed for the Devonian of the Paraná Basin, but they have never been properly revised. This study focused on reviewing the supposed occurrences of "*Coelospira*? *colona*", "*Meristella septata*," and "*Chonostrophia andina*." From this, the following conclusions were reached: *Chonostrophia andina* is synonymous with the new species recognized here and named *Chonostrophia raquelae* sp. nov.; the presence of *Coelospira* in the Devonian of the Paraná Basin was not confirmed; the specimens have been called "*C*? *colona*" in the literature are actually *Australocoelia*; the genus *Meristelloides* and its type species were revised, and "*Meristella septata*" is synonymous with *Meristelloides riskowskii*. Finally, it was recognized that the migration between the Emsian and Eifelian of *Chonostrophia* to Bolivia may be related to the Upper Zlichov-Daleje or Choteč events. The migration from the Eifelian of *Australocoelia* to the Parnaíba Basin (Brazil) may be related to the Lower Kačák event. All species discussed here preferred to inhabit the transitional offshore environment.

Keywords: Brachiopoda, *Chonostrophia*, *Australocoelia*, *Meristelloides*, Devonian, Gondwana

Resumen. *Sobre los braquiópodos (Strophomenata y Rhynchonellata) del Devónico de la Cuenca del Paraná, Brasil.* Los braquiópodos Rhynchonelliformea del Devónico de la Cuenca del Paraná se conocen y estudian desde el siglo XIX. Desde entonces, se han propuesto varios taxones de braquiópodos para el Devónico de la Cuenca del Paraná, pero nunca se han revisado adecuadamente. Este estudio se centró en revisar las supuestas apariciones de «*Coelospira*? *colona*», «*Meristella septata*» y «*Chonostrophia andina*». A partir de ello, se llegó a las siguientes conclusiones: *Chonostrophia andina* es sinónimo de la nueva especie reconocida aquí y denominada *Chonostrophia raquelae* sp. nov.; no se confirmó la presencia de *Coelospira* en el Devónico de la Cuenca del Paraná; las muestras denominadas «*C*? *colona*» en la literatura son en realidad *Australocoelia*; y se confirmó la validez del género *Meristelloides*, siendo «*Meristella septata*» sinónimo de *Meristelloides riskowskii*. Por último, se reconoció que la migración entre el Emsiense y el Eifeliense de *Chonostrophia* a Bolivia puede estar relacionada con los eventos del Zlichov-Daleje superior o Choteč. La migración desde el Eifeliense de *Australocoelia* a la Cuenca del Parnaíba (Brasil) puede estar relacionada con el evento del Kačák inferior. Todos las espécies aquí discutidas preferían habitar el offshore de transición.

Palabras clave. Strophomenata, Rhynchonellata, Gondwana

Introduction

Brachiopods are a phylum of solitary, sessile, and benthic marine animals that emerged in the Cambrian and still exist today, although they reached the peak of their diversification and abundance during the Paleozoic (Curry and Brunton, 2007; Fonseca, 2011). In turn, Rhynchonelliformea are a brachiopod subphylum corresponding more or less to the traditionally recognized articulate brachiopods and have been reported from the Devonian rocks of the Paraná Basin since the second half of the 19th century (Derby, 1878; 1895), having been more widely studied since the work of Clarke (1913).

Clarke (1913) proposed the occurrence of "*Coelospira*? *colona*" and "*Meristella septata*" in the Devonian of the Paraná Basin, but these species were never properly reviewed, although more recent studies cite them (e.g., Bosseti et al., 2012; Sedorko et al., 2021). Isaacson (1977) recognized the species *Meristelloides riskowskii* Ulrich, 1892 in the Devonian of Bolivia and considered "*Meristella septata*" to be its junior synonym, but without analyzing any Brazilian specimens.

In turn, Quadros (1987), in her doctoral thesis, proposed the occurrence of "*Chonostrophia andina*" in the Devonian of the northwestern edge of the Paraná Basin, with the holotype of *Chonostrophia reversa* var. *andina* Levy and Nullo, 1972. However, this proposal lacks a formal nomenclatural act, and the species "*Chonostrophia reversa* var. *andina*" is currently recognized as a synonym of ?*Sanjuanetes andina* (see Racheboeuf & Herrera, 1994).

Therefore, given the taxonomic problems outlined here, the objective of this article was to review the presumed occurrences of "*Coelospir*a", "*Meristella*," and "*Chonostrophia*" in the Devonian of the Paraná Basin. Subsequently, after the taxonomic review, paleobiogeographic and paleoenvironmental considerations were made.

Institutional abbreviations. MCT/CPRM/SGB (DGM-I), Museu de Ciências da Terra/Serviço Geológico do Brasil, Rio de Janeiro, Brazil; UFMT (MP, FUFMT MP), Universidade Federal de Mato Grosso, Cuiabá, Brazil; UFPR (NR), Departamento de Geologia/Universidade Federal do Paraná, Curitiba, Brazil; MCN/UFPR (MCN), Museu de Ciências Naturais/Universidade Federal do Paraná, Curitiba, Brazil; UEPG (MPI), Universidade Estadual de Ponta Grossa, Ponta Grossa, Brazil; USP (GP 1E), Universidade de São Paulo, São Paulo, Brazil; and NYSM (NYSM I), New York State Museum, Albany, USA.

Geological Setting

The Paraná Basin is one of the largest intracratonic basins in South America, extending over an area of ~1,500,000 km², covering parts of Argentina, Paraguay, Uruguay, and south-central Brazil (Melo, 1988; Grahn, 1992; Milani et al., 2007). The Devonian of the Paraná Basin, in Brazil, crops out in the states of Paraná (Figure 1), Mato Grosso (Figure 2), Mato Grosso do Sul, and Goiás (Melo, 1988). Although traditionally divided into two sub-basins: Alto Garças, to the north, and Apucarana to the south (Nothfleet et al., 1969; Ramos, 1970), more recent studies have indicated that this individualization did not occur completely until at least the late Emsian (Sedorko et al., 2018a; Scheffler et al., 2020).

According to Grahn et al. (2013), the Devonian of the Paraná Basin is divided into the Furnas (Lochkovian), Ponta Grossa (late Pragian–early Emsian), and São Domingos (late Emsian–Frasnian) formations (Figure 3). The Devonian fauna of the Paraná Basin is part of the Malvinoxhosan Realm, formerly Malvinokaffric (see Penn-Clarke & Harper, 2021, 2023).

The Ponta Grossa Formation is notable for being quite fossiliferous and with records of the typical Malvinoxhosan fauna (e.g., Clarke, 1913; Petri, 1948; Caster, 1954; Lange, 1967; Melo, 1985, 1988; Bosetti et al., 2012). It is stratigraphically located between the Furnas and the São Domingos formations (figure 3), and it is interpreted as being of marine origin, covering environments in the shoreface and in the offshore (Sedorko et al., 2018b).

According to Grahn et al. (2013), the lower part of the Ponta Grossa Formation consists of sandstones interspersed with siltstones. This basal part is followed by sandy shales with calcareous nodules or sandy clay. Finally, the uppermost portion consists of a hard shale, rich in pyrite and organic matter, being quite dark. Grahn et al. (2010) suggested a late Pragian to early Emsian age for this succession.

The outcrops of the Ponta Grossa Formation studied here are in the Brazilian states of Paraná (outcrops Rivadávia, Curva II, Ponta Grossa of Clarke, 1913; Bosque Mistral and Jaguariaíva) and Mato Grosso (outcrop Estrada) (see Sedorko et al., 2021, regarding the age of the rocks in this outcrop).

In the São Domingos Formation, the impoverished Malvinoxhosan fauna occurs in its basal part, and after the Givetian, the typical elements of the Malvinoxhosan fauna disappear or are rare (Bosetti et al., 2010, 2012).

This formation is stratigraphically located between the Ponta Grossa Formation and the Itararé Group (Carboniferous). The São Domingos Formation is marine in origin and comprises foreshore to offshore environments (Sedorko et al., 2018b), consisting of poorly sorted conglomeratic sandstones, followed by rarely bituminous shales, and micaceous siltstones that are rich in plant fragments. According to Melo and Loboziak (2003) and Grahn et al. (2013), this succession is late Emsian–Frasnian in age. The outcrops of the São Domingos Formation studied here are in the Brazilian state of

Paraná (outcrops Metalúrgica Águia and Boa Vista) (see Sedorko et al., 2021 for age of the outcrops).

(FIGURE 1 HERE)

(FIGURE 2 HERE)

(FIGURE 3 HERE)

Material and methods

The specimens studied here are held in the collections of the Museu de Ciências da Terra/Serviço Geológico do Brasil (DGM-I), Universidade Federal de Mato Grosso (MP, FUFMT MP), Departamento de Geologia/Universidade Federal do Paraná (NR), Museu de Ciências Naturais/Universidade Federal do Paraná (MCN), Universidade Estadual de Ponta Grossa (MPI), Universidade de São Paulo (GP 1E), and New York State Museum (NYSM I).

