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Systematic revision of the Devonian Brachiopods (Terebratulida) from the Paraná Basin, Brazil

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Abstract

Terebratulids comprise one of the most successful orders of brachiopod, having emerged in the mid-Paleozoic and persisting to the present day. Although the Devonian paleontology of the Paraná Basin is among the best studied of the Brazilian basins, the Terebratulida taxa still lack a well-defined systematic classification. Therefore, this study aimed to conduct a taxonomic review of the Devonian Terebratulida of the Paraná Basin (Ponta Grossa and São Domingos formations). The taxonomic review was conducted using samples from the Brazilian states of Paraná, Goiás, and Mato Grosso housed in Brazilian scientific collections. The results achieved include: recognition of the first occurrences of the genera *Mutationella* (*Mutationella grahni* nov. sp. and *Mutationella* sp.) and ?*Rhipidothyris* in the Paraná Basin; as well as confirmation of the validity of the species *Cryptonella baini* and *Paranaia margarida*. The migration of *Cryptonella* and *Mutationella* from Bolivia to the Paraná Basin may be related to the Lochkovian-Pragian sea-level-rise events, whereas the migration of ?*Rhipidothyris* from the Parnaíba Basin or Bolivia to the Paraná Basin was possibly related to the Kačák event. Finally, it was possible to infer that the terebratulids analyzed here are inferred to have inhabited the offshore transition paleoenvironment.

KEYWORDS: Rhynchonelliformea; Devonian; Malvinoxhosan realm; Gondwana.

1. INTRODUCTION

Terebratulids comprise a diverse order of brachiopods that include approximately 600 genera. This order can be considered one of the most successful among the brachiopod orders, having emerged in the Silurian/Devonian and persisting to the present day (Lee & MacKinnon, 2006; Jansen et al., 2025).

Members of the order Terebratulida are distinguished from those of other brachiopod orders by the presence of an endopunctate shell, a loop, and a generally functional pedicle. Their valves are generally biconvex, often smooth or occasionally ribbed, astrophic, and frequently characterized by a ventral sulcus and dorsal fold (Lee & MacKinnon, 2006; Jansen et al., 2025).

To date, only the terebratulid genera *Derbyina*, ?*Cryptonella*, *Podolella*, and *Scaphiocoelia* have been recognized in the Devonian of the Paraná Basin (e.g., Clarke, 1913a; Boucot & Caster, 1984; Quadros, 1987; Videira-Santos et al., 2023).

The first records of Terebratulida in the Devonian of the Paraná Basin date back to the second half of the 19th century, with reports of "*Terebratulae*", "*Centronella*" sp., and "*Notothyris*? *smithi*" from outcrops in the Brazilian state of Mato Grosso (Smith, 1883; Ammon, 1893; Derby, 1895). Since then, terebratulids such as *Derbyina*, *Cryptonella,* and ?*Globithyris* have been reported from the Devonian of the Paraná Basin (Clarke, 1913a; Erichsen & Lofgreen, 1940; Petri, 1948; Lange & Petri, 1967; Andrade & Camarço, 1978, 1980; Quadros, 1987; Bosetti & Quadros, 1996; Marques, 2006; Bosetti et al., 2012; Kunzler, 2012; Carbonaro & Ghilardi, 2016; Sedorko et al., 2021).

Although the Devonian paleontology of the Paraná Basin is among the best studied relative to other Brazilian basins, Terebratulida still require revision (Videira-Santos et al., 2023). For example, *Cryptonella*? *baini* has never been formally revised and has remained in open nomenclature since Clarke (1913a). In turn, some authors have questioned the validity of the genus *Paranaia* (e.g., Lee, 2006).

To further clarify knowledge about the Devonian Terebratulida of the Paraná Basin, this paper aims to provide a taxonomic review of selected taxa of this order. Such a review is essential because Paleozoic brachiopods are useful for paleoenvironmental and paleobiostratigraphic interpretations which require a well-defined systematic classification (Boucot, 1971; Racheboeuf, 1990; Ponciano & Machado, 2007; Jansen, 2016; Penn-Clarke & Harper, 2021, 2023; Jansen et al., 2025).

2. GEOLOGICAL SETTING

The Paraná Basin is one of the largest intracratonic basins in South America (Melo, 1988; Grahn, 1992; Milani et al., 2007) (Figures 1, 2, and 3). The Devonian succession of this basin is divided into the Furnas (Lochkovian), Ponta Grossa (late Pragian–early Emsian), and São Domingos (late Emsian–Frasnian) formations (Grahn et al., 2010a; Melo & Loboziak, 2003; Grahn et al., 2013). All these formations occur along

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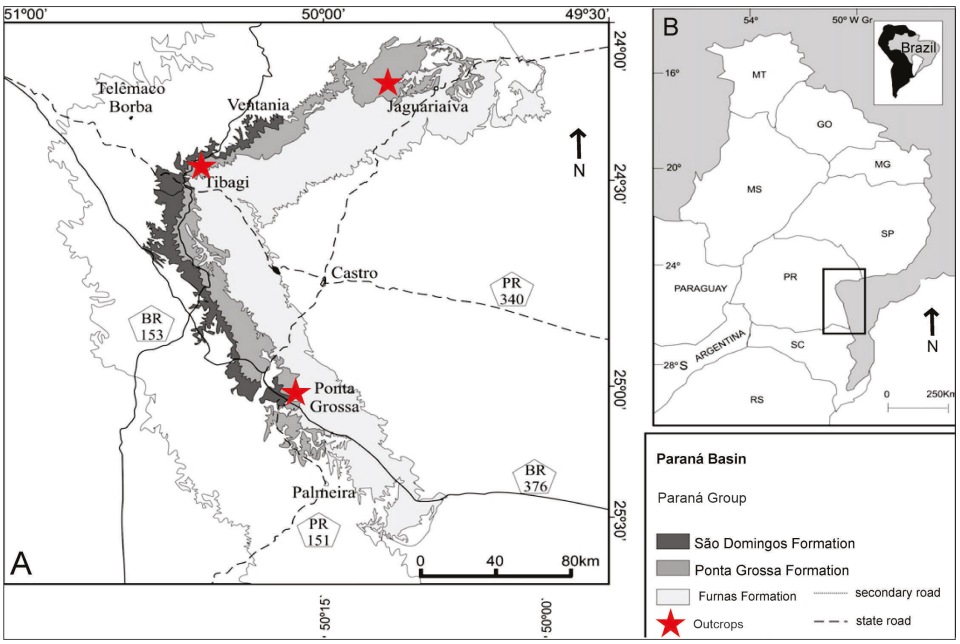


Figure 1. A. Outcrops studied in the state of Paraná indicated with stars. **B.** Paraná Basin, with emphasis on Devonian outcrops of the central part of Paraná (adapted from Grahn et al., 2013).

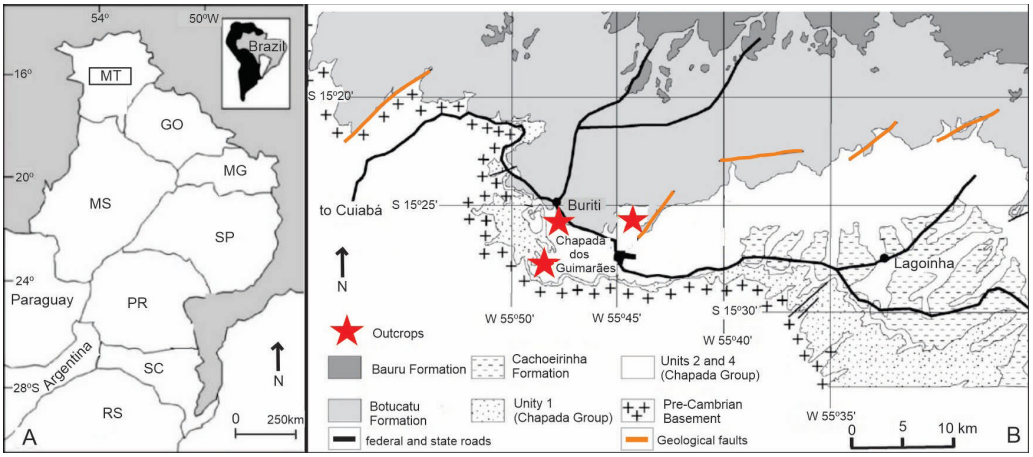


Figure 2. A. Paraná Basin, with emphasis on Devonian outcrops of the central part of the state of Mato Grosso. **B.** Outcrops studied in the state of Mato Grosso (Chapada dos Guimarães region) indicated by stars (adapted from Grahn et al., 2010b).

