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Permian bivalves of the Taciba Formation, Itararé Group, Paraná Basin, and their biostratigraphic significance

Bivalves permianos da Formação Taciba, Grupo Itararé, Bacia do Paraná e seu significado bioestratigráfico

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Abstract
A small and poorly diversified bivalve fauna from Taciba Formation, Itararé Group, Paraná Basin (State of Santa Catarina, Mafra Municipality), is described in this paper for the first time, based on new findings. The fauna is recorded in a 30 cm thick interval of fine sandstone locally at the top of Taciba Formation, in the Butiá quarry. The studied fossil-bearing sandstone bed is a marine intercalation recording a brief eustatic rise in sea-level, probably following glacier retreat and climate amelioration at the end of a broad glacial scenario. The fauna is mainly dominated by productid brachiopods, which are not described here, and rare mollusk shells (bivalves and gastropods). Two bivalve species were identified: *Myonia argentinensis* (Harrington, 1955), and *Aviculopecten multiscalptus* (Thomas, 1928). The presence of *Myonia argentinensis* is noteworthy since this species is also present in the Baitaca assemblage found in marine siltstones (Baitaca assemblage) of the Rio do Sul Formation, cropping out at the Teixeira Soares region, Paraná State. This species is also recorded in the bivalve fauna from the Bonete Formation, Pillahinco Group, Sauce Grande Basin, Buenos Aires Province, in Argentina. Hence, the marine bivalves of the Taciba Formation are associated with the transgressive event that characterizes the *Eurydesma* fauna, indicating a Late Asselian-Sakmarian age for the bivalve fauna. Presence of the *Myonia argentinensis* megadesmid species reinforces the Gondwanic nature of the studied fauna.

Keywords: Bivalvia; Megadesmidae; Permian; Paraná Basin; Taciba Formation; *Eurydesma* fauna.

Resumo
Uma pequena e pouco diversificada assembleia de bivalves permianos da Formação Taciba, Grupo Itararé, Bacia do Paraná (Estado de Santa Catarina, Município de Mafra) é descrita pela primeira vez, com base em novos achados. A fauna foi registrada em um intervalo de 30 cm de espessura de arenito bioturbado, localizado no topo da Formação Taciba, na pedreira Butiá. A camada de arenito fossilífero representa uma intercalação marinha, que registra variação estática do nível do mar, provavelmente como reflexo do evento de deglaciação. A fauna é principalmente dominada por braquiópodes productídeos (não descritos neste artigo) e raras conchas de moluscos (bivalves e gastrópodes). Duas espécies de bivalves foram identificadas: *Myonia argentinensis* (Harrington, 1955) e *Aviculopecten multiscalptus* (Thomas, 1928). A presença de *Myonia argentinensis* é notável, pois esta espécie está também presente na assembleia de Baitaca, encontrada em siltitos marinhos, no topo da Formação Rio do Sul, na região de Teixeira Soares, Estado do Paraná. É registrada também na fauna de bivalves da Formação Bonete, Grupo Pillahinco, Bacia Sauce Grande, Província de Buenos Aires, Argentina. Desse modo, os bivalves marinhos da Formação Taciba estão associados ao evento transgressivo que caracteriza a fauna de *Eurydesm*a, indicando uma idade Asseliana Tardia-Sakmariana para a fauna. A presença do megadesmídeo *Myonia argentinensis* reforça a natureza Gondwânica da fauna estudada.

Palavras-chave: Bivalvia; Megadesmidae; Permiano; Bacia do Paraná; Formação Taciba; Fauna de *Eurydesma*.

INTRODUCTION

Contrary to Argentina, where thick lower carboniferous up to Permian sequences yield abundant and diversified marine fossiliferous records (González and Saravia, 2007; Pagani and Taboada, 2010), coeval occurrences in the Brazilian portion of the huge, up to 1,600,000 km^2 (Holz et al., 2010), foreland Paraná Basin are rare and poorly diversified (Rocha-Campos and Rösler, 1978; Simões, Rocha-Campos, Anelli, 1998).

In the last decade, several papers (Pagani, 2000, 2004a, 2004b, 2005, 2006, 2006b; Sterren, 2000, 2003, 2004, 2005; González, 2002a, 2002b, 2006; Pagani and Sabattini, 2002; Cisterna and Sterren, 2010; Pagani and Taboada, 2010; Sterren and Cisterna, 2010; Taboada, 2010; Taboada and Pagani, 2010; Pagani and Ferrari, 2011) about the marine invertebrate faunas of the Gondwana succession of Argentina were published (González and Saravia, 2007; Pagani and Taboada, 2010; Sterren and Cisterna, 2010; Taboada, 2010; Taboada and Pagani, 2010). Hence, there were recent advances in our understandings of the paleobiogeography and biostratigraphy of brachiopod- and bivalve-dominated faunas, with obvious implications to the provincial affinities and age of these assemblages (Pagani and Taboada, 2010). Indeed, such faunas have been long recognized as essentials tools to constrain the age of major geologic and biotic events of the Southeastern portion of Gondwana supercontinent, during the Late Paleozoic (Simões, Rocha-Campos, Anelli, 1998; González and Saravia, 2007; Sterren and Cisterna, 2010; Anelli et al., *in press*).