For taxonomic identification, we consulted the Treatise on Invertebrate Paleontology (Williams et al., 2000, 2002) and papers on Strophomenata and Rhynchonellata taxonomy, mainly from the Malvinoxhosan Realm and adjacency.

Systematic Paleontology

Phylum Brachiopoda Duméril, 1805

Subphylum Rhynchonelliformea Williams et al., 1996

Class Strophomenata Williams et al., 1996

Order Productida Sarytcheva and Sokolskaya, 1959

Suborder Chonetidina Muir-Wood, 1955

Superfamily Chonetoidea Bronn, 1862

Family Chonostrophiidae Muir-Wood, 1962

Genus ***Chonostrophia*** Hall and Clarke, 1892

Type species. *Chonetes reversa* Whitfield, 1882.

Chonostrophia raquelae nov. sp.

Figure 4(A-F)

1987 "*Chonostrophia andina*" Quadros; Quadros, p. 41, est. 5, fig. 1-23.

1994 [*non*] ?*Sanjuanetes andina* (Levy and Nullo, 1972); Racheboeuf and Herrera, p. 548, fig. 1a-d.

2022 *Chonostrophia*? aff. *truyolsae* Racheboeuf, 1992; Videira-Santos et al., p. 13.

Etymology. In honor of the Brazilian paleontologist Raquel Quadros (? – 2024), who contributed greatly to the development of Paleontology in the Brazilian state of Mato Grosso.

Holotype. MP 63e (ventral valve, figure 4A).

Paratypes. MP 63a-d, f-k, MP 67b (figure 4F), MP 109a, b, c, d(figure 4B), e, f-f, MP 110a-b, MP 111, MP 112a-h, MP 113, MP 114 (figure 4D), MP 115a (figure 4E), be, c,d,e,fe, MP 116, MP 117, MP 118a,b (figure 4C), d, MP 119a-i, MP 120, MP 121a-b, MP 122 and MP 123a-b.

Material. MP 63 (external ventral mold),b (external dorsal mold),c (external dorsal mold),d (external ventral mold),e (internal ventral mold),f (undefined),g (external ventral mold),h, i (internal ventral mold),j (external ventral mold),k (internal ventral mold), MP 67b (internal ventral mold), MP 109a (undefined),b (external ventral mold),c (external ventral mold),d (external ventral mold),e (internal ventral mold),f (external ventral mold), MP 110a (external ventral mold),b (internal ventral mold), MP 111 (internal dorsal mold), MP 112a (internal ventral mold),b (internal dorsal mold?),c (external ventral mold), d (internal ventral mold), e (internal ventral mold), f (internal ventral mold), g (external ventral mold),h (undefined), MP 113, (external ventral mold) MP114 (internal dorsal mold), MP 115 (internal ventral mold), b (external ventral mold), c (internal dorsal mold), d (external dorsal mold), e (external dorsal mold), MP 116 (undefined), MP 117 (internal dorsal mold), MP 118a (external ventral mold),b (external ventral mold), d (external ventral mold), MP 119a (external ventral mold),b (external ventral mold), c (internal ventral mold), d (internal ventral mold), e (external ventral mold), f (external dorsal mold?), g (external dorsal mold), h (internal ventral mold), i (internal ventral mold), MP 120 (external ventral mold), MP 121a (external ventral mold), b (external dorsal mold), MP 122 a(internal ventral mold) and MP 123a (external ventral mold),b (external ventral mold).

Geographic occurrence. Estrada, Chapada dos Guimarães, Mato Grosso, Brazil.

Stratigraphic occurrence. Ponta Grossa Formation (late Pragian– early Emsian).

Diagnosis. *Chonostrophia* species with a smaller size (no larger than 4 mm) larger developed muscle field both in relation to other known species of *Chonostrophia,* spines of the type oblique orthomorphic, parvicostellate ornamentation, maximum of 32 ribs; and in the ventral valve interior there is a sharp septum dividing the muscle field

Occurrences of the genus *Chonostrophia*. Canada, Forillon, Shiphead and York River formations – Pragian to Emsian (Racheboeuf & Lesperance, 1995); United States of America, Onondaga Limestone – Emsian to Eifelian (Racheboeuf & Lesperance, 1995); Argentina, Talacasto Formation – Pragian (Herrera, 1995); Colombia, Floresta Formation – Frasnian (Caster, 1939); Bolivia, Icla and Humampampa formations – Eifelian (Racheboeuf, 1992; Racheboeuf et al., 2012), Brazil, Ponta Grossa Formation –

late Pragian to early Emsian (Videira-Santos et al., 2022; this paper) and Venezuela – unknown formation – Middle Devonian (Benedetto, 1985).

Description. Small shell, 43 specimens mensurated, varying in length from 1.2 mm to 3.4 mm (average of 1.7 mm; standard deviation of 0.47 mm) and width from 1,7 mm to 4.0 mm (average of 2.25 mm; standard deviation of 0.6 mm) (figure 5), width/length ratio from 1,2 to 1,4; contour weakly transverse to transverse, maximum width at the hinge, resupinated shell, reduced umbo protruding slightly from the posterior edge of the ventral valve, at least one oblique orthomorphic spine on each side of the umbo, ornamentation with a parvicostellate appearance consisting of up to 32 rounded ribs in total multiplying mainly by intercalation and subordinately by bifurcation, maximum of 7 ribs per mm. Presence of concentric growth lines. **Ventral interior:** well-developed muscle field, rounded triangular, sharp septum dividing the muscle field. **Dorsal interior:** very poorly preserved, no relevant morphological features can be distinguished.

Description (according to Quadros, 1987): Shells of varying sizes (small 1 mm, medium 2-3 mm and large 4-5 mm), subcircular to subquadrangular outline, plano-convex valves. Long and straight cardinal line with the greatest width of the shell. Straight cardinal angle, ventral interarea aprsacline (smaller forms) to catacline (larger forms), dorsal anacline. The interarea of the pedicular valve is comparatively larger than that of the dorsal valve. Umbo projecting slightly beyond the cardinal line. In smaller forms, a pair of tubular spines, wider at the base, project from the cardinal line at an internal angle of 115º to 130º. In some specimens, these spines emerge from the cardinal angle. In larger forms, a second pair of spines is observed on each side, with an internal angle varying from 120º to 130º. The ventral valve begins with pronounced convexity that decreases in stages like steps until almost half its length, where it becomes gently convex until it appears flat on the anterior margin. In larger specimens, this convex area does not follow the growth pattern, remaining restricted to the posterior third. The ornamentation consists of thin, low, sparse ribs arranged radially. A parvicostelate pattern is observed in some specimens. Two or three pronounced and continuous growth lines mark the decreases in the convex portion. On the anterior margin and flanks, thin and discontinuous growth lines give the valve surface a reticulated appearance. **Ventral interior:** small teeth, divergent with respect to the plane of symmetry and subparallel to the cardinal line. Pronounced median septum, triangular in cross-section. In small specimens it is more widened. Its length follows the pattern of the convex portion, that is, it does not follow the growth rate of the valve, resulting in a long septum in small specimens and a short one in large ones. In some specimens it bifurcates in the posterior region and thins in the anterior region (larger forms), in others, it shows sub-equal width with widened and shallow ends (smaller forms). Oval triangular muscular area, well marked, lateral to the median septum. The pronounced convexity of the valve is due to these strong muscular markings. Not infrequently its length slightly exceeds that of the median septum. In some specimens, pustules are observed that are arranged radially following the outline of the ribs. **Dorsal interior:** slightly curved dental fossae limited by internal and external ridges arranged subparallel to the cardinal line. Internal ridges comparatively higher. Median septum or myophragm absent. Short anderidia symmetrically subparallel and perpendicular to the cardinal line. Muscular area of the adductors indistinct. The internal ridges join with the anderidia in the posterior portion forming a low platform, probably for the cardinal process, which, in the few available specimens of this valve, was not preserved. Pustules follow the rib lineament.

