Eurydesma–Lyonia fauna (Early Permian) from the Itararé group, Paraná Basin (Brazil): A paleobiogeographic W–E trans-Gondwanan marine connection

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ABSTRACT

Here, the biocorrelation of the marine invertebrate assemblages of the post-glacial succession in the uppermost portion of the Late Paleozoic Itararé Group (Paraná Basin, Brazil) is for the first time firmly constrained with other well-dated Gondwanan faunas. The correlation and ages of these marine assemblages are among the main controversial issues related to Brazilian Gondwana geology. In total, 118 brachiopod specimens were analyzed, and at least seven species were identified: *Lyonia rochacamposi* sp. nov., *Langella imbituvensis* (Oliveira),? *Streptorhynchus* sp.,? *Cyrtella* sp., *Tomiopsis* sp. cf. *T. harringtoni* Archbold and Thomas, *Quinquenella rionegrensis* (Oliveira) and *Biconvexiella roxoi* Oliveira. The presence of *Tomiopsis* sp. cf. *T. harringtoni* and the bivalve *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington) in the Teixeira Soares beds plus *Myonia argentinensis* (Harrington) and *Heteropecten paranaensis* Neves *et al.*, both of which recorded in deposits in the Teixeira Soares and Mafra beds (Butiá), suggests a biocorrelation with the *Eurydesma* fauna from the Bonete Formation, Sauce Grande-Colorado Basin, Argentina. Furthermore, the presence of *Lyonia* Archbold and *Praeundulomya* cf. *subelongata* Dickins in the Taciba Formation indicates affinities with deposits in the Lyons Group, Carnarvon Basin, and the Fossil Cliff Member, Perth Basin (Western Australia), suggesting a late Asselian–early Sakmarian age. Even more importantly, the collected data suggest the existence of an W–E trans-Gondwanan marine seaway between the Paraná (Brazil), Sauce Grande-Colorado (Argentina), Huab (Hardap shale of the Dwyka Group, Aranos area, Namibia, southwest Africa), the Carnavon (Western Australia) basins, and beyond eastward to the Cimmerian region. A V proto-rift system through two major axes of extensional basin development facilitated the W–E marine connection. Main axes formed by a north-northwesterly trending axis paralleling the future South Atlantic and a broadly north-northeasterly trending line of separation related to the future Indian Ocean. This proto-rift system coupled with a sea-level rise of at least 100 m, favored the establishment of a long narrow shallow seaway, allowing the exchange of *Eurydesma* fauna between eastern and western Gondwana.

1. Introduction

The Gondwanan affinity of the Permian marine macrofossils of the Itararé Group (Bashkirian/Moscovian–early Permian, Holz et al. 2010), Paraná Basin, is well known on the basis of its molluskan faunas, particularly those recorded in some strata from southern Brazil (Rocha Campos and Rösler, 1978; Neves et al., 2014a, b). The marine assemblages recorded in the upper portion of the Taciba Formation cropping out in the Mafra and Teixeira Soares regions, in the states of Santa Catarina and Paraná, respectively, are especially noteworthy. The Taciba Formation records a succession of depositional environments tied to the demise of late Paleozoic glaciation (França and Potter, 1988; Santos et al., 1996; Mineropar, 2007). The faunal assemblages are poorly diversified, showing a scattered distribution, both vertically and geographically, and are mainly dominated by bivalve mollusks (Rocha Campos, 1967; Simões et al., 1998, 2012; Neves et al., 2014a, b). These occurrences have been known since E.P. Oliveira announced the discovery of marine macrofossils in that unit in 1908 in a letter to Woodworth (1912, in Lange, 1954). These fossils were

subsequently studied by various authors (Oliveira, 1930; Mendes, 1952; Lange, 1952; Kegel and Costa, 1952; Beurlen, 1954; Rocha Campos, 1966, 1969, among others). However, more comprehensive contributions regarding the taxonomic composition, age and affinities of these marine fossils have only been reported recently (Simões et al., 2012; Neves et al., 2014a, b). On the basis of the presence of *Myonia argentinensis* (Harrington, 1955), *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington, 1955) and *Heteropecten paranaensis* (Neves et al., 2014a), researchers have emphasized the correlation of the Taciba bivalve fauna with those of the *Eurydesma*-bearing Bonete Formation, Pillahuincó Group, Sauce Grande-Colorado Basin, Buenos Aires Province, Argentina. This indicates a possible Asselian age for the post-glacial bivalve fauna of the Taciba Formation. However, our view regarding the marine fossils of the Taciba Formation is mainly "bivalvecentric" (=biased towards this mollusk class). Indeed, much less is known about the identity, affinities and age of the brachiopods of the Taciba Formation, which co-occur in the same lithofacies. In this paper, we describe, illustrate and discuss, in modern terms, a surprisingly "diverse" and well-preserved brachiopod fauna of the Taciba Formation. Although these faunas have been known since Oliveira (1930) and Rocha Campos (1966, 1969), we have added new information on the composition and age of the marine invertebrate faunas recorded in the uppermost portion of the Itararé Group. Furthermore, re-examination of faunal affinities allowed us to improve our understanding of the paleobiogeographical relationships between close and/or co-eval Gondwanan faunas of southern Brazil (Paraná Basin) with other South American and Patagonian late Paleozoic basins (Sauce Grande-Colorado, Uspallata-Iglesia and Tepuel-Genoa basins) as well as those of South Africa (western Kalahari/Aranos Basin) and Western Australia (Carnarvon, Canning, Perth basins). In this context, a new paleobiogeographic hypothesis is presented and discussed.

2. General geological setting

Carboniferous to early Permian glacial-related successions in the intracratonic Paraná Basin (Brazil) are recorded at the base of the Gondwana 1 Supersequence (Milani et al., 2007). These glacial non-marine and glaciomarine rocks are referred to as the Itararé Group, a ~1500 m thick unit that includes conglomerates, diamictites, sandstones, rhythmites, mudstones, shales, and a few coal seams (Milani et al., 2007; Holz et al., 2008, 2010). These rocks rest unconformably either on metamorphic/igneous Precambrian–pre-Silurian basement or sedimentary Devonian strata (Rocha Campos, 1967; Holz et al., 2008).

In the study area, in the states of Santa Catarina and Paraná (Fig. 1), the Itararé Group comprises rocks belonging to the Taciba Formation. According to França and Potter (1988), this unit encompasses a third major fining upward cycle of the Itararé Group including three members (i.e., in ascending order the Rio Segredo sandstone, Chapéu do Sol diamictite, and Rio do Sul rhythmite, siltstone, and shale; see also Castro, 1999; Weinschutz and Castro, 2004, 2005, 2006). The Taciba Formation is equivalent to the Rio do Sul Formation, in the sense of Schneider et al. (1974) (excluding the basal Lontras shale).

