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Taphonomic aspects and the Lilliput Effect on Devonian discinoids of the Paraná Basin, Apucarana Sub-basin, Brazil

Jeanninny Carla Comniskey
Universidade de São Paulo. Av. Bandeirantes, 3900, Monte Alegre, 14040-901, Ribeirão Preto, SP, Brasil. comniskey@gmail.com

Elvio Pinto Bosetti
Universidade Estadual de Ponta Grossa. Av. General Carlos Cavalcanti, 4748, Uvaranas, 84030-900, Ponta Grossa, PR, Brasil. elvio.bosetti@pq.cnpq.br

Rodrigo Scalise Horodyski
Universidade do Vale do Rio dos Sinos. Av. Unisinos, 950, Cristo Rei, 93022-750, São Leopoldo, RS, Brasil. rshorodyski@gmail.com

ABSTRACT

Discinoids are exclusively marine, epibenthic, inarticulate brachiopods, which use their pedicle to attach to the substrate. The global stratigraphic range of the genera range from the ?Ordovician to Holocene, but the Devonian period was the climax of this group. They have a broad geographical distribution and, in Brazil, are found in the Paraná, Amazonas, Parnaíba and Parecis basins. The discinoids from the Paraná Basin are found in the Ponta Grossa and São Domingos formations. Three genera of discinoids are recorded in the Brazilian Devonian strata, *Orbiculoidea*, *Gigadiscina* and *Rugadiscina*. Five species are recognized in the Paraná basin (*Orbiculoidea baini*, *Orbiculoidea bodenbenderi*, *Orbiculoidea excentrica*, *Gigadiscina collis* and *Rugadiscina* sp.). As far the taphonomy is concerned, the discinoids can be found isolated or in clusters, as complete and articulated valves, or as complete and disarticulated valves and/or fragmented valves, and constitute assemblages of shoreface and offshore settings. The analysis presented herein establishes the stratigraphic range of the Discinidae family between the late Pragian and the early Givetian. *Orbiculoidea baini* and *Orbiculoidea excentrica* showed phenotypes with reduced size attributed to the Lilliput Effect. This effect resulted of a biotic crisis recorded shortly before the collapse of Malvinokaffric fauna that caused a global extinction, the Kačák Event, in the Eifelian-Givetian transition.

Keywords: Discinoids, Lilliput Effect, Devonian, Kačák Event, Taphonomy.

RESUMO

ASPECTOS TAFONÔMICOS E O EFEITO LILLIPUT EM DISCINOIDEOS DO DEVONIANO DA BACIA DO PARANÁ, SUB-BACIA APUCARANA, BRASIL. Os discinídeos são braquiópodes inarticulados, exclusivamente marinhos, epibentônicos, que utilizam o pedículo para fixação ao substrato. Eles têm distribuição estratigráfica do ?Ordoviciano ao Holoceno, mas foi no período Devoniano o clímax desse grupo. Possuem ampla distribuição geográfica e, no Brasil, são encontrados nas bacias do Paraná, Amazonas, Parnaíba e Parecis. Na Bacia do Paraná, os discinídeos são encontrados nas Formações Ponta Grossa e São Domingos. Três gêneros de discinídeos são encontrados nos estratos devonianos brasileiros (*Orbiculoidea*, *Gigadiscina* e *Rugadiscina*). Cinco espécies são reconhecidas para a Bacia do Paraná (*Orbiculoidea baini*, *Orbiculoidea bodenbenderi*, *Orbiculoidea excentrica*, *Gigadiscina collis e Rugadiscina* sp.). Em relação à tafonomia, os discinídeos podem ser encontrados isolados ou agrupados, como valvas completas e articuladas, ou valvas completas e desarticuladas e/ou valvas fragmentadas, e constituem assembleias em sucessões de *shoreface* a *offshore*. A análise da distribuição estratigráfica estabelece a família Discinidae entre o final do Praguiano e o início do Givetiano. *Orbiculoidea baini* e *Orbiculoidea excentrica* mostraram tamanhos fenotípicos reduzidos atribuídos ao Efeito Lilliput. Esse efeito resultou de uma crise biótica registrada pouco antes do colapso da fauna Malvinocáfrica, que causou uma extinção global, o Evento Kačák, na passagem Eifeliano-Givetiano.

Palavras-chave: Discinídeos, Efeito Lilliput, Devoniano, Evento Kačák, Tafonomia.

INTRODUCTION

The discinoids are extinct marine invertebrates belonging to the Family Discinidae. The representatives of this group have epibenthic behavior and a shell formed by two valves. The group is common in middle shoreface sandstones and siltstones successions as well as in offshore-transition to offshore shales. Discinoids have stratigraphic distribution between the Ordovician and Holocene.

The present study presents the occurrence of five species of discinoids:

O. baini, *O. bodenbenderi*, *O. excentrica*, *G. collis* and *Rugadiscina* sp. The analysis has defined the stratigraphic range of the Discinidae family between the latest Pragian to early Givetian.

In the study area the species *Orbiculoidea bodenbenderi*, *Gigadiscina collis* and *Rugadiscina* sp. are recorded from late Pragian to Emsian, whereas *Orbiculoidea baini* and *Orbiculoidea excentrica* are recorded from latest Pragian to early Givetian. The species *O. baini* and *O. excentrica* showed phenotypes with reduced size in adult forms, characteristic of a relictual fauna. Despite occurring in all types of rocks, their presence is well marked in black shales, in which they are often the only taxa found.

