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NEW OCCURRENCES OF MALVINOKAFFRIC CHONETOIDEA (BRACHIOPODA) IN THE PARANÁ BASIN, DEVONIAN, BRAZIL

ROBERTO VIDEIRA-SANTOS
Programa de Pós-Graduação em Geociências: Patrimônio Geopaleontológico, Laboratório de Paleoinvertebrados - LAPIN, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, s/n, 20940-040, Rio de Janeiro, RJ, Brazil. *robvidsan@yahoo.com.br* (corresponding author)

SANDRO MARCELO SCHEFFLER & ANTONIO CARLOS SEQUEIRA FERNANDES
Laboratório de Paleoinvertebrados - LAPIN, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, s/n, 20940-040, Rio de Janeiro, RJ, Brazil.
schefflersm@mn.ufrj.br, *af07509@gmail.com*

ABSTRACT – Brachiopods of the superfamily Chonetoidea are abundantly found in Devonian rocks in the Paraná Basin (Brazil). Despite this, only two species were formally known: *Pleurochonetes falklandicus* and *Australostrophia mesembria*, while at least 34 other taxa are known in other locations also within the Malvinokaffric Realm. In this contribution we present nine new taxa of Chonetoidea from the Ponta Grossa (late Pragian–early Emsian) and São Domingos (late Emsian–Frasnian) formations in the Paraná Basin: *Babinia parvula maxima* ssp. nov., *Kentronetes*? *iclaense*, *Kentronetes*? *ortegae*?, *Sanjuanetes*? sp., *Chonostrophia*? aff. *truyolsae*, Chonetidae indet., *Pleurochonetes*? *comstocki*?, *Notiochonetes skottsbergi* and *Pleurochonetes surucoi*?. Additionally, we emended the diagnosis of *Babinia parvula*. This expands the known diversity of Devonian Chonetoidea of the Paraná Basin. We also discuss the likely living environment of the identified taxa, based on the outcrops from which they came. The identification of these taxa provide new paleobiogeographic and chronostratigraphic information, allowing interpretations about possible affinities and migration routes of these benthic organisms within the Malvinokaffric Realm regions.

Keywords: chonetoideans, Malvinokaffric Realm, Lower–Middle Devonian, systematic, paleoenvironments, paleobiogeography.

RESUMO – Os braquiópodes da superfamília Chonetoidea são abundantemente encontrados em rochas Devonianas na Bacia do Paraná (Brasil). Apesar disso, apenas duas espécies eram formalmente conhecidas: *Pleurochonetes falklandicus* e *Australostrophia mesembria*, enquanto pelo menos 34 outros táxons são conhecidos em outros locais também dentro Domínio Malvinocáfrico. Nesta contribuição apresenta-se nove novos táxons de Chonetoidea das formações Ponta Grossa (Pragiano tardio–Emsiano inicial) e São Domingos (Emsiano tardio–Frasniano) da Bacia do Paraná: *Babinia parvula maxima* ssp. nov., *Kentronetes*? *iclaense*, *Kentronetes*? *ortegae*?, *Sanjuanetes*? sp., *Chonostrophia*? aff. *truyolsae*, Chonetidae indet., *Pleurochonetes*? *comstocki*?, *Notiochonetes skottsbergi* e *Pleurochonetes surucoi*?. Adicionalmente, emenda-se a diagnose de *Babinia parvula*. Isso amplia significativamente a diversidade conhecida de Chonetoidea do Devoniano Bacia do Paraná. Também discute-se o provável ambiente de vida dos táxons identificados, com base nos afloramentos de onde eles vieram. A identificação desses táxons fornece novas informações paleobiogeográficas e cronoestratigráficas, permitindo interpretações sobre possíveis afinidades e rotas de migração desses organismos bentônicos pelas regiões do Domínio Malvinocáfrico.

Palavras-chave: Chonetoidea, Domínio Malvinocáfrico, Devoniano Inferior–Médio, sistemática, paleoambientes, paleobiogeografia.

INTRODUCTION

Chonetoideans are productid brachiopods that are characterized mainly by having spines along the ventral interarea, although there are rare exceptions, and a pair of anderidia within the dorsal valve (Racheboeuf, 2000). These brachiopods appeared in the Ordovician and probably became extinct during the late Permian, although there are questionable occurrences of some specimens from the Lower Triassic of South China (Sheng *et al*., 1984).

The fossils of marine invertebrates found in the Devonian strata of the Paraná Basin are part of what Clarke (1913) defined as "Austral Fauna". Later, Richter (1941) introduced the concept of the "Malvinocaffrischen Fauna", whilst Richter & Richter (1942) introduced the 'Malvinocaffrischen Provinz'. Boucot (1975) elevated the Malvinokaffric Province to the status of Realm, a biogeographic unit with a higher rank than "province" (Kauffman, 1973), thus being called the Malvinokaffric Realm. However, more recently, Penn-Clarke & Harper (2021) proposed the name "Malvinoxhosan" to replace "Malvinokaffric", due to the racist connotations of the latter term.

Until then, in the Paraná Basin, only two species of chonetoideans – *Australostrophia mesembria* (Clarke, 1913) and *Pleurochonetes falklandicus* (Morris & Sharpe, 1846) – were formally described (Ammon, 1893; Clarke, 1913;

Isaacson, 1977; Fonseca, 1998). However, in other locations also covered by the Malvinokaffric Realm, the diversity of Chonetoidea is significantly greater. In Bolivia, South Africa, Argentina, Malvinas/Falkland Islands, Uruguay and Paraguay, for example, at least 34 other Chonetoidea taxa are recognized, in addition to those identified for the Paraná Basin so far (*e.g.*, Clarke, 1913; Isaacson, 1977; Racheboeuf & Branisa, 1985; Proyecto PAR 83/005, 1986; Racheboeuf, 1992; Benedetto *et al*., 1992; Hiller, 1995; Herrera, 1995; Presser *et al*., 2004; Martinez & Verde, 2008; Racheboeuf *et al*., 2012).

The Paraná Basin (Brazil) Malvinokaffric fauna (late Pragian–?early Givetian) has been considered as abundant, but not very diverse (Melo, 1985, 1988; Bosetti *et al*., 2010a, 2012), mainly in relation to the Old World and Eastern Americas realms fauna. However, recent publications have indicated that the diversity of invertebrate fauna in the Paraná Basin was greater than traditionally considered (*e.g.*, Soares *et al*., 2008; Simões *et al*., 2009; Bosetti *et al*., 2010b; Carbonaro *et al*., 2016; Scheffler *et al*., 2017; Comniskey & Bosetti, 2017; Comniskey & Ghilardi, 2018; Fraga & Vega, 2019; Videira-Santos & Scheffler, 2019).

In this contribution we describe the first formal occurrences of *Babinia parvula maxima* ssp. nov., *Kentronetes*? *iclaense*, *Kentronetes*? *ortegae*? *Sanjuanetes*? sp., *Chonostrophia*? aff. *truyolsae*, Chonetidae indet., *Pleurochonetes*? *comstocki*?, *Notiotochonetes skottsbergi* and *Pleurochonetes surucoi*? from the Devonian of Paraná Basin. In this way, the diversity of the Chonetoidea superfamily known in the Devonian of the Paraná Basin is significantly increased.

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, Mato Grosso, Mato Grosso do Sul and Goiás (Melo, 1988). According to Northfleet *et al*. (1969) and Ramos (1970) the Parana Basin in Brazil comprises two discrete sub-basins, namely the Apucarana, to the south, and Alto Garças to the northwest. However, recent publications have indicated that these two sub-basins perhaps were not completely individualized until at least Emsian (Sedorko *et al*., 2018a; Scheffler *et al*., 2020).

This study employs the stratigraphic subdivision proposed by Grahn *et al*. (2013) for the entire Paraná Basin, including the eastern (Paraná state) and northwest (Mato Grosso, Mato Grosso do Sul and Goiás states) borders. 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 1).

PONTA GROSSA AND SÃO DOMINGOS FORMATIONS

The Ponta Grossa Formation is stratigraphically located between the Furnas Formation and the São Domingos Formation. It is interpreted as being of marine origin, covering environments in the shoreface and the offshore (Sedorko *et al*., 2018b). This formation is notable for being one of the most fossiliferous of the Devonian of the Paraná Basin, having records of the typical climax of Malvinokaffric fauna (*e.g.*, Clarke, 1913; Petri, 1948; Caster, 1954; Lange, 1967; Melo 1985, 1988; Bosetti *et al*., 2010a, 2012).

According to Grahn *et al*. (2013), the lower portion of Ponta Grossa Formation consists of sandstones interspersed with siltstones. This basal portion 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*. (2010b) suggested a late Pragian and the early Emsian age for this succession.

The studied chonetoideans samples from the Ponta Grossa Formation are from the states of Paraná [outcrops Ponta Grossa, São Domingos Road, São Domingos Creek, Vila Francelina, Campus UEPG, Tibagi (Lange and Petri), Curva I and Jaguariaíva; Figures 2 and 3], Mato Grosso do Sul (outcrop Barreiro da Figueira; Figures 4 and 5) and Mato Grosso (outcrop Estrada; Figure 6) (see Sedorko *et al*., 2021, for outcrop age).

The São Domingos Formation is stratigraphically located between the Ponta Grossa Formation and the Itararé Group (Carboniferous). It is marine in origin and comprises foreshore to offshore environments (Sedorko *et al*., 2018b). The São Domingos Formation consists of poorly sorted conglomeratic sandstones, followed by rarely bituminous shales, and micaceous siltstones that are rich in plant fragments. In this succession, the impoverished Malvinokaffric fauna occurs in its basal portion and after the Givetian the typical elements of Malvinokaffric fauna disappear or are rare (Bosetti *et al*., 2010a, 2012). According to Melo & Loboziak (2003) and Grahn *et al*. (2013), this succession is late Emsian–Fransnian in age.

The examined chonetoideans specimens from the São Domingos Formation come from the states of Paraná (outcrops Desvio Ribas and Rio Caniú; Figure 2), Goiás (outcrop Doverlândia; Figures 5 and 7) and Mato Grosso (outcrop Monjolo dos Padres; Figures 6 and 7) (see Sedorko *et al*., 2021 for age of the outcrops).