Remarks. Quadros (1987, p.41) proposed the species *Chonostrophia andina* with the holotype of *Chonostrophia reversa* var. *andina* Levy and Nullo, 1972. This species was synonymized as ?*Sanjuanetes andina* by Racheboeuf and Herrera (1994, p. 548). 1994). However, the Brazilian specimens differ from ?*Sanjuanetes andina* by lacking an enlarged median rib and by having less developed structures inside the dorsal valve. Based on the morphological characteristics described (valve size, muscle field, ornamentation, and spine type), the Brazilian specimens belong to the genus *Chonostrophia*. These specimens differ from *Chonostrophia reversa* (Whitfield, 1882) by the development of the muscular field and thicker ribs; from *Chonostrophia montrealensis* Schuchert, 1901, by their smaller size (less than 4 mm compared to more than 9 mm), maximum width at the hinge and not halfway along the valve, more developed ribs; from *Chonostrophia cartieri* Racheboeuf and Lespérance, 1995 by their smaller size (maximum of 4 mm compared to maximum of 15 mm), smaller number of spines (in *C. cartieri* there are up to 7 spines) and greater development of the muscular field; from *Chonostrophia dawsoni* (Billings, 1874) by its smaller size (up to 4 mm against up to 21 mm), smaller number of spines (up to 10 pairs of spines in *C. dawsoni*), septum inside the ventral valve slightly thicker and shorter, muscle field better developed, ribs thicker and less numerous; from *Chonostrophia elenae* Herrera, 1995, by its smaller size (maximum 4 mm against maximum 20 mm), apparently thicker ribs, a thicker myophragm inside the ventral valve, and valves more resupinated; and finally from *Chonostrophia truyolsae* Racheboeuf, 1992 from the Devonian of Bolivia the larger development of the muscular field and thicker ribs. In the present study, it was not possible to recognize any dorsal valve interior, although Quadros (1987, p.41) described it in her thesis. Furthermore, not all specimens studied by Quadros (1987) were located in the present study, which is why Quadros' (1987) descriptions are longer than those presented in this paper. It was also not possible to observe any further details in the photos presented by Quadros (1987) beyond those already described in this paper. However, even so, the characteristics of the ventral valve are significantly different from those of the *Chonostrophia* species known so far, as described previously. Because of this, a new species is proposed, here called *Chonostrophia raquelae*. It should be noted that Racheboeuf and Lespérance (1994, p.42) proposed the new species *Chonostrophia cartieri*, although its dorsal interior was unknown. The only other record of the genus *Chonostrophia* in this basin is in the state of Mato Grosso do Sul (*Chonostrophia*? aff. *truyolsae* according to Videira-Santos et al., 2022).

Observation 1. Videira-Santos et al. (2022) when analyzing specimens of *Chonostrophia* deposited in the collection of the Universidade Federal de Mato Grosso erroneously referred to the ascension numbers FUFMT-MP 632, FUFMT-MP 633, FUFMT-MP 634, FUFMT-MP 635a, b, FUFMT-MP 636a, b, FUFMT-MP 638, FUFMT-MP 1121a, b FUFMT-MP 1131, FUFMT-MP 1151, FUFMT-MP 1152, FUFMT-MP 1171, FUFMT-MP 1172, FUFMT-MP 1182, FUFMT-MP 1183, FUFMT-MP 1184, FUFMT-MP 1192, FUFMT-MP 1193, FUFMT-MP 1222 and FUFMT-MP 1223. The correct ascension numbers are, respectively, FUFMT-MP 63b, FUFMT-MP 63c, FUFMT-MP 63d, FUFMT-MP 63e (holotype, figure 4A), MP 63f, FUFMT-MP 63g, h, FUFMT-MP 63j, FUFMT-MP 112a, b FUFMT-MP 113a, FUFMT-MP 115a (paratype, figure 4F), FUFMT-MP 115b, FUFMT-MP 117a, FUFMT-MP 117b, FUFMT-MP 118b (paratype, figure 4C), FUFMT-MP 118c, FUFMT-MP 118d, FUFMT-MP 119b, FUFMT-MP 119c, FUFMT-MP 122b and FUFMT-MP 122c.

Observation 2. Caster (1939), based on a poorly preserved Devonian ventral valve from Colombia, proposed a new species which was named *Chonostrophia knodi*, however Boucot and Amsden (1964) suggested that this species may actually belong to the genus *Chonostrophiella*.

(FIGURE 4 HERE)

(FIGURE 5 HERE)

Class Rhynchonellata Williams et al., 1996

Order Rhynchonellida Kuhn, 1949

Superfamily Rhynchotrematoidea Schuchert, 1913

Family Leptocoeliidae Boucot and Gill, 1956

Genus ***Australocoelia*** Boucot and Gill, 1956

Type species. *Atrypa palmata* Morris and Sharpe, 1846.

Australocoelia palmata (Morris and Sharpe, 1846)

Figure 6(A-B)

1913 *Coelospira*? *colona* Clarke; Clarke, p. 275-276, pl. XXII, fig. 8-12.

2013 *Coelospira* sp.; Cerri, p. 13, fig. 4d-f.

Material. DGM 214-I (internal ventral mold), DGM 215-I (internal ventral mold), DGM 216-I (internal ventral mold), DGM 217-I (internal ventral mold), GP 1E 7537 (external dorsal mold), and GP 1E 7812 (articulated exterior mold).

Provenance. Ponta Grossa of Clarke (1913) (late Pragian – early Emsian) and Jaguariaíva (late Pragian – early Emsian).

Occurrences. Islas Malvinas , Fox Bay Formation – Early Devonian (Morris and Sharpe, 1846); Brazil, Ponta Grossa, São Domingos and Pimenteira formations – late

Pragian to Givetian (Clarke, 1913; Gama Jr., 2008; Rezende et al., 2019, Queiroz et al., 2013; Ribeiro et al., 2021; this paper); South Africa, Bokkeveld Group- ?late Emsian to late Givetian (Reed, 1925); Argentina, Talacasto and Punta Negra formations – Lochkovian to Emsian (Castellaro, 1966; Rezende et al., 2019), Bolivia, Belen, Icla, Huamamampampa and Sica Sica formations – Pragian to Frasnian (Isaacson, 1977; 1993); Peru, Lampa Formation – Early/Middle Devonian (Laubacher et al., 1982); Uruguay, Cordobés Formation - Pragian to Emsian (Mendez-Alzola, 1938) and Venezuela, Caño Grande Formation - ?Emsian (Benedetto, 1984; Rezende et al., 2019).

Description. Shell small to moderate size, six specimens mensurated, 3 mm to 15 mm in length (average of 11.25 mm; standard deviation of 4.47 mm), 4 mm to 18 mm in width (average of 12.15 mm; standard deviation of 4.6 mm), width/length ratio of 1,2; about 12 ribs, angular, subrounded in the anterior portion, rarely bifurcating, multiplying mainly by intercalation, subcircular outline, convex valves, small umbo, in some specimens the umbo region has no ribs, in the dorsal valve some specimens of a median rib slightly larger than the others and with a small groove on top of it, without traces of punctuation, ribs are thin posteriorly, but thicken towards the anterior commissure; ribs have a slightly curved appearance, reduced interspaces, presence of concentric growth lines, sub-rectangular beak. **Dorsal and ventral interiors**: poorly preserved.

Remarks. The specimens described as *Coelospira*? *colona* by Clarke (1913, p. 275) and *Coelospira* sp. by Cerri (2013, p.13) are not *Coelospira* and diverge from this genus for the following reasons: absence of a central rib that is thinner than the adjacent ones and a shell without a naviculated aspect (see Boucot & Johson, 1967; Amsden, 1983; Alvarez & Copper, 2002). Although Clarke (1913) stated that in the specimens there would be one rib embedded in the ventral valve groove, this characteristic was not observed when we analyzed the same material studied by Clarke (1913), which is deposited in the Museu de Ciências da Terra/Serviço Geológico do Brasil (MCT/SGB-CPRM). Although the interiors of the valves are not well preserved in the material studied, the characteristics that can be observed in the specimens allow them to be classified as *Australocoelia palmata*, distinguished from *A. boucoti* by their more rounded ribs anteriorly and larger interspaces (see Rezende et al., 2019). Copper (1977) had previously suggested that *C.*? *colona* was probably *Australocoelia*, but did not explain why. In the Brazilian state of Mato Grosso, Quadros (1987) claimed to have found *Coelospira* sp. in Devonian layers, but when analyzing the specimens studied by Quadros (1987) deposited in the collection of the Universidade Federal de Mato Grosso, it was noticed that these specimens do not have the thinned central rib. Quadros' (1987) specimens are actually *Derbyina smithi* (Videira-Santos and Scheffler, in preparation). Therefore, to date, there are no genuine records of *Coelospira* in the Devonian of the Paraná Basin.

(FIGURE 6 HERE)

Order Athyridida Boucot, Johnson, and Staton, 1964

Suborder Athyrididina Boucot, Johnson, and Staton, 1964

Superfamily Meristelloidea Waagen, 1883

Family Meristellidae Waagen, 1883

Subfamily Meristellinae Waagen, 1883

Genus ***Meristelloides*** Isaacson, 1977

Type species. *Meristella riskowskii* Ulrich, 1892.

Diagnosis. Large meristellid with a short, stout median septum in the dorsal valve. Ventral valve without secondary shell modifications, jugum, cardinal plate, and spiralia present (Isaacson, 1977).

Remarks. *Meristelloides* is a genus whose validity was questioned by Alvarez and Rong (2002) because there was little information on this taxon. However, here we agree with the diagnosis and distinctions made by Isaacson (1977), thus considering *Meristelloides* as a valid genus. *Meristelloides* differs from *Meristina* and *Merista* by lacking dental plates. *Meristelloides* differs from *Meristella* by the possession of a stout and short dorsal median septum (see Isaacson, 1977).

Meristelloides riskowskii (Ulrich, 1892)

Figure 7(A-F)

1892 *Meristella riskowskii*; Ulrich, pl. IV, figs. 16-18.