In the Mafra region, in the state of Santa Catarina (Fig. 1C), Weinschutz and Castro (2006) have recognized two main depositional sequences within the Taciba succession, which were generated under glacial and post-glacial conditions (Taciba I and II), respectively (Fig. 2). In outcrops, the deglacial interval (Taciba II) comprises a succession of a 10 m-thick stratified diamictite, overlain by thin stratified conglomerate and sandstone and an intensely bioturbated, fossil-rich sandstone, which is succeeded by shales (Weinschutz and Castro, 2006; Simões et al., 2012) (Fig. 2). As noted below, most of the studied brachiopods come from that sandstone bed (= Butiá assemblage, sense Rocha Campos and Rösler, 1978) (Table 1).

In the Imbituva and Teixeira Soares regions, in the state of Paraná (Figs. 1A, B, respectively), only the upper portion of the Taciba Formation crops out (Lange, 1952; Mineropar, 2007; Neves et al., 2014b),

which includes diamictites, sandstones, siltstones and mudstones (Passinho shale), succeeded by the sand-dominated, coal-bearing deposits of the lower portion of the Sakmarian–Artinskian, Rio Bonito Formation (Fig. 3) (see below in Stratigraphy and Locality).

## 3. Material and methods

3.1. Fossil collection

In total, 118 brachiopod specimens from the Taciba Formation were examined: 1 specimen from fossil site A, 11 from fossil site B and 106 from fossil site C (see Tables 2 and 3). These specimens are housed in distinct Brazilian invertebrate fossil collections, including a-CENPALEO (Centro de Paleontologia), Universidade de Contestado, Mafra, Santa Catarina State; b- Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), Botucatu, São Paulo State; and c- Instituto de Geociências, Universidade de São Paulo, São Paulo State. Other material (*Crurithyris* sp.) is housed at the Laboratorio de Investigaciones em Evolución y Biodiversidad (LIEB), Universidad de la Patagonia "San Juan Bosco", Esquel, Chubut, Argentina.

Abbreviations.- CP, Cenpaleo collection; DZP, Department of Zoology, Paleontology collection, UNESP, Botucatu campus; DGM, Division of Geology and Mineralogy, National Department of Mineral Production, Rio de Janeiro State. Materials with the DGM prefix are housed in the University of São Paulo collection, while GP-1E indicates Institute of Geosciences collection, University of São Paulo, USP, São Paulo, Brazil, and LIEB-PI indicates the LIEB invertebrate fossil collection.

In the laboratory, the fossil material was prepared according to standard paleontological procedures (see Feldmann et al., 1989) using precision tools. Latex casts and plasticine molds were prepared for most of the shells. Brachiopod and bivalve shells were also coated with magnesium oxide sublimate to enhance diagnostic morphological characters for photography (see Neves et al., 2014a, b and references therein). The applied classification largely follows Waterhouse (2013) for Linproductidina, Williams and Brunton (2000) for Orthotetidina, Carter et al. (2006) for Spiriferidina, Carter and Johnson (2006) for Spiriferinidina, Racheboeuf (2000) for Chonetidina and Williams et al. (2000) for Lingulida.

3.2. Stratigraphy and locality

Brachiopods come from three main fossil sites in the states of Paraná (Teixeira Soares) and Santa Catarina (Mafra) in southern Brazil. Table 1 summarizes the main geographic and geologic information for the sampled localities (fossil sites A, B and C). In the study area, the geology and the correlation of the strata of the Itararé Group are relatively well known (see Almeida, 1945; Rocha Campos, 1966; Weinschutz and Castro, 2006; Mineropar, 2007; Neves et al., 2014b). Here the Taciba Formation (França and Potter, 1988) comprises the uppermost unit of the Itararé Group (Fig. 4). In Teixeira Soares County, in the state of Paraná, the rocks of this formation are exposed along the Almas River Valley, ~4 km SE of the town of Teixeira Soares (Oliveira, 1930; Lange, 1954; Almeida, 1945; Mineropar, 2007; Neves et al., 2014b). Locally, the Taciba Formation is a ~45 m thick, siliciclastic succession including, in ascending order, a thick (~10 m), polymitic, matrix-supported, massive diamictite with rounded, striated and faceted clasts (granules/boulders) of granites, which may grade upward to crudely stratified mudstones (Mineropar, 2007, p. 106). These are succeeded by a ~7 m-thick package of medium-to-fine grained sandstones (Rio da Areia sandstone) with planar cross-stratifications (see Mineropar, 2007, p. 107). In these sandstones, *Planolites*-like traces are associated with ripple marks, and bivalve-dominated shell pavements occur in the uppermost (2 m) portion, above which thin (50 cm), deeply bioturbated fossil-bearing siltstones (Baitaca siltstone) including scattered, splayed-out bivalve shells are recorded (Neves et al., 2014b, p. 212).
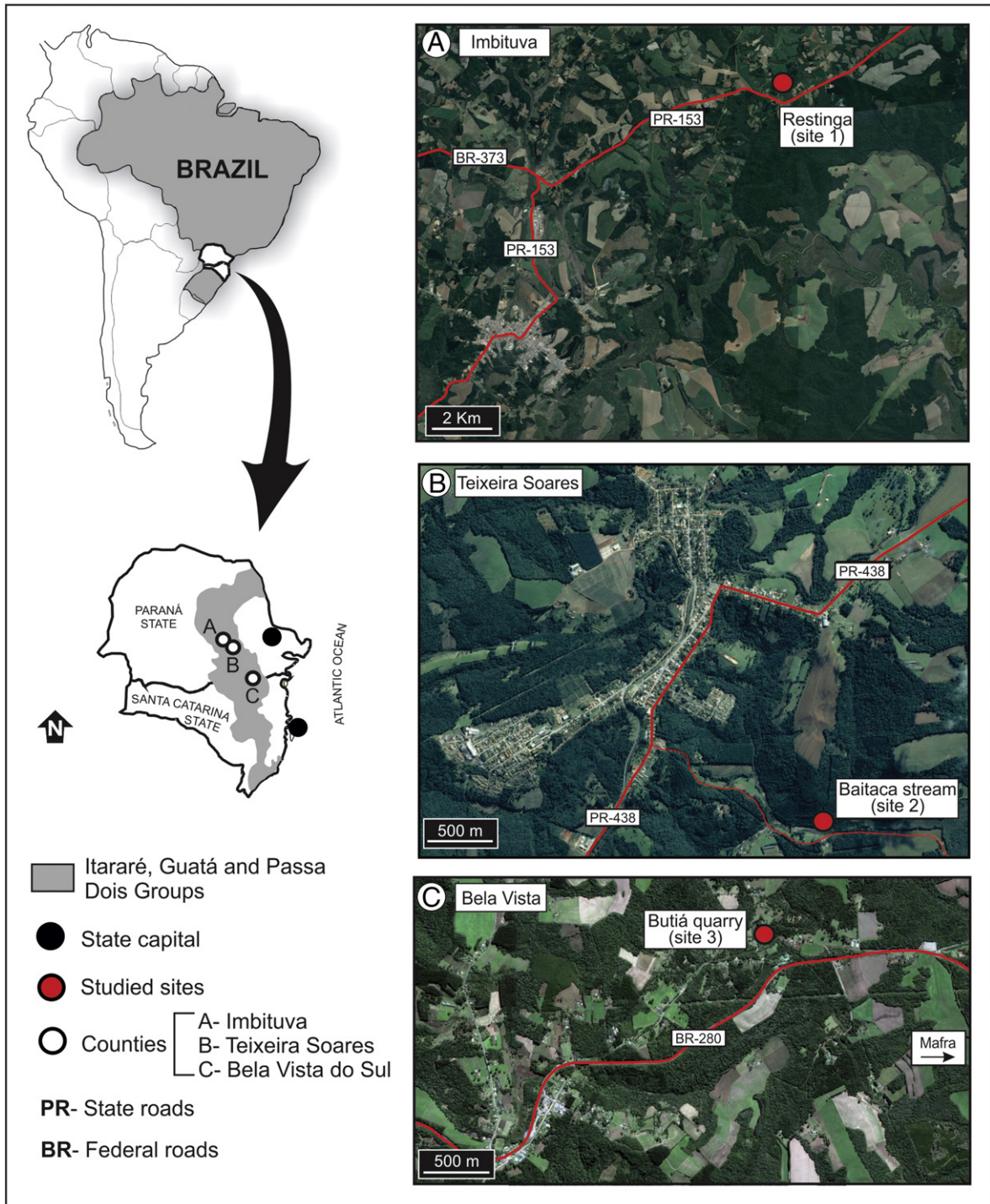
Fig. 1. Location map of the studied sites. A: Imbituva County, State of Paraná, at the Restinga locality (site 1); B: Teixeira Soares County, State of Paraná, at the Baitaca stream locality (site 2); C: Mafra County, State of Santa Catarina, at the Bela Vista do Sul locality, Butiá quarry, (site 3).

