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TAXONOMY OF DEVONIAN CONULARIIDS (CNIDARIA) FROM MATO GROSSO DO SUL, PARANÁ BASIN, BRAZIL

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ABSTRACT – Devonian conulariids (Cnidaria) from the Ponta Grossa Formation, Paraná Basin, have been studied since 1913, when the fauna composed of *Paraconularia africana* (Sharpe), *Conularia quichua* Ulrich, and *Paraconularia ulrichana* (Clarke) was first described. Since then, much work has been done encompassing their taphonomy, systematics, and paleobiology. However, until now the studies have relied on conulariids from the eastern border area of the basin. Therefore, there was a lack of information on the conulariids of the northwestern border area of the Paraná Basin, particularly from the Mato Grosso do Sul, for which there are no previous descriptions of these fossils. The present analysis of specimens from the Ponta Grossa Formation in Mato Grosso do Sul revealed the presence of *Conularia quichua*, *Paraconularia africana*, *P. ulrichana*, and *Reticulaconularia caetensis* sp. nov. Therefore, the diversity of the conulariid fauna recorded from the northwest border area of the basin is greater than that of the eastern border area, where the genus *Reticulaconularia* has not yet been found, and the presence of *Paraconularia ulrichana* still needs confirmation. Furthermore, our data suggest that the Paraná Basin had narrow connections with the Devonian seas of Bolivia, at least during sea-level rise, as indicated by the shared benthic marine fauna.

Keywords: Conulariids, Lower Devonian, Ponta Grossa Formation, Paraná Basin.

RESUMO – Os conulariídeos (Cnidaria) devonianos da Formação Ponta Grossa, da Bacia do Paraná, são estudados desde 1913, quando a fauna composta por *Paraconularia africana* (Sharpe), *Conularia quichua* Ulrich e *Paraconularia ulrichana* (Clarke) foi descrita pela primeira vez. Desde então, foram feitos muitos trabalhos envolvendo sua tafonomia, sistemática e paleobiologia. No entanto, até então os estudos foram feitos com conulariídeos da borda leste da bacia. Portanto, há uma falta de informações sobre conulariídeos provenientes da borda noroeste da Bacia do Paraná, especialmente do Mato Grosso do Sul, onde não há descrições formais desses fósseis. A análise de espécimes da Formação Ponta Grossa, no Mato Grosso do Sul, indica a presença de *Conularia quichua*, *Paraconularia africana*, *P. ulrichana* e *Reticulaconularia caetensis* sp. nov. Portanto, a diversidade da fauna de conulariídeos registrada na borda noroeste da bacia é maior que da borda leste, onde o gênero *Reticulaconularia* ainda não foi encontrado e a espécie *Paraconularia ulrichana* ainda carece de confirmação. Além disso, os dados sugerem que a Bacia do Paraná poderia manter conexões com os mares devonianos da Bolívia, pelo menos nos períodos de aumento do nível do mar, como indicado pela similaridade da fauna marinha bentônica.

Palavras-chave: Conulariídeos, Devoniano Inferior, Formação Ponta Grossa, Bacia do Paraná.

INTRODUCTION

Conulariids are an extinct group of benthic marine cnidarians, related to scyphozoans, which ranged from the terminal Ediacaran to the Late Triassic (Van Iten *et al*., 2006, 2014; Leme *et al*., 2022). They are characterized by a four-sided elongate pyramidal theca composed of francolite (Babcock, 1991; Van Iten, 1991; Leme, 2002; Leme *et al*., 2008). Conulariids have been found on all continents except Antarctica (Lucas, 2012).

In South America, there are significant occurrences of conulariids in Argentina (*e.g*., Leme *et al*., 2003), Uruguay (*e.g*., Mendéz-Alzola & Sprechmann, 1973), Peru (*e.g*., Steinmann, 1930), Paraguay (*e.g*., Babcock *et al*., 1990), Bolivia (*e.g*., Babcock *et al*., 1987; Babcock, 1988) and Brazil (*e.g*., Clarke, 1913; Kozlowski, 1913; Simões *et al*., 2000;

Leme, 2002; Rodrigues, 2002; Siviero, 2002; Leme *et al*., 2004). They are ubiquitous in marine Devonian strata of the Malvinokaffric Realm, including the "conulariids beds" of Bolivia (Babcock *et al*., 1987). However, although conulariids are abundant, they are not very diverse. In the Devonian of Bolivia, for example, Babcock *et al*. (1987) recognized only six valid species: *Conularia albertensis* Reed, 1925; *C. quichua* Ulrich, 1890; *Malvinoconularia cahuanotensis* (Branisa & Vanek, 1973); *Paraconularia africana* (Sharpe, 1856); *P. ulrichana* (Clarke, 1913); and *Reticulaconularia baini* (Ulrich, 1892).

In Brazil, conulariids occur in the Silurian and Devonian successions of the Amazonas Basin (*e.g*., Fonseca & Machado, 1999), Devonian of the Paraná Basin (*e.g*., Clarke, 1913), Devonian of the Parnaíba Basin (*e.g*., Siviero, 2002) and in the Ediacaran Corumbá Group (Leme *et al*., 2022). In the Amazonas Basin, Clarke (1899) and Katzer (1933) identified *Conularia amazonica* Clarke, 1899 in Silurian beds and Sivieiro (2002) identified *C. amazonica* in the Pitinga Formation and ?*Paraconularia* sp. nov. in the Maecuru Formation. In the Parnaíba Basin, Kegel (1953) identified *Paraconularia* cf. *africana* from the Pimenteira Formation and *Conularia undulata* from the Itaim Formation, and Siviero (2002) identified two species: "*Conularia*" sp. nov. from the Itaim Formation and *Conularia* sp. nov. 2 from the Pimenteira Formation. Finally, Leme *et al*. (2022) recently identified *Paraconularia ediacara* in the Ediacaran Corumbá Group.