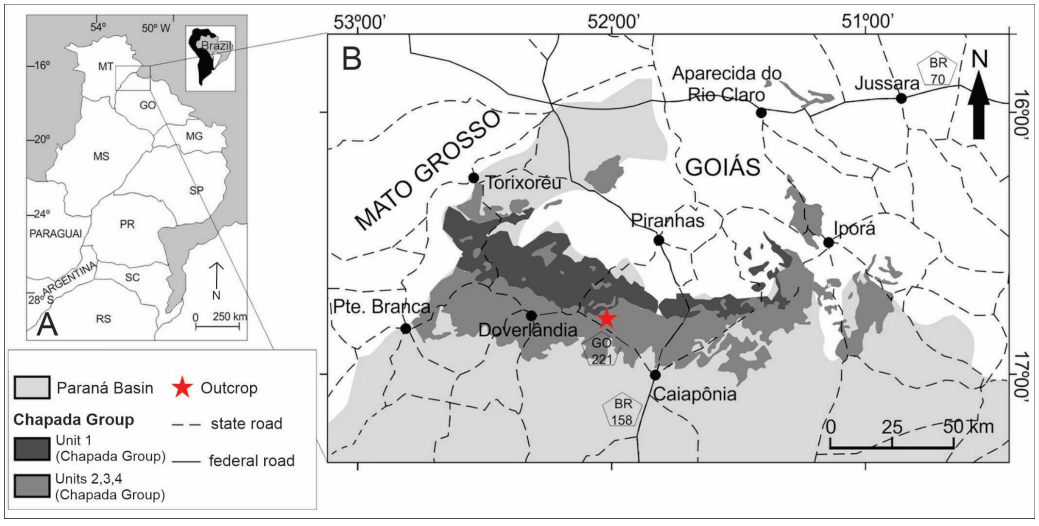


Figure 3. A. Paraná Basin, with emphasis on Devonian outcrops of the central part of Goiás. **B.** Outcrops studied in the state of Goiás indicated by a star (adapted from Carbonaro & Ghilardi, 2016).

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both the eastern and northwestern margins of the Paraná Basin, but brachiopods have been reported only from the Ponta Grossa and São Domingos formations.

The Ponta Grossa Formation is notably fossiliferous, and contains the typical Malvinoxhosan fauna (e.g., Clarke, 1913a; Petri, 1948; Caster, 1954; Lange, 1967; Melo, 1985, 1988; Bosetti et al., 2012; Penn-Clarke & Harper, 2021, 2023). The Ponta Grossa Formation is undivided, and the Jaguariaíva Member *sensu* Lange & Petri (1967) is considered a junior synonym of the Ponta Grossa shales *sensu* Oliveira (1912) according to Grahn et al. (2013). The Ponta Grossa Formation is interpreted as being of marine origin, encompassing shoreface and offshore environments (Sedorko et al., 2018).

According to Grahn et al. (2013), the Ponta Grossa Formation consists of sandstones interspersed with siltstones, sandy shales with calcareous nodules or sandy clay, and hard, dark shale, rich in pyrite and organic matter. The contact between the Ponta Grossa and Furnas formations is marked by a transgressive ravinement surface (Grahn et al., 2010a), whereas the contact between the Ponta Grossa and São Domingos formations is predominantly conformable (Vargas et al., 2020). In the São Domingos Formation, an impoverished Malvinoxhosan fauna occurs in its basal portion, and after the Givetian, the typical elements of the Malvinoxhosan fauna disappear or become rare (Bosetti et al., 2010, 2012).

The São Domingos Formation is subdivided only into the Tibagi Member, which constitutes the lowermost part of the formation. The succession displays cyclic alternation between sandstone and micaceous shale layers, although arenaceous beds dominate toward the top. The lithology consists of coarse- to fine-grained sandstones, siltstones, and claystones, and the age of this member is early late Emsian (Grahn et al., 2013).

The São Domingos Formation is marine in origin and comprises foreshore to offshore environments (Sedorko et al., 2018). It consists of poorly sorted conglomeratic sandstones, locally bituminous shales, and micaceous siltstones rich in plant fragments (Grahn et al., 2013). The contact between the São Domingos Formation and the Itararé Group is characterized by a low-angle erosional unconformity (Trzaskos et al., 2006).

3. MATERIAL AND METHODS

The specimens studied here are housed in the collections of the Museu Nacional/Universidade Federal do Rio de Janeiro (MN), Instituto de Geociências/Universidade Federal do Rio de Janeiro (UFRJ-DG Bq), Museu de Ciências da Terra/Serviço Geológico do Brasil (DGM-I), Universidade Federal de Mato Grosso (MP), Museu de História Natural de Mato Grosso (MHN MT), Departamento de Geologia/Universidade Federal do Paraná (UFPR PI), Museu de Ciências Naturais/Universidade Federal do Paraná (MCN), Universidade Estadual de Ponta Grossa (MPI), Universidade de São Paulo (GP 1E), National Museum of Natural History/Smithsonian Institution (USNM), New York State Museum (NYSM) and Cincinnati Museum Center (CMC IP). All the specimens analyzed are preserved as molds.

For taxonomic identification, the Treatise on Invertebrate Paleontology (Williams et al., 2006) was consulted, together with papers on Terebratulida taxonomy mainly from the Malvinoxhosan Realm, but also from the Eastern Americas Realm and the Brazilian Amazonas and Parnaíba basins (e.g., Clarke, 1913a; Cloud Junior, 1942; Suárez-Riglos, 1967; Carvalho, 1972; Isaacson, 1977).

4. SYSTEMATIC PALEONTOLOGY

Phylum Brachiopoda Duméril, 1806
Subphylum Rhynchonelliformea Williams et al., 1996
Class Rhynchonellata Williams et al., 1996
Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Stringocephaloidea King, 1850
Family Meganteriididae Schuchert and LeVene,1929
Subfamily Mutationellinae Cloud Junior, 1942
Genus *Mutationella* Kozłowski, 1929

Type species. *Waldheimia podolica* Siemiradzki, 1906.

Mutationella grahni nov. sp.
Figure 4(A-I)

Derivation of the name. In honor of the Swedish paleontologist Carl Yngve Grahn (1945-2025), who contributed greatly to our knowledge of the Devonian of the Paraná Basin.

Holotype. MPI 15747.

Paratype. MPI 18086, MPI 16056, MPI 16002, MPI 16202, MPI 16144, MPI 17747, MPI 17412, and MPI 15747.

Type locality. Bosque Mistral, Ponta Grossa, Paraná, Brazil.

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

Diagnosis. *Mutationella* species ranging from 8 mm to 20 mm in length, with a well-developed muscular field, a maximum of approximately 35 ribs, and a non-uniplicate anterior commissure.

Material. MPI 12974, MPI 13001, MPI 14020, MPI 14026, MPI 14076, MPI 14082, MPI 14090, MPI 14176, MPI 14211, MPI 14298, MPI 14350, MPI 14369, MPI 14384, MPI 14396, MPI 14398, MPI 14428, MPI 14621, MPI 14625, MPI 14688, MPI 14701, MPI 14740, MPI 14789, MPI 14966, MPI 15181, MPI 15261, MPI 15324, MPI 15338, MPI 15363, MPI 15394, MPI 15747, MPI 15756, MPI 15840, MPI 15852, MPI 16002, MPI 16056, MPI 16071, MPI 16089, MPI 16144, MPI 16202, MPI 16398, MPI 16460, MPI 16545, MPI 16672, MPI 16976, MPI 17007, MPI 17233, MPI 17389, MPI 17412, MPI 17527, MPI 17677, MPI 17747, MPI 17892, MPI 17897, MPI 17902, MPI 17903, MPI 17931, MPI 17963, MPI 17981, MPI 18050, MPI 18061, MPI 18072, MPI 18086, MPI 18357, MPI 18566, MPI 18583, MPI 18639, MPI 18875, and MPI 18988.