In spite of that, the use of the Late Paleozoic marine invertebrate faunas of South America to regional scale correlations is limited, since many of the Brazilian faunas remain virtuously undescribed and/or poorly described or illustrated. Among those, the Butiá assemblage, known since Rocha-Campos (1966), in the upper most portion of the Itararé Group is of particular interest to regional correlations. This assemblage is associated with a short transgressive-regressive episode at the end of the Late Paleozoic glaciation in the Paraná Basin (Simões, Anelli, Rocha-Campos, 1998), and record the first appearance of typical Gondwanian marine bivalves in the basin (Rocha-Campos and Rösler, 1978; Simões, Anelli, Rocha-Campos, 1998). Therefore, the aim of this contribution was to describe, by the first time, the bivalve species of the Butiá assemblage found in the Taciba Formation in the top of Itararé succession at the State of Santa Catarina, Southern Brazil. By accomplishing this, we add herein new palaeobiogeographic and biostratigraphic information to Late Paleozoic bivalve faunas of Western Gondwana.

BACKGROUND

Bivalves and other marine invertebrates are poorly diversified and sparsely distributed in the glacial (Itararé Group) and post-glacial successions (Guatá Group) of Paraná Basin (Simões, Anelli, Rocha-Campos, 1998, p. 445). However, some of these are key faunas for interbasinal correlations since data on checklists available (Rocha-Campos, 1970; Rocha-Campos and Rösler, 1978) indicate that such assemblages at the top most portion of the Rio do Sul or Taciba Formations (upper third of Itararé Group) may show affinities with the Lower Permian bivalves, from the Bonete Formation, Sierras Australes, Buenos Aires Province, in Argentina (Harrington, 1955; Pagani, 2000).

Rocha-Campos (1966) had listed (but not described or illustrated) the presence of marine invertebrates (e.g., brachiopods and mollusks) associated with glaciogenic rocks (e.g., diamictites) at the top of Itararé succession, in the Butiá Quarry. As well noted by Rocha-Campos (1966), this fauna can be distinguished from all other coeval ones (Capivari, Rio da Areia, Baitaca, Budó assemblages) by the uncommon numeric dominance of brachiopods, mainly productids, over mollusks (e.g., bivalves and gastropods).

Renewed interest in this fauna, in the broad context of a join scientific project, including São Paulo State University – UNESP, São Paulo University – USP and the Paleontological Center – CENPALEO of the University of Constestado, have lead to the discovery of new bivalve specimens in the same horizon sampled by Rocha-Campos in 1966, which allowed us to do a better stratigraphic correlation with the "Butiá horizon" and other coeval marine intercalations of Paraná Basin, Brazil, and Sauce Grande Basin, Argentina (Figure 1).

GEOLOGICAL SETTING

In the Paraná Basin, the Gondwanian glacial-postglacial sedimentary succession of the Itararé Group consists of thinly-laminated rhythmite and mudstone, dark gray to black shale, massive siltic-argilaceous matrix diamictite, heterolithic siltstone and sandstone, and fine- to medium-grained sandstone with trough cross-stratification, parallel to sub-parallel stratification, climbing ripple cross-lamination, and wave ripples (Rocha-Campos, 1967; Schneider et al., 1974). Intraclasts and mud drapes are common in the sandy deposits (Balistieri, 2003).

In Southern Paraná, as well as in the neighboring Santa Catarina State, the Itararé succession is divided into three units, namely Campo do Tenente Formation at the bottom, Mafra and Rio do Sul (Schneider et al., 1974) or Taciba Formations (França and Potter, 1988) above. The Taciba Formation records the third major fining upward cycle of Itararé Group, encompassing three members: Rio Segredo sandstone, Chapéu do Sol diamictite, and Rio do Sul (rhythmite, siltstone, and shale).