The aim of this paper is to document taphonomic aspects, record the reduced sizes in discinoids found in Devonian outcrops of the Paraná Basin, and discuss the Lilliput Effect in Orbiculoidea. The discinoid taphonomic signatures, diagnosed on the material, support the characterization of two taphonomically-controlled modes (classes) of preservation.

DISCINOIDS IN THE PARANÁ BASIN

Derby (1877) reported the first occurrence of Devonian, organophosphatic discinoids (Family Discinidae) from the Paraná Basin in the Paraná State, south of Brazil. Clarke (1890) described different fossil groups previously collected by Luiz Felipe Gonzaga de Campos in 1888, in the vicinity of the Jaguariaíva municipality. Clarke did not participate of any fieldwork in Brazil but he noticed that the discinoid fossil exhibited a cosmopolitan character independently of the sedimentary facies in which they occurred. Clarke (1913) and Kozlowski (1913) were the first to describe discinoids from the Devonian rocks of the Paraná State. Clarke (1913) recognized *Orbiculoidea baini* and Sharpe (1856) proposed two new species: *O.bodenbenderi* and *O.collis*. Kozlowski (1913), in the same year, published "Devonian fossils from the Paraná State", in which he described a new discinoid species: *Orbiculoidea grandissima*. However, these new species have the same characteristics of *O. collis* Clarke (1913), which led to the priority of *Orbiculoidea collis* once Clarke's article (1913) was published a few months before Kozlowski's (1913). Many years later, Lange (1943) proposed a new species, *Orbiculoidea excentrica*.

After Clarke's (1913), Kozlowski's (1913) and Lange's (1943) researches, Brazilian Devonian discinoids were not studied for more than 60 years. Comniskey (2011), Comniskey and Bosetti (2012), and Zabini *et al.* (2013) retake the study of this group approaching questions of systematic, biostratigraphy, paleoecology and taphonomy.

MATERIAL AND METHODS

The outcrops analyzed in this study have been widely studied by the authors through time. The methodology used is adapted from the systematic protocols proposed by Simões and Ghilardi (2000), Bosetti (2004) and Ghilardi (2004). The outcrop area was prospected in accordance with the specific methodology (Bosetti, 2004) in which stratigraphic pavements and grid squares are demarcated and fossils are collected with concomitant detailed description from the top to the bottom of each area.

The method used in the fieldwork consists of the following steps, subdivision of the outcrop in squares (at least 3m wide and 2m high) and/or pavements controlled from the base to the top. This procedure allows the observation of the evolution of the taxonomic and taphonomic associations throughout the section; position (x, y and z axes) of bioclasts in the squares; bioclasts orientation relative to bedding plane; degree of fragmentation of bioclasts; degree of disarticulation of the shells; concavity and convexity in relation to bedding plane; orientation of bioclasts regarding possible paleocurrent; and description of lithofacies (Speyer and Brett, 1986; Speyer and Brett, 1988; Speyer and Brett, 1991; Holz and Simões, 2002). This data set makes it possible to get maps, photos, and to perform stratigraphic correlation between different outcrops based on the regional stratigraphic framework of sequences (Bergamaschi, 1999; Grahn *et al*., 2013).

The fossil distribution in the studied sedimentary succession and their taphonomic signatures allowed to recognize different taphonomical classes, related to siltstone, sandstone and shale deposits. The parameters used for Taphonomy follow the same of Rodrigues' *et al.* (2003) and Zabini' *et al.* (2010), among others.

The interpretation of the assemblage in relation to the lithofacies was followed from the concepts of Walker and James's (1992) the facies models and a number of subsequent articles of different authors, adding inferences of models of distribution of fossiliferous associations related with the environments they represent. Additionally, the parameters used to determine degrees of autochthonous/allochthonous followed observations of anatomy, presumed mode of life and taphonomic signatures of concentrations as life position, disarticulation and degree of fragmentation of bioclasts.

The samples analyzed were collected from Devonian outcrops at the following cities and localities (Figure 1), as follow:

(a) Ponta Grossa

Outcrops Boa Vista (S 25^{0} 04' 38,01"; W 50^{0} 11' 25,01"),

Vendrami (S 25^{0} 08' 57,07"; W 50^{0} 11' 25,01"),

Desvio Ribas - Tibagi (S 25^{0} 12' 02,73"; W 50^{0} 03' 58,55"),

Caça e Pesca (S 25^{0} 11' 24,15"; W 50^{0} 08' 27, 36"),

Fazenda Rivadávia (S 25^{0} 15' 05,47"; W 50^{0} 03' 06,21"),

Curva I (S 25^{0} 03' 34,56"; W 50^{0} 08' 04,09"),

Curva II (S 25^{0} 04' 03,06"; W 50^{0} 07' 56,18"),

Vila Francelina (S 25^{0} 04' 55"; W 50^{0} 06' 54"),

Pilão de Pedra (S 25^{0} 05' 17,95"; W 50^{0} 09' 15,43") and

Vila Vilela (S 25^{0} 05' 17,40"; W 50^{0} 09' 16,37"),

(b) Jaguariaíva

Railroad Outcrop at Jaguariaíva – Arapoti railroad (S 24^{0} 14' 05"; W 49^{0} 42' 34"),