Clarke (1913) reported three species from the Paraná Basin, including *Paraconularia africana* (Sharpe, 1856); *Conularia quichua* Ulrich, 1890, and *P. ulrichana* (Clarke, 1913). Lange (1954) revised Clarke's descriptions and identified three species: *Paraconularia africana* (originally described as *Mesoconularia africana*), *Conularia quichua* (identified by Lange (1954) as *Plectoconularia quichua*), and *P. ulrichana*. Siviero (2002) identified four species in the Ponta Grossa Formation: *Paraconularia ulrichana*; *Conularia* sp. 1; *Conularia* sp. nov.; and *Reticulaconularia baini*. Finally, Leme (2002) and Leme *et al*. (2004) published a major revision of 133 specimens of conulariids from the Ponta Grossa Formation at Jaguariaíva. They reported only two species from the Paraná Basin: *Paraconularia africana* and *Conularia quichua*. Leme's (2002) and Leme et al. (2004) studies are the most recent large-scale taxonomic revision of conulariids from the Paraná Basin.

Although conulariids from the Paraná Basin are the most intensively studied in Brazil in terms of taphonomy, taxonomy, and paleobiology, they are restricted to the Devonian strata of the eastern border area of the basin (*e.g*., Clarke, 1913; Kozlowski, 1913; Simões *et al*., 2000; Leme, 2002; Rodrigues, 2002; Rodrigues *et al*., 2003, 2006; Leme *et al*., 2004). Therefore, there is a lack of information on conulariids from the northwestern border area of the Paraná Basin, especially in the Mato Grosso do Sul State, for which there are no formal descriptions of conulariids.

This study aimed to carry out a taxonomic analysis of the conulariids from Mato Grosso do Sul and to recognize the species composition and diversity.

GEOLOGICAL SETTING

The Paraná Basin is a polycyclic intracratonic sedimentary basin. It includes parts of southern Brazil, eastern Paraguay, northeastern Argentina, and northern Uruguay and covers an area of approximately 1,500,000 km^2 (Milani *et al*., 2007). According to Ramos (1970) and Pereira *et al*. (1998), the Paraná Basin in Brazil had two sedimentary depocenters during the Early Paleozoic: the northern Alto Garças and southern Apucarana sub-basins. However, Sedorko *et al*. (2018a) and Scheffler *et al*. (2020) concluded that these sub-basins may not have been completely differentiated until at least the Emsian.

The Devonian of the Paraná Basin in Brazil comprises portions of the states of Mato Grosso do Sul, Mato Grosso, Goiás, and Paraná (Melo, 1988). It consists of the upper unit of the Furnas (Lochkovian, *sensu* Sedorko *et al*., 2017), the Ponta Grossa (Late Pragian – Early Emsian, *sensu* Grahn *et al*., 2013), and the São Domingos (Late Emsian – Frasnian, *sensu* Grahn *et al*., 2013) formations. These marine strata consist of transgressive-regressive cycles related to relative sea level oscillations (Milani *et al*., 2007). This study dealt with conulariids collected from the Ponta Grossa Formation.

The Ponta Grossa Formation comprises shoreface and offshore settings (Melo, 1988; Assine, 1996; Bergamaschi, 1999; Milani *et al*., 2007; Grahn *et al*., 2013; Sedorko *et al*., 2018b). Grahn *et al*. (2013) reported that the basal lithologies of the Ponta Grossa Formation are sandstones with intercalated siltstones. Overlying these lithologies are sandy shales with limestone nodules or arenaceous clays. The uppermost portion of the Ponta Grossa Formation consists of hard, pyrite-bearing shales.

The studied conulariid specimens were collected in Mato Grosso do Sul, from the Estância Nhecolândia and Corredeira do Caeté outcrops (Figure 1). The Corredeira do Caeté outcrop is located in the Taquari River, above the Palmeiras waterfall, in the municipality of Coxim (18º18'31.06" S 54º36'30.60" W; altitude: 224 m). The specimens occur within concretions, recorded in tabular beds of fine sandstones on the riverbed. The Estância Nhecolândia outcrop is located along the MS080 highway, two kilometers from Rio Verde de Mato Grosso, in the municipality of Rio Negro (19º24'41.91" S 54º58'59.92" W; altitude: 252 m). The specimens occur in tabular to lenticular beds of fine to medium grained sandstone and in laminated sandy siltstones (Figure 2).

MATERIAL AND METHODS

The studied conulariid specimens are deposited in the paleoinvertebrate collection of the Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro (Table 1).

All specimens were rescued following the fire that impacted the institution's collection. Therefore, the first stage of this research was to identify the samples and their provenance. Each sample was assigned a rescue number to specify its position in the collection. The next step was to