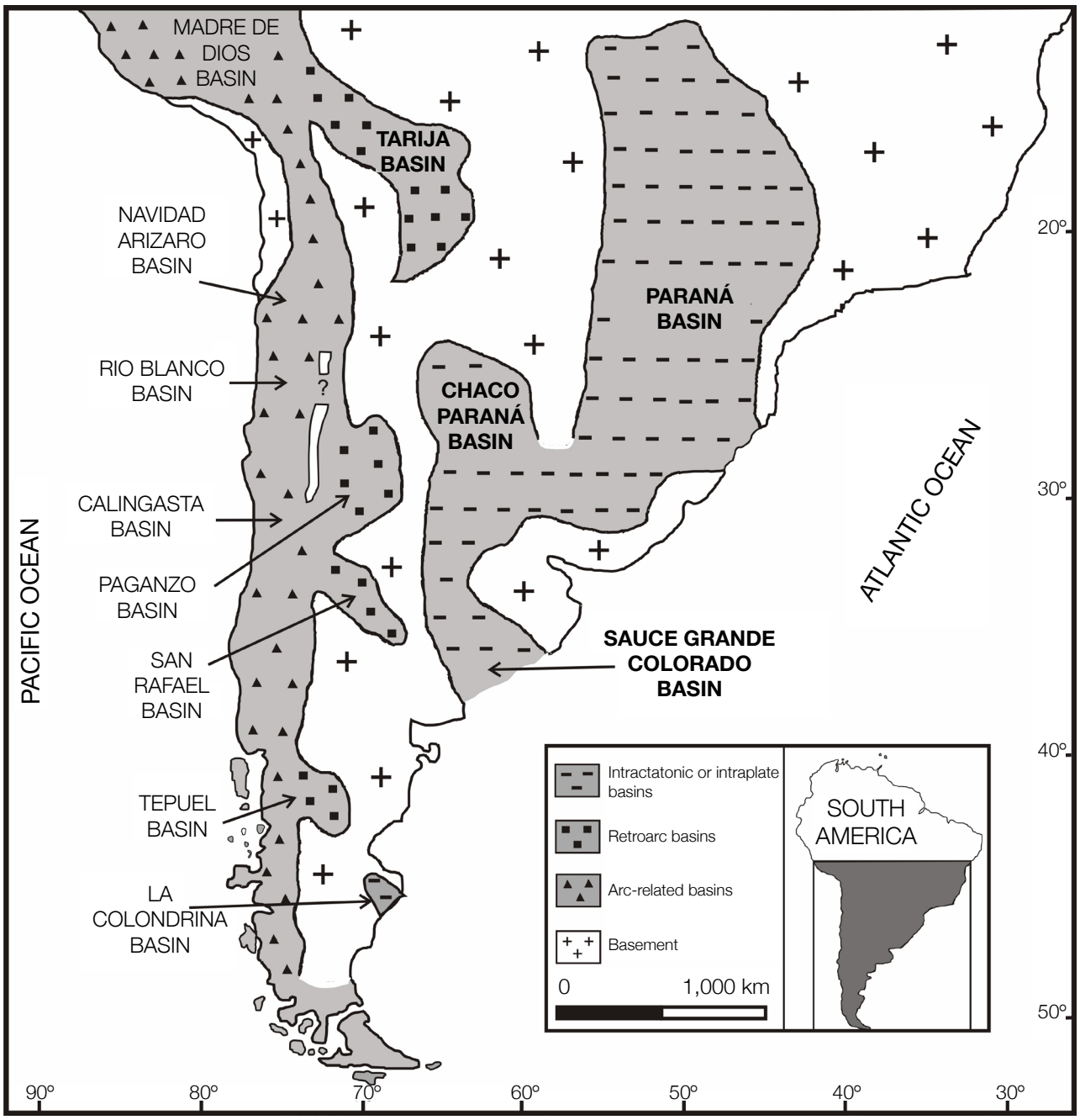

Figure 1. Sketch map showing the main Late Paleozoic basins of southern South America (modified from Limarino and Spalletti, 2006).

Weinschütz and Castro (2006) identified two depositional sequences in Taciba Formation. A 65 m-thick interval of diamictite with intercalations of massive argillaceous sandstone (*slurry*), siltstone and thin rhythmite, which characterizes the lower Taciba-I sequence (TC-I). Slumping, contorted beds, sandstone dykes, and a large, *in situ*, turbidite block with dropstone are also recorded in those rocks. In its upper part, the diamictite is stratified and includes abundant dropstones. In core, it passes laterally to a coarsening-upwards succession of varvic shale, siltstone and slumped thin rhythmites (Weinschütz and Castro, 2006). All the lithofacies can be assigned to transgressive and high-stand system tracts. In outcrops, the deglaciation interval is made-up of a 10 m-thick stratified diamictite, overlain by thin stratified conglomerate and sandstone; bioturbated, fossiliferous

sandstone and shale, representing the transgressive systems tract (Weinschütz and Castro, 2006). The sandstone includes numerous fossils, such as: brachiopods and mollusks (bivalves and gastropods).

MATERIAL AND METHODS

The material described herein is from the Butiá Quarry (Figures 2 and 3), Mafra Municipality, Santa Catarina State, in Southern Brazil. We also analyzed fossil specimens from the Teixeira Soares region, Paraná State (Figure 3). All the studied material is reposited in three main scientific collections and coded as: DGM (*Departamento de Geologia e Mineralogia*, *IGc*/USP, São Paulo, SP); DZP (*Departamento de Zoologia*, IBB/UNESP, Botucatu, SP), and CP (*Centro Paleontológico*/CENPALEO, *Universidade do Contestado*, Mafra, SC).