(c) Tibagi
Outcrops Tibagi II (S 24^0 29’ 51”; W 50^0 25’ 00”),
Furnas/Ponta Grossa contact (S 24^0 46’ 04”; W 50^0 09’ 24”),
Sítio Wolff (S 24^0 28’ 11,21”; W 50^0 32’ 08,46”),
Fazenda Fazendinha (S 24^0 28’ 04,50”; W 50^0 26’ 28,01”),
Km 211 (S 24^0 34’ 29,19”; W 50^0 27’ 05,03”),
Km 217 (S 24^0 36’ 34,88”; W 50^0 26’ 37,73”),
Km 220 (S 24^0 38’ 02,19”; W 50^0 27’ 40,35”) of the BR 153 highway and Fazenda Zezito = Tibagi Member type section *sensu* Lange and Petri, 1967 (S 24^0 31’ 32,65”; W 50^0 27’ 52,05”), and
(d) Palmeira
Rio Caniú outcrop (S 25^0 18’ 48” e W 50^0 05’ 32”).

A number of the fossils analyzed in the present research had already been deposited in the UEPG collection. This material is constantly enriched by fossils collected during each new field campaign.

GEOLOGY

The Paraná Basin is an intracratonic, intercontinental and polycyclic sedimentary basin. It has about 1.5 million km^2 (Milani *et al.*, 2007). This basin has two depocenters, the northern Alto-Garças Sub-Basin and the southern Apucarana Sub-Basin, which constitute the east-central portion of the South American continent (Figure 1). Milani *et al.* (2007) recognized six major rock packages that represent depositional periods of tens of millions of years. These units are demarcated by inter-regional discontinuities. The Devonian Paraná supersequence, which bears the discinoids studied herein, is represented by successive transgressive-regressive cycles that are linked to second order sea-level oscillations (Milani *et al.*, 2007).

The studied outcrops are part of the Campos-Gerais Group (Grahn *et al.*, 2000; Gaugris and Grahn, 2006; Grahn *et al.*, 2013; Mendlowicz Mauller *et al.*, 2009), which consists of the Furnas, Ponta Grossa and São Domingos formations (see Grahn *et al.*, 2013). Regional unconformities are recorded during the latest Early Emsian and the earliest late Emsian as a result of the Andean Pre-Cordilleran epirogenesis (Grahn *et al.,* 2013). The Ponta Grossa Formation overlies the Furnas Formation. Lithologically, it is composed of black to light gray shales, massive dark mudstones or laminated siltstones and, interspersed with sandy layers or sandy lenses, with wavy-laminated or hummocky-like structures (Grahn *et al.*, 2013). This unit is characterized by marine shoreface to offshore deposits in a transgressive context that has its major evidence in the contact Furnas-Ponta Grossa (Horodyski *et al.*, 2014). The São Domingos Formation is positioned stratigraphically above the Ponta Grossa formation (Grahn *et al.*, 2013) and it is lithologically composed of mudstones, shales, siltstones, sandstones and conglomeratic sandstones whose main sedimentary structures are horizontal laminations with sporadic occurrence of small to medium hummocky cross stratification (HCS), flaser and wavy bedding, as well as occasional bioturbation. These rocks record marine deposits of the inner and outer shelf.

STRATIGRAPHIC DISTRIBUTION

Orbiculoidea had a wide geographical distribution during the Devonian and has been recorded in the Paraná, Parecis, Amazonas and Parnaíba basins (Clarke, 1913; Lange, 1943; Boucot *et al.*, 2001; Melo, 1988). *Gigadiscina collis* (= *Orbiculoidea collis* sensu: Clarke, 1913; Lange, 1954; Melo, 1988; Boucot *et al.,* 2001) has been recorded in the Paraná and Parecis basins up to now, whereas *Rugadiscina* is found only in the Paraná Basin. Based on the field data and the recent relative dating of the outcrops (see Grahn *et al.,* 2010, 2013; Bosetti *et al.,* 2011, 2012), it was possible to determine the discinoid stratigraphic distribution during the Devonian.

Orbiculoidea baini and *O. excentrica* are the species that have the broadest paleogeographic and biostratigraphic distributions. They range from the latest Pragian until the early Givetian (Figure 2). In comparison with *O. baini*, *O. excentrica* is less abundant. Previously, *O. excentrica* had not been recorded from early Eifelian strata, but since it has been recorded in early Givetian age, its absence in the Eifelian units must be a taphonomic artifact. *O. baini* is very abundant in all the studied stages and regions, independently of the lithology. *O. baini* is very abundant between the early and the middle of Emsian. *Orbiculoidea bodenbenderi* and *G. collis* have been recorded in the late Pragian to late Emsian. *Rugadiscina* sp. was found until now at only one locality (?latest Pragian – Emsian). The five species of discinoids found on the Devonian, in the Paraná basin, were associated with other invertebrates of the Malvinokaffric Realm. During the late Emsian, the discinoid biogeographic range begins to decrease accompanied by a lower abundance. *Orbiculoidea bodenbenderi*, *G. collis* and *Rugadiscina* sp. disappeared from the fossil record together with other very common Malvinokaffric representatives (see Bosetti *et al.,* 2012). The early Eifelian is marked by the decline in diversity of all the faunal elements that were common during the previous stages (sensu: Melo, 1988; Bosetti *et al.,* 2010a, 2010b, 2012; Horodyski, 2014); it caused the Eifelian/Givetian transition Kačák Event (House, 2002) registered by Horodyski *et al.* (2014) in the Paraná Basin. This has been confirmed by the discinoid record, which declined in species richness from this stage. Only *O. baini* and *O. bodenbenderi* have been recorded in the early Eifelian and with reduced abundance than that of underlying beds. The cosmopolitan species *O. baini* becomes abundant from the earliest Givetian. *Orbiculoidea excentrica*, as previously cited, is present only in low abundance.