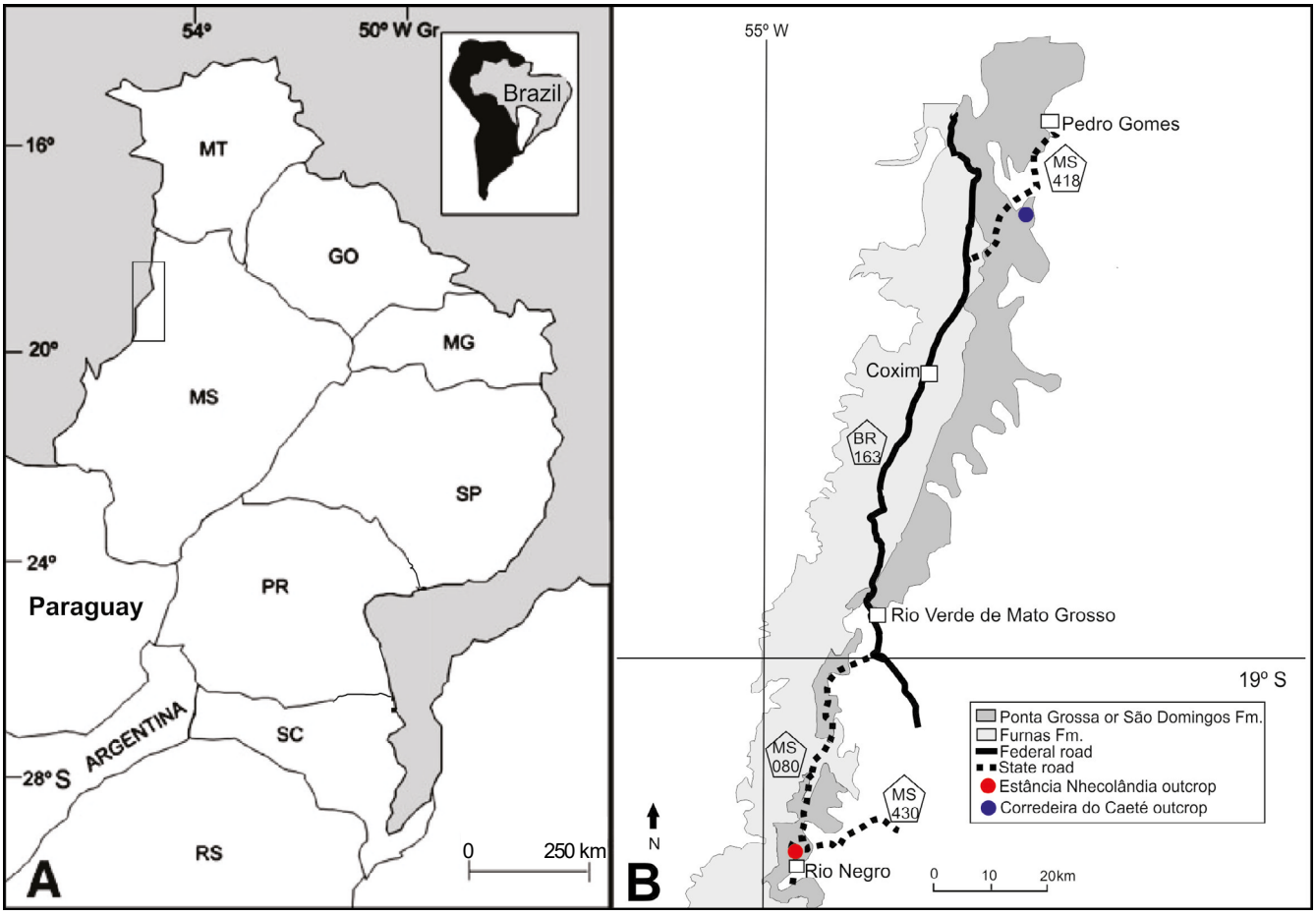

Figure 1. A–B, Location map of the outcrops with conulariid specimens from the Mato Grosso do Sul State. **A**, adapted from Grahn *et al*., 2013; **B**, adapted from Scheffler *et al*. (2020).

Table 1. Locality and identification code of each studied specimen.

Institution	Code	Locality
Museu Nacional (UFRJ)	MN-PRO-2-I / MN-PRO-3-I	MS14 (Estância Nhecolândia outcrop) 19º 24' 41" S 54º 58' 59" W
	MN12037-I / MN12038-I / MN12039-I / MN12040-I / MN12041-I / MN12042-I / MN12043-I / MN12044-I / MN12045-I / MN12046-I / MN12047-I	MS65 (Corredeira do Caeté outcrop) 18º 18' 31" S 54º 36' 30" W

identify the original code of each sample. It was possible to retrieve the original code of all but two specimens (127E374.001 – rescue number), to which we assigned a provisional code until they can be properly identified and reincorporated into the original collection. The provisional codes have acronyms pertaining to the Museu Nacional (**MN**), provisional code (**PRO**), number of the sample (2–3) and invertebrate collection (**I**).

The specimens from the Corredeira do Caeté outcrop are well preserved inside the concretions, allowing detailed morphological descriptions. However, they are usually incomplete owing to the absence of the apical region, a taphonomic condition also commonly noted in the conulariid specimens of the Ponta Grossa Formation from the Apucarana Sub-basin (Simões *et al*., 2000; Leme, 2002; Rodrigues, 2002; Siviero, 2002; Leme *et al*., 2004). The same is true for the specimens of the Estância Nhecolândia outcrop, where they are preserved in sandstones.

The anatomical terminology (Figure 3) employed in this study was based on Babcock & Feldmann (1986a), Van Iten *et al*. (1996) and Leme *et al*. (2003, 2008), in order to follow the standard terminology of conulariids in the literature. However, some quantitative characters, such as "rib angle" and "apical angle", can be modified by taphonomic processes (see Simões *et al*., 2003 for a detailed discussion about this issue). Therefore, these characters are only measured in well-preserved fossils, in which taphonomic factors have not influenced the morphometric characteristics of the fossil. The specimens were examined using a stereomicroscope, and the morphometric parameters were measured in the Leica Imaging System and Corel Draw 2018.