In the laboratory, the material was prepared according to standard paleontological procedures (Feldmann, Chapman, Hannibal, 1989), using precision tools. Most of the shells are represented by internal and external moulds. The material was coated with magnesium oxide sublimate to enhance anatomical details (i.e., ornamentation, muscle scars etc.) for photography (Anelli, Rocha-Campos, Simões, 2006; Anelli et al., 2009; Pagani and Ferrari, 2011). Finally, the suprageneric systematics is based on Morris, Dickins and Astafieva-Urbaitis (1991), and, at the family level, on Runnegar and Newell (1971), Runnegar (1974) and Simões et al. (1997).

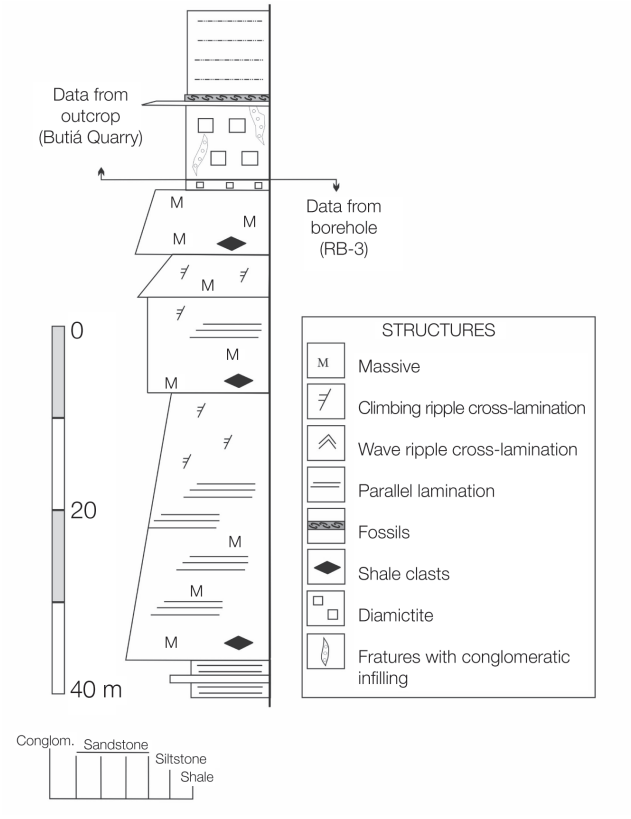

Figure 2. Composite columnar section of the upper portion of the Taciba Formation, Mafra region, State of Paraná.

RESULTS

Systematic

Superfamily Pectinacea Rafinesque, 1815
Family Aviculopectinidae Meek; Hayden, 1865
Genus *Aviculopecten* M'Coy, 1851

Type species

Aviculopecten planoradiatus M'Coy, 1851, p. 171, by latter designation of Hind, 1903, p. 66.

Aviculopecten multiscalptus Thomas, 1928,
(Figures 4A to F.)

Aviculopecten sp. Lange, 1944, p. 279.
Aviculopecten sp. Kegel, 1952, p. 84, Figure 4.
Aviculopecten sp. Kegel; Costa, 1951, p. 171.
Aviculopecten sp. Lange, 1954, p. 54.
Aviculopecten multicalptus Thomas; Beurlen, 1954; *In* Lange, 1954, p. 54.
Prosopecten alternatus Beurlen, 1954; *nom. nud.*, *in* Lange, 1954, p. 55.
Prosopecten elegans Beurlen, 1954; *nom. nud.*, *in* Lange, 1954, p. 55.
Prosopecten densicostatus Beurlen, 1954; *nom. nud.*, *in* Lange, 1954, p. 55.
Prosopecten radiatus Beurlen, 1954; *nom. nud.*, *in* Lange, 1954, p. 55.
Aviculopecten? sp. Rocha-Campos, 1967, p. 29, Figure 15.
Aviculopcten multiscalptus Thomas, 1928; Rocha-Campos, 1969, p. 41.
Aviculopcten cf. *A. multiscalptus* Rocha-Campos; Rösler, 1978, p. 5.

Material

Two fragmented internal molds of the left valve were used.

Description

Left valve slightly convex, with inflated umbones, and faintly orthogyrate beaks. Posterior auricle acuminate,