The stratigraphic framework adopted herein is based on Bergamaschi (1999), Bergamaschi and Pereira (2001), Bosetti *et al.* (2012), Grahn *et al.* (2013), and Horodyski *et al.* (2014). The five discinoid species (*O.baini*, *O. bodenbenderi*, *O. excentrica*, *G. collis,* and *Rugadiscina* sp.)

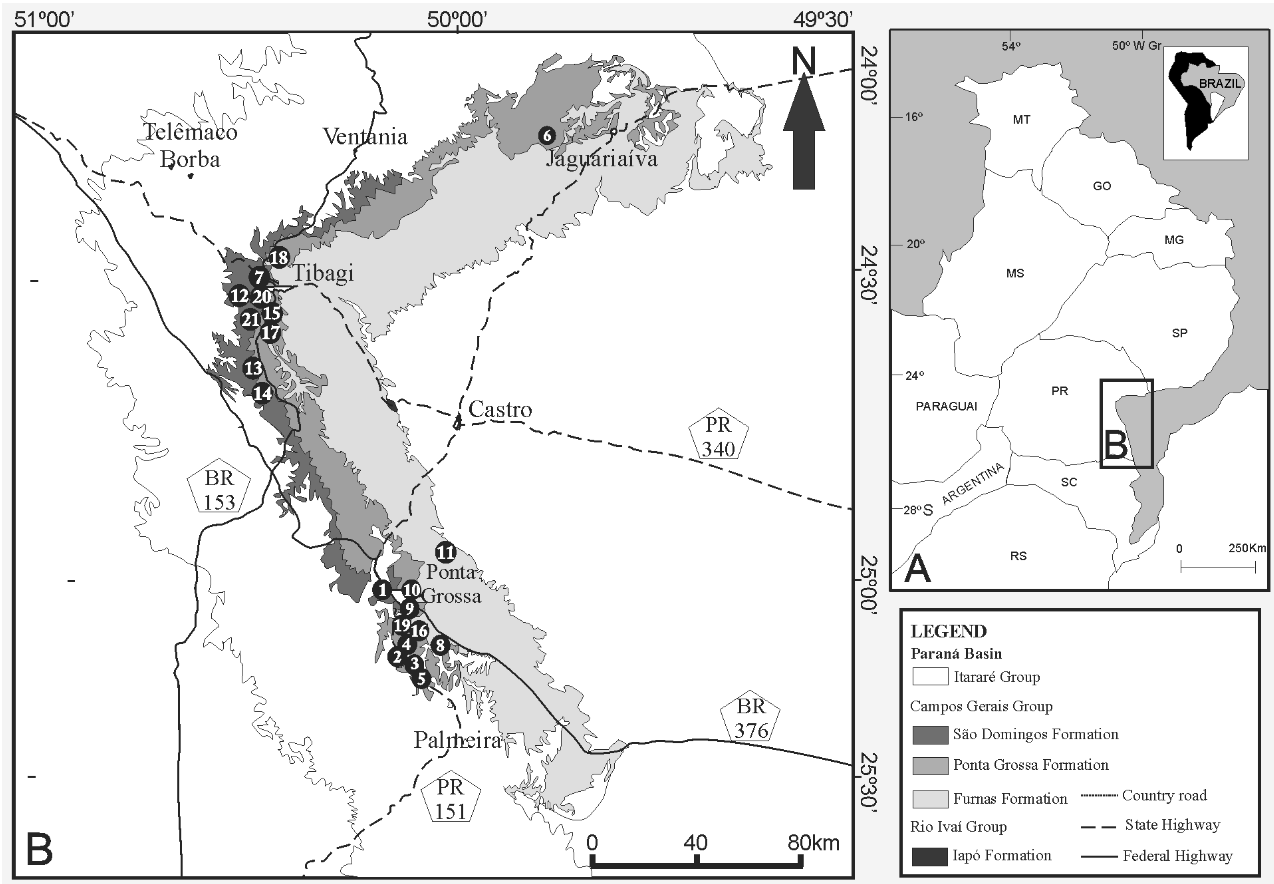


Figure 1. Study area. **A)** Location map of the study area in the Paraná Basin record. **B)** Location of formations and outcrops analyzed (after Grahn *et al.*, 2013).

were analyzed in relation to their relative abundance and stratigraphic range based on the field data. The prospected outcrops have been correlated to each other based on outcrop data published by Bergamaschi (1999), Bosetti *et al.* (2010, 2012) and Grahn *et al.* (2010, 2013).

At the latest Pragian-early Emsian, a major discinoid domain of the group is recorded, represented by their abundance and the paleobiodiversity climax of all the Malvinokaffric fauna (sensu Bosetti *et al.*, 2012). In the Eifelian-Givetian interval, discinoids were rare, and only *O. excentrica* and *O. baini* have been recorded. The decrease in the abundance of discinoids is due to the decline of the Malvinokaffric Fauna (*cf.* Bosetti *et al.,* 2012; Horodyski, 2014).