MALVINOKAFFRIC REALM

The Devonian, mainly between the Pragian and Eifelian, was marked by the existence of large areas of endemic marine invertebrates. There were three major paleobiogeographic realms in this period: Old World (30ºN–30ºS, Lower Devonian–Carboniferous), Eastern Americas (30ºS–60ºS,

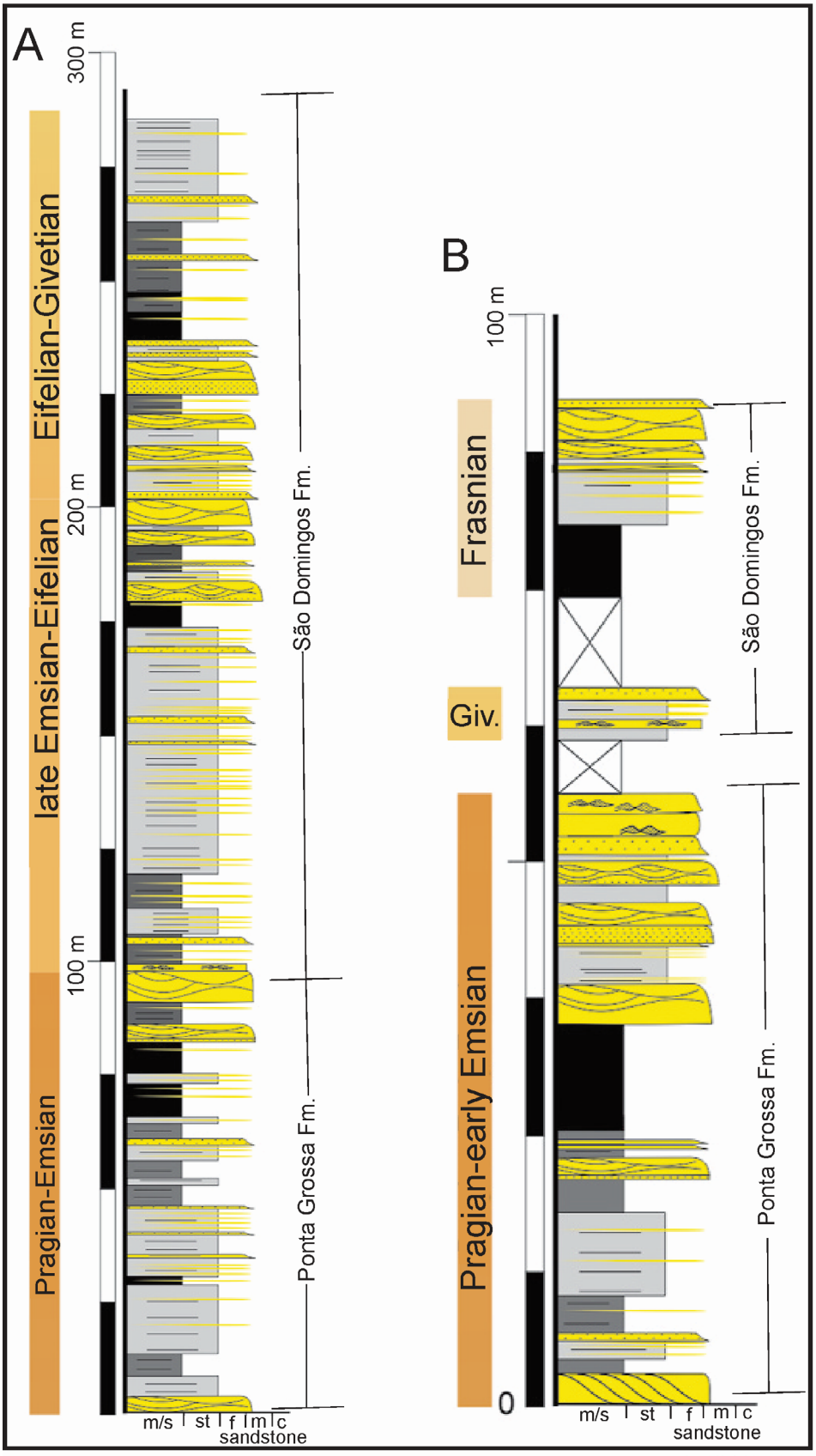

Figure 1. Schematic sedimentological profile of the Ponta Grossa and São Domingos formations. **A**, sedimentological profile representing the east edge of the Paraná Basin (State of Paraná), **B**, sedimentological profile representing the northwestern edge of the Paraná Basin (states of Mato Grosso do Sul, Mato Grosso and Goiás) (adapted from Sedorko *et al*., 2021).

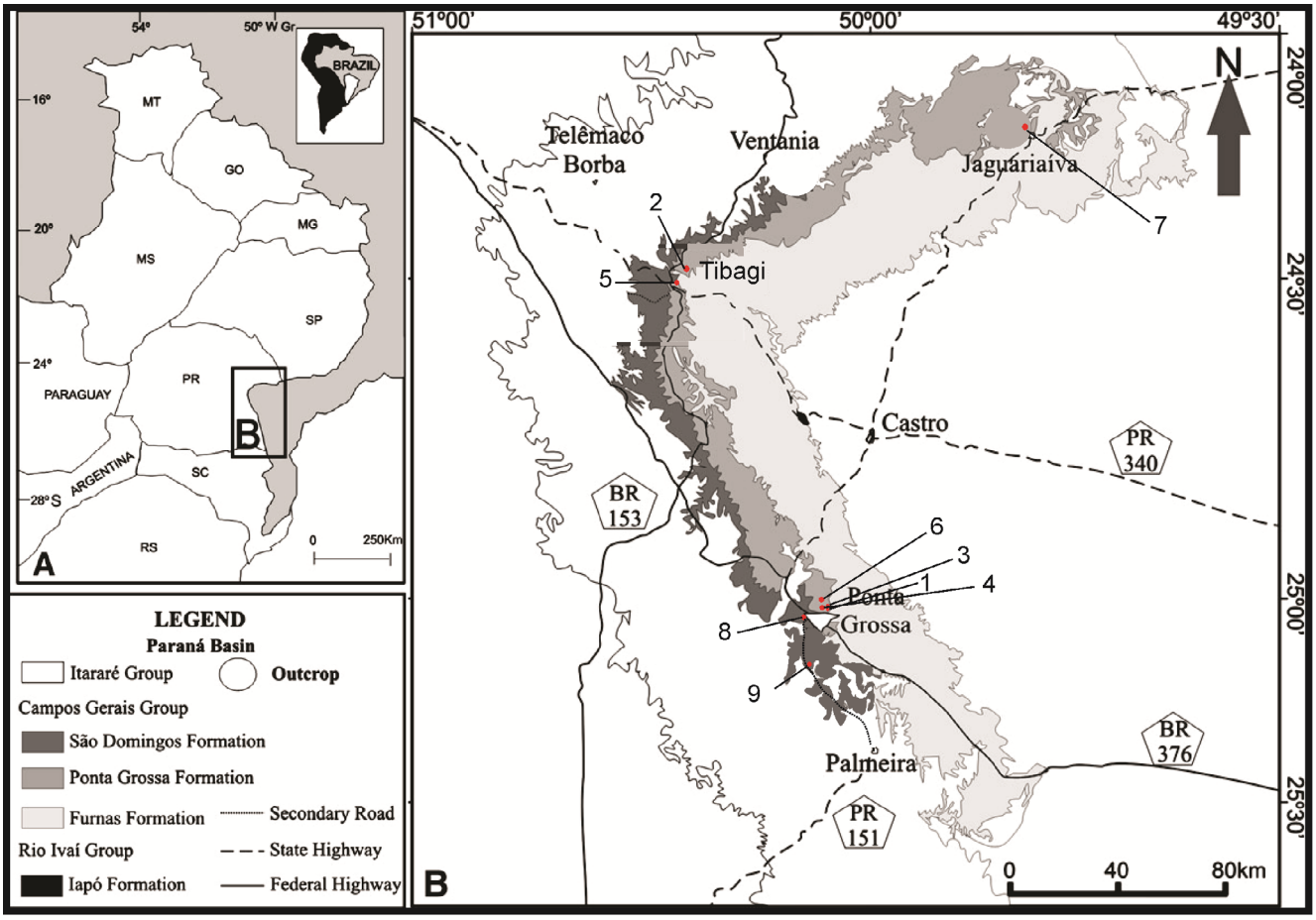

Figure 2. A–B, map of outcrops with chonetoideans in the State of Paraná. **1**, Ponta Grossa; **2**,São Domingos Road; **3**, Vila Francelina; **4**, Campus UEPG; **5**, Tibagi (Lange and Petri); **6**, Curva I; **7**, Jaguariaíva; **8**, Desvio Ribas; **9**, Rio Caniú (adapted from Grahn *et al*., 2013).

Silurian–Carboniferous) and Malvinokaffric (60ºS–90ºS, Pragian-Givetian) (Boucot *et al*., 1969). In the Upper Devonian, Dowding & Ebach (2018) recognized the Western Gondwana Realm encompassing cold waters from parts of North America, South America, South Africa and Antarctica.

The Malvinokaffric Realm (or Malvinoxhosan according to Penn-Clarke & Harper, 2021) encompassed epicontinental seas with cold and with a large amount of terrigenous sediment. It covered parts of Brazil (Paraná and Parecis basins), Argentina, Malvinas/Falkland Islands, Bolivia, Paraguay, southern Peru, South Africa, Antarctica, Ghana and Chile, the latter two with doubts (Melo, 1985; Isaacson & Sablock, 1988; Melo, 1988; Presser *et al*., 2004; Bosetti, 2010a; Torsvik & Cocks, 2013; Boucot *et al*., 2013; Penn-Clarke & Harper, 2021).

This Realm had low faunal diversity, being its outstanding characteristics the absence of graptolites, conodonts and stromatoporoid sponges; the rarity of corals, bryozoans and amonoids; and the high degree of endemism of rhynchonelliform brachiopods and trilobites (Dowding & Ebach, 2018; Penn-Clarke & Harper, 2021). Among the endemic brachiopods we highlight the chonetoideans *Aseptonetes*, *Australostrophia*, *Austronoplia*, *Babinia*, *Kentronetes*, *Lomaella*, *Montsenetes*, *Notiochonetes*, *Pleurochonetes* and possibly *Sanjuanetes* (Penn-Clarke & Harper, 2021).

The Malvinokaffric fauna is believed to have originated from the Appalachian Basin, during the Silurian (Koch & Boucot, 1982; Hallam, 1994), although more recently some authors have considered that certain taxa from the Malvinokaffric Realm were derived from other taxa already existing in regions currently corresponding to South America and Africa (see Penn-Clarke & Harper, 2021).

In the Paraná Basin, the Malvinokaffric fauna reached its peak in the interval between the late Pragian and the early Emsian, having declined from the late Emsian onwards. Possible causes of this decline are likely to be related to changes in ocean circulation due to basin restrictions and anoxic events in the Middle Devonian. The transgression recorded in the late Emsian introduced a reduced and less provincial fauna into the Paraná Basin (Bosetti *et al*., 2012; Sedorko *et al*., 2019), while other groups showed radical faunal changes, such as the echinoderms (Scheffler *et al*., 2017).

At the end of the Givetian the Malvinokaffric Realm disappeared and only the Old World (expanded) and Eastern

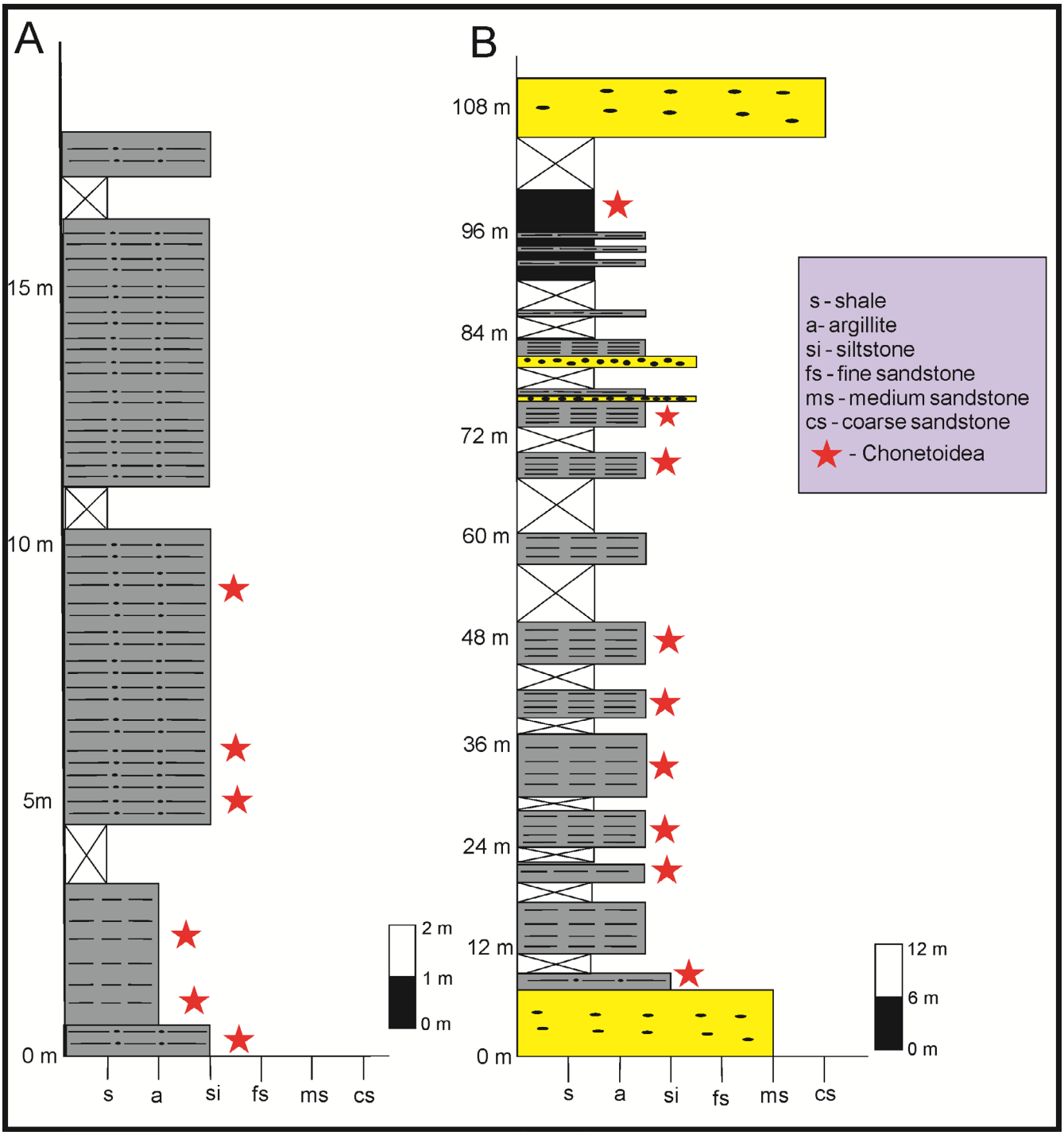

Figure 3. A, sedimentological profile of outcrop São Domingos Road (Ponta Grossa Formation, adapted from Petri, 1948); **B**, sedimentological profile of outcrop Jaguariaíva (Ponta Grossa Formation, adapted from Rodrigues, 2002).