Provenance. Bosque Mistral (late Pragian - early Emsian).

Occurrences of the genus *Mutationella*. Algeria, Atafaitafa Formation - Lochkovian (Dubois & Mazelet, 1964); Argentina, Punta Negra and Talacasto formations - Pragian to Emsian (Herrera, 1995; Herrera & Bustos, 2001); Brazil, Ponta Grossa and Pimenteira formations - late Pragian to middle Givetian (Suárez-Riglos, 1967; this paper); Bolivia, Lower Icla Formation – Pragian (Isaacson, 1977); Canada, Torbrook Formation - Lochkovian (Boucot, 1999); Czechia, Lochkow and Praha formations – Lochkovian to Pragian (Mergl, 1986; Havlicek & Storch, 1999); Poland, unknown formation - Lochkovian (Tomczyk et al., 1977); South Africa, Hex River Formation - Eifelian (Penn-Clarke & Harper, 2023); Spain, Lebanza and Furada formations - Lochkovian (Binnekamp, 1965;

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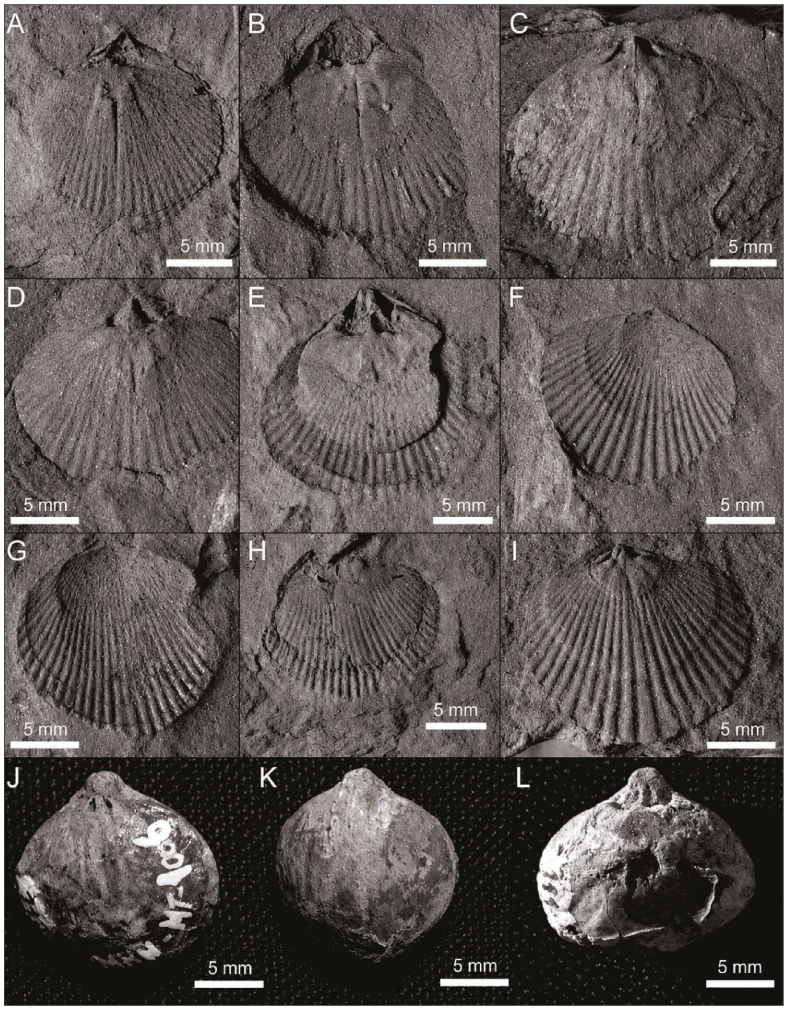


Figure 4. A-I. *Mutationella grahni* nov. sp., MPI 18086 (dorsal valve, paratype) (A), MPI 16056 (dorsal valve, paratype) (B), MPI 16002 (dorsal valve, paratype) (C), MPI 16202 (dorsal valve, paratype) (D), MPI 16144 (dorsal valve, paratype) (E), MPI 17747 (ventral valve, paratype) (F), MPI 17412 (ventral valve, paratype) (G), MPI 16976 (ventral valve, paratype) (H), MPI 15747 (dorsal valve, holotype) (I). **J-L.** *Mutationella* sp., MHN-MT-1006 (dorsal valve) (J), MHN-MT-1006 (ventral valve) (K) and MNH-MT-1107 (dorsal valve) (L).

García-Alcalde, 2011); United States of America, Tarratine Formation - Early Devonian (Boucot, 1973).

Description. Biconvex valve, suberect umbo, length ranging from 8 mm to 18 mm, width ranging from 8 mm to 20 mm, width/length ratio of 0,9-1,0; subrounded outline, with approximately 35 rounded ribs covering the entire valve, less distinct in the umbo region and separated by narrow interspaces. **Ventral interior:** poorly preserved and defined muscular field, separated by a thin myophragm; inclined cardinal plates, limiting the dental fossae, which are generally narrow and elongated. **Dorsal interior:** poorly preserved but large muscular field extending to approximately one-third of the valve with a subtriangular shape. Presence of a thin, short myophragm separating the muscular field and sometimes extending slightly beyond it; presence of incipient crural plates. Brachidium unknown.

Remarks. *Derbyina* and *Mutationella* are two similar genera that differ mainly in the umbo morphology: in general, the umbo of *Derbyina* is smooth, whereas that of *Mutationella* it is entirely costellate, although exceptions occur (Lee, 2006). Cloud Junior (1942) stated that the cardinal plate also serves to differentiate the two genera but the cardinal plate was not preserved in any of the *Derbyina* specimens analyzed here. Other proposed differences are dubious. Isaacson (1977) stated that *Derbyina* has shorter dental lamellae, a poorly impressed muscle field inside the ventral valve, fewer ribs than *Mutationella* (8-24 in *Derbyina* versus 22-34 in *Mutationella*), and a costellate valve, whereas in *Mutationella* the ribs extend only one-third of the way along the valve from the anterior margin, which is the opposite of the condition described in the revised Treatise on Invertebrate Paleontology (see Lee, 2006). Although Isaacson (1977, 1993) proposed the presence of *Mutationella* in the Devonian of Bolivia, Isaacson (1977) recognized the possibility that *Mutationella* and *Derbyina* might be synonyms as more specimens were studied. To clarify this issue, this study compared the specimens of *Mutationella* and *Derbyina* (DGM 222-I, DGM 223-I, DGM 224-I, DGM 225-I, DGM 226-I, DGM 227-I, DGM 229-I, DGM 231-I) from the Paraná Basin with specimens of *Mutationella* from the Devonian of Bolivia (unknown formation) (USNM 209036, and USNM 126164E) and the United States of America (Maine, Tarratine Formation) (USNM 126185A, USNM 126168B, USNM 126166B, USNM 126185A, USNM 126168B, USNM 126166B, USNM 126178A, USNM 126171, USNM 126173A, B, and USNM 126671). The morphological characteristics, including the ribs, cardinal plates, incipient crural plates, and the muscle field size, are identical among the Bolivian, U.S., and Brazilian *Mutationella* specimens but differ from those *Derbyina* specimens, such as DGM 222-I, considered a syntype of "*Derbyina whitiorum* Clarke, 1913a". This is the basis for considering the specimens analyzed here to belong to *Mutationella*, representing the first record of this genus in the

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Devonian of the Paraná Basin. *Mutationella grahni* differs from *M. salasica* García-Alcalde, 2011, *M. comtei* García-Alcalde, 2011, *M. podolica* (Siemiradzki, 1906), *M. sarrobi* Renouf, 1971, and *M. barroisi* (Asselberghs, 1930), in its larger size and better-developed muscle field (see García-Alcalde, 2011). *M. grahni* differs from *M. plicata* Mergl, 1986 mainly by lacking an uniplicate anterior commissure (see Mergl, 1986).

M. grahni differs from *M. fresnoensis* García-Alcalde, 2011 and *M. parlinensis* Boucot, Caster, Ives, and Talent, 1963 in having a significantly smaller number of ribs (approximately 35 in *M. grahni* compared with 44 and 64 in *M. fresnoensis* and to between 40 to 60 in *M. parlinensis*) (see Boucot, 1973; García-Alcalde, 2011).