TAPHONOMY

The discinoid taphonomic signatures support the characterization of two taphonomic classes: A – clustered bioclasts – and B – isolated bioclasts. The taphonomic class A occurs in the shoreface environment. In deposits interpreted as situated above the fair-weather wave base (FWWB), such as middle and lower shoreface, the lithofacies are fine-to-medium sandstones and fine sandstones to coarse siltstones, bearing thin sand lenses with wavy ripple and hummocky cross stratification. The taphonomic class B occurs in the offshore-transition to offshore deposits. The siltstones are often intercalated with thin sandstones lenses and indicate the offshore-transition zone, below the shoreface. This region is located between the FWWB and the storm wave base level (SWB), marking the transition with the offshore. Dark shales formed by decantation of fine sediment below the SWB after the storm surge is the lithofacies, which represent the deepest portions of the sedimentary setting, interpreted as offshore deposits.

These classes can be subdivided into 5 subclasses, as follows (Figure 3):

Subclass A1: articulated valves near or overlapping each other.

Subclass A2: dorsal and ventral valves complete, disarticulated, near or overlapping each other.

Subclass A3: fragmented valves associated with complete valves, articulated or disarticulated.

These three subclasses have been found in shoreface deposits.

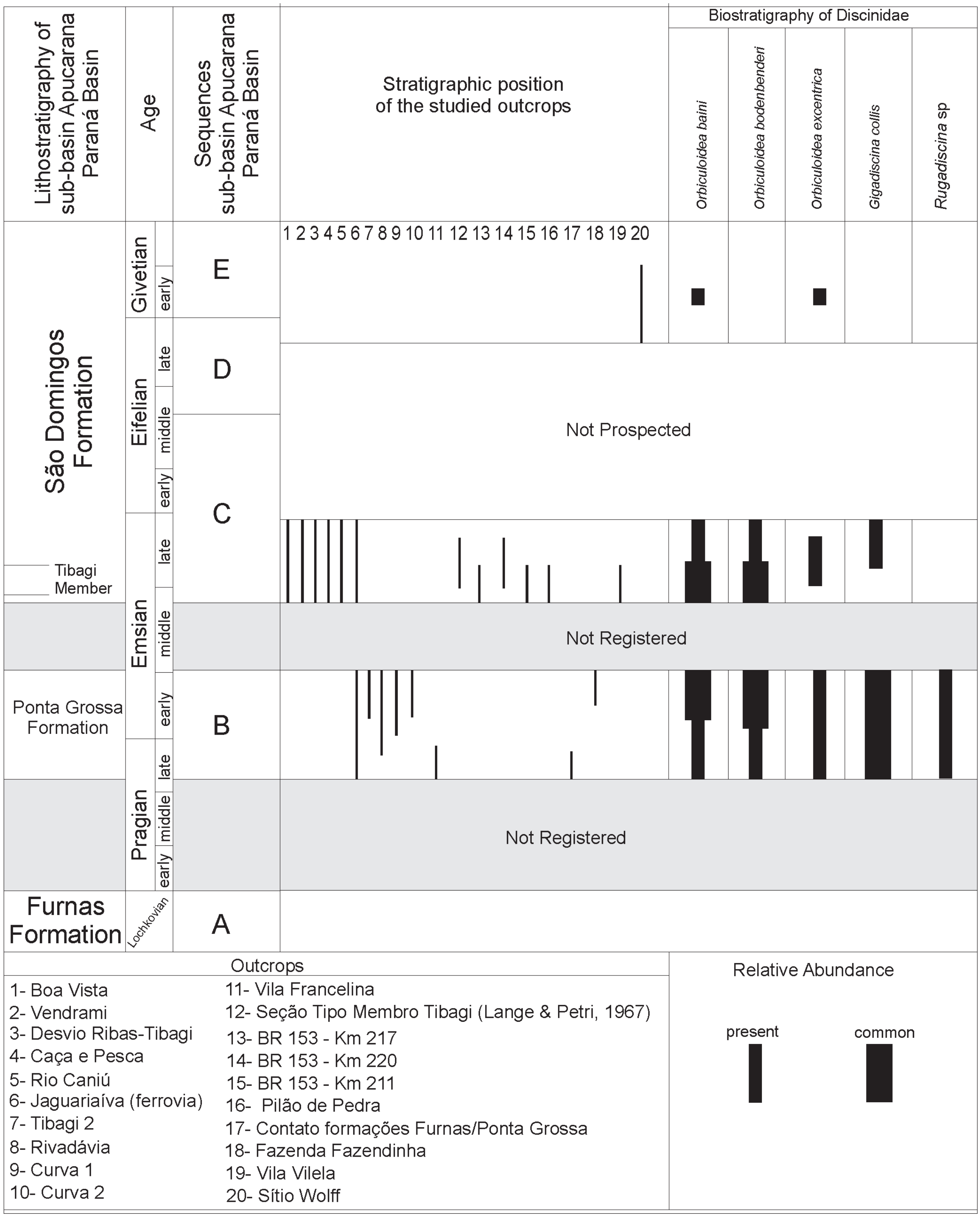


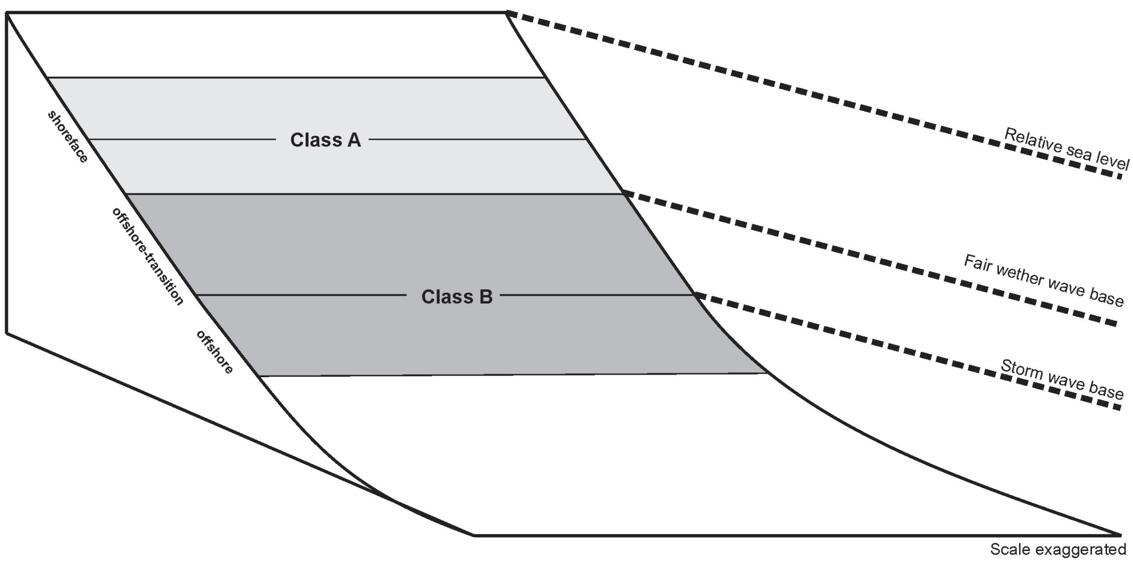
Figure 2. Distribution of discinoids in the Devonian of the Paraná Basin (late Pragian to early Givetian). The group presented stratigraphic range between stratigraphic sequences B and E (for more information see: Bergamaschi, 1999). The figure shows the position of the Tibagi member, between the middle and the end of Emsian. We can see a higher abundance and more diversity between the sequences B and C, which is represented by a relative increase in the relative sea-level. At the end of the sequence C, the decrease in the discinoids in abundance and diversity becomes evident. In the D-E sequence, in which the Lilliput Effect is recorded, we only recorded the presence of *O. baini* and *O. excentrica*. For geological setting information of the Paraná Basin, see Grahn *et al*. (2013).

Subclasses A1 and A2 represent *in situ* preservation and autochthonous accumulations, whereas subclass A3 represents little or no transport, time-averaging and an autochthonous to parautochthonous pattern. All specimens in clusters have been found in medium-grained siltstone to fine-grained sandstones.

Subclass B1: complete and articulated valves, associated with offshore transition to offshore deposits and an autochthonous pattern.