Toward the top, a thick (2.15 m) succession including fine-to-very fine, well-sorted sandstones with low-angle trough cross-stratifications occurs. This sandstone is intensely bioturbated, including *in situ* bivalve shells, escape structures, and rare rhynchonelliform brachiopods. Above this, thick (>30 m), laterally persistent (tabular), dark grey (or white-yellowish when weathered), thinly laminated mudstones (Passinho shale) are recorded (Almeida, 1945; Mineropar, 2007; Neves et al., 2014b, p. 206), which may contain rare splayed-out bivalve shells or isolated valves of linguliform brachiopods (Oliveira, 1930).

The succession described above reflects a stratigraphy composed of alternating units, including (a) proximal re-deposited diamictites generated in proximal settings, succeeded by (b) strata deposited in nearshore (upper shoreface) and (c) inner (lower shoreface)- to (d) outer-shelf (offshore) environments (Mineropar, 2007; Neves et al., 2014b) tied to the demise of the LPIA (Late Paleozoic Ice Age). Regionally, the Passinho shale marks the maximum flooding surface of the Itararé succession (Santos et al., 1996; Mineropar, 2007; Holz et al., 2010; Neves et al., 2014b) (Fig. 2). These mudstones are capped by the fluvio-deltaic, coal-bearing deposits of the Sakmarian–Artinskian Rio Bonito Formation (Santos et al., 1996; Holz et al., 2010). At the Restinga locality, near Imbituva County, in the state of Paraná (Fig. 1A), the Passinho shale also crops out at Km 42 of the PR-153
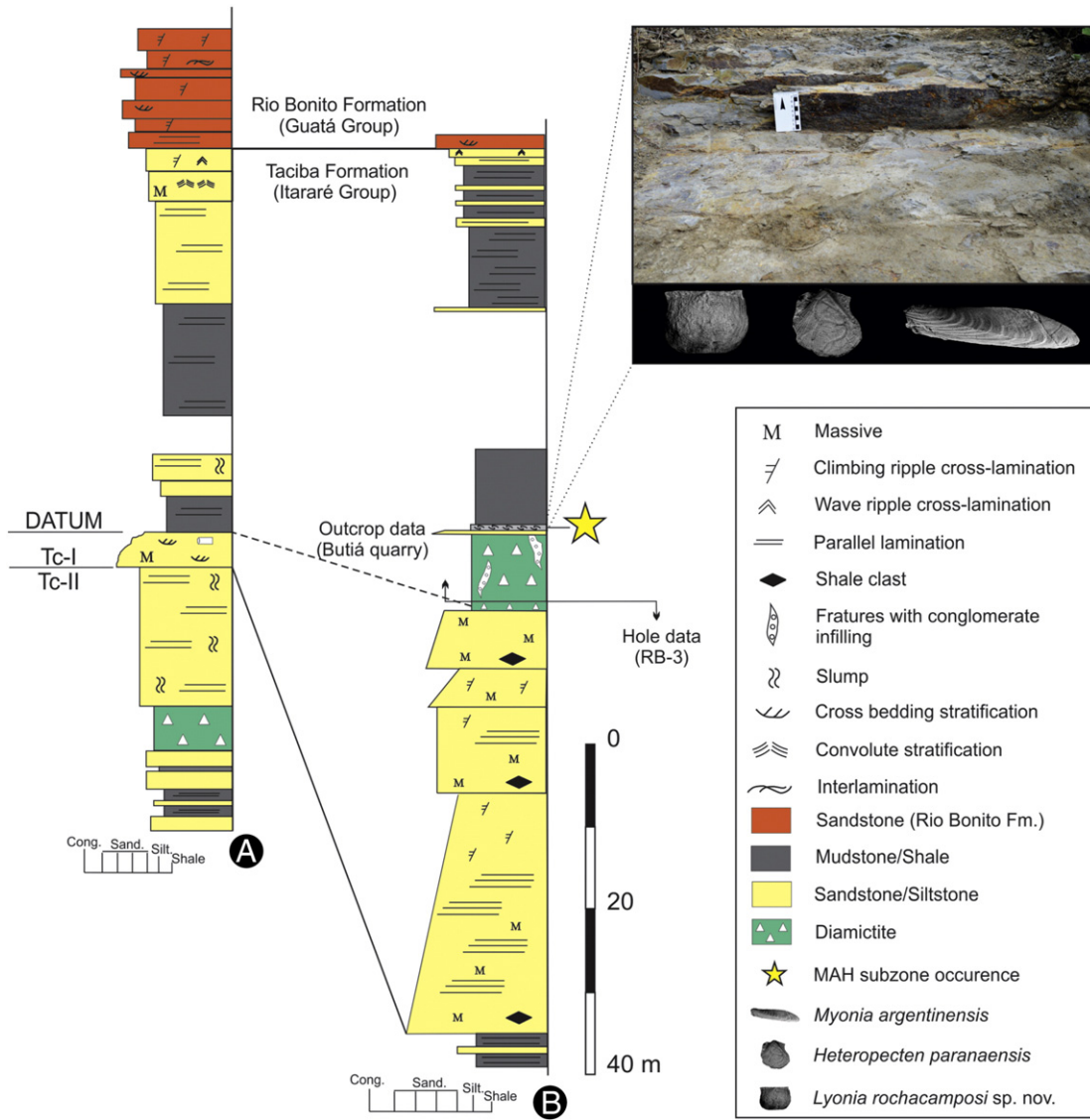
Fig. 2. Columnar sections of the uppermost portion of the Taciba Formation at Bela Vista do Sul locality, Butiá quarry. A: PP-10 borehore and B: RB-3 borehole plus surface data, modified from Weinschutz and Castro (2006) and Neves et al. (2014b).

road between Ponta Grossa-Imbituva (see Lange, 1952, p. 82). This author described some brachiopods from that locality, which are also revised herein (see in Systematic Paleontology).