1913 *Meristella septata*; Clarke, p. 264-267.

1977 *Meristelloides riskowskii* (Ulrich); Isaacson, pl. 2, figs. 25-29; pl. 3, fig.1.

1993 *Meristelloides riskowskii* (Ulrich); Isaacson, pl. 4, figs. 25-29; pl. 5, fig.1.

Material. DGM 1958-I (internal ventral mold), DGM 1959-I (internal ventral mold), MPI 1705 (external articulated mold), MPI 2282 (internal dorsal mold), MPI 2424 (internal ventral mold), MPI 12920 (internal ventral mold), MPI 13453 (internal dorsal mold), MPI 13459 (external dorsal mold), MPI 14259 (undefined), MPI 16016 (internal ventral mold), MPI 16528, MPI 16898 (internal dorsal mold), MPI 17342 (internal ventral mold), MPI 17421 (internal ventral mold), MPI 17431 (internal ventral mold), MPI 17433 (internal ventral mold), MPI 17498 (internal ventral mold), MPI 17565 (undefined), MPI 17580 (undefined), MPI 17824 (external ventral mold), MPI 18921 (internal dorsal mold), MPI 19028 (internal ventral mold), MPI 19031 (internal ventral mold), NR 6252 (articulated exterior mold), MCN P 1107 (internal articulated mold), NYSM I 19745 (internal ventral mold), NYSM I 19746 (internal dorsal mold) and NYSM I 19747 (internal ventral mold).

Provenance. Rivadávia (Pragian), Curva II (Pragian), Bosque Mistral (late Pragian – early Emsian), Jaguariaíva (late Pragian – early Emsian), Metalúrgica Águia (?late Emsian), and Boa Vista (late Emsian).

Occurrences of the genus *Meristelloides*. Bolivia, Lower Icla, Lower Belen, Upper Icla, Upper Belen, Sica Sica, and Huamampampa formations – Pragian to Frasnian (Isaacson, 1977, 1993); Argentina, Pescado Formation – Pragian to Emsian (Noetinger et al., 2016); South Africa, Bokkeveld Group- ?late Emsian to late Givetian (Reed, 1925) and Brazil, Ponta Grossa and São Domingos formations – Pragian to late Emsian (Clarke, 1913; this paper).

Description. Shells biconvex, seven specimens mensurated, length between 11 mm and 30 mm (average 25.2 mm; standard deviation 6.0 mm); and width between 10 mm and 38 mm (average 33.5 mm; standard deviation 10 mm) (figure 8); width/length ratio from 1,1 to 1; umbo wide, erect, and margins rounded, ventral groove not very prominent, anterior commissure without ribs, pyriform outline, presence of faint concentric growth lines in some specimens. **Ventral interior:** weakly impressed muscle field. **Dorsal interior:** thick median septum extending a little more than halfway along the valve, thicker posteriorly and tapering anteriorly. The muscle field is weakly impressed and poorly defined.

Remarks. Clarke (1913) presented the identification of a species of brachiopod that was relatively large in size and had a large septum, which he named *Meristella septata*

Clarke, 1913, from Jaguariaíva. However, after Clarke's (1913) work, few studies have even mentioned the presence of this species in the Devonian of the Paraná Basin (e.g., Bosetti et al., 2012; Sedorko et al., 2021), based on Clarke (1913). Isaacson (1977) synonymized the species *Meristella septata* with *Meristelloides riskowskii* from the Devonian of Bolivia, but provided no clear explanation for this decision. The original material, illustrated by Clarke (1913) (type series of "*Meristella septata*"), is in the collection of the New York State Museum. These specimens come from Jaguariaíva and were collected by Eusebio de Oliveira. The samples still bear the original type-material marking from the MCT/SGB-CPRM, because they were originally part of the MCT/SGB-CPRM collection. The fossils were sent by O. Derby, then director of the Geological and Mineralogical Service of Brazil, to the New York State Museum for Clarke to analyze between 1907 and 1912. Confirmation that these were indeed Clarke's (1913) specimens was made by comparing the specimens with the illustrations presented by Clarke (1913). Specimens of *Meristelloides* from the Paraná Basin are very similar to those from Bolivia, classified by Isaacson (1977) as *Meristelloides riskowskii*. Isaacson (1977) stated that the specimens he studied are similar to those described as *Meristella riskowskii* by Ulrich (1892). Looking at Ulrich's (1892) illustrations, it is possible to see that these specimens have apparently a deeper sulcus, but *M. riskowskii* is a species that has great morphological variety (Ulrich, 1892), so even though it is not possible to see internal characters in the Brazilian material, it is reasonable to classify it as *M. riskowskii*. Nevertheless, the need to search for specimens with the best-preserved interior of both valves cannot be ruled out, since meristelloids are quite similar in their external morphology, and often the difference lies in the characteristics of the cardinalia and brachidium.

(FIGURE 7 HERE)

(FIGURE 8 HERE)

Discussion

Paleobiogeography. Meristelloides is a genus, as far as is known, endemic to the Malvinoxhosan Bioregion. *Australocoelia* and *Chonostrophia* are found in other non-Malvinoxhosan regions (see Caster, 1939; Benedetto, 1984; Racheboeuf and Lésperance, 1995; Rezende et al., 2019).

Throughout the Devonian, several anoxic transgressive events occurred, such as the Zlichov-Daleje (early-middle Emsian), Choteč (early Eifelian), and Kačák (late Eifelian-Givetian) events, which are often linked to extinction events (e.g., Bosetti et al., 2010; Dowding and Ebach, 2018). However, these events may also have facilitated the faunal dispersion when sea levels reached their maximum amplitude (e.g., Grahn et al., 2016; Videira-Santos et al., 2022; Goltz et al., 2025).

Meristelloides appeared in the Pragian and dispersed rapidly to the different malvinoxhosan regions (Clarke, 1913; Reed, 1925; Isaacson, 1977, 1993; Noetinger et al., 2016). *Chonostrophia*, on the other hand, possibly dispersed from the Paraná Basin to Bolivia between the early Emsian and the Eifelian (Caster, 1939; Benedetto, 1985; Racheboeuf, 1992; Racheboeuf and Lésperance, 1995; Herrera, 1995; Racheboeuf et al., 2012; Videira-Santos et al., 2022). This may be related to the Zlichov-Daleje or Choteč events (Sedorko et al., 2019). This had already been noticed by Videira-Santos et al. (2022) not only for *Chonostrophia*, but also for other Chonetoidea such as *Kentronetes iclaensis* and *Pleurochonetes surucoi.*

Australocoelia is a genus that arose in the Early Devonian of the Malvinoxhosan Realm, Devonian of the Islas Malvinas, Paraná Basin (Brazil), South Africa, Argentina, Bolivia, southern Peru, and Uruguay (Morris and Sharpe, 1846; Clarke, 1913; Reed, 1925; Mendez-Alzola, 1938; Castellaro, 1966; Isaacson, 1977, 1993; Laubacher et al., 1982; Rezende et al., 2019). Its dispersal from the Eifelian is recorded in the Pimenteira Formation of the Parnaíba Basin (Queiroz et al., 2013) may also be related to the Lower Kačák event (see Grahn et al., 2016). The record of *Australocoelia* in the Early Devonian of Venezuela (Benedetto, 1984) lacks confirmation. This possible presence of *Australocoelia* in Venezuela has also not been included by Savage (2002) in the revised edition to the Treatise on Invertebrate Paleontology.

Paleoenvironment. *Meristelloides* is found in the Paraná Basin in outcrops ranging from the shoreface to the offshore (see Kurovski, 2023). They are most commonly found articulated in sandy facies, although one specimen with a semi-open valve was found at Rivadávia outcrop ("iron oxide level", MCN P 1107), which is interpreted as offshore transitional (see Kurovski, 2023). Here, it was considered that *Meristelloides* occupied an offshore transition environment.

Taphonomically, the specimens of *Chonostrophia* analyzed here are very similar to the specimens of *Chonostrophia* analyzed by Videira-Santos et al.(2022) in the Brazilian state of Mato Grosso do Sul, showing small size, disarticulated valves with spines preserved in siltstones to sandy siltstones. Videira-Santos et al. (2022) interpreted that the genus occurred in an offshore transition to offshore paleoenvironment, while here it was interpreted that it was more restricted to the offshore transition, at least the species *Chonostrophia raquelae*, since it is not possible to interpret the Estrada outcrop as an offshore environment.

In turn, *Australocoelia*, due to the morphology of its shell and the outcrops where it is recorded, would have a preference for the transitional offshore environment (e.g., Queiroz et al., 2013; Ribeiro et al., 2021, 2024). Also, according to Ribeiro et al.

(2024), specimens of *Australocoelia* that lived in a transgressive marine environment had varied sizes, while those that lived in a regressive context had body sizes 25% smaller (in length and width), probably as a consequence of anoxia related to the Maximum Flooding Surface (MFS).