Subclass B2: complete or fragmented disarticulated valves, associated with different offshore-transitional deposits in a paraautochthonous to allochthonous pattern.

The classes identified are correlated with the inferred paleobathymetry obtained from the integrated analysis of lithology and sedimentary structures in which bioclasts were found (Figure 4). Fragmented material is rare, whereas complete and articulated specimens prevail. This suggests that the associations are close to their life habitat and that they were distributed throughout a wide area. *G. collis*, *O. bodenbenderi* and *Rugadiscina* sp. have been frequently found in the outcrops in which rock, sedimentary structures and bioestratinomics features strongly indicate marine, high energy shoreface deposits bearing fine sand with hummocky stratification and wavy bedding. In general, the Malvinokaffric fauna found at deeper settings, *i.e.*, offshore, shows evidence of some transportation, carrying living



Taphonomic Class	Paleoenvironmental	Sub-class	Observed features	Implications
A	shoreface	A1	Complete and articulated valves, closely or overlapping	*in situ* preservation and autochthonous patterns to classes A1 and A2
		A2	Disarticulated valves (dorsal or ventral), closely or overlapping	
		A3	Fragments associated with disarticulated or articulated valves	No significant transport, time averaging and parautochthonous to autochtonous patterns
B	Offshore transition to offshore	B1	Complete and articulated valves	Allochthonous patterns to both classes
		B2	Fragments, articulated and/or disarticulated valves	

Figure 3. Vertical distribution of the taphonomic discinoid classes in a bathymetric profile. The taphonomic class A is subdivided into three classes because of the intrinsic characteristics that occur in the shoreface (*e.g.* articulation/disarticulation and fragmentation degree, and overlapping). The taphonomic class B is subdivided into two classes because of the intrinsic characteristics that occur in the offshore-transition to offshore environments (e.g., articulation/disarticulation and fragmentation degree). The high sedimentation rate and the short residence time controlled the quality of the preservation of the skeletal remains (articulation; A1 and B1 classes), whereas low sedimentation rate and high residence time controlled taphonomic damage on the skeletal remains (e.g., disarticulation and fragmentation; A2-A3 and B2 classes).

organisms and valves, (sensu Kidwell, 1986; Kidwell and Bosence, 1991) and also exhibits evidence of settling in a different setting. *Orbiculoidea baini* and *O. excentrica* might have been transported to deeper waters via energetic water influx of greater intensity (Brett and Seilacher, 1991), where they attempted to reestablish themselves. This can explain the isolated valves found in the offshore black shales.