Finally, *M. grahni* differs from *M. guerangeri* (Verneuil, 1850) in lacking two ribs in the median sector of the ventral valve that are thicker than the other ribs in the same shell (see Binnekamp, 1965), and *M. grahni* differs from *M.* aff. *guerangeri* in having thinner ribs (see Mergl, 1986).

Observation. The types of what was termed "*Mutationella falklandica* (Clarke, 1913a)" by Boucot (1973) are in the collection of the New York State Museum (NYSM 8477 and NYSM 8478), and after analysis, it was concluded that they belong to the genus *Pleurothyrella*.

Mutationella sp.

Figure 4(J-L)

Material. MHN MT 1006, and MHN MT 1107.

Provenance. Chapada dos Guimarães region (unknown outcrop, Devonian).

Occurrences of the genus *Mutationella*. Same as above.

Description. Small, with a maximum length of 11 mm and a maximum width of 13 mm; ribs very poorly marked; concentric growth lamellae present. The pedicle foramen is relatively large.

Remarks. The specimens display the typical characteristics of the genus *Mutationella* as discussed above. *Mutationella salasica, M. comtei, M. podolica, M. sarrobi,* and *M. barroisi* differ from *Mutationella* sp. in their larger size and better-developed muscle fields. *Mutationella* sp. differs from *Mutationella plicata* mainly in lacking a uniplicate anterior commissure (Mergl, 1986). It differs from *Mutationella grahni* in its smaller size and poorly marked and less numerous ribs. It may represent a new species of *Mutationella*; however, confirmation requires analysis of the interior of the specimens, which was not available. Therefore, additional specimens need to be analyzed.

Genus *Paranaia* Clarke, 1913a

Type species. *Centronella*? *margarida* Derby, 1895.

Diagnosis (emended from Derby, 1895**;** Clarke, 1913a**;** Cloud Junior, 1942**).** Externally homeomorphic to *Derbyina* but differentiated by the shape of the loop inside the dorsal valve. In *Paranaia,* the descending lamellae join in the median region of the shell in a "V" shape and extend into a single vertical median lamella.

Paranaia margarida (Derby, 1895)

Figure 5(A-E)

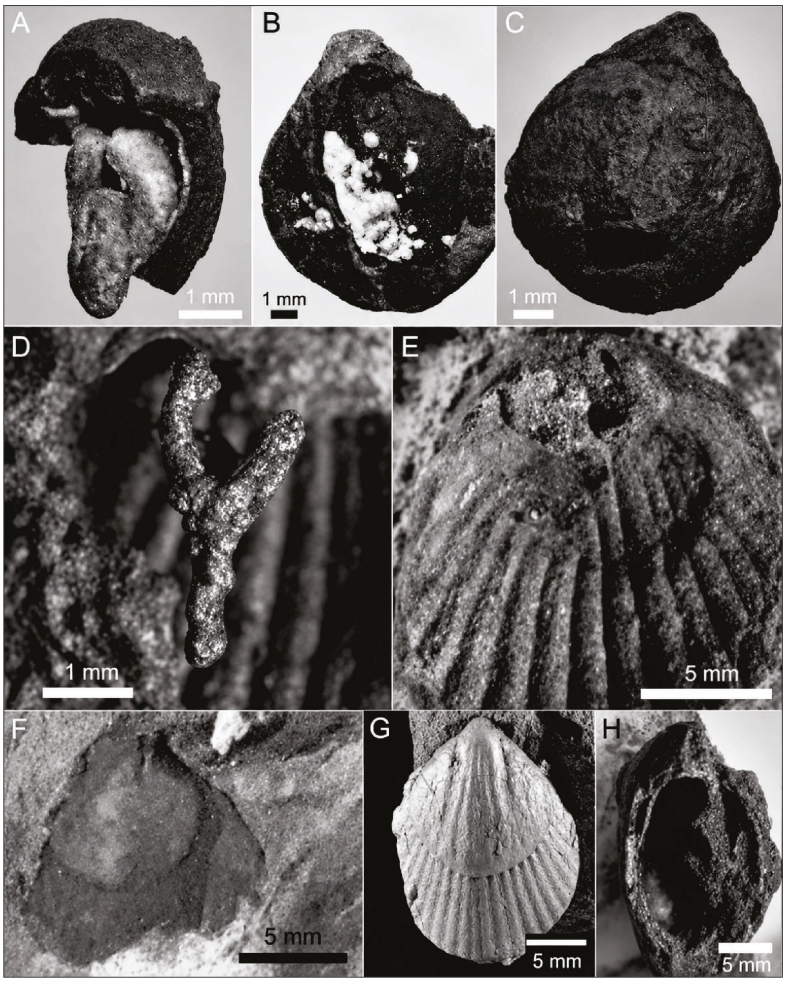


Figure 5. A-E. *Paranaia margarida* (Derby, 1895), MP 203 (dorsal valve, shape of the loop) (A), MP 258 (dorsal valve) (B), MP 307 (ventral valve) (C), MN 3321-I (dorsal valve, shape of the loop, lectotype. adapted from Kunzler, 2012) (D) and MN 3326-I (dorsal valve, paralectotype, adapted from Kunzler, 2012) (E). **F-H.** ?*Rhipidothyris* sp., UFRJ-DG 056 Bq (ventral valve) (F), MN 7079-I (ventral valve, Kunzler, 2012) (G) and MN 7080-I (dorsal valve, Kunzler, 2012) (H).

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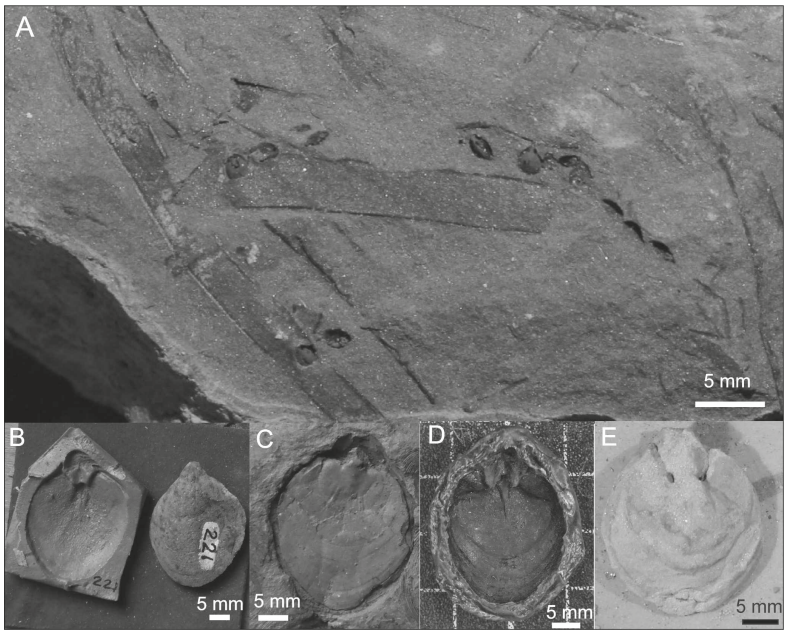


Figure 6. A-E *Cryptonella baini* (Sharpe, 1856), MCN P 1042a-n (juvenile *Cryptonella* symbiosis) (A), DGM 221-I (dorsal valve) (B), DGM 218-I (dorsal valve) (C), GP 1E 3933 (dorsal valve) (D) and NYSM 19752 (dorsal valve) (E).

1895 *Centronella*? *margarida*; Derby, p. 84, fig. 4a-b.

1913 *Paranaia margarida* (Derby); Clarke, pl. 21, fig. 7-8.

1913 *Brazilia margarida* (Derby); Clarke, est. XVII, figs. 18-19.

1920 *Chapadella* sp.; Greger, p. 70.

1920 *Brasilica* sp.; Greger, p.70.

1921 *Brasilina* sp.; Clarke, p. 139.

1934 *Oliveirella margarida* (Derby); Oliveira, p. 168.

1942 *Paranaia margarida* (Derby); Cloud Jr., p. 122-123, est. 21, figs. 9-14.

1967 *non Paranaia margarida* (Derby); Suárez-Riglos, pl. 1, fig. 21-23.

1981 *Paranaia* sp.; Quadros, p. 780, est. 4, fig. 4.