In Mafra County, rocks of the Taciba Formation are well exposed on the walls of abandoned quarries, such as the so-called Butiá quarry (Rocha Campos, 1966) at the margins of the eponymous river. Detailed subsurface stratigraphic data (cored wells) are also available

(Weinschutz and Castro, 2006). These data indicate that, locally, the Taciba Formation is represented by five meters of laminated siltstones and rithmites (= varvites) belonging to the glacial Taciba I sequence (sense Weinschutz and Castro, 2006). Above this, a 52.5 m-thick sandstone body occurs, which is succeeded by a ~ 12 m-thick grey diamictite that is itself overlaid by thin stratified conglomerate and sandstone beds. In ascending order these are succeeded by bioturbated,

Table 1
Summary of the main features of the studied lithofacies of the uppermost portion of the Taciba Formation, in the Teixeiras Soares and Bela Vista do Sul (Butiá) regions.

Facies	Local Designation	Processes	Environment	Brachiopod species	n.
Parallel-laminated or massive mudstones	Passinho Shale	Deposition of background sediments from suspension under low-energy conditions, in oxygen deficient, organic-rich bottoms, below storm wave base	Outer shelf	Biconvexiella roxoi	2
				Quinquenella rionegrensis	3
				Langella imbituvensis	1
Laminated siltstones	Baitaca Siltstone	Low-energy, suspension fall-out deposition during fair-weather periods punctuated by erosional events, as indicated by the splayed valves of burrowing bivalves. Deposition above storm wave base	Inner to middle shelf	?Streptorhynchus sp.	1
				?Cyrtella sp.	1
				Tomiopsis sp. cf. T. harringtoni	1
				Biconvexiella roxoi	1
				Quinquenella rionegrensis	2
Highly bioturbated fine sandstones	Butiá Sandstone	Low-energy lower shoreface aerated bottoms. Sandstones may record deposition from storms, with bioturbation recording post-event periods. Deposition mostly above storm-wave base and below fairweather-wave base.	Middle shelf	Lyonia rochacamposi sp. nov.	106
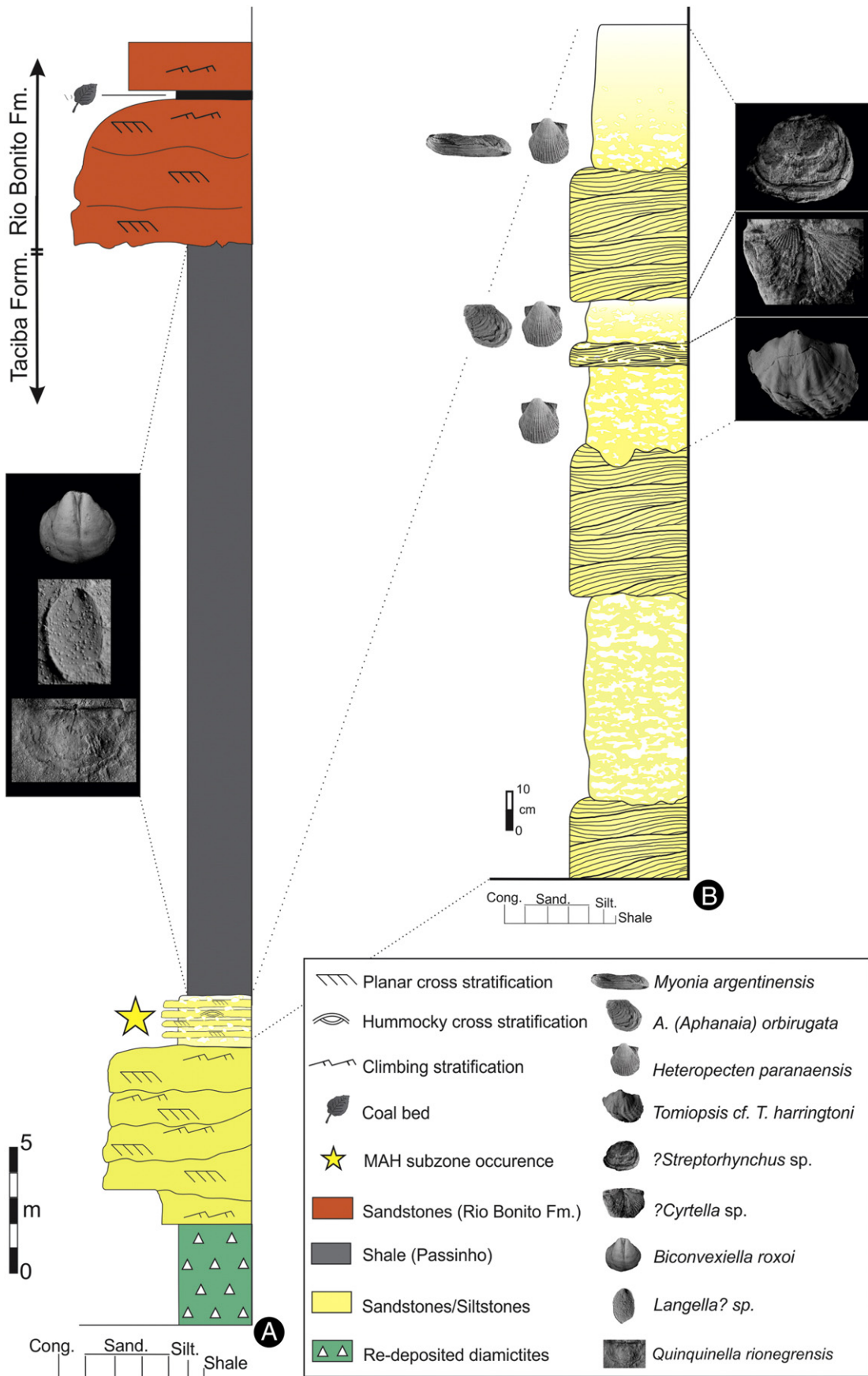
Fig. 3. A: Composed columnar section of the uppermost portion of the Taciba Formation at Teixeira Soares County. B: Detailed columnar section of the "Baitaca siltstone" at Baitaca stream locality, where mostly of the studied brachiopods where collected (Modified from Neves et al., 2014b).