In relation to discinoid biostratinomy, samples of *O. baini* showed bryozoa incrustation (Figure 5a). Bryozoa zooecia are prismatic in outline, sometimes elongated, incrusted at the marginal portions of the dorsal and ventral valves. This taphonomic signature has not been recorded in any other species of the Malvinokaffric Realm. Another signature is the presence of cracks on the valve margins of *O. baini* and *O. bodenbenderi* (Figure 5b). This feature does not show relation with the type of rock. As the Lingulida valves are organophosphatic, it is assumed that this feature is developed during compaction as result of the rigidity caused by mineralization during the early diagenesis. The final burial of the organisms causes the rigid valves to crack (Speyer and Brett, 1988). This feature usually occurs in valves which have an original pellicle as part of its constituent. The deposition of sediments over the valves results in pressure capable to break the edges of the hardened shells.

LILLIPUT EFFECT IN *ORBICULOIDEA*

According to Bosetti *et al.* (2011), the term "Lilliput Effect" was introduced by Urbanek (1993) to describe the size changes in faunas impacted by extinction events. In the aftermath of biotic crises, the organisms tend to be much smaller than before. According to Twitchett (2006), this effect is one of the most widespread evolutionary phenomena, but it stays unstudied. Body size is a key element in animal evolution, and many paleontologists have noted that the organisms that survived to mass extinctions often have a body size much smaller than their predecessors. There are many reasons associated with organism shrink, including drastic environmental changes (*e.g.*, effects of volcanic activity, increasing of competition, etc). Although previously demonstrated by several authors, the subject of subnormal phenotypes size of the fossil record still requires further study. According to Harries and Knorr (2009), the more ubiquitous trend seen in the evolutionary history in a broad taxonomic spectrum is the size changes, an easily recognized characteristic. Authors also warn the necessity to investigate in detail the effect considering not only the small size of the fauna, but also the general conditions of the causes of extinction on a multidisciplinary analysis.

Among other invertebrate groups, discinoids were also studied by Bosetti *et al.* (2010a, 2011) and Horodyski *et al.* (2014), at the Barreiro section (latest Eifelian-earliest Givetian transition-Kačák event), Tibagi city, Paraná State. Their taxonomic analysis indicated that they represent a Malvinokaffric Realm relictual assemblage, dominated by adult organisms of smaller size. According to these authors, discinoids represented the most abundant group of the assemblage. Discinoids brachiopods are abundant and represented exclusively by the genus *Orbiculoidea*. The adult *Orbiculoidea* has the length of approximately 1.8 to 3.2 cm, while an *Orbiculoidea* with downsizing has been found with 3 mm length at the maximum. *Orbiculoidea baini* and *O. excentrica* presented subnormal size phenotypes, with a drastic size reduction of 90% if compared with adult forms. This small size characterizes them as a consequence of the Lilliput Effect during the earliest Givetian. This effect resulted of a biotic crisis recorded shortly before the collapse of Malvinokaffric fauna after the global 'Kačák Event' (early Givetian).

The first decline of the Malvinokaffric fauna began in the late Emsian (Bosetti *et al.,* 2012) when trilobites, brachiopods, rhynchonelids, cephalopods and bivalves species apparently disappeared from the fossil record of the Devonian of the Paraná Basin. The

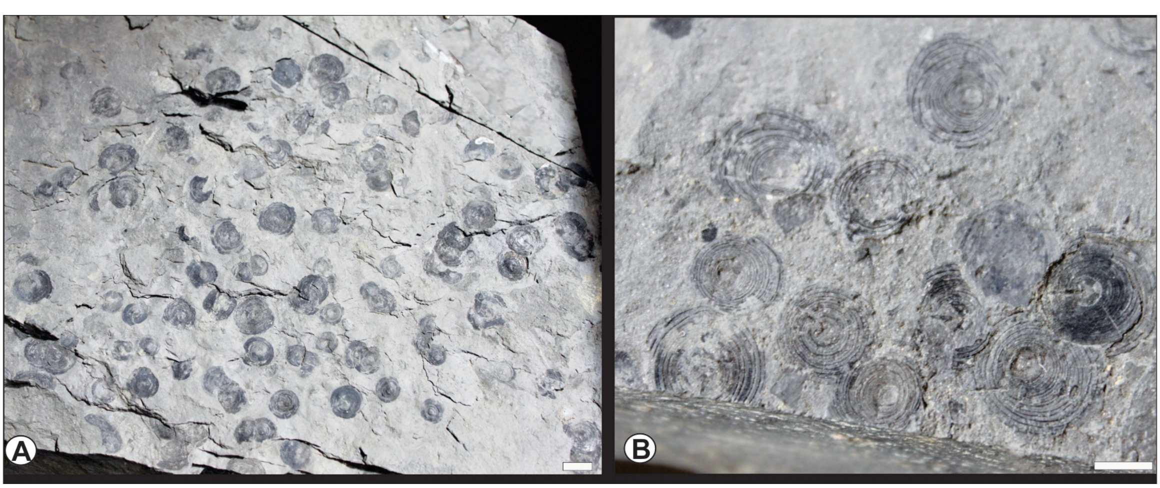


Figure 4. Examples of taphofacies of the type A2. A-B. *Orbiculoidea baini*; the figure shows specimens with complete, disarticulated, dorsal and ventral valves. Scale is 0.3 cm.