Finally, it should be noted that all the paleoenvironmental inferences were made based on material deposited in different scientific collections, most of which were not collected with a taphonomic bias. Therefore, more taphonomic works in different outcrops across the Paraná Basin are necessary to corroborate the inferences made here.

Conclusion

In this paper a new species of Chonetoidea, herein designated *Chonostrophia raquelae*, was identified in the Devonian of the Paraná Basin. The validity of the genus *Meristelloides* and the occurrence of the species *M. riskowskii* in this basin were also corroborated in this paper.

Furthermore, the occurrence of *Coelospira* in the Devonian of the Paraná Basin was not recognized. The specimens that have been assigned to this genus in previous papers (e.g., Clarke, 1913) are actually *Australocoelia*.

The migration of *Chonostrophia* to Bolivia during the transition between the early Emsian and Eifelian may be related to the Zlichov-Daleje or Choteč events. The migration from the Eifelian of *Australocoelia* to the Parnaíba Basin (Brazil) may be related to the Lower Kačák event.

Finally, the genera discussed in this article (*Chonostrophia*, *Australocoelia,* and *Meristelloides*) preferred to inhabit the transitional offshore environment.

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Figure captions

Figure 1. A. Outcrops studied in the state of Paraná: 1 - Ponta Grossa of Clarke (1913), 2 - Bosque Mistral, 3 - Curva II, 4 - Metalúrgica Águia, 5 - Rivadávia, 6 - Boa Vista, 7 - Jaguariaíva (adapted from Grahn et al., 2013); B. Paraná Basin, with emphasis on Devonian outcrops of the central part of Paraná.

Figure 2. A. Paraná Basin, with emphasis on Devonian outcrops of the central part of the state of Mato Grosso; B. Outcrop studied in the state of Mato Grosso (Chapada dos Guimarães region): 1 - Estrada (adapted from Grahn et al., 2010).

Figure 3. Stratigraphic context of the Devonian (Lochkovian-Givetian) of the Paraná Basin. TST – Transgressive Systems Tract, MFS – Maximum Flooding Surface, HST – Highstand Systems Tract, SB – Sequence Boundary, TS – Transgressive surface. Siluro-Devonian, Devonian I, and Devonian II are Sequence Stratigraphy proposed by Sedorko et al. (2018b) (adapted from Sedorko et al., 2018b).

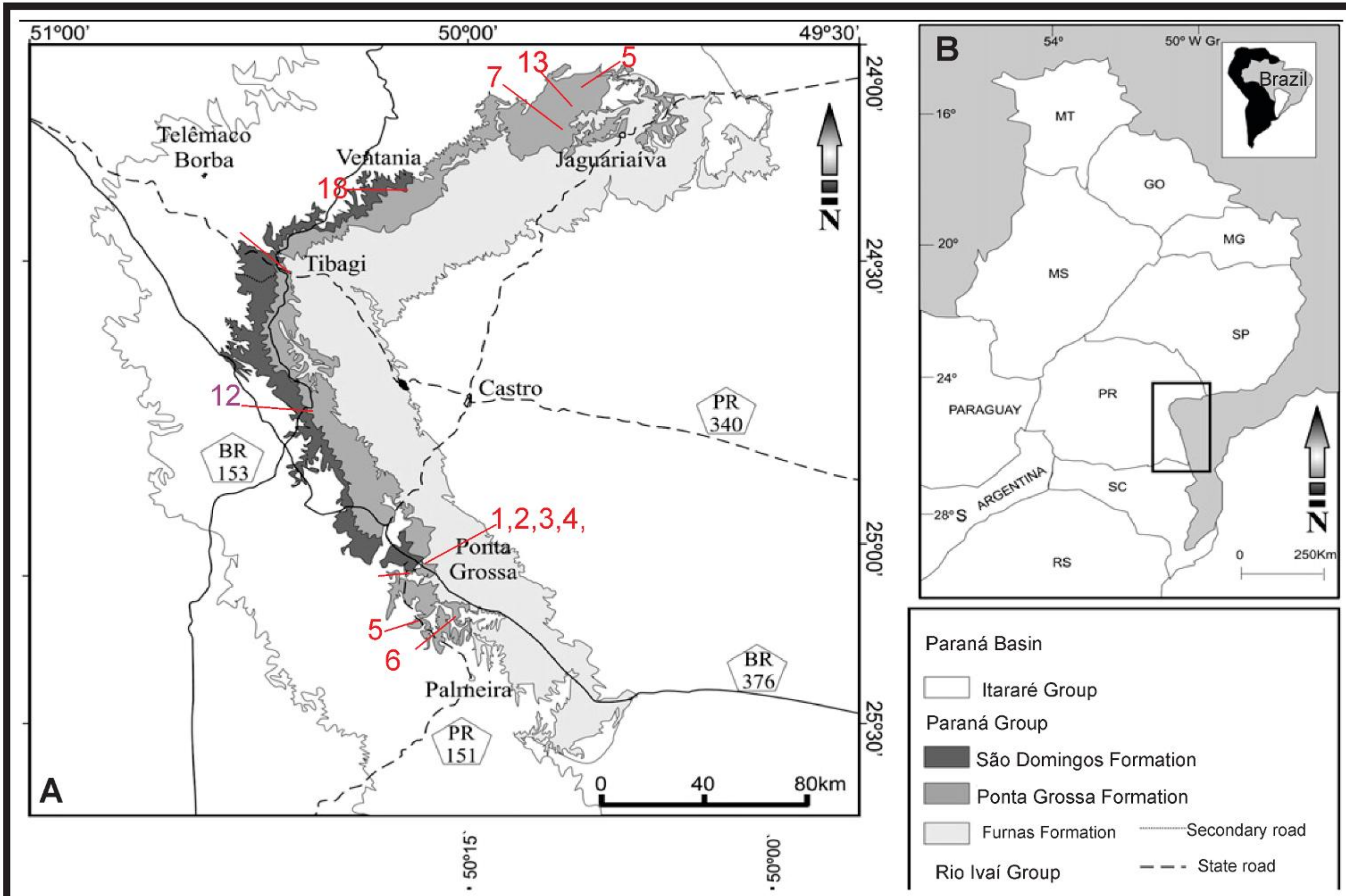
Figure 4. A-F. *Chonostrophia raquelae* nov. sp., MP 63e (ventral valve, holotype) (A), MP 109d (ventral valve, paratype) (B), MP 118b (ventral valve, paratype) (C), MP 114 (ventral valve, paratype) (D). MP 115a (ventral valve, paratype) (E), and MP67b (ventral valve, paratype) (F). Scale bars equal 1 mm.

Figure 5. Length x Width relationship of the *Chonostrophia raquelae* specimens analyzed.

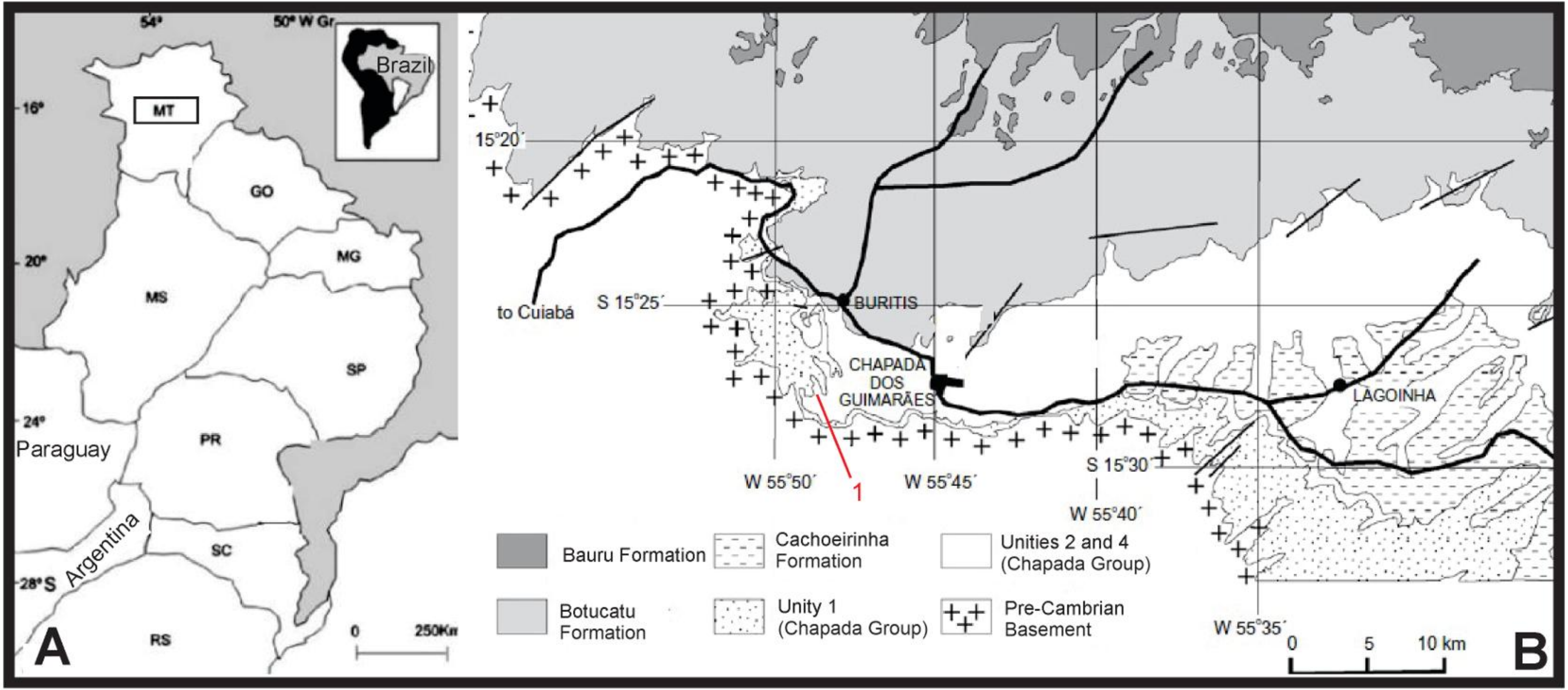
Figure 6. A-B. *Australocoelia palmata* (Morris and Sharpe, 1846), DGM 216-I (ventral valve) (A) and DGM 217-I (ventral valve) (B). Scale bars equal 5 mm.