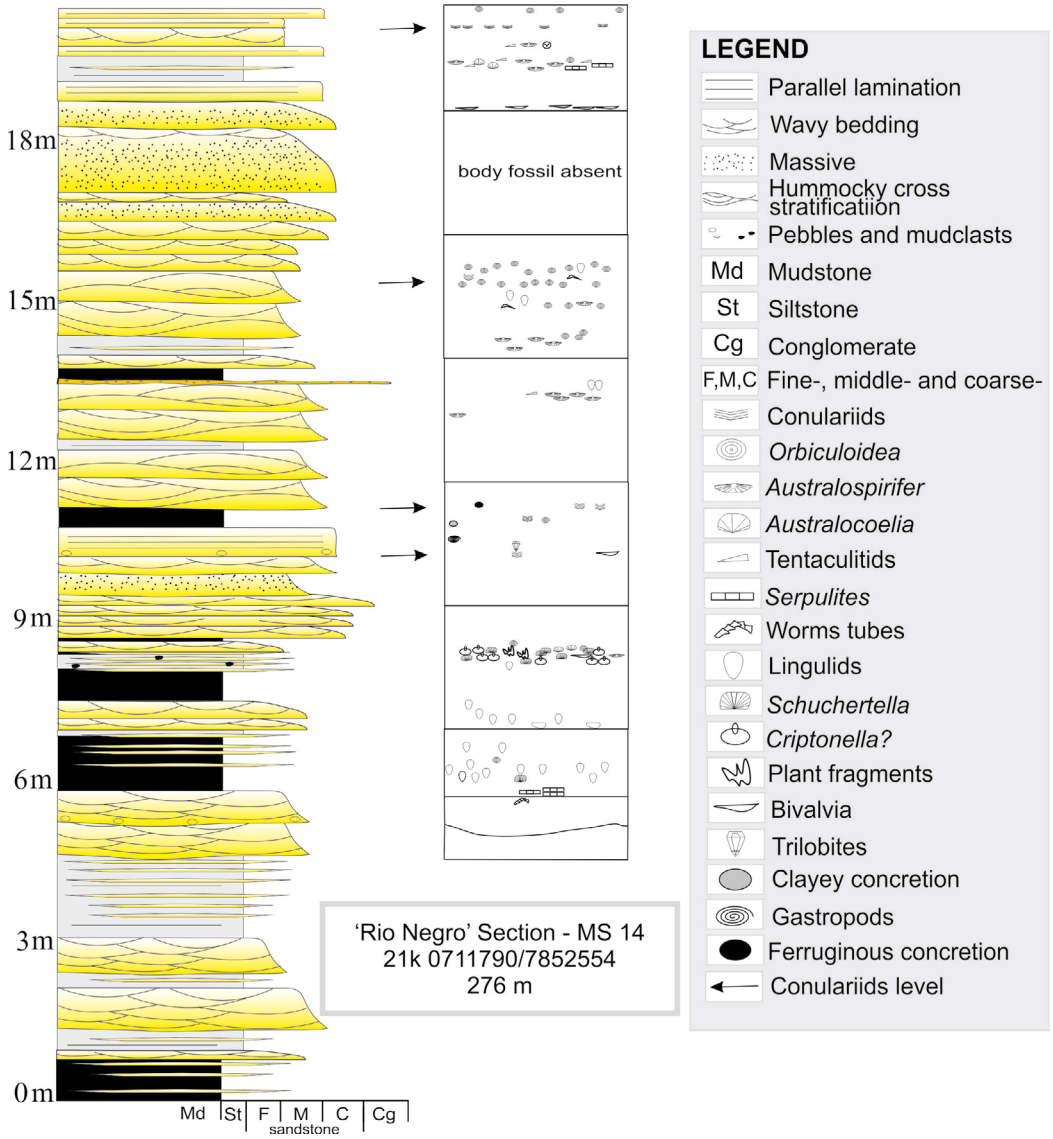

Figure 2. Vertical section of the Estância Nhecolândia outcrop. Conulariid levels are indicated by arrows. The studied specimens were collected at the top of the outcrop.

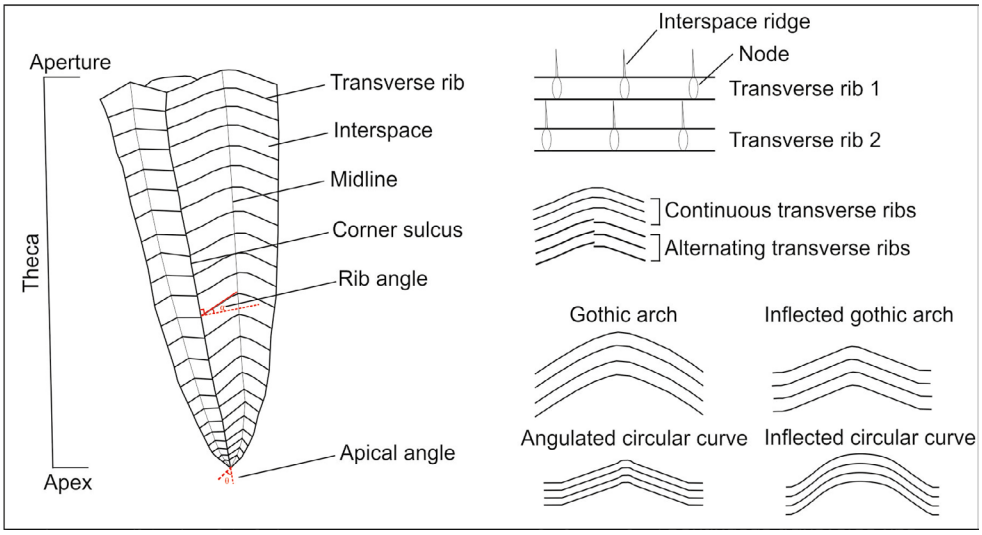

Figure 3. Conulariid morphology with the main characters used in the descriptions (modified from Babcock & Feldmann, 1986a; Van Iten *et al*. 1996; Leme *et al*., 2003).

SYSTEMATIC PALEONTOLOGY

Phylum CNIDARIA Verrill, 1865
Subphylum MEDUSOZOA Peterson, 1979
Class SCYPHOZOA Götte, 1887
Order CONULARIIDA Miller & Gurley, 1896

Conularia Sowerby, 1820

Type species. *Conularia quadrisulcata* Sowerby, 1820.