2012 *Paranaia margarida* (Derby); Kunzler, fig. 22b-c.

Lectotype. MN 3321-Ia (this paper).

Paralectotype. MN 3326-Ia (this paper).

Diagnosis. Same as the genus, by monotypy.

Material. MP 52, MP 54, MP 56, MP 203, MP 211, MP 241, MP 243, MP 252, MP 258, MP 268E, MP 306, MP 307, MP 313, MP 315, MP 319, MN 3321-Ia, and MN 3326-Ia.

Provenance. Estrada (late Pragian-early Emsian), Tope de Fita (late Pragian-early Emsian), and Chapada dos Guimarães - ?São Domingos Formation (early Givetian).

Occurrences. Brazil, Ponta Grossa and ? São Domingos formations – late Pragian to? early Givetian (Derby, 1895; Clarke, 1913a, b; Cloud Junior, 1942; Quadros, 1981; Kunzler, 2012; this paper).

Description. Small shell; length from 2 mm to 10 mm, and width from 2 mm to 9 mm, width/length ratio from 0,9 to 1,0; biconvex, with rounded ribs on both valves, not widely spaced, no folds or sulcus; subcircular outline, presence of growth lines present; suberect beak; and rounded foramen. **Ventral interior:** poorly preserved. **Dorsal interior:** brachial structure with the bases of the crura arising from the inner margin of the hinge plates, diverging anteriorly and extending to the point where the descending lamellae of the loop arise; the descending lamellae join in the median region of the shell in a "V" shape (Figure 5A) and extend into a single vertical median lamella. In younger specimens, the loop tends to be thicker than in older specimens.

Remarks. Derby (1895), when studying material from Mato Grosso, recognized some specimens that he identified as *Centronella*? *margarida*. This species was later assigned to various genera, including *Paranaia*, *Brazilia*, *Brasilina*, *Chapadella*, *Brazilica,* and *Oliveirella* (Clarke 1913b, 1921; Greger, 1920; Oliveira, 1934). Cloud Junior (1942), however, briefly discussed the different terms used to refer to *Centronella*. *margarida* and reinstated the term *Paranaia* as the valid name. Kozłowski (1929) suggested that *Paranaia* and *Derbyina* might be synonyms because they showed polymorphism similar to that observed in *Mutationella podolica*. In turn, Isaacson (1977) considered *Paranaia* and *Derbyina* to be synonyms, since variations in loop shape, and in presence or absence of a sulcus, and folds could represent intraspecific variation. However, Quadros (1981) compared his study specimens with those of Carvalho (1972), Derby (1895), and Clarke (1913a) and considered *Paranaia* to be distinct from *Derbyina*.

Lee (2006) treated *Derbyina* and *Paranaia* as synonyms, although Lee & MacKinnon (2006) stated that differences in loop shapes are an important morphological characters even for distinguishing superfamilies. Analysis of the material studied here showed that the specimens are externally very similar to *Derbyina* but the shape of the loop inside the dorsal valves differs markedly from *Derbyina*. This difference is also evident when comparing the specimens studied here with *Derbyina* of similar size, ruling out the possibility that it is due to ontogenetic differences. Homeomorphic genera are very common in brachiopods (Schuchert & Cooper, 1932; Ager, 1967; Rudwick, 1970; Cooper, 1972; Alvarez, 2003; Afanasjeva, 2016; Halamski, 2023).

Therefore, because the loop of the specimens analyzed here is identical to that described by Derby (1895) and illustrated by Kunzler (2012), but very different from the loop of *Derbyina* at the same ontogenetic stage, the specimens studied here are considered to belong to the genus *Paranaia*,

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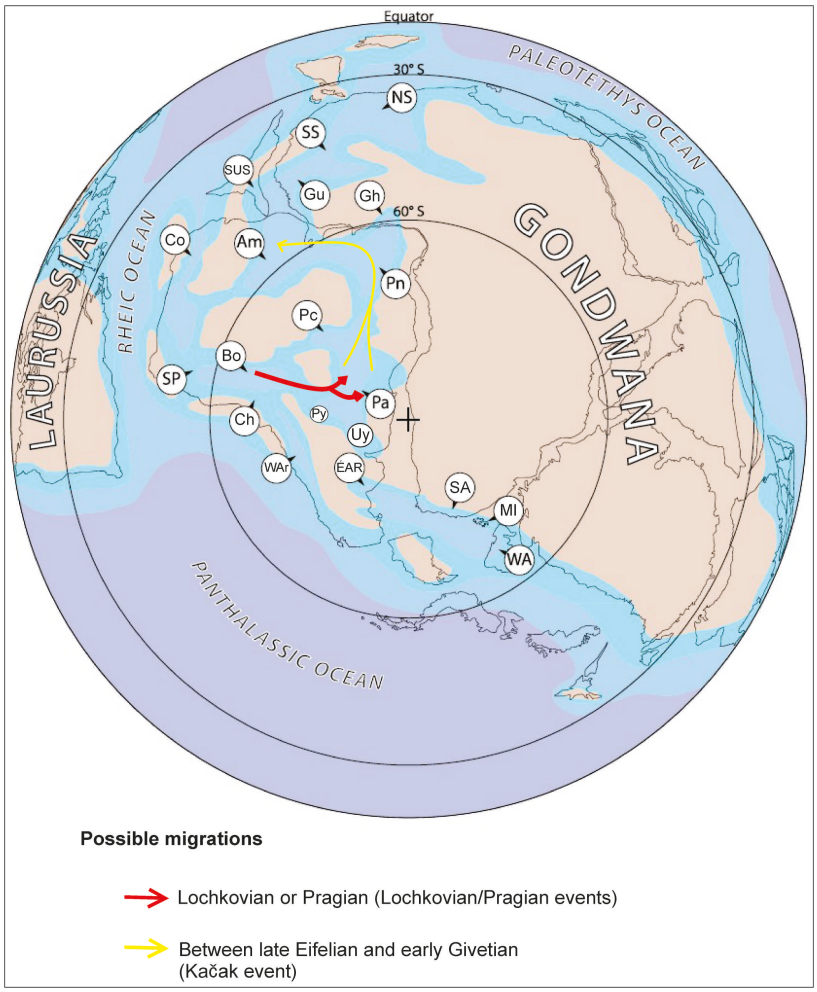


Figure 7. Possible dispersion of terebratulid brachiopods in part of the Malvinoxhosan Realm throughout the Devonian. Pa-Paraná Basin (Brazil), Uy-Uruguay, EAr-East Argentina), War-west Argentina, Py-Paraguay, Ch-Chile, Bo-Bolivia, Pc-Parecis Basin (Brazil), Pn-Parnaíba Basin (Brazil), Am-Amazonas Basin (Brazil), SP-South Peru, Co-Colombia, SA-South Africa, MI-Malvinas Islands, WA-West Antarctica, Gh-Ghana, SS-South Sahara, NS-North Sahara, SUS-South United States of America and Gu-Guinea (adapted from Penn-Clarke & Harper, 2021 and references therein).

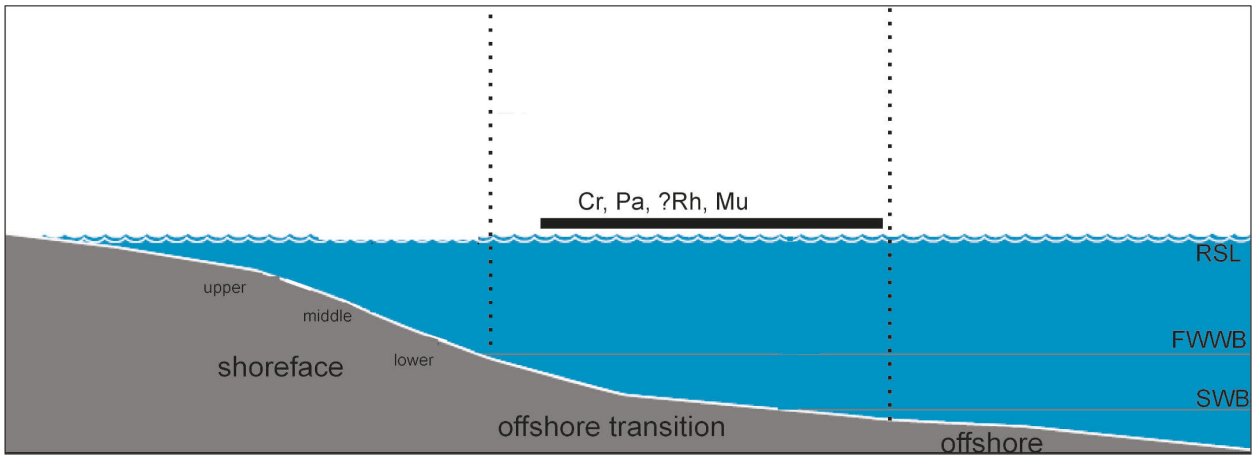


Figure 8. Preferential distribution across the shelf in the Paraná Basin of the taxa identified in this paper. Abbreviations: Cr, *Cryptonella* sp.; Mu, *Mutationella* sp.; Pa, *Paranaia* sp.;?Rh, ?*Rhipidothyris* sp.. RSL, Relative Sea Level; FWWB, fair-weather wave base; SWB, storm wave base level (adapted from Horodyski et al., 2019).

supporting its validity as a genus. *Paranaia* and *Derbyina* are therefore externally homeomorphic genera, that differ in the shape of the loop inside the dorsal valve.