Table 2
Dimensions of the specimens of *Lyonia rochacamposi* of the Taciba Formation from the Bela Vista do Sul locality (Butiá quarry). Dimensions in millimeters. Frag. = fragmented valve; ~ = estimate.

Specimen number	Maximum width	Hinge width	Dorsal length	Ventral length	Thickness	Costae number/5 mm[a]
CP.I 769 I	50	Frag.	32	–	–	8
CP.I 763	~38	~38	29	–	–	12
CP.I 765	~35	–	–	17	–	10
CP.I 755 II	37	36	27	–	–	10
CP.I 754	31	~16	28	–	–	9
CP.I 5011	40	~32	32	–	–	9
CP.I 2156	40	38			–	12
CP.I 769 II	~44	42	–	37	12	9
CP. I 753	~34	Frag.	–	~28	–	8
CP. E 4396B	~45	Frag.	–	40	–	9
CP.E 536	Frag.	43	–	~30	–	11
DZP 18913	34	32	22	–	16	10
DZP 18906	Frag.	41	–	~25	–	12
DZP 19133B	33	24	29	–	–	12

[a] Costae number/5 mm at middle portion of shell.

brachiopod-rich sandstones, which are in turn followed by dark shales (Weinschutz and Castro, 2006) (Fig. 2). This sandstone has also yielded mollusk shells, including both gastropods (Rocha Campos, 1966) and bivalves (Simões et al., 2012). All of these rocks are referred to the glacial succession of the Taciba II sequence (sense Weinschutz and Castro, 2006), which is succeeded locally by the Rio Bonito Formation (Weinschutz and Castro, 2006) (Fig. 2).

4. The Eurydesma fauna

4.1. The Taciba–Bonete Eurydesma faunal composition: an updated chrono-biocorrelation
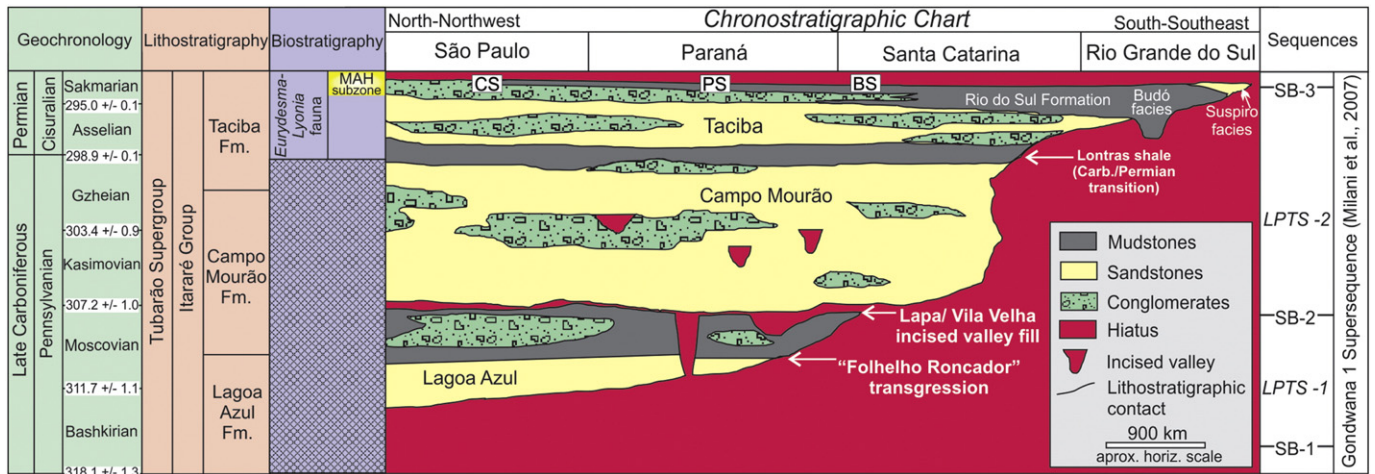
The studied material from the uppermost section of the Taciba Formation exhibited significant, but low-diversity brachiopod assemblages, being monotypic in Bela Vista do Sul, where *Lyonia rochacamposi* sp. nov. is recognized in large numbers (~110/m^2), whereas the scarce fossil records in Texeira Soares include *Biconvexiella roxoi* (Oliveira, 1936),? *Cyrtella* sp., *Langella imbituvensis* (Oliveira, 1930), *Quinquenella rionegrensis* (Oliveira, 1930),? *Streptorhynchus* sp. and *Tomiopsis* sp. cf. *T. harringtoni* Archbold and Thomas, 1986 (see Table 4). These brachiopods co-occur in association with a more diverse bivalve fauna that was recently described by Simões et al. (2012) and Neves et al. (2014a, b). In total, six bivalve assemblages were identified, which are mainly dominated by four species: *Heteropecten paranaensis* Neves et al. (2014a), *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington, 1955), *Praeundulomya* cf. *P. subelongata* Dickins, 1963 and *Myonia argentinensis* (Harrington, 1955) (see Plate I). These bivalves were demonstrated to be key species for establishing regional and interbasinal biocorrelations (Simões et al., 2012; Neves et al., 2014a, b). For example, *Heteropecten paranaensis*

Table 3
Dimensions of the brachiopod species of the Taciba Formation from Teixeira Soares and Imbituva counties. Dimensions in millimeters; ~ = estimate.

Specimen number	Dorsal width	Ventral width	Dorsal length	Ventral length	Thickness
GP-1E 2056	9	–	6		–
GP-1E 4402	–	7	–	5	–
GP-1E 4439	4	–	6	–	–
GP-1E 4364	–	15	–	~10	~3
GP-1E 4367	–	9	–	11	~2
GP-1E 4437	9	9	6	6	~4
GP-1E 4373	~8	~10	~8	5	~4
GP-1E 4339a	–	9	–	6	–
GP-1E 4339b	8	–	5	–	–
DGM 4355	17	–	~14,5	–	–
DZP 18829	~26	~25	~20	~12	7
DZP 19139	6	–	4	–	–

(Plate I, Figs. A-D) and *Myonia argentinensis* (Plate I Figs. K-M, O-P) are recorded in both deposits of the Itararé Group (Teixeira Soares and Bela Vista do Sul (Butiá quarry)) and in the *Eurydesma* fauna of the Bonete Formation (Sauce Grande-Colorado Basin, Argentina) (Neves et al., 2014a). The bivalve *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington) (Plate I Figs. E-H) is also shared by the Taciba (Teixeira Soares) and Bonete formations, which provides even more support for this faunal affinity hypothesis.