Conularia quichua Ulrich, 1890
(Figure 4)

1890 *Conularia quichua* Steinmann & Döderlein, p. 343, fig. 395d–e.
1913 *Conularia quichua* Clarke, p. 163.
1948 *Mesoconularia quichua* Sinclair, p. 119.
1954 *Plectoconularia quichua* Lange, p. 34.
1987 *Conularia quichua* Babcock *et al.*, p. 218, fig. 4.
2002 *Conularia quichua* Leme, p. 33, est. 1 e 2.
2004 *Conularia quichua* Leme *et al*., p. 217, fig. 4.

Type material. Lost holotype (Babcock *et al*., 1987). YPFB 3432 and USNM 409818 (neotypes).
Material. Part and counterpart of a fragment of a pyramidal theca; MN12040-I.
Occurrence. Corredeira do Caeté (Pragian–early Emsian) outcrop.
Description. Pyramidal theca measuring 17 mm long, without apex and aperture. The preserved faces are mutually adjacent and similar in width. The transverse ribs are continuous across the midline and are adaperturally arcuate. The transverse ribs exhibit a gothic arch style near the apical region and an angulated circular curve style elsewhere. Within the corner sulcus the transverse ribs are continuous, but their poor preservation in this region prevents further observations. The ribs ranges from 27 to 33 per cm and are ornamented by nodes, which range from 4 to 5 per mm.
Remarks. The major revision of the conulariids of Leme (2002) showed the predominance of *Conularia quichua* in the Ponta Grossa Formation. However, only one specimen of *C. quichua* was identified from Mato Grosso do Sul. The articulation pattern of the transverse ribs (where the gothic arch style predominates near the apical region and angulated circular curve style is present elsewhere), the continuity of the ribs at the midline and the close spacing of the transverse ribs and nodes were key characteristics to properly identify the specimen as *Conularia quichua*. All the characteristics here described agree with those observed by Leme (2002) and Leme *et al*. (2004) in *Conularia quichua* from the Ponta Grossa Formation.

Paraconularia Sinclair, 1940

Type species. *Conularia inaequicostata* Koninck, 1883.

Paraconularia africana (Sharpe, 1856)
(Figure 5)

1856 *Conularia africana* Sharpe, p. 214, est. 27, figs. 13a–b.
1913 *Conularia africana* Clarke, p. 160.
1954 *Mesoconularia africana* Lange, p. 34.
1987 *Paraconularia africana* Babcock *et al*., p. 221, fig. 7.
2002 *Paraconularia africana* Leme, p. 42, est. 3.
2004 *Paraconularia africana* Leme *et al*., p. 218, fig. 5.

Type material. BM (NH) 4279 (lectotype) and BM (NH) 4278 (paralectotype).
Material. The specimens are preserved in concretions, generally with two adjacent faces on both the part and counterpart: MN12037-I / MN12038-I / MN12039-I / MN12041-I / MN12042-I / MN12044-I / MN12045-I / MN12046-I / MN12047-I.
Occurrence. Corredeira do Caeté (Pragian–early Emsian) outcrop.
Description. Specimens measure up to 75 mm long, faces equal in width. Corner sulcus with internal carina and ornamented with alternating, disrupted transverse ribs. At the midline, the transverse ribs predominantly alternate and exhibit inflected gothic arch style. The transverse ribs number up to 28 per cm in the apical region and from 12 to 20 per cm elsewhere. Apical angles vary between 10º and 25º, and rib angles measure from 13º to 20º. Nodes and interspace ridges are absent in all specimens.
Remarks. *Paraconularia africana* differs from other species of the genus in having an internal carina at the corners, widely spaced transverse ribs, inflected gothic arch style,

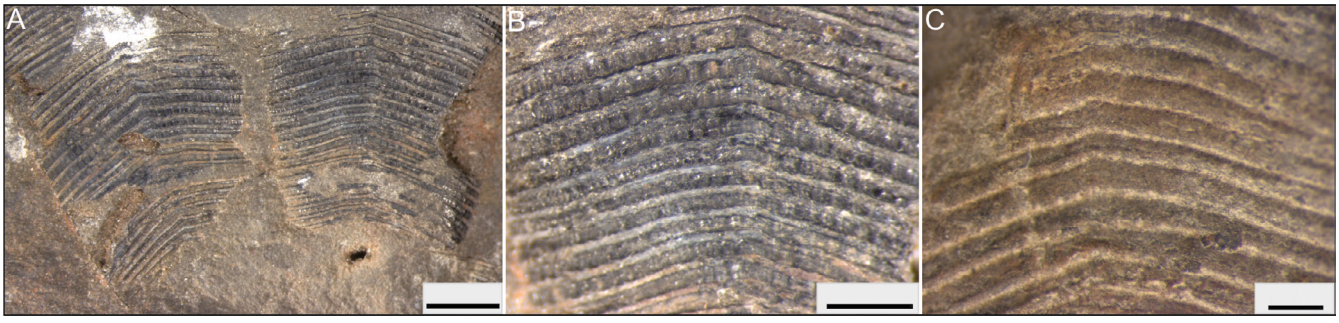

Figure 4. A–C, *Conularia quichua*, MN12040-I: **A**, two faces preserved, with the apex missing; **B**, transverse ribs continuous at the midline and nodes present; **C**, transverse ribs adaperturally arcuate at the midline. Scale bars: A = 2 mm; B = 1 mm; C = 500 µm.