In addition, the specimens studied here exhibit no other characteristics that distinguish them from the species described by Derby (1895). We therefore identify the specimens as belonging to the *Paranaia margarida* species. It should be noted, however, that Carvalho (1972) recognized a supposed species, *Paranaia wardiana*, in the Devonian of the Amazonas Basin but when illustrating the dorsal interior,

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the author actually only reproduced the dorsal interior of the species *Paranaia margarida* from the Paraná Basin (MN 3321-Ia and MN 3326-Ia). The other specimens illustrated by Carvalho (1972) ("MN 08" and "MN 09") are external dorsal and ventral valves, making it impossible to reliably differentiate *Derbyina* from *Paranaia*. Therefore, this supposed species ("*Paranaia wardiana*") requires revision. The genus *Paranaia* is currently considered to be monospecific, with *Paranaia margarida* as its type species

Observation 1. The lectotype and paralectotype proposed here (MN 3321-Ia and MN 3326-Ia) were lost in the fire that affected the facilities of the Museu Nacional/UFRJ in 2018. However, Article 74 of the International Code of Zoological Nomenclature (International Comission On Zoological Nomenclature, 1999) allows the designation of lectotypes by means of illustrations or descriptions, and the fact that a specimen no longer exists or cannot be traced does not invalidate the designation.

Observation 2. Suárez-Riglos (1967) cited the occurrence of *Paranaia margarida* in the Pimenteira Formation (Parnaíba Basin, Brazil), but analysis of the original material deposited at the Cincinnati Museum Center (CMC IP 38452) indicates that it probably belongs to ?*Globithyris,* since this genus is externally homeomorphic to *Derbyina* and does not have a strongly incurved umbo like that of the specimens from the Parnaíba Basin. Therefore, the occurrence of *Paranaia* in the Parnaíba Basin is not considered here.

Observation 3. In the Universidade de São Paulo collection, replicas of the specimens "MN 08" and "MN 09" considered by Carvalho (1972) to be *Paranaia wardiana* were not found. It is important to note that although they are cited as "MN 08" and "MN 09", indicating that they belong to the collection of the Museu Nacional/UFRJ, this is not an official numbering system, since these numbers refer to specimens from France in the accession-number book of that institution.

Family Rhipidothyrididae Cloud Junior, 1942

Subfamily Rhipidothyridinae Cloud Junior, 1942

Genus *Rhipidothyris* Cooper and Williams, 1935

Type species. *Rhipidothyris plicata* Cooper and Williams, 1935.

?*Rhipidothyris* sp.

Figure 5(F-H)

2012 *Globithyris*? sp.; Kunzler, p. 89-90, fig. 22d-f.

Material. MN 7079-I, MN 7080-I, MHN MT 995, MHN MT 1041, and UFRJ-DG 056 Bq.

Provenance. Cachoeira Véu da Noiva (early Givetian), Independência (Middle Devonian?), and Chapada dos Guimarães (Devonian).

Occurrences of the genus *Rhipidothyris*. Australia, Etonvale Formation -?Eifelian (McKellar, 1966); South Africa, Karoopoort Formation – Givetian (Boucot & Theron, 2001);?Brazil, São Domingos Formation – Eifelian to Givetian (this paper); Bolivia, Chakjeri Formation – Givetian (Isaacson, 1993; Boucot & Theron, 2001); China, Yingtang Formation – Eifelian (Chen & Qiao, 2008); Libya, ?al Qasr Formation – Eifelian (Havlicek & Röhrlich, 1987); and United States of America, Gilboa beds, Ludlowville Formation -?Givetian (Cloud Junior, 1942; Boucot & Theron, 2001).

Description. Small size, length from 6 mm to 10 mm, and width from 6 mm to 12 mm, width/length ratio from 1,0 to 1,1; with some specimens being wider than long. Subcircular to oval outline; up to 25 thin to medium ribs, separated by interspaces of approximately width; concentric growth lines present; in umbo region, a prominent lamella without ribs is usually present; ventral beak erect and slightly incurved. **Ventral interior:** poorly preserved muscle field, thin and separated by a thin myophragm; short, subparallel, anteriorly diverging dental lamellae present. **Dorsal interior**: crura extending approximately one-third of the shell length, lamellae descending from the brachidium with a slight backward curvature. At approximately two-thirds of the shell length, the lamellae ascend again and join in an inverted "U" shape in the median region of the valve, ending in a well-developed deltiform loop.

Remarks. Cloud Junior (1942), when proposing the genus *Globithyris,* based it on the characteristics of the foramen and crural plates, which could not be observed in the material analyzed here. However, these specimens are externally similar to what Isaacson (1977) identified as *Globithyris* aff. *G. diana* (Clarke, 1907). Isaacson (1993) reclassified *Globithyris* aff. *G. diana* as *Rhipidothyris ava* Isaacson, 1993, because *Globithyris* was considered restricted to the Early Devonian (see Havlicek & Röhrlich, 1987). Isaacson (1993) rejected the possibility that it represented *Neoglobithyris* based on morphological criteria but did not explain in detail why it was then considered *Rhipidothyris* other than for supposed biostratigraphic reasons. In fact, neither the Brazilian nor the Bolivian specimens are *Globithyris*, because when compared with specimens of *Globithyris* from the United States of America deposited at the NMNH/SI (USNM 126182, USNM 126165, USNM 125994, and USNM 125946), it can be seen that *Globithyris* has a much more inflated valve, a more strongly curved umbo, and thicker ribs. The specimen MN 7080-I illustrated by Kunzler (2012) may represent the first record of a brachidium of the genus *Rhipidothyris*. However, this specimen was probably lost in the fire at the Museu Nacional/UFRJ in 2018. Because the brachidium is a key feature for identifying this taxon (see Lee, 2006; Chen & Qiao, 2008) and is poorly preserved, the specimens studied here were classified using open nomenclature. According to Boucot & Theron (2001), all occurrences of *Rhipidothyris* are in the Givetian, although older occurrences have been reported in the literature (e. g., Chen & Qiao, 2008).

Observation. Suárez-Riglos (1967) recorded *Rhipidothyris* from the Cabeças Formation (Parnaíba Basin, Brazil) but Boucot & Theron (2001) considered this occurrence is questionable because of the poor quality of the images presented by Suárez-Riglos (1967). In the present study, this material deposited at the Cincinnati Museum Center under the number CMC IP 38460a-n was analyzed and is probably *Derbyina* based on the shape of its sulcus; therefore, its occurrence in the Parnaíba Basin is not considered here. However, there are other specimens in this collection identified by Suárez-Riglos (1967) as other genera may represent *Rhipidothyris* (CMC IP 38465, CMC IP 38466, and CMC IP 38477).

Superfamily Cryptonelloidea Thomson, 1926

Family Cryptonellidae Thomson, 1926

Subfamily Cryptonellinae Thomson, 1926

Genus *Cryptonella* Hall, 1861

Type species. *Terebratula rectirostra* Hall, 1860.

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Cryptonella baini (Sharpe, 1856)
Figure 6(A-E)

1913 *Cryptonella*? *baini*; Clarke, p. 208-210, est. XVII, figs. 10-17.