The *Eurydesma* fauna in eastern Argentina was recorded in the lower half of the Bonete Formation through a stratigraphic section nearly 155 m-thick, although *Eurydesma* is notably absent in level 4 (=BM6), which is 15 m-thick, located at 1285 to 1270 m above the base of the overlying Pillahuinco Group, 70 m above and 70 m below the first and last appearance of *Eurydesma*, respectively (Harrington, 1955). This fossil-bearing bed is characterized only by two brachiopods, *Tivertonia pillahuincensis* (Harrington, 1955) (= *Chonetes pillahuincensis* Harrington, 1955; Archbold and Gaetani, 1993; Pagani, 1998) and *Tomiopsis harringtoni* Archbold and Thomas, 1986 (= *Notospirifer darwini* (Morris) Harrington, 1955), and a diverse bivalve assemblage including *Myonia argentinensis* (Harrington, 1955) (= *Stutchburia? argentinensis* Harrington, 1955; Pagani, 2000; Simões et al., 2012), *Exochorhynchus inflectoventris* (Harrington, 1955) (Neves et al., 2014b; = *Allorisma inflectoventris* Harrington, 1955; Pagani, 2000), *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington, 1955) (= *Aphanaia? orbirugata* Harrington, 1955; Pagani, 2000) and *Leptodesma* (*Leiopteria*) *dutoiti* (Harrington, 1955) (= *Liopteria? dutoiti* Harrington, 1955; Pagani, 2000). More recent fossil records from this stratigraphic interval (BM6) have added *Deltopecten harringtoni* Rocha Campos and de Carvalho, 1975, *Vacunella camachoi* Rocha Campos and de Carvalho, 1975, *Promytilus acinaciformis* Harrington, 1955 (Pagani, 2000) and *Heteropecten paranaensis* Neves et al., 2014a. This assemblage shares various genera (the bivalves *Palaeoneilo*, *Phestia*, *Promytilus*, *Exochorhynchus* and *Schizodus*) with those from Texeira Soares and Bela Vista do Sul as well as three three bivalve species *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington), *Myonia argentinensis* (Harrington) and *Heteropecten paranaensis* Neves et al., 2014a. In addition a species remarkably similar to *Leptodesma* (*Leiopteria*) *dutoiti* (Harrington), referred as *Leptodesma* (*Leiopteria*) aff. *dutoiti* from Texeira Soares, was indicated by Neves et al. (2014b). Likewise, *Tomiopsis* cf. *T. harringtoni* Archbold and Thomas described herein reinforces the recognition of the *Eurydesma* fauna in the Paraná Basin, as postulated by Simões et al. (1998, 2012), Pagani (2000) and Neves et al. (2014a, b). Furthermore, this biocorrelation between the Bonete and Taciba formations is refined to a short interval within the recognized level 4 (BM6) of the *Eurydesma* Biozone (Dickins, 1985) by Harrington (1955) and the thin fossil-bearing beds (<5 m) of Texeira Soares and Bela Vista do Sul. The

Fig. 4. Chronostratigraphic chart of the Itararé Group in the Paraná Basin (modified from Holz et al. 2010). In the Taciba Formation the MAH subzone interval, here proposed, is indicated in yellow. Explanation: CS = Capivari Shale; PS = Passinho Shale; BS = Butiá Shale.

absence of *Eurydesma* in these last stratigraphic intervals was explained by Neves et al. (2014b; see also Runnegar, 1979) as being due to ecological competition with Pachydomidae bivalves, especially *Myonia*, which can cause local extinction of *Eurydesma* populations. This same mechanism could also be valid for the *Eurydesma*-lacking fossil-bearing level 4 (BM6) of the Bonete Formation in Argentina. The *Myonia argentinensis-Atomodesma* (*Aphanaia*) *orbirugata-Heteropecten paranaensis* association (MAH) is proposed here to recognize this regional stratigraphic interval, or Subzone, within the Biozone of *Eurydesma*. The MAH assemblage includes some bivalve species, such as *Praeundulomya* cf. *subelongata* Dickins, 1963 (Neves et al., 2014b) and *Limipecten capivariensis* (= *Aviculopecten capivariensis* Mendes, 1952) that are also recognized in the Capivari Formation (Simões et al., 2015) as well as *Lyonia rochacamposi* (classification by one of the authors: ACT), thus extending the boundary of the *Eurydesma* transgression northward to the northernmost Paraná Basin in São Paulo State.

Rocha Campos (1970) indicated the Bonete Formation as supraglacial, while the Taciba Formation is more closely associated with diamictite beds (Figs. 2 and 3). The first appearance of the *Eurydesma* fauna in the Bonete Formation occurs at its base, 300 m above (the entire Piedra Azul Formation) the glacial-related Sauce Grande Formation. This thick interval and another of 70 m, that separates from MAH at the base of level 4 (BM6) of Harrington (1955) are absent in the upper section of the Taciba Formation, where MAH also occurs. This circumstance suggests a brief, but significant hiatus just above the diamictite interval of the Taciba Formation and a subsequent northward delay of the *Eurydesma* postglacial transgression (Fig. 5).

In the Sauce Grande Basin, SHRIMP radiogenic isotope dating of zircons in tuffs of the uppermost section of the Tunas Formation (500 m thick) provided an early Kungurian age of 280.8 ± 1.9 Ma for this unit (López Gamundi et al., 2013; see also Tohver et al., 2007, 2008 and Alessandretti et al., 2010), constraining the *Eurydesma*-bearing beds (~700 m below) of the underlying Bonete Formation to pre-Kungurian times (after Cohen et al., 2013, the age of the base of the Kungurian is 283.5 ± 0.6, 4 Ma older than the previous age of 279.3 ± 0.5 Ma indicated in the stratigraphic chart of Gradstein et al., 2012). In the Paraná Basin, U–Pb SHRIMP ages obtained from tonsteins interbedded in coal seams of the Rio Bonito Formation indicated a radiometric age of 291 ± 1.2 Ma (Simas et al., 2012, 2013; see also Matos et al., 2001; Guerra-Sommer et al., 2008a, b, c; Rocha Campos et al., 2006, 2007, 2011; Mori et al., 2012), constraining the *Eurydesma*-bearing beds of the underlying Taciba Formation to pre-Artinskian (Neves et al., 2014b) or, more precisely, to pre-latest Sakmarian times, which is also valid for the coeval fauna of the Bonete Formation. Common genera, such as *Eurydesma*, *Deltopecten*, *Lyonia* and *Tomiopsis* as well as *Praeundulomya* cf. *elongata* Dickins, close species and possible *Punctocyrtella*, along with the relative bivalve diversity of the South American *Eurydesma* fauna, strongly suggest a coeval condition for the *Eurydesma* assemblage of the uppermost Lyons Group/Carrandibby Formation (Carnarvon Basin) of Western Australia. Collectively, faunal affinities of the *Eurydesma-Lyonia* fauna based in common records of genera mainly of bivalves (*Eurydesma*, *Deltopecten*, *Praeundulomya* and *Astartila*), brachiopods (*Lyonia*, *Neilotreta*, *Punctocyrtella*, *Tomiopsis*, *Tivertonia*, *Biconvexiella*) and gastropods (*Peruvispira*, *Keenia*), extend eastward the trans-gondwanan marine connection. This faunal linkage reinforces previous correlations to geographical areas that were adjacent or close to western Australia during Asselian–early Sakmarian times (Dickins and Shah, 1981, 1987; Shi and Archbold, 1993). Biocorrelation among the Lyons Group and Carrandibby Formation to Talchir, Umaria and Bap formations of India (Archbold et al., 1996, and references provided therein), Nilawan Group in Salt Range and the Agglomeratic Slate in Kashmir, Pakistan, eastern Himalaya (Waagen, 1881; Reed, 1936; Sahni and Srivastava, 1956; Dickins, 1985; Singh and Archbold, 1993) were suggested (Fig. 6). Comparable faunas to those of western Australia were also recognized even further east,