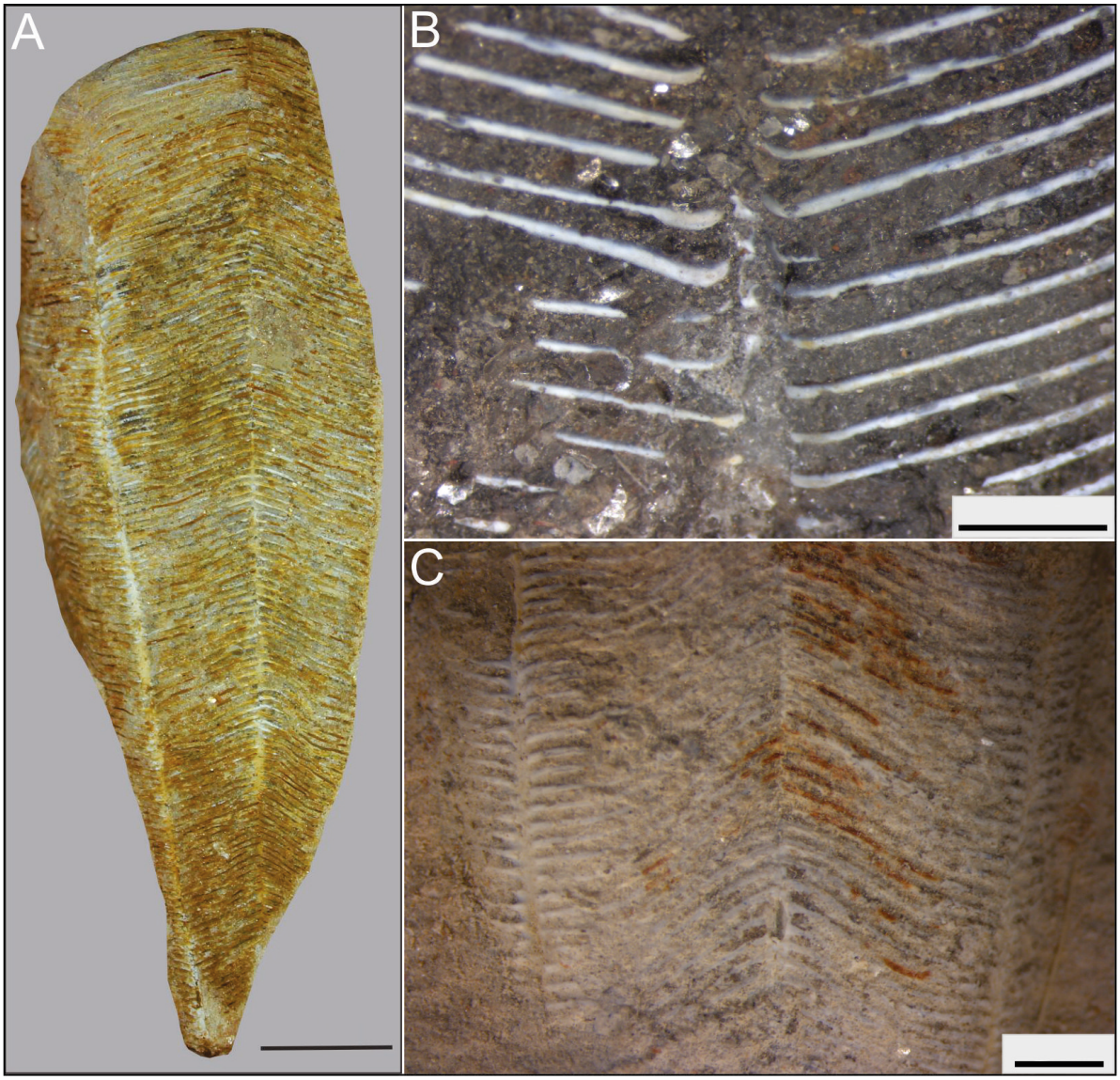

Figure 5. A–C, *Paraconularia africana*: **A**, MN12038-I, almost complete specimen preserved in a concretion. Transverse ribs exhibiting an inflected gothic arch style and predominantly alternating at the midline; **B**, MN12037-I, corner sulcus with alternating, disrupted transverse ribs; **C**, MN12044-I, transverse ribs showing an inflected gothic arch style. Scale bars: A = 1 cm; B–C = 2 mm.

and in lacking nodes and interspace ridges. Leme (2002) redescribed the species and observed gothic arch style in *Paraconularia africana*. However, our specimens exhibit an inflected gothic arch style, also documented by Babcock *et al*. (1987) in specimens from Bolivia. This could be related to morphological variation within the species.

Paraconularia ulrichana (Clarke, 1913)
(Figure 6)

1892 *Conularia* cf. *acuta* (Roemer) Ulrich, p. 30, fig. 5a, 5b.
1913 *Conularia ulrichana* Clarke, p. 161, est. VIII, fig. 16–21.
1954 *Conularia ulrichana* Lange, p. 33.
1987 *Paraconularia ulrichana* Babcock *et al*., p. 223, fig. 8.
2002 *Paraconularia ulrichana* Sivieiro, p. 47, est. I, II, figs. 1–8, 1–10.

Type material. DGM 93-I (lectotype); DGM 91-I, DGM 92-I, DGM 94-I, DGM 95-I (paralectotype).
Material. MN-PRO-2-I / MN-PRO-3-I.
Occurrence. Estância Nhecolândia (Pragian–early Emsian) outcrop.
Description. The specimens are preserved as parts and counterparts of fragmented conulariid thecae in sandstone, measuring approximately 10 mm in length. The transverse ribs alternate and are disrupted within the corner sulcus, and apparently there is no internal carina. At the midline, the transverse ribs predominantly alternate and exhibit an inflected circular curve style. In addition, an internal carina is present at the midline and there is no ornamentation. The apex is completely missing. The transverse ribs range from 14 to 17 per cm. Nodes and interspace ridges are absent.
Remarks. This species is distinct from all other *Paraconularia* described in the literature. It is the only one with rib articulation

exclusively of the circular curve style, interspace ridges or nodes absent, and an internal carina along the midline. Our description is consistent with those from Bolivia (*e.g*., Babcok *et al*., 1987) and Brazil (*e.g*., Clarke, 1913; Siviero, 2002). The occurrence of the species in the eastern border area of the Paraná Basin still requires confirmation, as it was not reported by Leme (2002) and Leme *et al*. (2004).