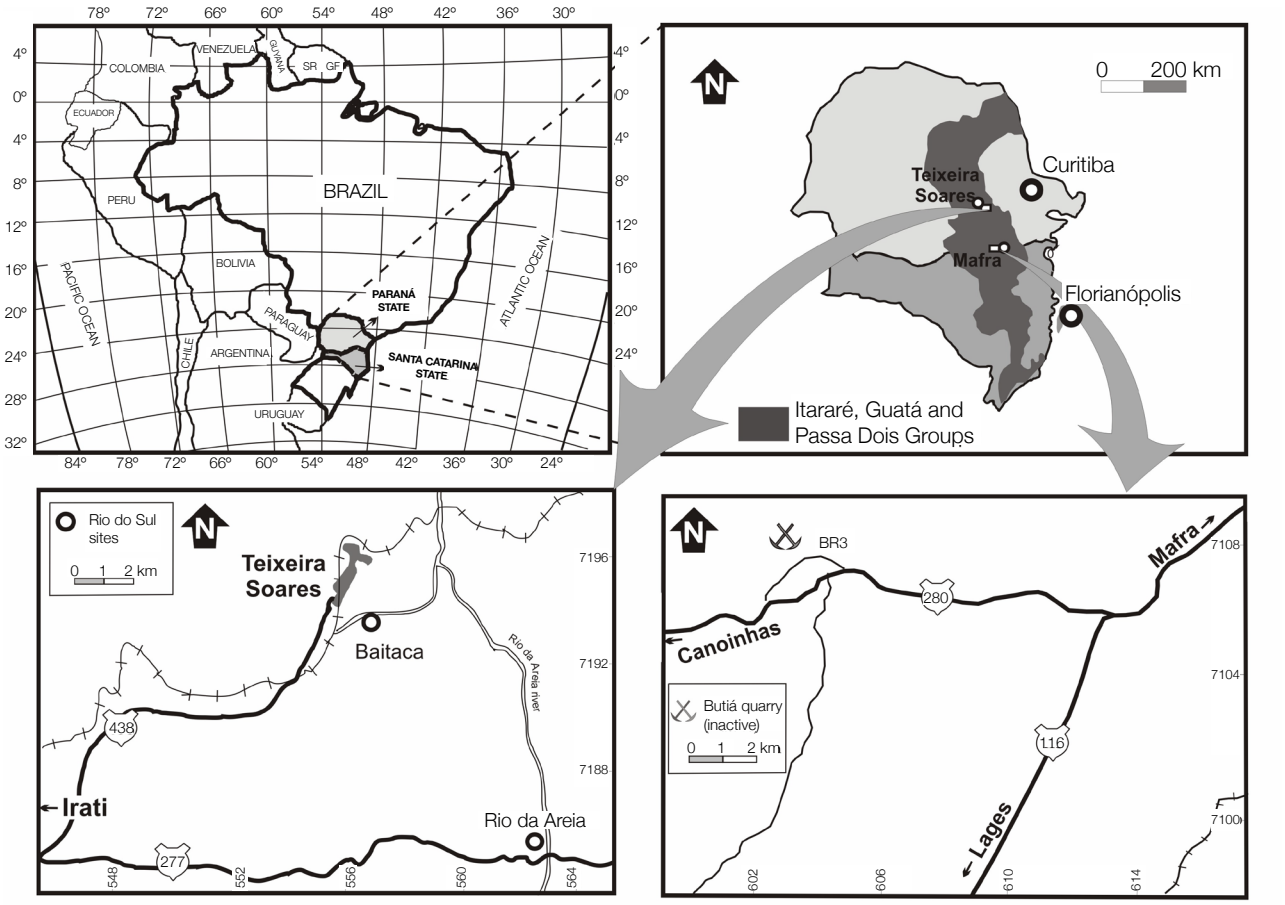

Figure 3. Location map of the studied marine fossil-rich intercalations in the upper portion of the Itararé Group.

with slightly concave ventral margin, separated from the shell body by weak curved fold. Surface ornament of the left valve consisting of primary radial costae beginning at umbonal region and extending until ventral margin; secondary costae begin high elevated on umbonal region by intercalation, extending until ventral margin. Around 20 to 23 primary costae are identifiable, always intercalated with secondary costae; dorsal area straight; and right valve is still unknown in Taciba Formation.

Table 1. Dimensions (mm) of the *Aviculopecten multiscalptus* shells.

Specimens	Length	Height	Weight
DGM 4358	28	30	8
DGM 4372	25	28	–
DGM 4360	23	24	–
DZP 18860	~ 31	~ 33	–
DZP 18820	29	35	–
DZP 18861	~ 21	~ 22	–

Comments

The material from Taciba Formation (Table 1) is highly similar to the one present in the Rio da Areia sandstone and Baitaca siltstone at the top of the Rio do Sul Formation, Teixeira Soares, Paraná State. It shows radial ornamentation (Figure 4G to M) with the same number of primary radial costae, with secondary costae added by intercalation. Usually, the primary ribs are thicker than the secondary ones. Additionally, specimens of both formations show the left valves slightly convex with posterior auricle acuminated and beaks typically above hinge line.