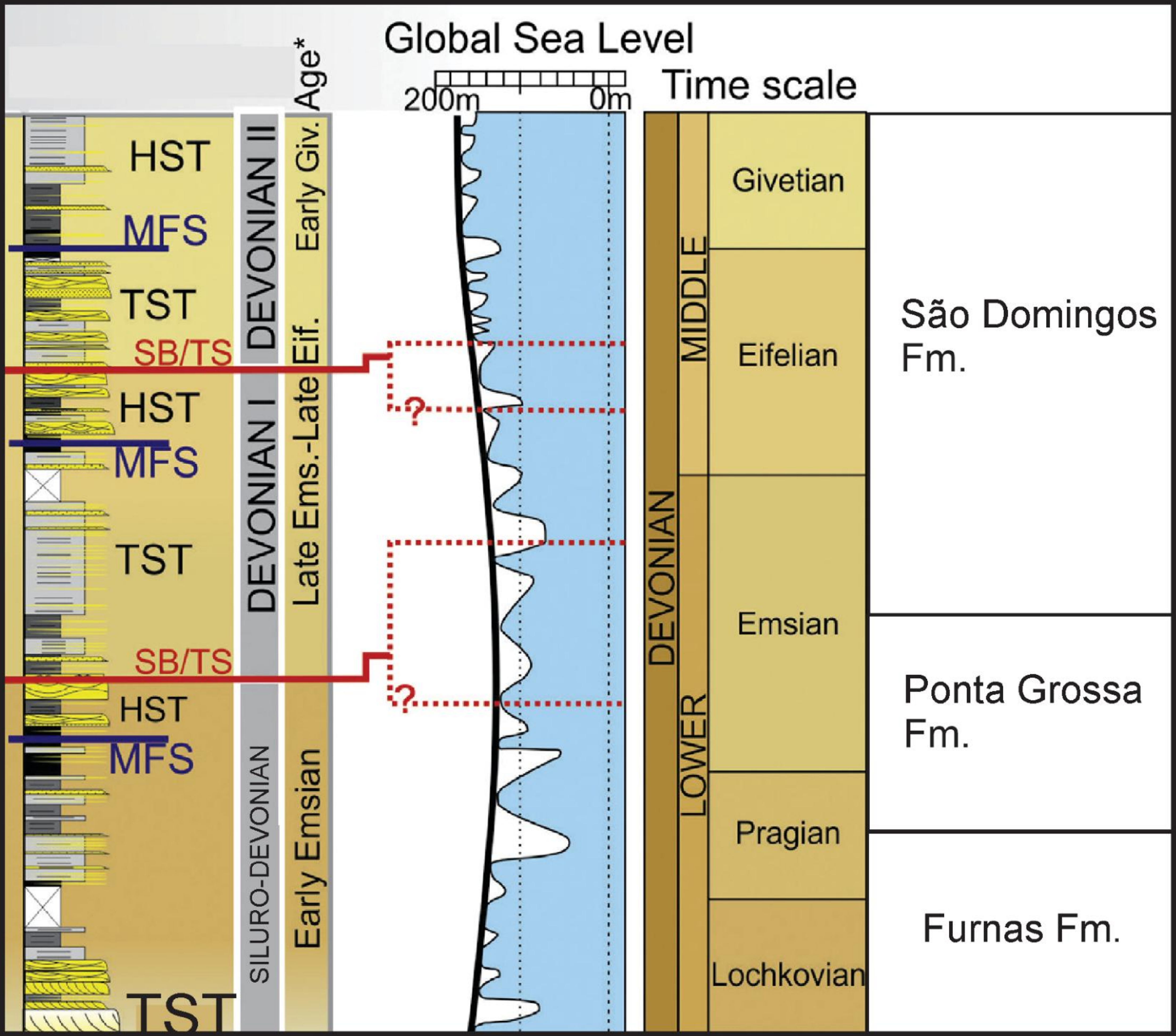
Figure 7A-F. *Meristelloides riskowskii* (Ulrich, 1892) MPI 17498 (ventral valve) (A), MPI 13453 (dorsal valve) (B), MCN P 1107 (specimen in butterfly) (C), NYSM I 19745 (ventral valve) (D), NYSM I 19746 (dorsal valve) (E), and NYSM I 19747 (ventral valve) (F). Scale bars equal 5 mm.

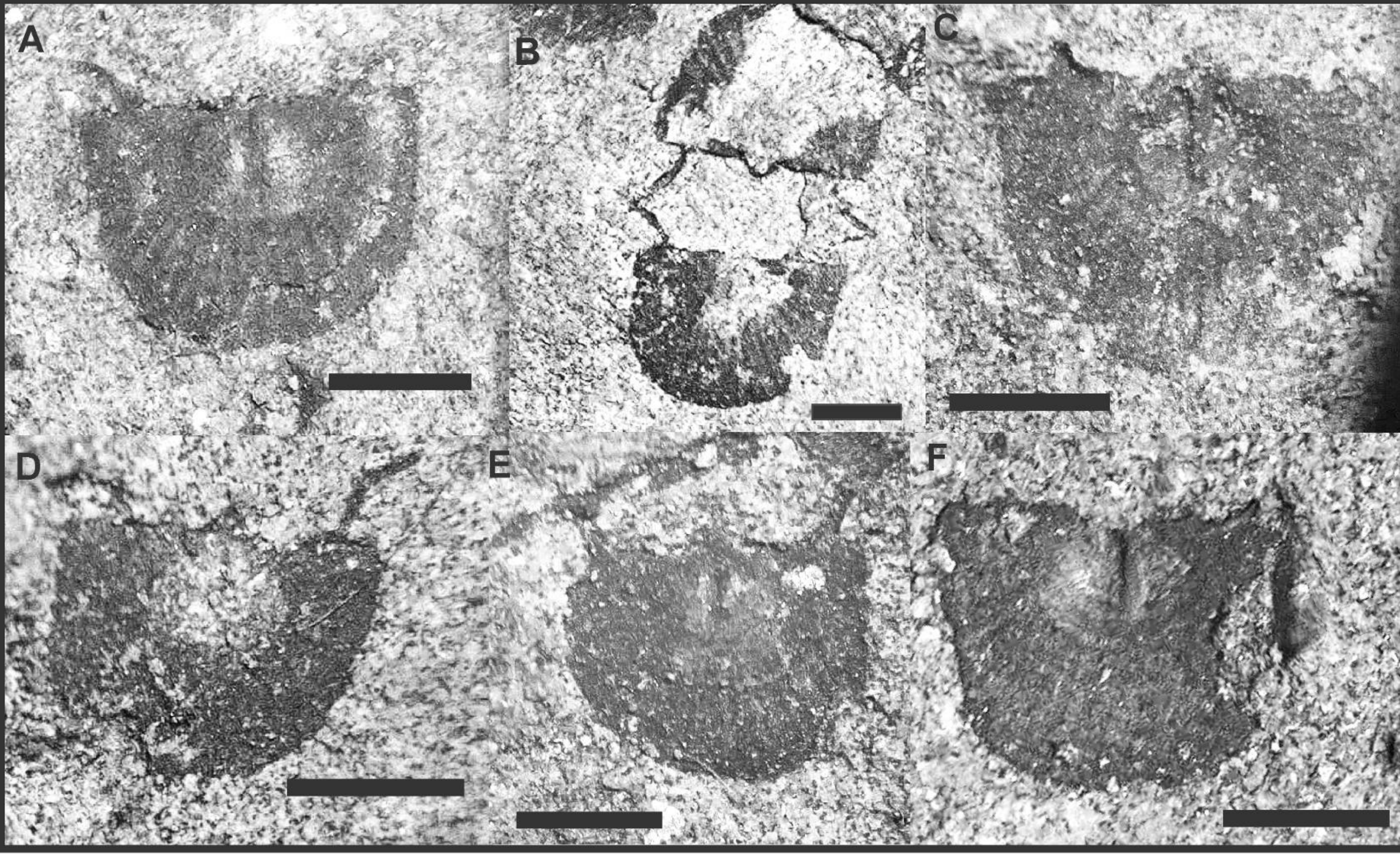
Figure 8. Length x Width relationship of the *Meristelloides riskowskii* specimens analyzed.