Reticulaconularia Babcock & Feldmann, 1986b

Type species. *Conularia penouili* Clarke, 1907.

Reticulaconularia caetensis sp. nov.
urn:lsid:zoobank.org:act:723A4EA9-84F9-49BD-91AE-ABDE167BC5B4
(Figure 7)

Diagnosis. Theca with long, thin, longitudinally aligned and closely spaced (4 to 6 per mm) interspace ridges and nodes. Transverse ribs always alternate at the midline, forming a gothic arch style and numbering 16-17 per cm. Transverse ribs are disrupted in the corner sulcus.

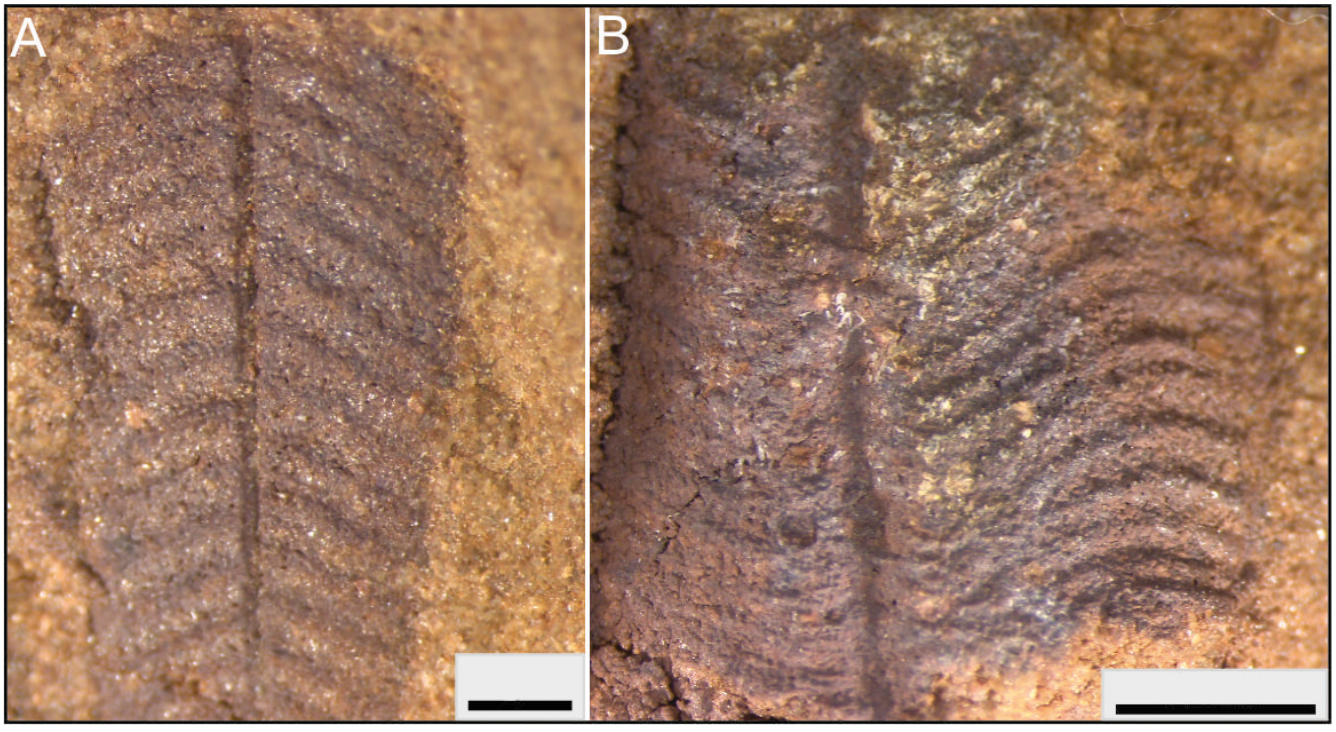

Figure 6. A–B, *Paraconularia ulrichana*: **A**, MN-PRO-2-I, one face preserved with internal carina along the midline; **B**, MN-PRO-3-I, transverse ribs exhibiting an inflected circular curve style. Scale bars: A = 1 mm; B = 2 mm.