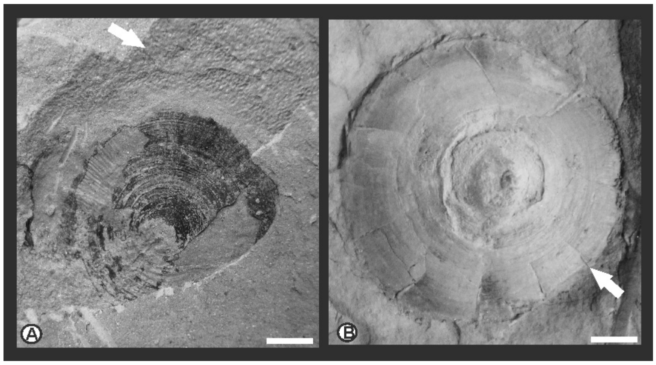


Figure 5. Examples of taphonomic signatures in discinoids. A. *Orbiculoidea baini*; note the encrustation by bryozoans; this feature occurs only in this species; B. *Orbiculoidea bodenbenderi*; cracked dorsal valve edges result of the rigidity caused by early diagenesis. Scale: 1 cm.

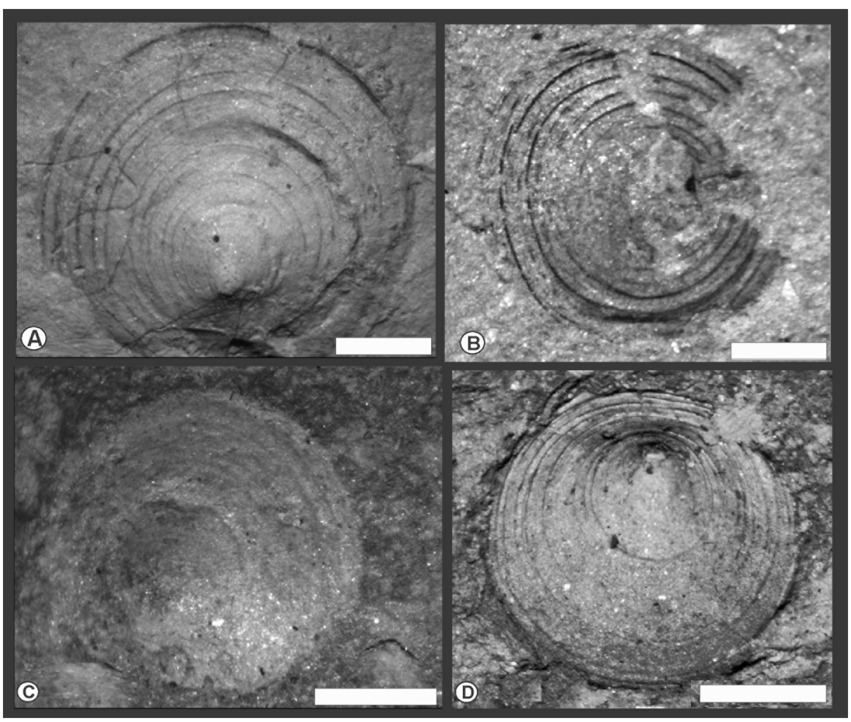


Figure 6. Examples of probable Lilliputs discinoids. A-B. *Orbiculoidea baini;* A. dorsal valve, internal mold, MPI 6053; B. ventral valve external mold, MPI 3678; C-D. *Orbiculoidea excentrica;* C. dorsal valve internal mold, MPI 6048; D. dorsal valve internal mold, MPI 3585. Scale: 0.5 cm.

total collapse of this fauna in the south of Brazil occurred at the latest Eifelian to the earliest Givetian transition and is based on other Devonian occurrences once related studies were performed only in south Brazil. Among the survivors, *O. baini* was the most abundant because it has the status of the most resistant species of the Malvinokaffric Realm. Other organisms were also present after the crisis, but they occurred at lower abundances, such as the trilobite *Pennaia pauliana* and the cnidarian *Conularia quichua*. It is interesting to note that very similar cases have been previously recorded for this group after biotic crises. Harries (1993) refers to the genera *Discina* as a disaster taxon in the Upper Cretaceous occurrences. This genus is typically scarce in some layers and is particularly abundant in levels interpreted as of stressed environments. Disaster taxa are groups of organism that resettle areas destroyed by natural disasters or that survived a major mass extinction. This seems to be the specific case of *O. baini* in occurrences of local earliest Givetian. The units above the extinction event were systematically prospected but none discinoid was found until now. Therefore, it is inferred that discinoids disappeared from the Devonian fossil record of the Paraná State at the end of the early Givetian.

FINAL REMARKS

Devonian discinoids from the Paraná Basin, Paraná state, are considered epibenthic and sessile. They can occur as isolated specimens (*Gigadiscina collis* and *Orbiculoidea bodenbenderi*) or in clusters (*O. baini, O. bodenbenderi* and *O. excentrica*). The *Orbiculoidea* have two taphonomic signatures. The first is an association with bryozoans in *O. baini*, and the second is the cracked valve edges recorded in *O. bodenbenderi*.

The analyzed species have a stratigraphic distribution during the latest Pragian to early Givetian. *Orbiculoidea baini* and *O. excentrica* had the widest paleogeographic and stratigraphic distribution. From the late Emsian, the discinoid fauna began to decline in terms of abundance and distribution, and *G. collis* disappeared from the paleontological record together with other Malvinokaffric representatives. Considering the five species found in the Paraná basin, only *O. baini* and *O. excentrica* present subnormal size phenotypes.

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