1977 *Cryptonella baini* (Sharpe); Isaacson, p. 210-211, pl. 7, figs. 4-19.

2013 *Cryptonella baini* (Sharpe); Cerri, figs. 3c, d, f.

Material. DGM 218-I, DGM 219-I, DGM 220-I, DGM 221-I, DGM 1537-I, DGM 1834-I, UFRJ-DG 105 Bq, MPI 2282, MPI 11901, MPI 14715, MN 12205-I, MN 12213-I, UFPR 1608 PI, UFPR 1609 PI, UFPR 1610 PI, UFPR 1611 PI, UFPR 1612 PI, UFPR 1613 PI, MCN P 1042a-n, GP 1E 3933a, b, GP 1E 3936, GP 1E 7511, GP 1E 7516a, b, and NYSM 19752.

Provenance. Tibagi of Clarke (1913a) (Eifelian), Ponta Grossa of Clarke (1913a) (late Pragian-early Emsian), Colégio Agrícola, km 255, Ponta Grossa-PR (?late Pragian-?early Emsian), Jaguariaíva (late Pragian-early Emsian), Monjolo dos Padres (Givetian), Rivadávia (Pragian), Jaguariaíva (late Pragian-early Emsian), Curva II (Pragian), Bosque Mistral (late Pragian-early Emsian), and Fazenda Sonho Meu (late Emsian-Eifelian).

Occurrences of the genus *Cryptonella*. Bolivia, Lower Icla and Lower Belén formations – Pragian to early Emsian (Isaacson, 1977); South Africa, Bokkeveld Group - ?late Emsian to late Givetian (Reed, 1903); Brazil, Ponta Grossa and São Domingos formations – late Pragian to Givetian (Clarke, 1913a; Cerri, 2013; this paper); ?Antarctica, Horlick Formation – Lower Devonian (Doumani et al., 1965); Spain, Portilla and Candás formations – Givetian (García-Alcalde, 2013); Czechia, Koneprusy Limestone – Pragian (Mergl, 1985); and United States of America, Jeffersonville, Norway Point, Three Forks and Jennings formations – Eifelian to Famennian (Kindle, 1900; Stumm, 1951; Robinson, 1963).

Description. Biconvex valves, ranging in length from 3 mm (juvenile forms) to approximately 30 mm (senile forms) and in width from 2.5 mm (juvenile forms) to approximately 28 mm (adult forms), with a width/length ratio of 0,8 to 0,9; with an oval to more rarely, circular profile; maximum width approximately half the length of the valve; shell without ribs, bearing only concentric lamellae, rectimarginate anterior margin. Umbo is erect to slightly curved. **Ventral interior:** elongate, thin, sparsely impressed muscle field extending halfway down the shell; thin myophragm extending slightly beyond the middle of the valve. **Dorsal interior:** thin hinge plate, initially united, and later becoming medially separated; perforated by a foramen at the posterior end; small dental plates; elongated dental fossae; incipient; thin, elongated muscular impression; presence of a crural base present in one specimen (GP 1E 3933); and a septum that thins anteriorly and does not support the hinge plate. No preserved loop was found in any specimen.

Remarks. According to Cloud Junior (1942) and Jin & Lee (2006) *Cryptonella* species are characterized by having a cryptonelliform brachidium, an unsupported and perforated hinge plate, well-impressed muscle fields, a submesothyrid foramen, and an erect to suberect umbo. The interiors of the *Cryptonella* valves found from the Paraná Basin are generally poorly preserved but the external morphology shows sufficient differences to allow comparison with other *Cryptonella* species and to support the validity of *Cryptonella baini*. *Cryptonella baini* (Sharpe, 1846) differs from *C. melonica* (Barrande, 1847) and *C. reimmani* Cloud, 1942 in having a rounded rather than subpentagonal outline. *C. baini* differs from *C. attenuata* (Whiteaves, 1898) and *C. chaconae* García-Alcalde, 2013 in its larger size. Adult specimens of *C. attenuata* are no larger than 10 mm (see Cloud Junior, 1942), whereas the largest specimens of *C. chaconae,* are approximately 20 mm. *C. chaconae* may not even belong to *Cryptonella* because it has a mesothyrid foramen, whereas *Cryptonella* has a submesothyrid foramen (see Jin & Lee, 2006); this species therefore requires revision. *C. baini* differs from *C. rectirostra* (Hall, 1860) in its rounded outline and more elongated shape (greater length/width ratio) and from *C. planirostra* (Hall, 1860) in lacking a sulcus on the external valve surface. Finally, *C. baini* differs from *C. eximia* Hall, 1862 in having less inflated valves and a less curved umbo. Other forms attributed in the literature to *Cryptonella*? *inortata* (d'Orbigny, 1850), *Cryptonella minor* García-Alcalde, 1988, and *Cryptonella truyolsi* García-Alcalde, 1999 were synonymized as *Monsenella inornatoides* (d'Orbigny, 1850), *Monsenella boucoti* García-Alcalde, 2013, and *Maisotia truyolsi* (García-Alcalde, 1999), respectively, by García-Alcalde (2013). Although some works that cite the occurrence of *Cryptonella baini* without questions in the Paraná Basin, following Clarke (1913a), no formal revision had been conducted to confirm its validity. Isaacson (1977) recognized the presence of *C. baini* in the Devonian of Bolivia and accepted its occurrence in Brazil, based on Clarke (1913a) but did not review the Brazilian material.

5. DISCUSSION

5.1 Plants or animals as a substrate for *Cryptonella*

Brachiopods depend on stable attachment for survival, both to ensure access to food and oxygen, and to facilitate the dispersal of reproductive products (Curry, 1981). There is good evidence that many articulated brachiopods with a free-living adult habit may have had an attached habit as juveniles (Curry, 1981).

In the Paleozoic, several records document plants or animals serving as substrates for brachiopods, as compiled by Vinn et al. (2024). In the collection of the Museu de Ciências Naturais/Universidade Federal do Paraná, there is a sample of approximately 14 juvenile *Cryptonella* (MCN P 1042a-n), about 3 mm long, with no ribs or concentric growth lines, a slightly recurved umbo, and very poorly preserved valve interiors, although the external morphology is typical of *Cryptonella*. These specimens appear to have used plants or animals as substrates, however, because of their preservation, the substrate cannot be identified with certainty. Three possibilities are considered: a land plant, a cnidarian, or algae.

Hypothesis 1 (land plant): This behavior is known in Recent brachiopods (Curry, 1981), and there are also records from the Mesozoic (see Fossa-Mancini, 1933; Weller, 1957; Thomson, 1971) and Paleozoic (Pashin & Ettensohn, 1992; Racheboeuf & Herrera, 1998), although few studies have confirmed that the brachiopods were actually attached to plants. Feldman (1980) considered that land plants could have served as substrates for *Coelospira* sp. in the Middle Devonian of New York, although he found no positive evidence. Racheboeuf & Herrera (1998), in turn,

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recognized an association between *Kentronetes variabilis* and plant fragments (*Cooksonia* sp.) in the Lochkovian of Argentina (Talacasto Formation). Notably this association occurred only in juvenile specimens of *K. variabilis,* and was probably not coincidental, as the spines are curved and oriented toward the plant fragments. From this, Racheboeuf & Herrera (1998) therefore interpreted that *K. variabilis* and other strophochonetids as potentially having an epiplanktonic life habit as juveniles. The same may be considered here for *Cryptonella*, which could potentially have had an epiplanktonic life habit as a juvenile. The specimens are aligned in the direction of the plant fragments, suggesting that the association was not coincidental.

Hypothesis 2 (tubiculous cnidarian): The brachiopods described here may have been associated with parts of a tubiculous cnidarian. Such an association has been reported since the Cambrian of Laurentia (Van Iten et al., 2002). Brachiopods may have benefited from this association by occupying a higher tier for suspension feeding (Vinn et al., 2024). In the Devonian of the Paraná Basin, tubiculous cnidarians such as *Sphenothallus* have been reported (Van Iten et al., 2019).

Hypothesis 3 (algae): The final hypothesis is that the organisms are algae, more specifically, coralline algae, sufficiently robust an association with brachiopods. Brachiopod–algae and bivalve–algae assemblages have been reported from the Paleozoic to the Recent (Ruedemann, 1934; Rudwick, 1965; Havlíček & Vaněk, 1966; McRoberts & Stanley Junior, 1989).