Family Megadesmidae Vokes, 1967
Subfamily Megadesminae Simões et al., 1997
Genus *Myonia* Dana, 1847

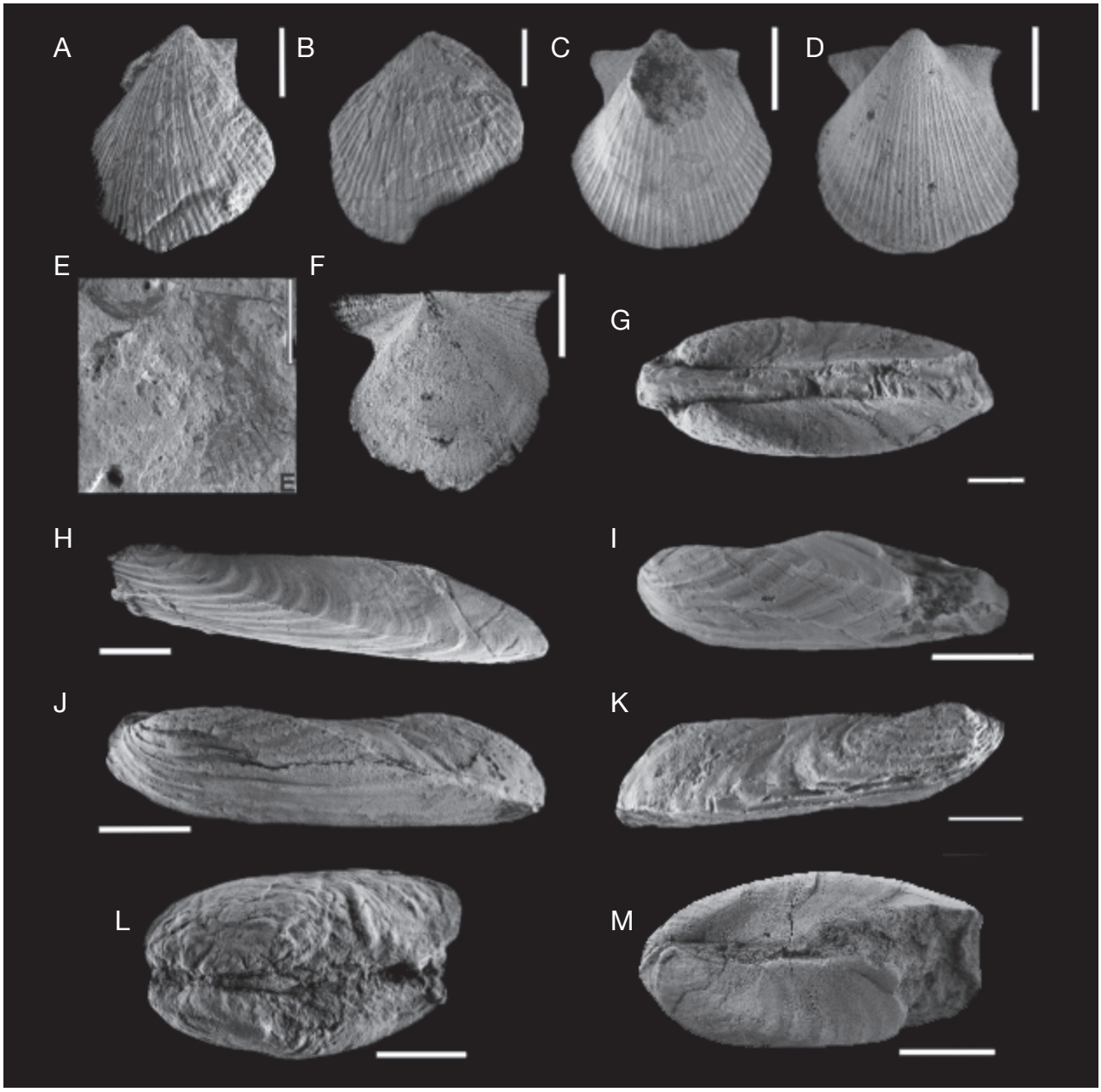

Figure 4. (A-F) *Aviculopecten multiscalptus* (Thomas, 1928); (A-D) internal mold of left valve; (A) DZP 18820; (B) DZP 18860; (C) DGM 4372; (D) DGM 4358; (E-F) internal mold of right valve; (E) DZP 18861; (F) DGM 4360; (G-M) *Myonia argentinensis* (Harrington); (G, L, M) internal mold of conjugated valves, dorsal view; (G) DGM 4341; (L) DZP 18859; (M) DZP 18826; (H-J) left valve; (H) CPI; 475; (I) DZP 18826; (J) DGM 4341; (K) right valve; DGM 4341. Specimens (A, B, E, H, L) Taciba Formation, Butiá Quarry, Mafra State of Santa Catarina. Specimens (C, D, F, G, I, J K, M) Rio do Sul Formation, Teixeira Soares, State of Paraná. Scale = 1 cm.

Type species

Myonia elongata Dana, 1847, p. 158, by posterior designation of Fletcher, 1932, p. 398.

Myonia argentinensis Harrington, 1955
(Figures 4G to M)

Stutchburia? *argentinensis* Harrington, 1955, p. 117, pl. 24, figures 1 to 3.
Praeundulomya argentinensis (Harrington); Dickins, 1963, p. 23.
Myonia (or *Vacunella*)? *argentinensis* (Harrington); Rocha-Campos, 1970).