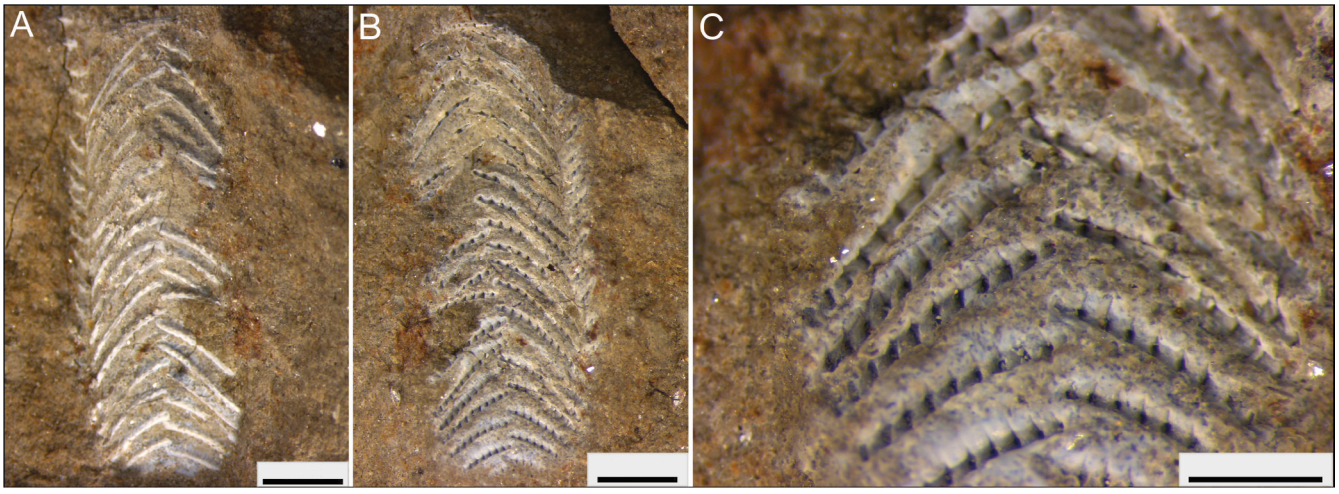

Figure 7. A–C, *Reticulaconularia caetensis* sp. nov., MN12043-I: **A**, Transverse ribs exhibiting a gothic arch style and alternating at the midline; **B**, one face preserved and one corner sulcus. Reticulate pattern derived from nodes and longitudinally aligned interspace ridges; **C**, closely spaced nodes and interspace ridges. Scale bars: A–B = 2 mm; C = 1 mm.

Holotype. Part and counterpart of a conulariid preserved in a concretion; MN12043-I.
Type locality. Corredeira do Caeté (Pragian–early Emsian) outcrop.
Etymology. The term *caetensis* refers to the Corredeira do Caeté rapids, where the fossil was found.
Description. Single specimen measuring 1.3 cm in length. Apex missing. The transverse ribs alternate at the midline and exhibit a gothic arch style. In the corner sulcus, the transverse ribs alternate and are disrupted, and there is no internal carina. Viewed in transverse cross section, the corner sulcus is angulated. The transverse ribs range from 16 to 17 per cm, and they exhibit nodes and interspace ridges, which range 4 to 6 per mm. The interspace ridges are longitudinally aligned, and together with the transverse ribs they form a "reticulated pattern".
Remarks. This specimen has all the morphological characters defined by Babcock & Feldmann (1986b), Van Iten *et al*. (2000) and Leme (2006) for the genus. However, it does not resemble the only species of the genus present in the Malvinokaffric Realm, *Reticulaconularia baini*. The specimen has a gothic arch style, instead of the inflected gothic arch style of *Reticulaconularia baini*, and nodes and interspace ridges are much closer together, numbering 4 to 6 per mm, while in *Reticulaconularia baini* they number 2 to 3 per mm (Babcock *et al*., 1987). Babcock & Feldmann (1986b) described two additional species within this genus, and these show clear differences from the specimen described above. *Reticulaconularia penouili* (Clarke, 1907) has two rib articulations along the theca: inflected circular curve style in the apical and apertural regions and angulated circular curve style in the middle region. Both styles are absent in *Reticulaconularia caetensis* sp. nov. Additionally, the spacing of the nodes and interspace ridges in *R. penouili* is much wider, numbering 1 to 2 per mm, and this species represents the only known conulariid having large, oblong, hollowed out interridge furrows on the exterior surface of the exoskeleton, as described by Babcock & Feldmann (1986b). The other species of the genus is *Reticulaconularia sussexensis* (Herpers, 1949), which differs from *Reticulaconularia caetensis* sp. nov. in its rib articulation (inflected gothic arch style). The transverse ribs in *R. sussexensis* usually abut at the midline, while in *R. caetensis* sp. nov. the transverse ribs always alternate at the midline. The nodes and interspace ridges are widely spaced, numbering 2 per mm, unlike the 4 to 6 nodes and interspace ridges per mm of *Reticulaconularia caetensis* sp. nov. For that reason, the present specimen does not fit any known species.

FINAL CONSIDERATIONS

This study is the first taxonomic assessment of conulariids in the Mato Grosso do Sul State, Brazil. The following species have been identified: *Conularia quichua*, *Paraconularia africana*, *Paraconularia ulrichana*, and *Reticulaconularia caetensis* sp. nov. Therefore, our results establish the occurrence of the genus *Reticulaconularia*, previously described by Siviero (2000) in Mato Grosso, in the northern border area of the Paraná Basin. Additionally, our results confirm the presence of *Paraconularia africana*, *Paraconularia ulrichana* and *Conularia quichua* in the State of Mato Grosso do Sul. Therefore, the diversity of conulariids in the Devonian of the northwestern border area of the Paraná Basin is greater than in the eastern border area, where, until now, *Reticulaconularia* is unknown and the presence of *Paraconularia ulrichana* still needs confirmation since it was not identified by Leme (2002) and Leme *et al*. (2004). It could be related to the climate barrier because the eastern border area of the basin was at higher latitudes and had colder waters than the northwestern border area, preventing the colonization of some species.

The stratigraphic range of the conulariids of the northern border area of the Paraná Basin is the same as that of the eastern border area, extending from the Praguian to the early Emsian. Our data also suggest that the Paraná Basin was not completely isolated from other South America basins, at least during the Early Devonian, based on the occurrence of the same species in the Devonian of Bolivia, including *Paraconularia africana*, *Paraconularia ulrichana*, *Conularia quichua* and the presence of the genus *Reticulaconularia* (Babcock *et al*., 1987).

A Bolivian faunal affinity on the northwestern border area of the Paraná Basin has been already suggested since Caster (1947), and the occurrence of the same species in both basins includes brachiopod genera such as *Scaphiocoelia* (see Boucot & Caster, 1984), *Babinia*, *Kentronetes*, *Saniuanetes,* and *Chonostrophia* (see Videira-Santos *et al*., 2022) as well as of bivalves (see Caster, 1947), and other groups. Therefore, this paper corroborates the idea that the northwest border area of the Paraná Basin had tenuous marine connections with the Devonian seas of Bolivia, at least during periods of sea level rise.

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