Table 4
Brachiopod groups present in the uppermost portion of the Taciba Formation, in the Bela Vista do Sul county (Butiá quarry), Santa Catarina State, and in the Teixeira Soares county, Paraná State.

Locality	Order	Superfamily	Family	Genus	Species
Bela Vista do Sul (SC)	Productida	Proboscidelloidea	Auriculispinidae	*Lyonia*	*Lyonia rochacamposi* sp. nov.
Teixeira Soares	Orthotetida	Orthotetoidea	Schuchertellidae	*Streptorhynchus*	?*Streptorhynchus* sp.
(PR)	Spiriferinida	Syringothyridoidea	Syringothyrididae	*Cyrtella*	?*Cyrtella* sp.
	Spiriferida	Martinioidea	Ingelarellidae	*Tomiopsis*	*Tomiopsis* sp. cf. *T. harringtoni*
		Cyrtospiriferoidea	Ambocoeliidae	*Biconvexiella*	*Biconvexiella roxoi*
	Chonetida	Chonetoidea	Rugosochonetidae	*Quinquenella*	*Quinquenella rionegrensis*
	Lingulida	Linguloidea	Lingulidae	*Langella*	*Langella imbituvensis*
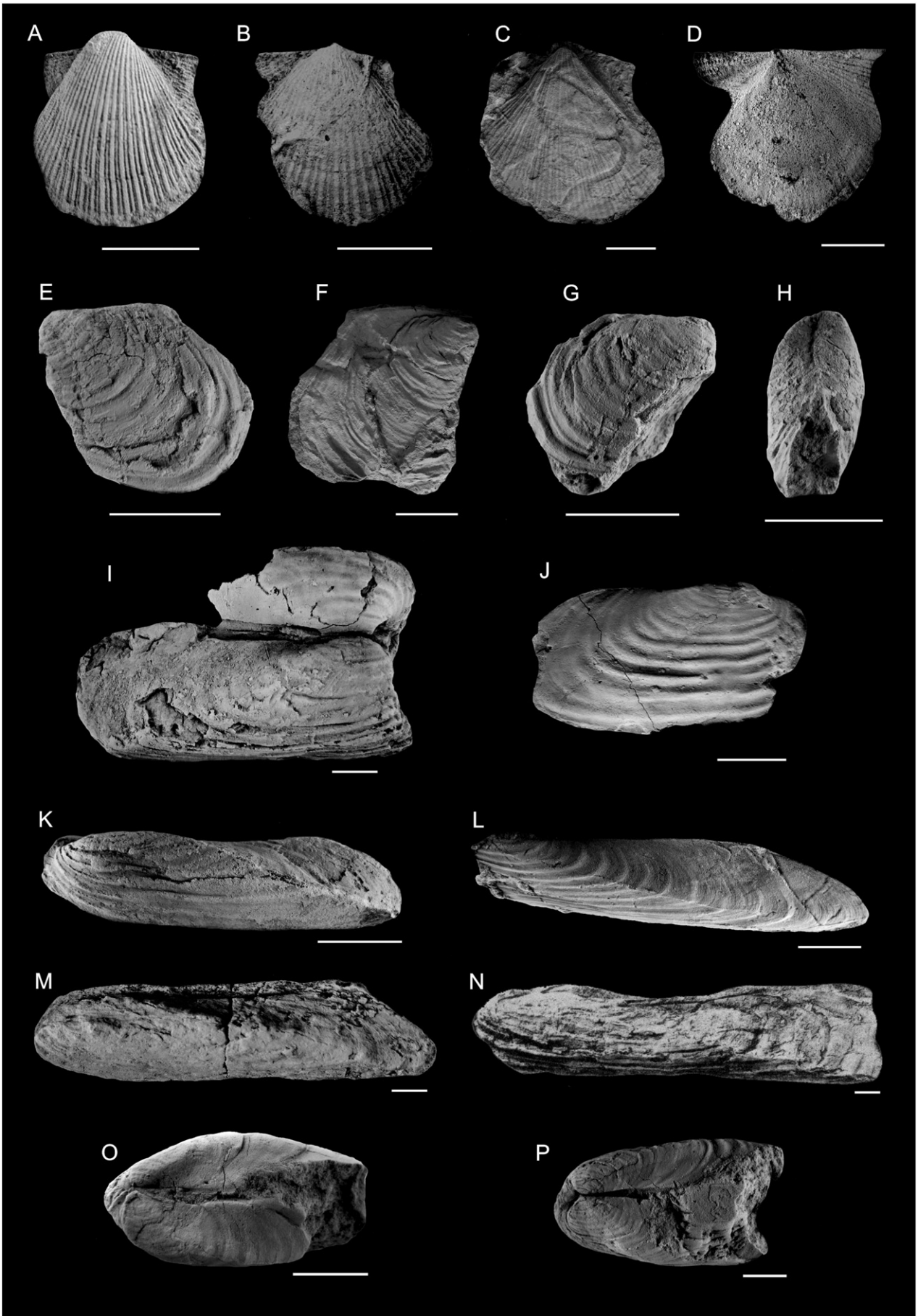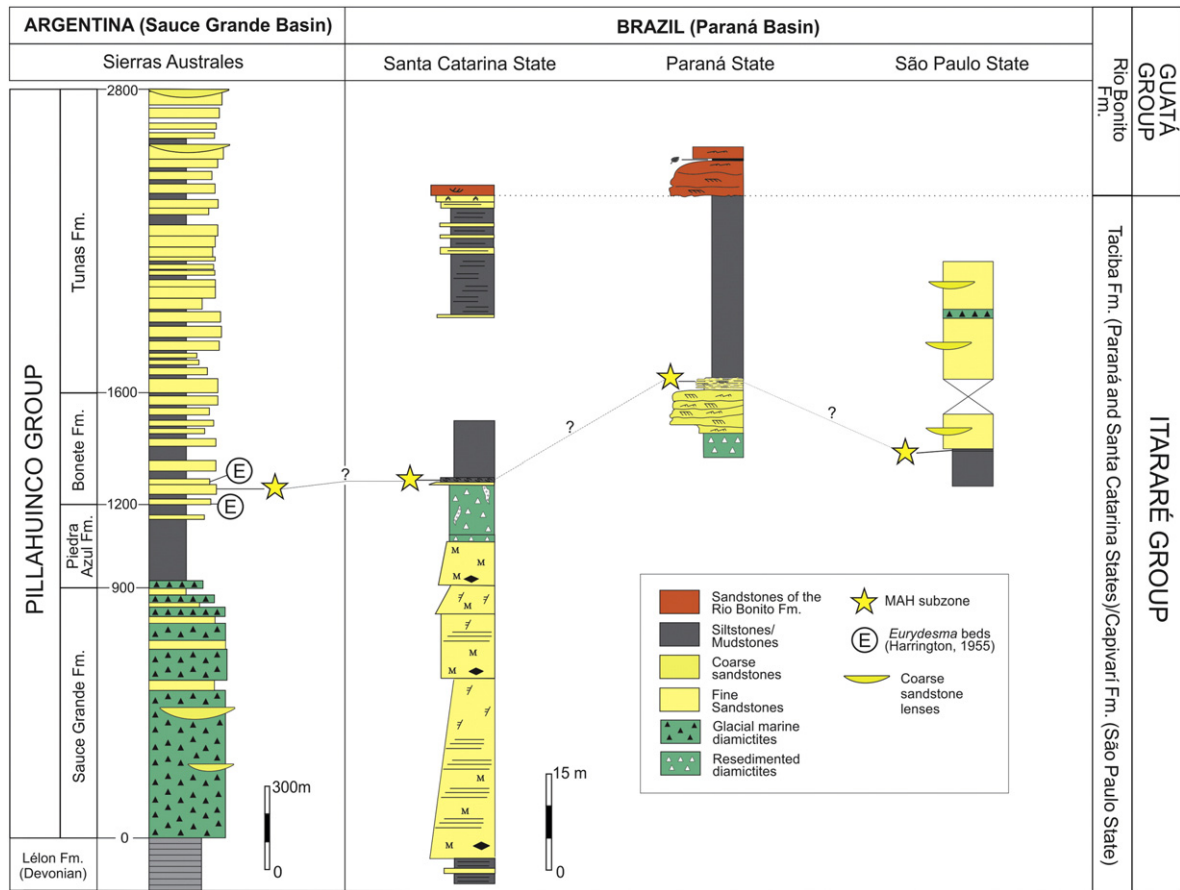
Fig. 5. Biostratigraphic correlation among the Brazilian columnar sections of the Taciba Formation (Teixeira Soares, Paraná State, and Bela Vista do Sul, Santa Catarina State), Capivari Formation (homonymous county, São Paulo State), and Bonete Formation (Sierras Australes), in Argentina.