Americas (reduced) realms remained (Dowding & Ebach, 2018). The end of the Malvinokaffric Realm is marked by the extinction of typically Malvinokaffric taxa and the appearance of warm water brachiopods such as *Tropidoleptus* and *Rhipidothyris*, as well as the abundance of the acritarch *Evittia* and the appearance of goniatite amonoids (Penn-Clarke & Harper, 2021).

MATERIAL AND METHODS

The specimens considered in this study are deposited in the collections of the Museu Nacional/Universidade Federal do Rio de Janeiro (**MN-I**), Museu de Ciências da Terra/Serviço Geológico do Brasil (**DGM-I**), Universidade Estadual de Ponta Grossa (**MPI**), Universidade Federal do Paraná (**NR**),

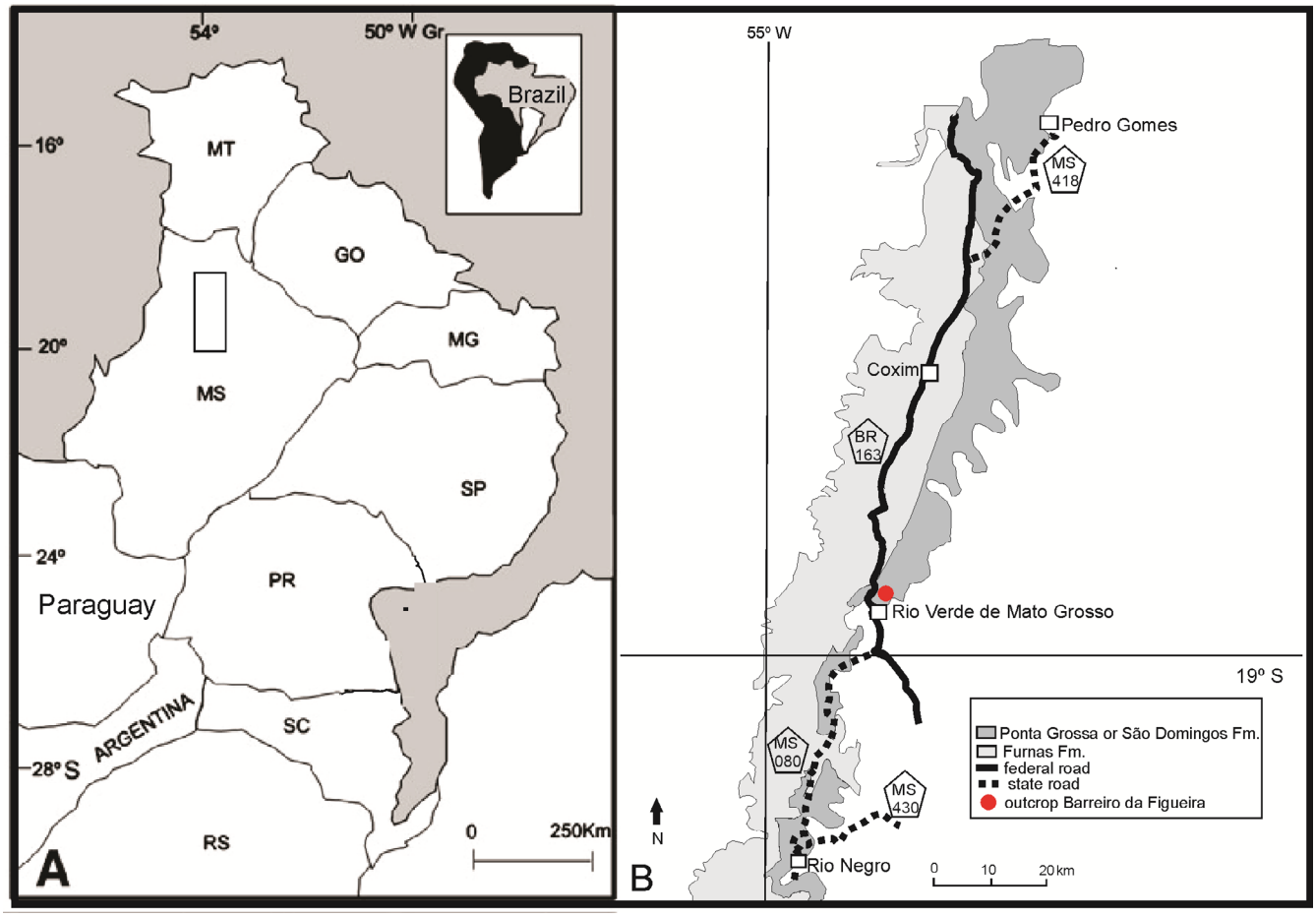

Figure 4. Location of the outcrop with Chonetoidea in the State of Mato Grosso do Sul (adapted from CPRM 2006, Grahn *et al*., 2013; Scheffler *et al*., 2020).

Universidade Federal do Estado do Rio de Janeiro (**UNIRIO-BQ**), Universidade Federal de Mato Grosso (**FUFMT-MP**) and Universidade Estadual Paulista Julio de Mesquita Filho (**CCLP**). We also examined chonetoideans from the Devonian of the Malvinas/Falkland Islands (replicas only) and Bolivia, deposited in the collections of the National Museum of Natural History/Smithsonian Institution (**USNM**) in order to compare them with the Brazilian specimens. Among the specimens deposited at the Museu Nacional/Universidade Federal do Rio de Janeiro, four (MN 10508-I, MN 10619-I, MN 10949-I and MN 10923-I) were completely lost due to fire that severely compromised this institution in 2018. The fossils collected during fieldworks after the fire were designated with the provisional code "MN MS Q1 F". Fossils from the so-called "Caster collection" that were not hit by the fire were designated with the provisional code "**MN MG**".

For taxonomic identification, we consulted the Treatise on Invertebrate Paleontology (Racheboeuf, 2000) and papers on Chonetoidea taxonomy from the Malvinokaffric and Eastern Americas realms, in addition to the Brazilian basins of Amazonas and Parnaíba. Stereoscopic microscopes were used to view and examine the fossils. For morphometry, digital and manual calipers with an accuracy of 0.02 mm were used to measure various features from the specimens. The standards proposed by Racheboeuf (2000) and Fonseca (2001) were used to assess the size and transversal elongation of the Chonetoidea shells (Tables 1 and 2).

Table 1. Shell size (Racheboeuf, 2000; Fonseca, 2001).

Size	Length (L)
Very Small	L< 5 mm
Small	5 mm < L < 10 mm
Medium	10 mm < L < 20 mm
Large	20 mm < L < 30 mm
Very Large	L > 30 mm

Table 2. Transverse elongation of chonetoidean shells (Fonseca, 2001). **Abbreviations: L**, length; **W**, width.

Transverse Elongation	L/W
Slightly Transverse	1,0 > L/W > 0,70
Transverse	0,70 > L/W > 0,65
Markedly Transverse	0,65 > L/W > 0,55

The safe identification of a given Chonetoidea taxon involves

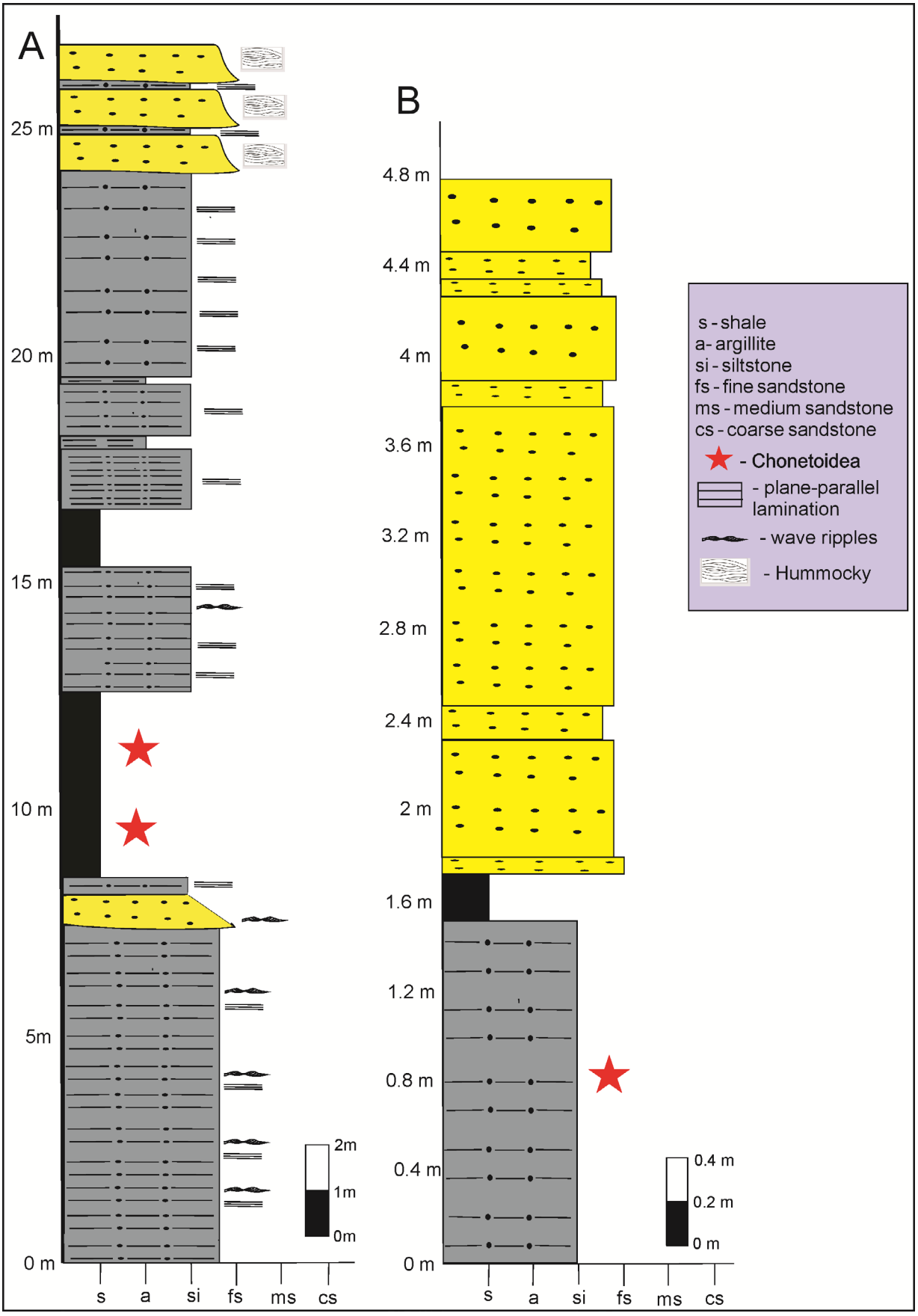

Figure 5. A, sedimentological profile of Barreiro da Figueira outcrop (Ponta Grossa Formation); **B**, sedimentological profile of Doverlândia outcrop (São Domingos Formation, Carbonaro & Ghilardi, 2016).