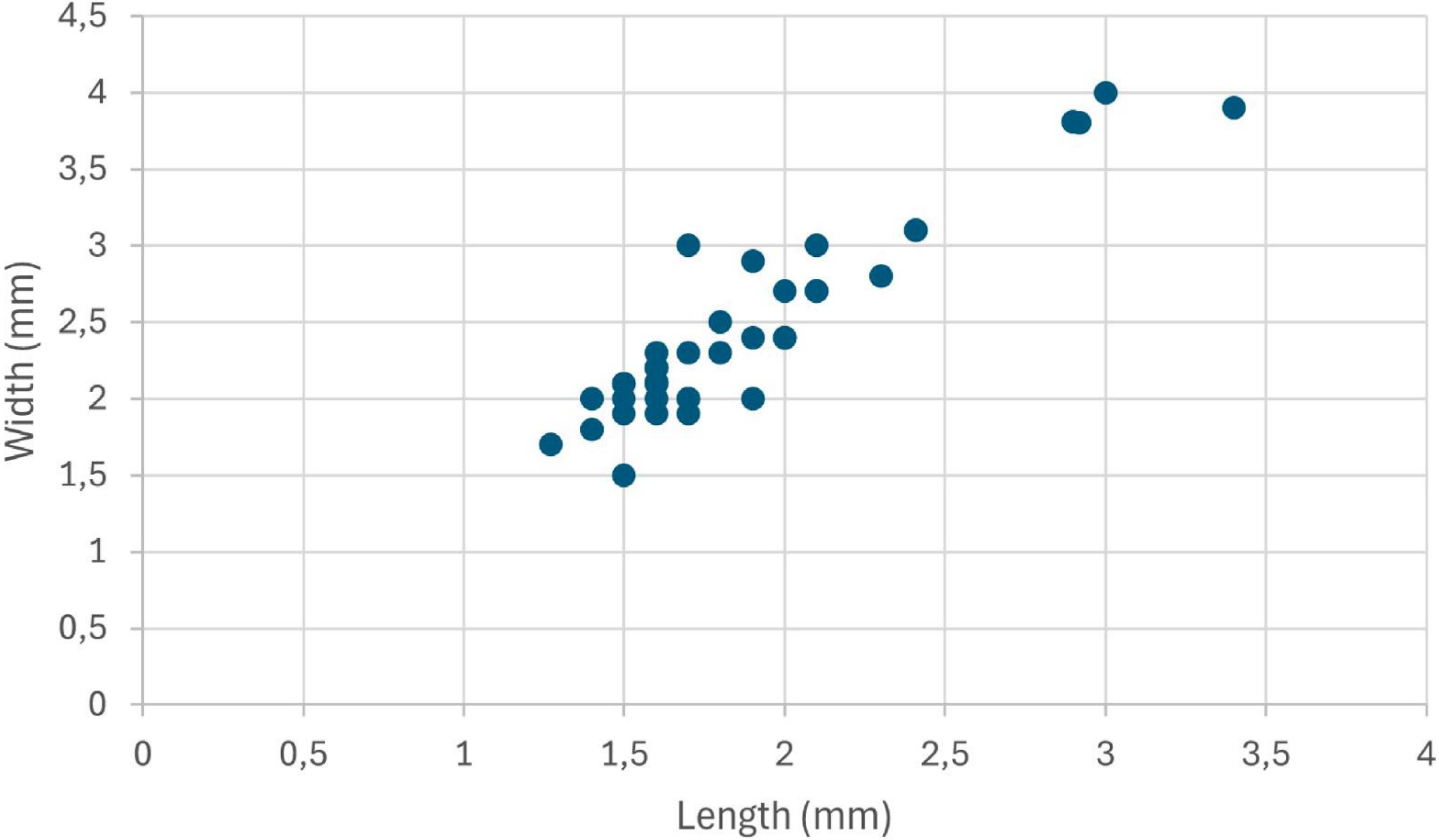


A
51º00'
50º00'
49º30'
24º00'
24º30'
25º00'
25º30'
50º15'
50º00'
Telêmaco Borba
Ventania
Jaguariaíva
Tibagi
Castro
Ponta Grossa
Palmeira
PR 340
BR 153
BR 376
PR 151
13
5
7
18
12
1,2,3,4,
5
6
N
0
40
80km
B
54º
50º W Gr
16º
20º
24º
28º S
Brazil
MT
GO
MG
MS
SP
PR
PARAGUAY
ARGENTINA
SC
RS
N
0
250Km
Paraná Basin
Itararé Group
Paraná Group
São Domingos Formation
Ponta Grossa Formation
Furnas Formation
Secondary road
State road
Rio Ivaí Group

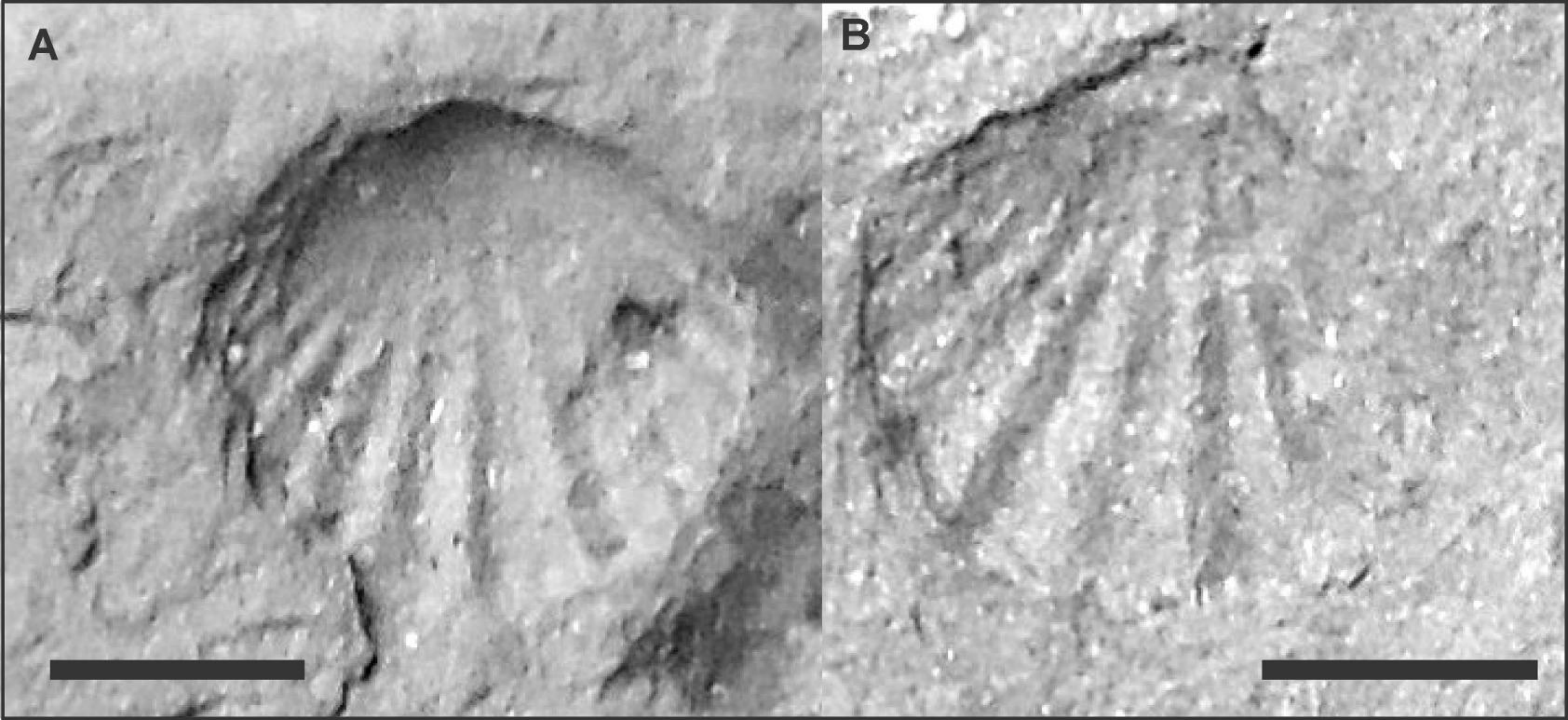

54°
50° W Gr
Brazil
MT
16°
GO
MG
20°
MS
SP
24°
Paraguay
PR
Argentina
SC
28° S
RS
0
250Km
A
15°20´
to Cuiabá
S 15°25´
BURITIS
CHAPADA
DOS
GUIMARÃES
LAGOINHA
W 55°50´
1
W 55°45´
S 15°30´
W 55°40´
W 55°35´
Bauru Formation
Cachoeirinha
Formation
Unities 2 and 4
(Chapada Group)
Botucatu
Formation
Unity 1
(Chapada Group)
Pre-Cambrian
Basement
0
5
10 km
B