Additionally, the Museu de Ciências Naturais/UFPR donated, through its curator Fernando Sedor, a large sample of algae to the Museu Nacional/UFRJ, containing hundreds a much larger number of clearly anchored individuals, more than hundreds. Unfortunately, the material was never studied, and the sample was lost in the fire at the Museu Nacional/UFRJ in 2018. However, it came from the same outcrop as the material analyzed here (Rivadávia), suggesting that this habit was not unusual.

5.2 Paleobiogeography

The genus *Paranaia* is possibly typical of Malvinoxhosan Realm (Penn-Clarke & Harper, 2021) from the middle/late Eifelian onward (Figure 7). The other genera analyzed here (*Mutationella*, *Cryptonella,* and *Rhipidothyris*) occur in other Malvinoxhosan regions, mainly in Bolivia but are not endemic to this realm.

Cryptonella is a genus that has achieved abroad geographic distribution across the globe and is highly adaptable to different ocean temperatures, occurring in the Old World, Eastern Americas, and Malvinoxhosan realms. There are records of *Cryptonella* from the Pragian of Czechia, Bolivia, and Brazil (Reed, 1903; Clarke, 1913a; Doumani et al., 1965; Kindle, 1900; Stumm, 1951; Robinson, 1963; Isaacson, 1977; Mergl, 1985; Cerri, 2013; García-Alcalde, 2013).

Mutationella is also a genus that appears to have adapted to different paleotemperatures and is also found in the Old World, Eastern Americas, and Malvinoxhosan realms. The genus arose in the Lochkovian of Europe, Algeria, or Canada and from the Pragian onward is found in the Malvinoxhosan regions of Bolivia and Brazil (Dubois & Mazelet, 1964; Suárez-Riglos, 1967; Boucot, 1973; Isaacson, 1977; Tomczyk et al., 1977; Mergl, 1986; Herrera, 1995; Havlicek & Storch, 1999; Boucot, 1999; Herrera & Bustos, 2001; García-Alcalde, 2011; Penn-Clarke & Harper, 2023).

According to Boucot & Theron (2001), all occurrences of *Rhipidothyris* are in the Givetian, although older occurrences have been reported in the literature (*e.g.*, Chen & Qiao, 2008). According to Penn-Clarke & Harper (2021), *Rhipidothyris* and *Tropidoleptus* are markers of the end of the Malvinoxhosan Realm. *Tropidoleptus* is found in the Paraná Basin and is, in principle, restricted to the northwestern edge of the basin, as is the possible occurrence of *Rhipidothyris* (Videira-Santos & Scheffler, 2023).

Among the genera studied here, *Paranaia* is the only typical Malvinoxhosan genus that was endemic to this realm. *Paranaia* was apparently restricted to the Paraná Basin; however, because the genus has been considered synonymous with *Derbyina*, the specimens identified as *Derbyina* in other Malvinoxhosan regions should be reviewed to determine whether they actually belong to this genus or could instead represent *Paranaia*.

The migration of *Cryptonella* from Bolivia to the Paraná Basin may be related to the Lochkovian/Pragian sea-level-rise events, as also reported for the chonetoids *Babinia* and *Sanjuanetes* (Videira-Santos et al., 2022) and the trilobite *Metacryphaeus* (Carbonaro et al., 2018).

Inferences about the migration of *Rhipidothyris* to the Paraná Basin must be made with caution, because its identification is based on open nomenclature. Even assuming that the generic identification is correct, it is difficult to infer the genus's dispersal pathway, given its widespread distribution during the Eifelian/Givetian (Cloud Junior, 1942; McKellar, 1966; Havlicek & Röhrlich, 1987; Isaacson, 1993; Boucot & Theron, 2001; Chen & Qiao, 2008). However, given the paleogeographic proximity, the genus may have entered the Paraná Basin from Bolivia during the Eifelian/Givetian. Another possibility is that it entered the Paraná Basin from the Parnaíba Basin (Brazil), given that Suárez-Riglos (1967) reported the presence of this genus from the Cabeças Formation (middle Givetian). However, this specimen is housed at the Cincinnati Museum Center (USA; CMC IP 38460) and its identification as *Rhipidothyris* is doubtful and requires taxonomic revision. Under either hypothesis (from Bolivia or the Parnaíba Basin), the migration may have been related to the Kačák event.

It is not possible to infer a migration pathway for *Paranaia*, because it was apparently restricted to the Paraná Basin, as explained above; its supposed occurrence in the Parnaíba Basin, as proposed by Suárez-Riglos (1967), is not considered valid here.

5.3 Paleoenvironments

Boucot (1975), based on brachiopods, proposed six Benthic Assemblages (BA 1-6) ranging from the intertidal to deep subtidal zones of Siluro–Devonian seas. Here, we preferred to divide the paleoenvironments into shoreface (= fair-weather deposits/BA 2 to upper BA 3), offshore transition (= storm-influenced or storm-dominated deposits/lower BA 3 to BA 4), and offshore (= deposits below the storm wave base level/BA 5 to BA 6) (see Horodyski et al., 2019) (Figure 8).

According to García-Alcalde (2013), in the Devonian of Spain, *Cryptonella* shells would have been suitable for more agitated reef environments but this type of environment

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is not known from the Devonian of the Paraná Basin. The specimens studied here were found in both sandy siltstones and fine sandstones, with articulated valves and commonly parallel to the bedding plane, suggesting that they are autochthonous to parautochthonous. A proximal to middle offshore transition environment is suggested for this genus in the Paraná Basin.

Boucot (1971) included mutationellids in the *Eocoelia* paleocommunity. Anderson (1971), on the other hand, stated that *Mutationella* inhabited very proximal environments (shoreface). In turn, García-Alcalde (2013) reported that *Mutationella* occurred in different environments in the Devonian of Spain, being found both in sandstones and shales as well as in sandy carbonates, indicating shallow environments with high turbidity. The *Mutationella grahni* specimens analyzed here are all from the Bosque Mistral outcrop and were found in dark siltstones to shales, parallel to the bedding plane and generally articulated, indicating that they are autochthonous to parautochthonous preservation. At Bosque Mistral, *Mutationella grahni* occurs in the same levels as chonetoids such as *Pleurochonetes* and *Kentronetes*, which were interpreted as having inhabited the offshore transition by Goltz (2023) and Goltz et al. (2025) in this outcrop. Videira-Santos et al. (2022) likewise interpreted that *Pleurochonetes* and *Kentronetes* as preferring the offshore transition, based on their occurrence in several other outcrops in the Paraná Basin. *Mutationella grahni* is therefore interpreted as having inhabited an environment corresponding to the middle to distal offshore transition. Regarding *Mutationella* sp., paleoenvironmental interpretations are not possible because the specimens are isolated in the collection and are not preserved in the rock matrix.

Paranaia and ?*Rhipidothyris* have so far been found only been found in the northwestern part of Paraná Basin but in silty facies. The specimens are commonly articulated in these facies, suggesting autochthonous to parautochthonous deposition and occupation of the offshore transition environment.

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 taphonomic bias. Therefore, additional taphonomic studies in different outcrops across the Paraná Basin are necessary to corroborate the inferences made here.

6. CONCLUSION

In this study, five terebratulid taxa were identified from the Devonian of the Paraná Basin. We recognize the first occurrences of the genera *Mutationella* (*Mutationella grahni* nov. sp. and *Mutationella* sp.) and ? *Rhipidothyris* in the Paraná Basin; and confirm the validity of the taxa *Cryptonella baini* and *Paranaia margarida* in the basin. The migration of *Cryptonella* and *Mutationella* from Bolivia to the Paraná Basin may be related to the Lochkovian/Pragian sea-level-rise events. The migration of ?*Rhipidothyris* from the Parnaíba Basin or Bolivia may have been related to the Kačák event.

In turn, paleoenvironmental considerations indicate that: *Cryptonella*, *Mutationella*, *Paranaia*, and ? *Rhipidothyris* inhabited the offshore transition environment.

The results presented here represent a further contribution to our knowledge of the Devonian faunal diversity of the Paraná and the distribution of terebratulid brachiopods throughout the Malvinoxhosan Realm.

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