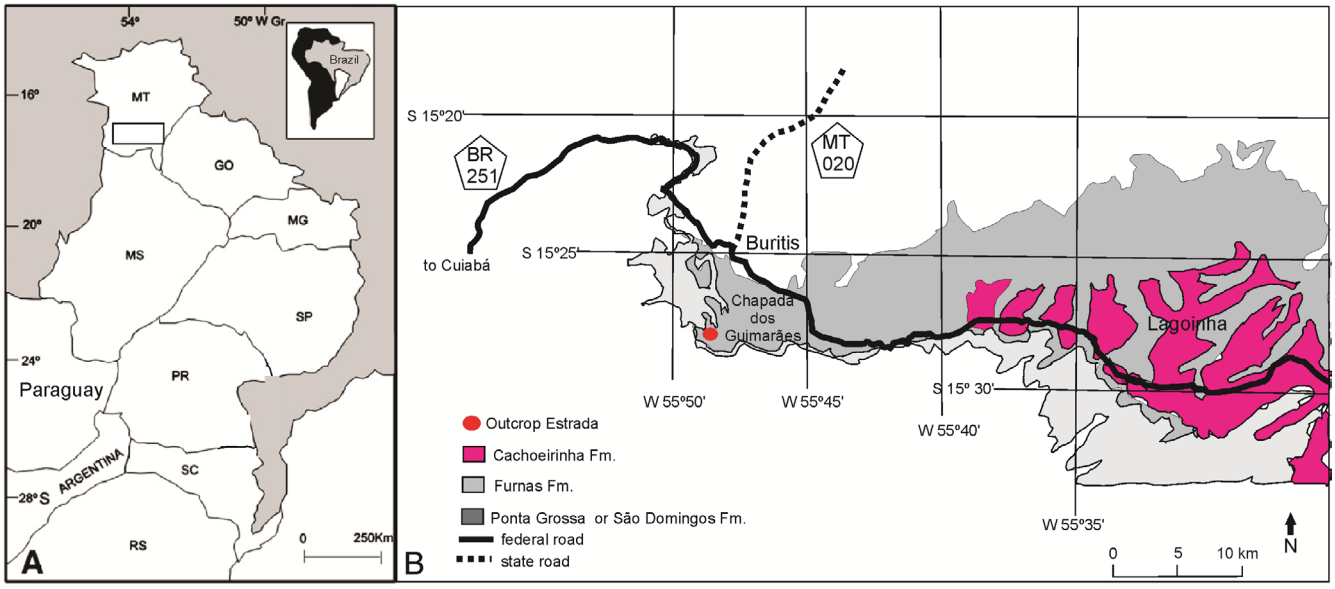

Figure 6. Location of the outcrop with Chonetoidea in the State of Mato Grosso (adapted from Grahn *et al*., 2010a).

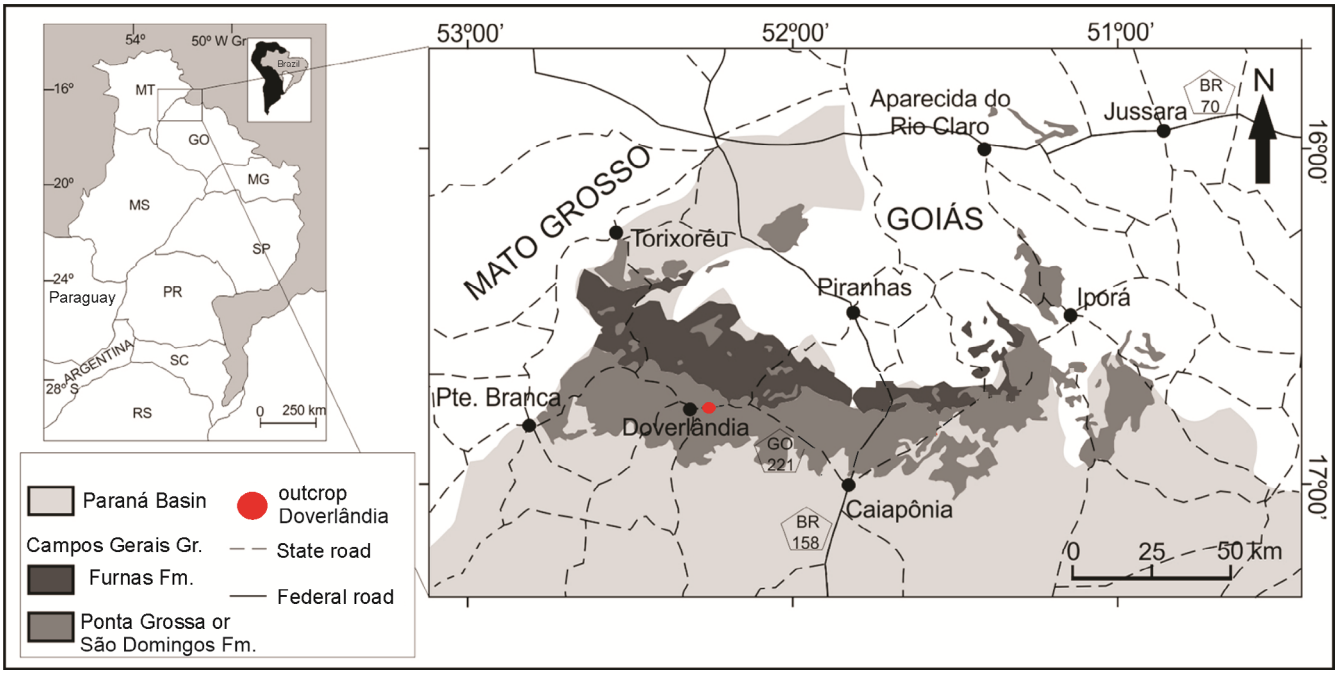

Figure 7. Location of the outcrop with Chonetoidea in the State of Goiás (adapted from Carbonaro & Ghilardi, 2016).

the analysis of the interior and exterior of the ventral and dorsal valves. However, not all these characteristics were always available in the analyzed specimens, and when they were available, they were often poorly preserved. For this reason, we widely use the open nomenclature in this work, following the recommendations of Bengtson (1988).

To assess the palaeoenvironmental distribution of the chonetoideans, Racheboeuf (1990), was used, who adopted the subdivision of the marine environments of Boucot (1975), Benthic Assemblages (**BA**). However, we do not used the communities proposed by Boucot (1975) for the Paraná Basin, considering that, as stated by Bosetti (2004), the fossil record of this basin is very biased, presenting a temporal mixture and taphonomic feedback.

Finally, the paleobiogeography method used was as follows: the oldest rock localities where the taxon was found are considered as its possible "emergence point" and the more recent rock localities where this same taxon was found are

considered as where this taxon migrated. This interpretation was possible to be made based on the data available at the time.

SYSTEMATIC PALEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Subphylum RHYNCHONELLIFORMEA Williams, Carlson, Brunton, Holmer & Popov, 1996
Class STROPHOMENATA Williams, Carlson, Brunton, Holmer & Popov, 1996
Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959
Suborder CHONETIDINA Muir-Wood, 1962
Superfamíly CHONETOIDEA Bronn, 1862
Famíly STROPHOCHONETIDAE Muir-Wood, 1962
Subfamíly STROPHOCHONETINAE Muir-Wood, 1962

Babinia Racheboeuf & Branisa, 1985

Type species. *Babinia parvula* Racheboeuf & Branisa, 1985.

Babinia parvula Racheboeuf & Branisa, 1985
(Figures 8A–C)

1913 *Chonetes falklandicus* (Morris & Sharpe); Clarke, p. 295, pl. 24, fig. 25.
2007 *Babinia*? sp.; Souza, p. 62, fig. 13F.
2018 *Babinia*? *larocquensis* Racheboeuf & Lesperánce; Videira-Santos & Scheffler, p. 42–43.

Holotype. VH 3451 (see Racheboeuf & Branisa, 1985).
Additional material. DGM 200-I, MN 10923-I, DGM 1532-I, MPI 10659, MPI 13025, MPI 13645, MPI 1372/1377, MPI 2081 and NR 1631.
Provenance of the additional material. Ponta Grossa (late Pragian–early Emsian), São Domingos Road (about 3 km from the Tibagi city – Pragian to early Emsian), Vila Francelina (late Pragian–early Emsian), Campus UEPG (late Pragian–early Emsian), Desvio Ribas (late Emsian), Tibagi – Lange and Petri (late Pragian–early Emsian) and Curva I (late Pragian).
Emended diagnosis. Length up to 12.5 mm, slightly transverse (C/L = 0.62 to 0.75), up to three straight orthomorphic spines on each side of the umbo, anderidia pair diverging around 70º, from three to eight ribs/mm and enlarged median rib reaching the anterior commissure in both valves.
Remarks. We emended the diagnosis of *Babinia parvula*, in relation to that presented by Racheboeuf & Branisa (1985), because of the following reasons: (i) *B. parvula* has up to three spines and not just two as stated by Racheboeuf & Branisa (1985) when they wrote the diagnosis of species, this is perceived in the Brazilian samples and also in the Bolivian samples analyzed by Racheboeuf & Branisa (1985) (see Racheboeuf & Branisa, 1985, fig. 3.17). This fact is mentioned in the description, but when writing the diagnosis the authors mistakenly placed only two spines; (ii) in the Brazilian material, it was noticed that the ribs of *B. parvula* can be thicker, with up to 4 ribs/mm, not restricted to having only between 6 and 8 ribs/mm; (iii) in the Brazilian material it was observed that the length of the *B. parvula* valve can reach up to 12 mm, not being restricted to just 7 mm as in the Bolivian samples; and (iv) the fact that the enlarged median rib reaches the anterior commissure is considered a diagnostic feature as it is for other Chonetoidea (see Racheboeuf & Branisa (1985) for an example).
Observation 1. *Babinia larocquensis* may not belong to the genus *Babinia*, as the pair of anderidia diverges around 50º, but one of the diagnoses of the genus *Babinia* is the pair of anderidia diverging around 70º (Racheboeuf, 2000). Therefore, this species needs revision.
Observation 2. Racheboeuf (1992) stated that *Babinia parvula* occurs in the Eifelian of Bolivia, but he also stated that some specimens were collected in the Lower Belen Member, which has an early Pragian–Emsian age (Isaacson & Sablock, 1988; Blieck *et al*., 1996).
Occurrence. ?Lochkovian–Emsian, Argentina (Herrera, 1993), late Pragian–late Emsian, Brazil (this paper) and Pragian–Eifelian, Bolivia (Racheboeuf & Branisa, 1985; Racheboeuf, 1992).