Myonia (or *Vacunella*)? *argentinensis* (Harrington); Rocha-Campos; Carvalho, 1975, p. 186, 189, plate 1, figures 13 to 14.
Stutchburia? *argentinensis* Harrington; Amos, 1979, p. 137.
Psedolomya? *argentinensis* (Harrington); Harrington, 1980, p. 974.
Stutchburia? *argentinensis* Harrington; Andreis et al., 1987, p. 221.
Stutchburia argentinensis Harrington; Andreis; Japas, 1996, p. 63.
Stutchburia argentinensis Harrington; Pagani, 2000, p. 312.

Material

Two articulated internal moulds, one from the Taciba Formation, Mafra, Santa Catarina State, and one from Rio do Sul Formation, Baitaca siltstone, Teixeira Soares region, Paraná State.

Description

Shell equivalve, strongly inequilateral, and elongated posteriorly. Posterior and ventral margins parallel to sub-parallel. The anterior dorsal margin is very short, straight; anterior extremity rounded; ventral margin straight to slightly convex; posterior extremity truncated, entirely occupied by respiratory margin. An obscure sulcus extends from beaks to ventral margin. Margins do not gap. The posterior dorsal margin is straight. Umbonal area slightly inflated, with beaks slightly elevated above hinge line. Umbonal carina well marked, running from beaks to postero-ventral angle. Lunule and escutcheon absent. Surface ornament of well-marked regular spaced comarginal rugae; slightly marked growth lines are visible near the posterior end of the shell. Narrow ligament furrow is present immediately posterior to beaks, until medial portion of the postero-dorsal margin. Hinge edentulous. The muscle scars are not observed.

Comments

Pagani (2000) designated under *Stutchburia*? *argentinensis* Harrington, 1955, specimens from the Lower Permian Bonete Formation. Similar material from Permian Rio do Sul Formation, Baitaca assemblage (Simões, Rocha-Campos, Anelli, 1998), studied by Rocha-Campos (1969, 1970), was designated under a different genus, *Myonia argentinensis* Harrington, 1955. *Stutchburia* is characterized by the presence of a well-marked radial costae and well-defined lunule and escutcheon. Furthermore, internally, *Stutchburia* also presents a well-marked buttress behind the anterior adductor scar. All these features are absent both in the Argentinean material from the Bonete Formation and the Brazilian specimens (Table 2) from the Rio do Sul Formation. The same is true for the material here studied from Taciba Formation. Therefore, by the lack of key characters of *Stutchburia* and the presence of well-defined carina, an obscure umbonal lateral sulcus and non-gaping margins, we recognize the Brazilian and Argentinean specimens under the genus *Myonia*.

Table 2. Dimensions (mm) of the *Myonia argentinensis* shells.

Specimens	Length	Height	Weight
DGM 4341	55	13	–
CP. I-475	~67	15	17
DZP 18826	~35	11	15
DZP 18859	32	~13	–

DISCUSSION

Contrary to Argentina, where the Late Paleozoic faunas are relatively diverse, better known, and more easily correlated with the Australian faunas, the use of the Late Paleozoic bivalves from the Paraná Basin (Figure 1) for correlations is limited. Therefore, the meager and poorly diversified marine invertebrate faunas recorded in the Itararé Group, their restrict vertical and lateral distribution, and high-degree of provincialism, due to basin isolation and strong climatic gradients recorded in the South American continent during the Late Paleozoic (Runnegar, 1972; Rocha-Campos, 1970; Pagani and Ferrarri, 2011), are among the main issues that mar the biocorrelations.

Elongate, probably dorsoventrally compressed bivalve specimens of the marine thin intercalations of the Itararé succession from the Santa Catarina State, Butiá assemblage, and Paraná State, Baitaca assemblage (Simões, Anelli, Rocha-Campos, 1998) are remarkable similar to specimens formerly assigned to *Stutchburia*? *argentinensis*, by Harrington (1955) and Pagani (2000) from the Bonete Formation. As commented, we here assign them to *Myonia argentinensis*. These specimens are also similar to that recorded by Rocha-Campos (1970) in the top of the Itararé Group (Rocha-Campos and Carvalho, 1975). In both the Argentinean and Brazilian specimens of *Myonia argentinensis*, a well-defined carina and an obliquely truncated posterior margin are visible.

As shown here, both *Myonia argentinensis* and *Aviculopecten multiscalptus* are present in the Baitaca siltstone of the Rio do Sul (or Taciba) Formation at the Teixeira Soares region, Paraná State. Hence, the Butiá and Baitaca assemblages are correlated to the "*Eurydesma* fauna" of the Bonete Formation (Asselian-Sakmarian) and with the fauna of the Amotape Formation (Middle Pennsylvanian) of Peru (Newell, Chronic, Roberts, 1953), as indicated by the common occurrence of *Aviculopecten multiscalptus* (Rocha-Campos, 1970; Rocha-Campos and Rösler, 1978).