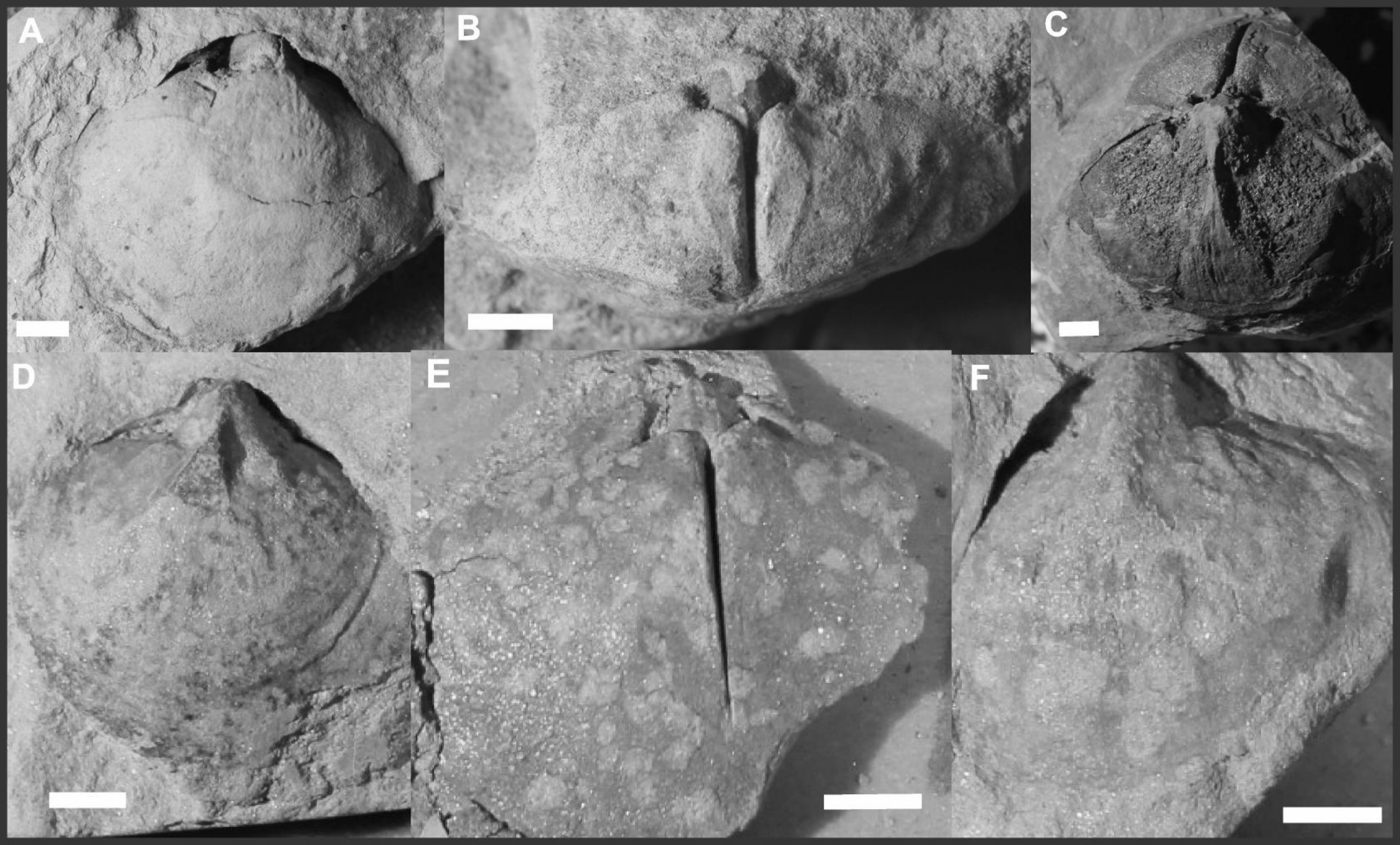

Global Sea Level
Age*
200m
0m
Time scale
HST
MFS
TST
SB/TS
HST
MFS
TST
SB/TS
HST
MFS
TST
DEVONIAN II
DEVONIAN I
SILURO-DEVONIAN
Early Giv.
Eif.
Late Ems.-Late
Early Emsian
?
?
DEVONIAN
MIDDLE
LOWER
Givetian
Eifelian
Emsian
Pragian
Lochkovian
São Domingos Fm.
Ponta Grossa Fm.
Furnas Fm.

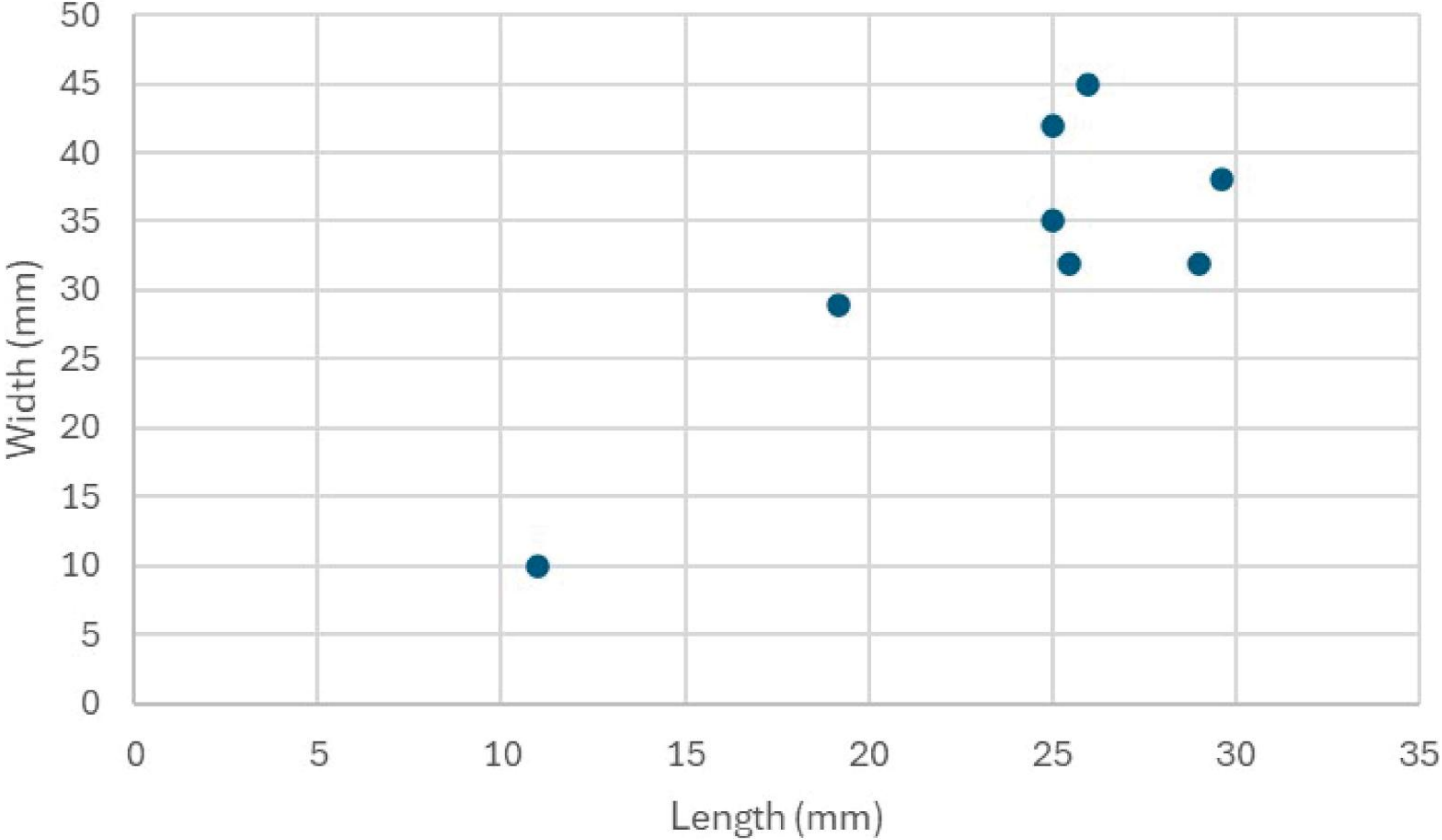

A
B
C
D
E
F



4,5
4
3,5
3
2,5
2
1,5
1
0,5
0
Width (mm)
0
0,5
1
1,5
2
2,5
3
3,5
4
Length (mm)


A
B


A
B
C
D
E
F



50
45
40
35
30
25
20
15
10
5
0
Width (mm)
0
5
10
15
20
25
30
35
Length (mm)