Babinia parvula maxima ssp. nov.
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(Figures 8A–C)

1913 *Chonetes falklandicus* (Morris & Sharpe); Clarke, p. 295, pl. 24, fig. 25.
2007 *Babinia*? sp.; Souza, p. 62, fig. 13F.
2018 *Babinia*? *larocquensis* Racheboeuf & Lesperánce; Videira-Santos & Scheffler, p. 42–43

Derivation of name. Due to the larger size.
Type locality. Ponta Grossa, Paraná, Brazil.
Stratigraphic horizon of the holotype. Ponta Grossa Formation (late Pragian–early Emsian).
Material. DGM 200-I (Holotype, Figure 8b), MN 10923-I, DGM 1532-I, MPI 10659, MPI 13025, MPI 13645, MPI 1372/1377, MPI 2081 and NR 1631 (Paratype).
Provenance. Ponta Grossa (late Pragian–early Emsian), estrada São Domingos (about 3 km from the Tibagi city – Pragian to early Emsian), Vila Francelina (late Pragian–early Emsian), Campus UEPG (late Pragian–early Emsian), Desvio Ribas (late Emsian), Tibagi – Lange and Petri (late Pragian–early Emsian) and Curva I (late Pragian).
Diagnosis. Characteristics as for the species except for having a length between 6 mm and 12.5 mm and about 3 or 4 ribs/mm.
Description. Small to medium shell, with length between 6 mm and 12.5 mm and width between 8.5 mm and 17 mm; sub-elliptical contour, transverse to slightly transverse (0.62 to 0.75), small umbo, maximum width before hinge line. About three or four ribs/mm close to the anterior commissure, multiplying mainly by intercalation; enlarged median rib reaching the anterior commissure in both valves; up to three straight orthomorphic spines on each side of the umbo in

the ventral valve. All ventral valves are slightly arched. Ventral interior: apparently flabelliform muscle field, poorly preserved diductor and addutor scars, small myophragm, external ornamentation printed inside the valve. Dorsal interior: anderidia pair diverging around 70º and apparently not merging with cardinalia, absent median septum.

Remarks. *Babinia parvula* specimens found in Brazil differ from those found in Bolivia by their larger size (maximum 12 mm in Brazilian specimens, against 7 mm in Bolivian specimens) and mainly by the thicker ribs (3 to 4 per mm in Brazilian specimens, against 6 to 8 per mm in Bolivian specimens). These features are not sufficient to indicate a new species, but represent only a new subspecies, here named *Babinia parvula maxima*. In turn, specimens of *Babinia parvula* from Bolivia now belong to the subspecies *Babinia parvula parvula*. Racheboeuf & Branisa (1985) had placed one of specimens of Clarke (1913, pl. 24, fig. 25) in the synonym of the species *Babinia parvula* but did not present the reasons for this. Therefore, in this paper, we made the first formal record of *Babinia parvula* in the Devonian of the Paraná Basin.

Occurrence. In late Pragian–late Emsian, Brazil (this paper).

Kentronetes Racheboeuf & Herrera, 1994

Type species. *Chonetes ruecki* Ulrich, 1893.

Kentronetes? *iclaense* (Racheboeuf & Branisa, 1985)
(Figures 8D–E)

2007 *Kentronetes* cf. *iclaensis* (Racheboeuf & Branisa), Souza, p. 65–66, fig. 14A–D.

Material. MN 10073-I, DGM 1602-I, DGM 1715-I, MPI 13282 and MPI 13608.

Provenance. São Domingos creek and São Domingos Road (late Pragian–early Emsian).

Description. Medium-sized shell, between 14 mm and 20 mm long and 21 mm to 25 mm wide, transverse (0.65), maximum width approximately in the middle of the valve; poorly preserved ribs present, between 16 and 19 ribs/5 mm close to the anterior commissure, in both valves. Ribs grow mostly by intercalation and subordinately by bifurcation in the ventral valve. Ventral valves with up to five intraversed cyrtomorphic spines on each side of the umbo. Ventral valves also have an enlarged median rib almost, or even, reaching the anterior commissure. Ventral interior: short myophragm, with internal surface completely covered by ornamentation, teeth not preserved. It was not possible to clearly observe the presence of the vascular media. Dorsal interior: very poorly preserved, it is not possible to observe any relevant morphological characteristics.

Remarks. Between 1985 and 1994 the South American Devonian strophochonetids were referred to the genus *Quadrikentron* Boucot & Gauri, 1966, but the South American specimens were reviewed by Racheboeuf & Herrera (1994), and they noticed some differences such as the fact that the specimens from South America have ventral median enlarged costa, intraversed cyrtomorphic spines, among other characteristics. With this in mind, Racheboeuf & Herrera (1994) created the genus *Kentronetes*. The genera *Kentronetes* and *Borealinetes* are very similar externally. The main difference between them resides inside the dorsal valve (morphology of the dental sockets). As in the Brazilian material there are no dorsal valves in a good state of conservation, it is not possible to classify them undoubtedly as *Kentronetes*, however, judging by the paleobiogeographic context, it is very likely that it is a *Kentronetes*, considering that *Borealinetes* occurs in the Devonian of the Canadian east coast (Eastern Americas Realm), while *Kentronetes* is registered in the Devonian of Bolivia (Malvinokaffric Realm). Due to the number of spines and the number of ribs/5 mm, the specimens analyzed here are remarkably similar to *Kentronetes iclaense* (Racheboeuf & Branisa, 1985). Based on the profiles made available by Petri (1948) it is possible to infer that at least some of the specimens analyzed here come from the Ponta Grossa Formation *sensu* Grahn *et al*. (2013), as they were collected at the same levels where there is a typical Malvinokaffric fauna. Such fact would represent the oldest occurrence of the species *K. iclaense*, since until then it is believed that this species is restricted to the Bolivian late Emsian–Eifelian (Racheboeuf, 1992, for age see Grahn, 2002).

Occurrence of the species *Kentronetes iclaense*. In late Pragian–early Emsian, Brazil (this paper) and late Emsian–Eifelian, Bolivia (Racheboeuf & Branisa, 1985; Racheboeuf, 1992).

Kentronetes? *ortegae*? Herrera, 1995
(Figures 8F–G)

Material. MPI 2071, MPI 12532, MPI 12554, MPI 13646, MPI 13649, UNIRIO 0157 BQ, UNIRIO 0162 BQ, NR 1036, NR 1044 and NR 4538.

Provenance. Curva I (late Pragian–early Emsian), Jaguariaíva (late Pragian–early Emsian), Vila Francelina (late Pragian–early Emsian) and Ponta Grossa (late Pragian–early Emsian).

Description. Medium-sized valves about 15 mm long and about 22 mm wide, markedly transverse (0.55 and 0.65). The ventral valve has up to four spines on each side of the umbo, all spines are cyrtomorph intraversed and symmetrically distributed. The dorsal valve has poorly preserved ribs that appear to be thin and sparse. It is not possible to specify the predominant type of multiplication. Between 12 and 16 ribs/5 mm close to the anterior commissure, maximum width close to half of the valve. Ventral valve with an enlarged median rib, poorly defined and that does not reach the anterior commissure. There is no enlarged median rib in the dorsal valve. Ventral interior: short myophragm, with internal surface completely covered by ornamentation, teeth not preserved. Dorsal interior: very poorly preserved, it is not possible to observe any relevant morphological characteristics.

Remarks. The discussion about the designation with doubts as *Kentronetes* is the same as that already mentioned in the

case of *Kentronetes*? *iclaense*. The specimens analyzed here, due to the number of spines and the average size, are similar to *Kentronetes ortegae* Herrera, 1995, however, the number of ribs and the position of the greatest width of the valve are close to the diagnosis of *K. ruecki* (Ulrich, 1893). Therefore, the specimens analyzed may represent a new species of *Kentronetes*, intermediate between *K. ortegae* and *K. ruecki* or just a polymorphic variation of *K. ortegae*. The second hypothesis seems more likely, since the number of spines, a diagnostic character widely used at a specific level for Chonetoidea (Racheboeuf, 1990), is typical of *K. ortegae*. However, for any of these hypotheses to be confirmed, it is essential to analyze the interiors of better preserved ventral and dorsal valves. If it is really *K. ortegae,* it would be the first occurrence of this species outside Argentina (Herrera, 1995), which would expand its geographical occurrence.

Occurrence of the species *Kentronetes ortegae*. In late Pragian–early Emsian (this paper) and Pragian, Argentina (Herrera, 1995).

Sanjuanetes Racheboeuf & Herrera, 1994

Type species. *Sanjuanetes dalenzae* Racheboeuf & Herrera, 1994.

Sanjuanetes? sp.
(Figure 8H)

Material. MN MS Q1 F7 (provisional code).

Provenance. Barreiro da Figueira (late Pragian–early Emsian).

Description. Very small shell, 3.5 mm long and 5.0 mm wide; maximum width in the middle of the valve, transverse (0.70); subcircular contour; small resupinate umbo, projected just beyond the hinge line; about seven ribs/mm; presence of an enlarged median rib that does not reach the anterior commissure. Ventral interior: short myophragm, oval, well-marked triangular muscle impressions. Dorsal interior: not found in the studied material.

Remarks. The resupinate nature of the valve and the presence of medium rib make the specimen more likely to be a *Sanjuanetes*. Due to the absence of the dorsal valve, we decided, to classify it with open nomenclature. However, the general shape of the ventral valve resembles that of *Sanjuanetes andina* (Levy & Nullo, 1972) (= *Chonostrophia reversa* var. *andina* Levy & Nullo, 1972). The number of ribs per millimeter, on the other hand, fits better in the diagnosis of *Sanjuanetes dalenzae* Racheboeuf & Herrera, 1994. If it is confirmed that the specimen analyzed here is in fact *Sanjuanetes*, it would be the most recent occurrence of this genus, considering that it was collected in the outcrop Barreiro da Figueira, with an age between the late Pragian and early Emsian (Scheffler *et al*., 2020; Sedorko *et al*., 2021), and until then the most recent known occurrence refers to the Lochkovian of Argentina and Bolivia (Racheboeuf & Herrera, 1994; Racheboeuf *et al*., 2012).

Occurrence of the genus *Sanjuanetes*. ?Lochkovian, Argentina (Levy & Nullo, 1972; Racheboeuf & Herrera, 1994), late Silurian–Lochkovian, Bolivia (Racheboeuf & Herrera, 1994; Herrera, 1995; Racheboeuf *et al*., 2012) and late Pragian–Early Emsian, Brazil (this paper).

Family CHONOSTROPHIIDAE Muir-Wood, 1962
Chonostrophia Hall & Clarke, 1892

Type species. *Chonetes reversa* Whitfield, 1882.

Chonostrophia? aff. *truyolsae* Racheboeuf, 1992
(Figure 8I)

1987 "*Chonostrophia andina*" (Levy & Nullo, 1972); Quadros, pl. 5, figs. 1–23.
2007 (non) *Chonostrophia*? sp.; Souza, p. 67–68, fig. 14E.

Material. MN MS Q1 F11 (provisional code), FUFMT-MP 111, FUFMT-MP 114, FUFMT-MP 118b, FUFMT-MP 123, 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.

Provenance. Barreiro da Figueira (late Pragian–early Emsian) and Estrada (Chapada dos Guimarães–late Pragian to early Emsian).

Description. Small to very small shells (between 1 mm and 4 mm long and between 2 mm and 5 mm wide), maximum width at the hinge, markedly slightly transverse (0.50 to 0.85); subcircular contour; small resupinate umbo, projected just beyond the hinge line; parvicostellar ornamentation, thin and low ribs, absence of an enlarged median rib; presence of concentric lines of growth; presence of oblique orthomorphic spines. Ventral interior: short and relatively thick myophragm, oval, well-marked triangular muscle impressions. Dorsal interior: absent median septum. We could not observe other relevant characteristics.

Remarks. The resupinate nature of the valves, the absence of a median rib and the presence of oblique orthomorphic spines make the specimens more likely to belong to the genus *Chonostrophia*. Such characteristics distinguish them from *Sanjuanetes*, a Chonetoidea similar to *Chonostrophia*. The general characteristics of the external ornamentation of the ventral valve and the morphology of the muscular field are similar to that of *Chonostrophia truyolsae* Racheboeuf, 1992 that occurred in the Eifelian of Bolivia, however the Brazilian specimens have less sparse ribs and a better developed muscular field, representing probably a new species of *Chonostrophia*. Due to the absence of better preserved dorsal valve interiors, we decided to classify the specimens using open nomenclature.

Observation. The specimens from Mato Grosso (FUFMT-MP) were analyzed based on the figures of Quadros (1987).