Our findings in Itararé succession of a bivalve species, which is typical of Bonetian fauna, open new avenues to better constrain the age of the marine intercalations recorded at the top of Itararé succession. In the Eastern Argentina, the Piedra Azul and Bonete Formations contain members of the typical *Eurydesma* fauna, and they are associated with the post-glacial transgression of the end of Gondwana Ice Age (Dickins, 1985; González and Saravia, 2007, Anelli et al., *in press*). As noted by González and Saravia (2007), the *Glossopteris* flora as well as the *Eurydesma* fauna in the Sauce Grande Basin (Harrington, 1955; Rocha-Campos and Carvalho, 1975; Archangelsky, 1996; Pagani, 1998, 2000) and Karoo-Kalahari Basin (Dickins, 1961; Mclachlan and Anderson, 1973) is suggestive of an Asselian age to this climatic deglatiation event (Dickins, 1985). Hence, Pagani (1998, 2000) have referred the *Eurydesma* fauna of the Saunce Grande Basin to the Late Asselian-Sakmarian, while González and Saravia (2007) to the Sakmarian.

Although *Eurydesma* has not been found yet in the marine assemblages of the Itararé succession of the Paraná Basin (Simões, Anelli, Rocha-Campos, 1998), the common occurrence of *Myonia argentinensis* in the Brazilian and Argentinean faunas indicate a Late Asselian-Sakmarian age for the assemblages. Therefore, new SHRIMP U-Pb zircon ages (Rocha-Campos et al., 2011, p. 9, Figure 6) from tuffs recorded at the top of the Itararé Group (Rio do Sul Formation) indicate that this portion of the Late Paleozoic succession of the Paraná Basin was deposited during the Asselian. Hence, the age of the section containing the studied fauna is sound with the age and biocorrelations with the Bonetian fauna of Argentina, as already suggested by other authors (Rocha-Campos and Rösler, 1978; González, 1997; Simões, Anelli, Rocha-Campos, 1998; Pagani, 1998, 2000). Finally, based on their mutual faunal content, both the Butiá and Baitaca assemblages are, indeed, an evident record of members of *Eurydesma*-fauna within the Late Paleozoic succession of Paraná Basin.

CONCLUSIONS

Until now, despite its close paleogeographic location within the Gondwana supercontinent, a free connection between Paraná Basin and Sauce Grande Basin (Figure 1), favoring the full interchange of members of the Paranian and Bonetian faunas, was very difficult to envisage. Despite the general suprageneric composition similarities of these faunas, as pointed out by previous authors (Rocha-Campos and Rösler, 1978; González, 1997; Simões, Anelli, Rocha-Campos, 1998; Pagani, 1998, 2000), the complete lack of bivalve species in common was always an evidence for some degree of faunal distinction among these basins (González and Saravia, 2007). Our new findings are, however, noteworthy, since they indicate that both faunas may yield species in common. Although *Eurydesma* is missing, *Myonia argentinensis* is the first conspicuous member of the Bonete Formation recorded in the Paraná Basin. We should highlight that Itararé faunas are virtually undescribed and still poorly sampled. This mars our comparisons with other Late Paleozoic faunas of Argentina.

In addition, the huge size of both basins (Paraná/Sauce Grande) and the pronounced climatic gradient, which was typical of the late Paleozoic times in the Gondwana supercontinent, may account for the development of several regional faunas, with variable degrees of endemism. One of the main differences between the Butiá assemblage and those of the upper portion of the unit in Teixeira Soares (Rio da Areia sandstone, Baitaca siltstone and Passinho shale), Paraná State, is that the first is largely dominated by productid brachiopods indicating distinct paleoenvironmental conditions. The marine invertebrates of the three main lithofacies of Itararé succession at Teixeira Soares region thrived in nearshore to inner and outer shelf environments (Simões, Rocha-Campos, Anelli, 1998). The studied fossiliferous sandstone found in the Butiá Quarry was probably deposited, under nearshore conditions.

Despite the paleoenvironmental similarities, this pattern is very interesting since the Paleozoic brachiopods and bivalves occupied different habitats and played different roles in the environment. As stated by Gould and Calloway (1980), there is no evidence that both groups actually competed with each other. Several Permian bivalves were shallow to deep burrowers, a new condition that characterizes the Late Paleozoic marine faunas (Bush and Bambach, 2011). The Baitaca assemblage is largely dominated by shallow to deep burrowers, mainly Anomalodesmatan bivalves (Simões, Rocha-Campos, Anelli, 1998). This is noticeable because the deep bioturbation (deep tiering) may have prevented the full colonization of the substrate by the brachiopods. The suspension-feeding organism may not coupe with intense bioturbation (deep tiering), which makes feeding more difficult or even impossible (Graham Budd at http://www.palaeontology.geo.uu.se/Download/Palaeobiology/Lecture_10.pdf). Bioturbation seems less intense (shallow tiering) in the fossiliferous siltstone of the Butiá Quarry, making the substrate more favorable to the brachiopod fauna. Hence, this may represent a good case study on trophic amensalim to be tested in the future.

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