Occurrence of genus *Chonostrophia*. In late Pragian, Argentina (Herrera, 1995), Eifelian, Bolivia (Racheboeuf, 1992; Racheboeuf *et al*., 2012), Pragian–Emsian, Canada (Racheboeuf & Lespérance, 1995), late Pragian–early Emsian, Brazil (this paper), Emsian–Eifelian, United States of America (Racheboeuf & Lesperance, 1995) and Middle Devonian, Venezuela (Benedetto, 1985).

Family CHONETIDAE Bronn, 1862

Chonetidae indet.
(Figure 8J)

2016 *Chonetidina* Muir-Wood; Carbonaro & Ghilardi, p. 142, fig. 6D.

Material. CCLP 935.
Provenance. Doverlândia, GO (early Givetian).
Description. Only one specimen of a very small shell, 1.7 mm wide and 1.2 mm long, slightly transverse (0.70), with a sub-rectangular shape; small umbo, protruding a little from the posterior edge of the shell; without ribs and spines. Most central portion of the shell slightly inflated, lateral regions flattened. Greater extension in the hinge region. Ventral interior: relatively long myophragm, almost reaching the half of the shell, triangular adductor and flabeled diductor scars. Dorsal interior: not found in the study material.
Remarks. Although the valve does not have many details, it is possible, due to the little transverse and inflated shape, in addition to the absence of sulcus and dentition on the hinge, to classify this specimen as a Chonetidae. However, as it is juvenile, in addition to the absence of a dorsal valve interior and ribs, it prevents a more refined taxonomic designation. The specimen studied here is only the second Chonetoidea registered in the Devonian of the state of Goiás (Almeida, 1948) and the first to be described. The small size of this specimen may be associated with the "Lilliput effect" described by Bosetti *et al*. (2010a) in fossils of correlated age levels in the state of Paraná.
Occurrence of the family Chonetidae. Cosmopolitan (Pragian–?Fammenian) (Racheboeuf, 2000).

Subfamily NOTIOCHONETINAE Racheboeuf, 1992
Notiochonetes Muir-Wood, 1962

Type species. *Chonetes skottsbergi* Clarke, 1913.

Notiochonetes skottsbergi (Clarke, 1913)
(Figures 8L–M)

1913 *Chonetes skottsbergi* Clarke; Clarke, p. 291, pl. 24, figs. 26–33.
1913 *Chonetes hallei* Clarke; Clarke, p. 293–295, pl. 24, fig. 34.
2019 *Notiochonetes skottsbergi* (Clarke); Videira-Santos, p. 38.
Material. NR 6152, NR 6550 e NR 8549a,b.
Provenance. Rio Caniú (late Emsian).
Description. Medium to large shell, between 18 mm and 23 mm long by a maximum of 37 mm wide, maximum width close to half of the valve, transverse (0.63); about nine ribs/5 mm that multiply apparently by intercalation, presence of pseudopunctation aligned to the interspaces, large muscle field. Dorsal interior: dental sockets slightly divergent and not curved posteriorly, pair of slightly divergent strong anderidia (less than 40º) and thick; median septum low, narrow, posterioly thickened. Ventral interior: well developed ventral median septum, large and poorly delimited muscle field.
Remarks. The main differences between the genus *Pleurochonetes* and *Notiochonetes* reside inside the dorsal valve, since the ventral valves of these two genera are very similar (Hiller, 1987; Rachebouef, 2000). The *Notiochonetes* differs from the *Pleurochonetes*, in that it has a more developed pair of anderidia, less divergent anteriorly, larger sockets, less curved posteriorly, less divergent and located less posteriorly. The comparison between the Brazilian material analyzed and the replicas of the type-series of *Notiochonetes*, deposited at the National Museum of Natural History/Smithsonian Institution (8075 NYSM, 8076 NYSM, 8077 NYSM, 8078 NYSM, 8079 NYSM, 8081 NYSM, 8082 NYSM), did not show significant differences in relation to the type-species of this genus, *N. skottsbergi*, that occurred in the Lower Devonian of the Malvinas Islands, Uruguay and in the Emsian-Eifelian of South Africa. The discovery of *N. skottsbergi* in the Paraná Basin expands the geographical scope of this species in the Malvinokaffric Realm.
Occurrence of *Notiochonetes skottsbergi*. In late Emsian–Eifelian, South Africa (Hiller, 1995); Lower Devonian, Malvinas Islands (Clarke, 1913); ?Eifelian, Bolivia (Racheboeuf *et al*., 1998); Lower Devonian, Paraguay (Harrington, 1950); late Pragian–early Emsian, Uruguay (Mendez-Alzola, 1938, for age see Daners *et al*., 2017) and late Emsian, Brazil (this paper).

Pleurochonetes Isaacson, 1977

Type species. *Chonetes (Pleurochonetes) lauriata* Isaacson, 1977.

Pleurochonetes surucoi? Racheboeuf, 1992
(Figure 8N)

2007 *Pleurochonetes surucoi?* Racheboeuf; Souza, p. 80, fig. 16b–c.

Material. MN 10508-I, MN 10619-I, MN 10949-I, UNIRIO 0226 BQ and DGM 1806-I.
Provenance. Jaguariaíva (late Pragian–early Emsian).
Description. Medium-sized shell, between 16 mm and 17 mm long and between 25 and 26 mm wide (UNIRIO 0226-BQ and DGM 1806-I, respectively), transverse (0.64 to 0.65); highly inflated shell, longitudinal profile clearly concave-convex, maximum width anterior to the hinge line, small umbo slightly protruding from the anterior edge. Ribs seemingly

narrow, gradually becoming sparser towards the commissure, pseudopunctation aligned and following the layout of the interspaces. Ventral interior: myophragm slightly exceeding half of the valve, muscular field covered by ornamentation. Dorsal interior: Not found in the analyzed material.

Remarks. *Pleurochonetes surucoi* Racheboeuf, 1992 differs from *P. anteloi* (Isaacson, 1977) in that it has a smaller, more inflated shell, less numerous spines, and radial ornamentation consisting of thinner ribs. Internaly *P. surucoi* differs from *P. anteloi* in that the pair of anderidia and dental sockets are more divergent, in addition to the lesser development of the median septum in *P. surucoi*. *P. surucoi* differs from *P. falklandicus* (Morris & Sharpe, 1846) by the greater development of these structures (Racheboeuf, 1992). The comparison of Brazilian specimens, especially DGM 1806-I and UNIRIO 0226-BQ, with Bolivian *P. surucoi*, deposited in the National Museum of Natural History/Smithsonian Institution collection (USNM 209085, USNM 209086, USNM 209087, USNM 209088, USNM 209165), showed great similarity based on the degree of transversality, very inflated shell and nature of the ornamentation. However, the absence of the dorsal valve in Brazilian material prevents the undoubted classification as *P. surucoi*, which is the reason we decided to identify Brazilian specimens with the open nomenclature.

Occurrence of the species *Pleurochonetes surucoi*. In late Pragian–early Emsian, Brazil (this paper), late Emsian–Eifelian, Bolivia (Racheboeuf, 1992, for age see Grahn, 2002), ?late Lochkovian–?early Pragian, Brazil (Boucot *et al*., 2001).

Pleurochonetes? *comstocki*? (Rathbun, 1874)
(Figure 8K)

Material. MN MG 839 (provisional code), MN MG 845 (provisional code), MN MG 873 (provisional code), MN MG 903 (provisional code), MN MG 928 (provisional code), MN MG 982 (provisional code) and MN MG 992B (provisional code).

Provenance. Monjolo dos Padres (early Givetian).

Description. large size valve, with length varying between 19 mm and 23 mm; width varying between 25 mm and 33 mm, slightly concave-convex, transverse to slightly transverse (0.69 to 0.77); rectangular contour, maximum width at the hinge line, rounded ribs, multiplying by intercalation and bifurcation and separated by narrow interspaces, about 10 ribs/5 mm in the best-preserved specimen (MN MG 873). Ventral interior: relatively long myophragm (reaching a little more than half of the valve of some specimens), weakly printed and variably developed muscle field, triangular adductor and flabeled diductor scars. Dorsal interior: not found in the study material.

Remarks. The specimens resemble *Pleurochonetes comstocki* (Rathbun, 1874) that occurred in the Middle Devonian of the Amazonas and Parnaíba basins (Ererê and Cabeças formations) (Fonseca, 2004). *P. comstocki* differs from other species of *Pleurochonetes* (*P. falklandicus* (Morris & Sharpe, 1846), *P. surucoi* Racheboeuf, 1992 and *P. anteloi* (Isaacson, 1977)) by the shape of the shell, external ornamentation, longer anderidia diverging with more acute angle and absence of accessory septa. Furthermore, *P. comstocki* is similar *to Notiochonetes skottsbergi* (Clarke, 1913) differing only by the cardinal process (Fonseca, 2004). However, the absence of the dorsal valve in material here studied prevents the undoubted classification as *P. comstocki*, even at a generic level, which is the reason why we decided to identify the specimens with the open nomenclature. If it is *P. comstocki* it would be one of the exogenous forms that entered the Paraná Basin in the early Givetian (Bosetti *et al*., 2010a).

Occurrence of *Pleurochonetes comstocki*. In late Eifelian–Givetian, Brazil (Fonseca, 2004; this paper).

PALEOBIOGEOGRAPHIC AND PALEOENVIRONMENTAL CONSIDERATIONS

Paleobiogeography

The species *Kentronetes iclaense*, *K. ortegae*, *Notiochonetes skottsbergi*, *Pleurochonetes surucoi*, and the genus *Sanjuanetes* are endemic to the Malvinokaffric Realm (*e.g*., Clarke, 1913; Racheboeuf & Branisa, 1985; Racheboeuf, 1992; Racheboeuf, 2000; Penn-Clarke & Harper, 2021).

The genera *Babinia* and *Chonostrophia* are found in Malvinokaffric regions (Rachebouef & Branisa, 1985; Hiller, 1987; Penn-Clarke, 2019; Penn-Clarke & Harper, 2021) but apparently, they were not endemic to this province, being also found in the Eastern Americas Realm (*e.g*., Rachebouef & Lespérance, 1995), although there are doubts about the real occurrence of *Babinia* in the Devonian of Canada, as discussed in the topic Systematic Paleontology.

The samples identified here as Chonetidae indet. and *Pleurochonetes*? *comstocki*?, found in layers of the Givetian of the Paraná Basin, may represent non-Malvinokaffric specimens that entered in the referred basin during from the early Givetian after the Kačák event (Bosetti *et al*., 2010a).

When comparing the occurrences of the taxa here identified in the Paraná Basin with their occurrences in other locations of the Malvinokaffric Realm (*e.g*., Clarke, 1913; Isaacson, 1977; Racheboeuf & Branisa, 1985; Proyecto PAR 83/005, 1986; Racheboeuf, 1992; Benedetto *et al*., 1992; Hiller, 1995; Herrera, 1995; Presser *et al*., 2004; Martinez & Verde, 2008; Racheboeuf *et al*., 2012), it is possible to infer some moments of fauna exchange in the Malvinokaffric Realm (Figures 9 and 10): one towards of Paraná Basin, coming from Bolivia, in the Lochkovian or in the Pragian, attested by the possible migration of the *Sanjuanetes* and probably *Babinia parvula*, related to the Lochkovian/Pragian events (Sedorko *et al*., 2019). Carbonaro *et al*. (2018) also reported migrations of trilobites *Metacryphaeus*, associated with the same transgression events, from Bolivia to the Paraná Basin; and another towards of Bolivia, coming from the Paraná Basin, in the late Emsian or in the Eifelian, attested by the possible migration of *Notiochonetes* probably related to the Choteč Event (Sedorko *et al*., 2019), it may represent the first paleontological evidence that this event influenced the migrations of the Malvinokaffric fauna.

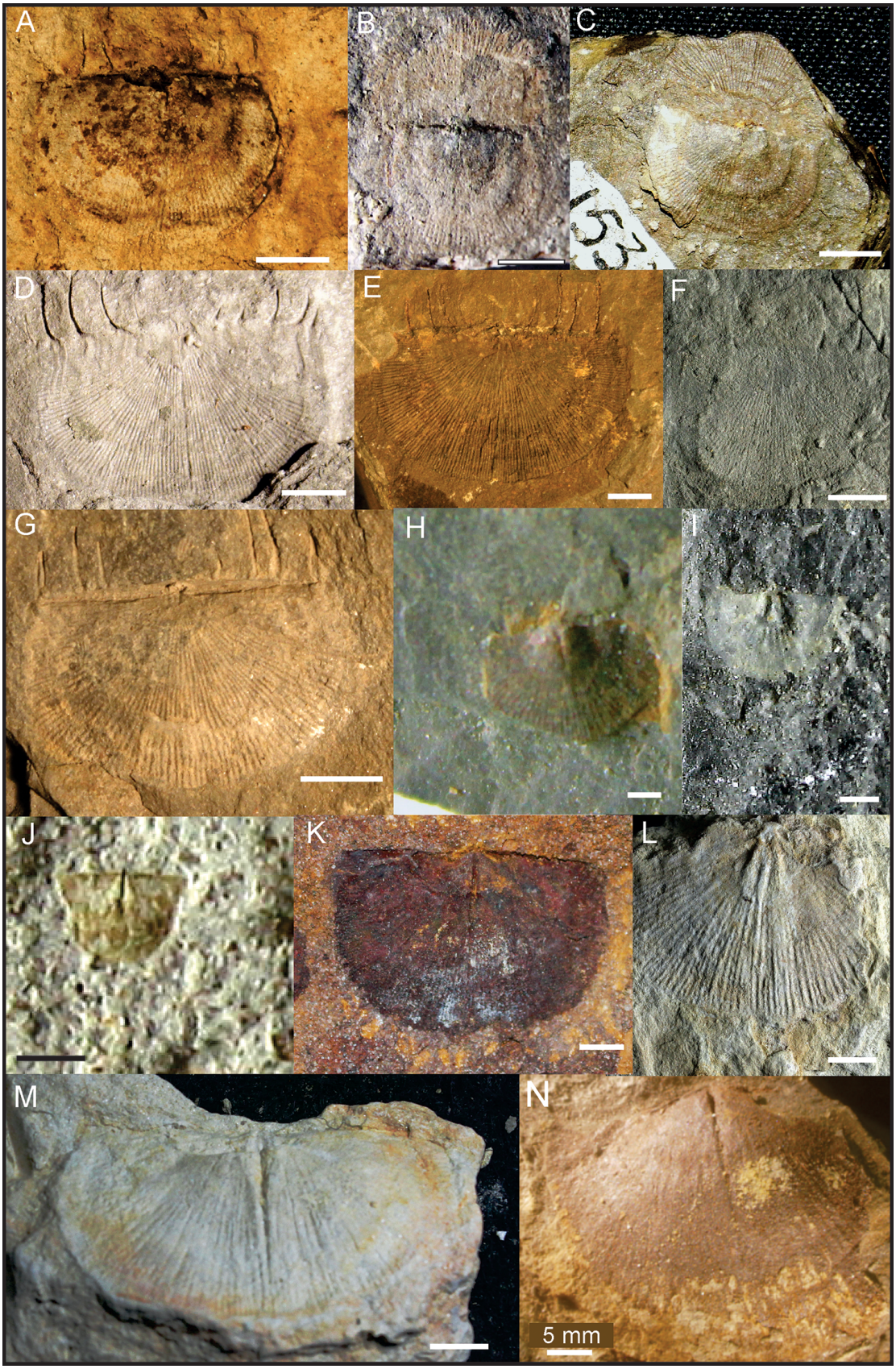

Figure 8. A–C, *Babinia parvula maxima* ssp. nov.: **A**, MPI 13645, Paratype; **B**, DGM 200-I, Holotype; **C**, DGM 1532-I, Paratype. **D–E**, *Kentronetes*? *iclaense*: **D**, DGM 1715-I; **E**, MPI 1382. **F–G**, *Kentronetes*? *ortegae*?: **F**, NR 1044; **G**, NR 12554. **H**, *Sanjuanetes*? sp.: MN MS Q1 F7. **I**, *Chonostrophia*? aff. *Truyolsae*: MN MS Q1 F11. **J**, Chonetidae indet.: CCLP 935. **K**, *Pleurochonetes*? *comstocki*?: MN MG 982.; **L–M,** *Notiochonetes skottsbergi*: **L**, NR 6550; **M**, NR 8549b. **N**, *Pleurochonetes surucoi*?: UNIRIO 0226 – BQ. Scale bars: A–G, K–N = 5 mm; H–J = 1 mm.

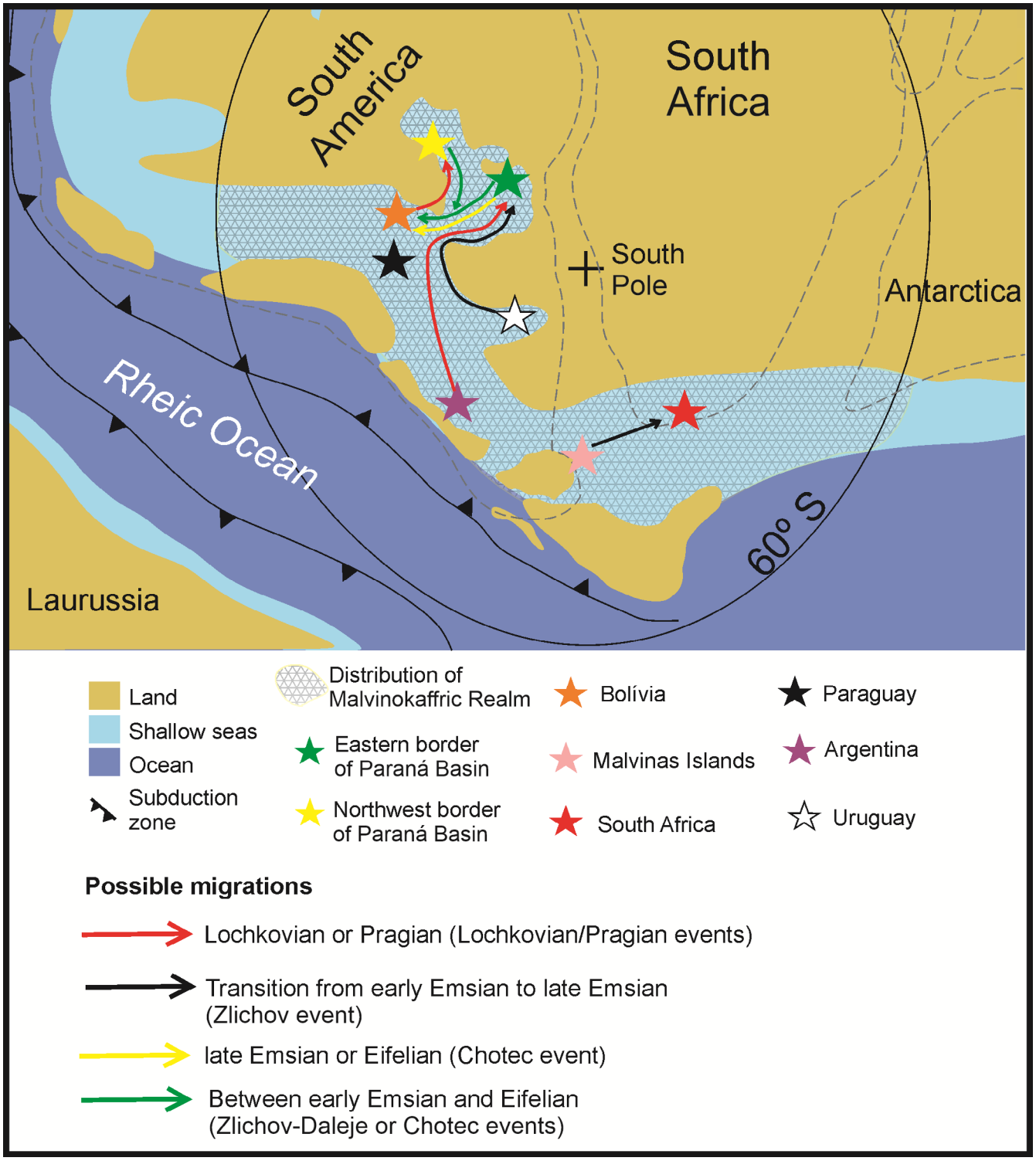

Figure 9. Possible migrations of Chonetoidea along the Devonian in the Malvinokaffric Realm. Arrows indicate the possible migrations (adapted from Sedorko *et al*., 2021 and references therein). Positioning of the Malvinas Islands followed Ramos *et al*. (2017).

There is also one more possible migration event towards Bolivia, coming from the Paraná Basin, attested by the possible migrations of *Chonostrophia truyolsae, Kentronetes iclaense* and *Pleurochonetes surucoi* between the early Emsian and the Eifelian that may be related to the Zlichov-Daleje or Choteč events (Sedorko *et al*., 2019). If it were related to the Zlichov-Daleje events, there would therefore be three moments of fauna exchange between the Paraná Basin and Bolivia, during the Devonian.

The migration of *Notiochonetes skottsbergi* from Uruguay to the Paraná Basin, in the transition from the early Emsian to the late Emsian, is possibly related to the Zlichov Event.

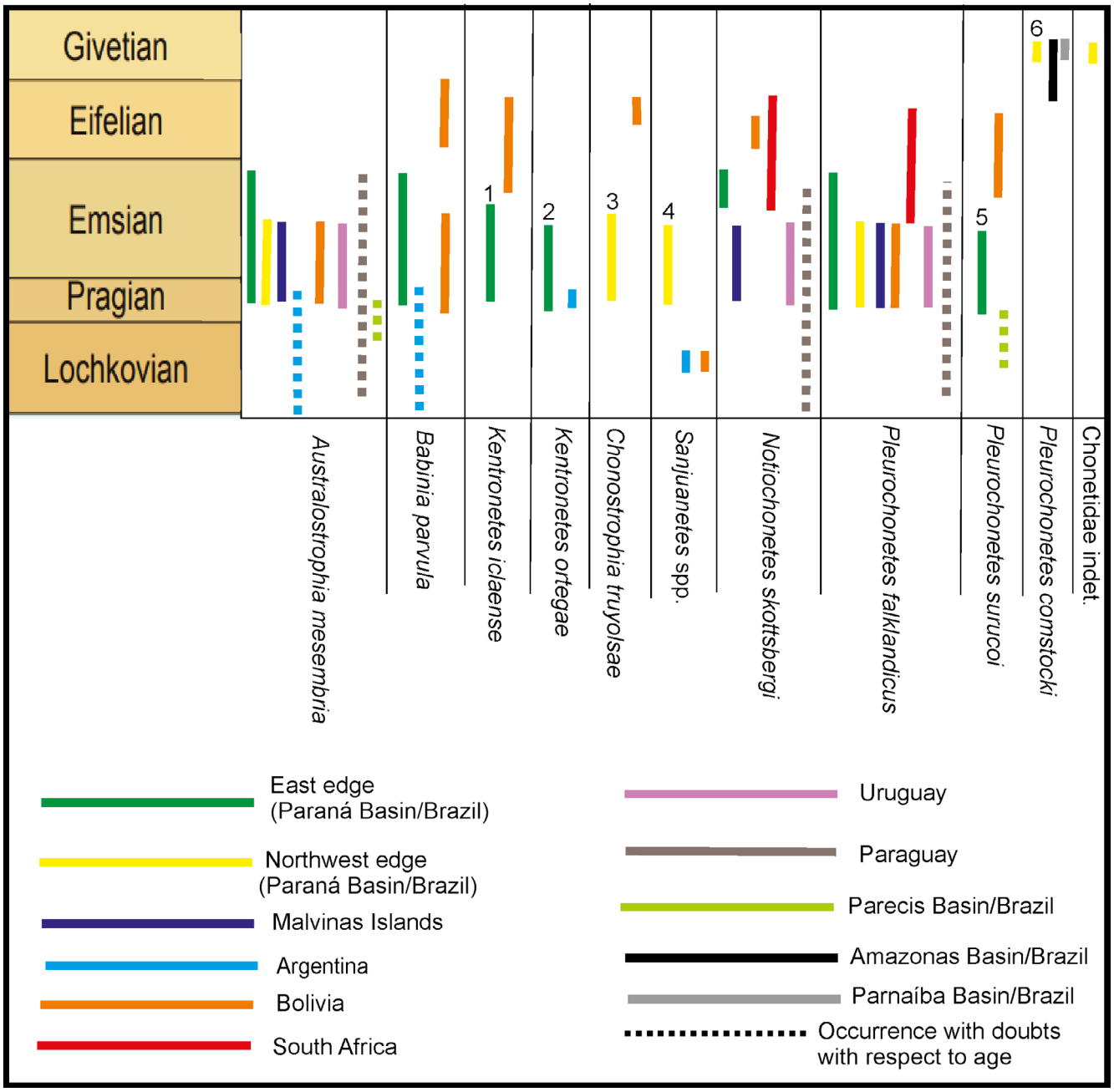

Figure 10. Geochronological distribution of taxa found in the Paraná Basin. **1**, identified in this paper as *Kentronetes*? *iclaense*; **2**, identified in this paper as *Kentronetes*? *ortegae*?; **3**, identified in this paper as *Chonostrophia*? aff. *truyolsae*; **4**, identified in this paper as *Sanjuanetes*? sp.; **5**, identified in this paper as *Pleurochonetes surucoi*?; **6**, identified in this paper as *Pleurochonetes*? *comstocki*? (occurrences follow Clarke, 1913; Mendez-Alzola, 1938; Castellaro, 1966; Quadros, 1981; Quadros, 1987; Racheboeuf, 1992; Herrera, 1993; Racheboeuf & Herrera, 1994; Hiller, 1995; Herrera, 1995; Boucot *et al*., 2001; Peralta *et al*., 2003; Presser *et al*., 2004; Martínez & Verde, 2008; Bosetti *et al*., 2012).

Paleoenvironment

About 75% of the analyzed specimens of *Babinia parvula maxima* ssp. nov. were found in rocks associated with relatively deeper environments, evidenced by quite dark siltstones, and about 25% of them in relatively shallow environments, evidenced by sandy siltstones. In sandy siltstones there are non-fragmented specimens with preserved spines (*e.g.*, MPI 13645 and MPI 1372), while in dark siltstones there are non-fragmented specimens in butterfly preservation (*e.g.*, DGM 1532-I and DGM 200-I). The presence of spines and the butterfly preservation suggests that the specimens analyzed were autochthonous to parautochthonous both in the samples of dark siltstone and sandy siltstone. This taxon is also found in these two lithologies in Bolivia and South Africa (Racheboeuf, 1992; Hiller, 1995). Despite the small size, *Babinia parvula maxima* ssp. nov., occurred in environments, preferably related to BA 3–4, due the presence of orthomorphic and not so long spines.

About 85% of the specimens of *Kentronetes*?, were found in dark siltstones, which shows a relatively anoxic environment, while the other 15% were also found in siltstones, but grayish. Apparently, this genus preferred this type of environment, since most of the analyzed specimens had spines, or at least their base, preserved, non-fragmented and disarticulated valves (*e.g*., DGM 1715-I, MPI 13282, MN 10073-I) indicating that they are parautochthonous. Moreover, this genus is only found in this type of lithology, or at least very similar, in Bolivia and South Africa (Racheboeuf, 1992; Hiller, 1995). In theory, *K. iclaense* would inhabit shallower positions and with greater hydrodynamic force action in relation to *K. ortegae*, because according to Racheboeuf (1990), there would be an increase in the number of spines, the shallower the Chonetoidea lived, in order to give greater stability to the same. *Kentronetes*? *ortegae*? Herrera, 1995 and *Kentronetes*? *iclaense* (Racheboeuf & Branisa, 1985) possibly lived in a preferential environment related to BA 4.

The specimens of *Chonostrophia*? aff. *truyolsae* analyzed in this paper were small and due to the small number of specimens it is not possible to say whether they are adults or juveniles. However, individuals referred to as *Chonostrophia* in Bolivia are small, including specimens considered adults. The specimen from Mato Grosso do Sul (MN MS Q1 F11) was collected close to the Maximum Flooding Surface (MFS) of the Barreiro da Figueira outcrop, probably associated with Siluro–Devonian sequence *sensu* Sedorko *et al*. (2018b), in a shale parallel to bedding, disarticulated, non-fragmented and with a preserved spine, suggesting that this specimen was parautochthnous in an offshore environment; however, they are also found disarticulated and with spines preserved in siltstones in Chapada dos Guimarães, judging by the illustrations by Quadros (1987), and even sandstones in other portions of the Malvinokaffric Realm (Racheboeuf, 1992), in a transitional offshore environment. Therefore, judging only by the small size of the valve, considering that the size of the spines is unknown, it is possible to infer that the specimens of *Chonostrophia* from the Malvinokaffric Realm preferred deeper environments referred to BA 4 or 5. In the Eastern Americas Realm, this genus could inhabit even portions referred to BA 3 (Racheboeuf & Lespérance, 1995).

The specimen of *Sanjuanetes*? sp. analyzed in this paper was parallel to the bedding, not fragmented, disarticulated, with downward convexity and without preserved spines, which indicates that the specimen did not undergo much transportation in relation to its living environment (autochthonous to parautochthonous). It was collected at the same level as one of the *Chonostrophia*? aff. *truyolsae* specimes in shales from Mato Grosso do Sul. Judging for this fact and only for the small size of the valve, considering that the size of the spines is unknown, it is possible that it occurred in the same preferred environment as *Chonostrophia*, that is, BA 4 or 5.

Notiochonetes from the Paraná Basin were found only in the Rio Caniú outcrop. All specimens analyzed are disarticulated, parallel to bedding and without preserved spines. The NR 8549a,b specimen is complete, while the NR 6550 and NR 6152 specimens are fragmented, but it was not possible to know if this occurred at the time of collection. Due to the morphology of the shells of this genus (large and little inflated), they possibly lived in BA 3, although they may also have inhabited environments of greater depths.

The specimens of *Pleurochonetes surucoi* were only found in the Jaguariaíva outcrop and one of the specimens (DGM 1806-I) is articulated, suggesting deposition *in situ*. The region of Jaguariaíva was shallower than the region of the city of Ponta Grossa (Petri, 1948) and in this outcrop there is an abundant occurrence of *Australostrophia mesembria* which appears to prefer the BA 3 environment, at least in the Paraná Basin (Videira-Santos, 2020). With this in mind, we believe that *P. surucoi* also occurred at BA 3 as well as *N. skottsbergi*. *P.*? *comstocki*? was found in sandstones in the Paraná Basin (Monjolo dos Padres outcrop) and we believe it also occurred in BA3. It is important to note that the morphotypes of the *Pleurochonetes* and *Notiochonetes* shells are similar and, therefore, these genera tend to have the same preferential occurrence environment (Racheboeuf, 1990).

In summary, the specimens of chonetoidean analyzed occurred in the offshore transition and offshore environments, as suggested by the lithology of the outcrops, most of which were previously studied by the authors in fieldwork in the Paraná Basin, and because the specimens are possibly autochthonous to parautochthonous as explained above. Here we correlate the relative benthic placements *sensu* Rachebouef (1990), as explained in Material and Methods, with the offshore transition and offshore environments (Figure 11).

FINAL CONSIDERATIONS

The diversity of chonetoideans in the Devonian in the Paraná Basin is greater than previously thought. In this contribution, we considerably increase the diversity known in this basin by identifying nine other taxa besides *Pleurochonetes falklandicus* and *Australostrophia mesembria*, including *Babinia parvula* with emended diagnosis and the new subspecies *Babinia parvula maxima* ssp. nov., although many identifications have been made with open nomenclature due to poor preservation of the studied material.

The species *Kentronetes iclaense* may have appeared in the Paraná Basin, if in the future the identity of the analyzed specimens is confirmed. In contrast, the occurrence of the genus *Sanjuanetes*, possibly, can be extended to the late Pragian–early Emsian.

The data presented indicate that possibly the Paraná Basin was not so isolated from the other basins in South America, at least, in the Lower Devonian. Possibly, there were several pulses of migration between the Paraná Basin and the other South American basins associated with marine transgressions.

Finally, we recognize that all paleobiogeographic and paleoenvironmental inferences presented here need to be corroborated in the future through the analysis of more specimens (well preserved) and taphonomic and sequence stratigraphy studies. However, these pioneering inferences are

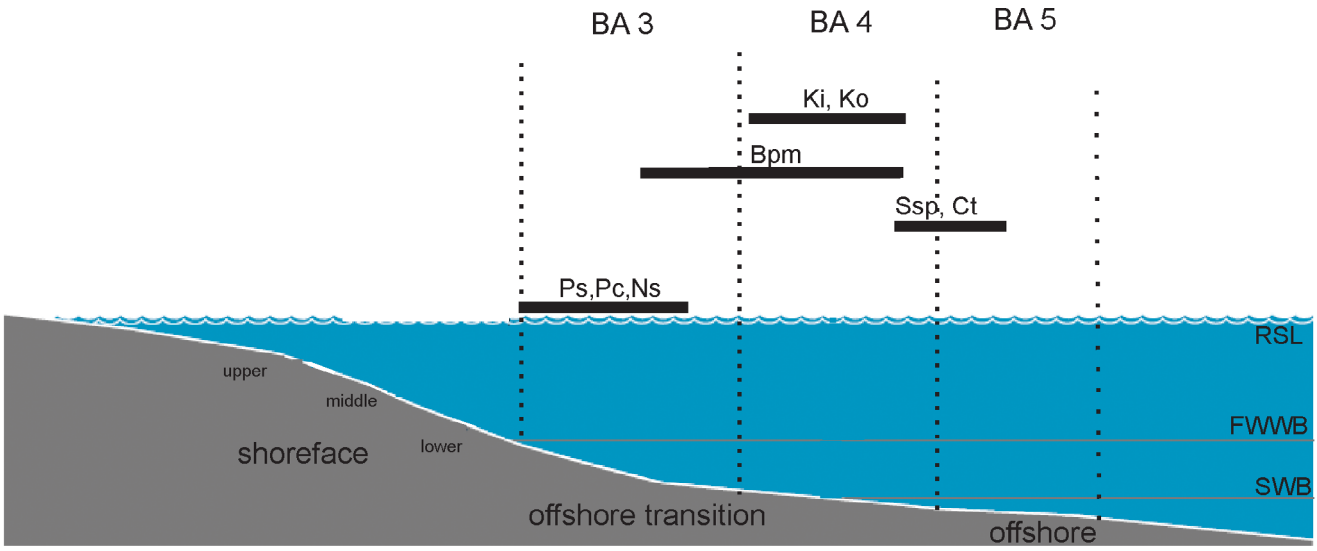

Figure 11. Preferential distribution across the shelf in the Paraná Basin, of the taxa identified in this paper. **Abbreviations: Ps**, *Pleurochonetes surucoi*?; **Pc**, *Pleurochonetes*? *comstocki*?; **Ns**, *Notiochonetes skottsbergi*; **Bpm**, *Babinia parvula maxima* ssp. nov.; **Ko**, *Kentronetes*? *ortegae*?; **Ki**, *Kentronetes*? *iclaense*; **Ssp**, *Sanjuanetes*? sp.; **Ct**, *Chonostrophia*? aff. *truyolsae*. **BA**, Benthic Assemblage; **RSL**, Relative Sea Level; **FWWB**, fair-weather wave base; **SWB**, storm wave base level (adapted from Horodyski *et al*., 2018).

important, as they open the way for a better understanding of the Malvinokaffric Chonetoidea brachiopods.

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