such as in Tibet of south China (Xinsheng, 1983), Malaysia (Shi et al., 1997), Western Yunnan (Shi et al., 1995, 1996), Irian Jaya (Archbold, 1982) and Timor (Archbold and Barkham, 1989; Archbold and Bird, 1989), in southeast Asia (Archbold, 2000; and references provided therein).

On the other hand, Cagliari et al. (2014) provided LA-ICP-MS U–Pb zircon age data, in parallel with the previous radiometric information mentioned above, which showed that deposition of the Rio Bonito Formation occurred between Sakmarian and Kungurian times, but suggesting the existence of significant hiatuses during its deposition. The period of time associated with such hiatuses suggests constraint deposition of the entire Itararé Group between Bashkirian–Moscovian times, contradicting absolute chronostratigraphy for most biochronology information (Cagliari et al., 2014) and significantly predating the age provided by marine fossil invertebrates in particular, including the *Eurydesma* fauna itself.

4.2. The Eurydesma fauna of the Dwyka (SW Africa) and Lyons Groups (Western Australia)

In western Gondwana, in addition to the South American *Eurydesma* faunal records, a poorly diversified *Eurydesma* assemblage was also recorded, interbedded within glaciomarine deposits of the Dwyka Group in Namibia (Aranos Basin), in southwest Africa (Dickins, 1961,

1985). In association with *Eurydesma mytiloides* Reed, 1932, the bivalve *Atomodesma* (*Aphanaia*) *haibensis* (Reed, 1936) and the gastropod *Peruvispira vipersdorfensis* Dickins, 1957 were described, while conulariids and fish remains were only mentioned (Reed, 1936; Martin and Wilczewski, 1970). The *Eurydesma* fauna occurs in a mudstone dropstone-rich to dropstone-free upward horizon with a maximum thickness of 76 m, which corresponds to the Deglaciation sequence III (DS III) of the Dwyka Group, referred to as the Hardap shale Member by SACS (1980; Stollhofen et al., 2000, 2008). Zircon separated from a tuffaceous horizon of the Hardap shale Member revealed a refined ^{206}Pb/^{238}U age of 297.1 ± 1.8 Ma age (see also Bangert et al., 1999; Stollhofen et al., 2000), which places the top of DS III in the early Permian Asselian Stage (Stollhofen et al., 2008). Although re-evaluation using information preferably provided by ID-TIMS data would be desirable, this early Asselian age (base of the Asselian Stage at 298.9 ± 0.15 Ma, according to the International Chronostratigraphic Chart of Cohen et al., 2013) could tentatively be taken as the oldest *Eurydesma* record. Its stratigraphic position, bounded below and above by glacial-related intervals, appears to be influenced by a higher paleolatitudinal location compared with the South American and Western Australian upward-free glacial influence, a circumstance that locally (Namibia) suggests a condensed stratigraphic interval where younger *Eurydesma* occurrences (latest Tastubian) are not represented or could be biased and might not reflect most records of the whole *Eurydesma*

Plate I. Associated bivalve fauna. A–D: *Heteropecten paranaensis* (Neves et al. 2014a), A–C: left valve view, A: DGM 4379; B: CPBA 5889; C: CP.I 2159; D: DGM 4360, right valve view; E–H: *Aphanaia orbirugata = Atomodesma* (*Aphanaia*) *orbirugata* (Harrington), E, G–H: DZP 18832; F: CPBA 5779; I–J: *Praeundulomya* cf. *subelongata*, I: DGM 4342; J: 4337; K–P: *Myonia argentinensis* (Harrington), K: DGM 4341; L: CP.I 475; M: CPBA 5778; N: UQF 48556; O: DZP 18826; P: GP/1E 700. Specimens A, D, E, G–K, O–P come from Teixeira Soares County (State of Paraná, Brazil), Taciba Formation; C and L come from Bela Vista do Sul (State of Santa Catarina, Brazil), Taciba Formation; B, F, M come from the *Eurydesma* beds in the Bonete Formation, Eastern Argentina, and the specimen N comes from Queensland, Australia (*Myonia* or *Vacunella*? sp. of Runnegar, 1967, plate 4, fig. 16). Scale bar = 10 mm.
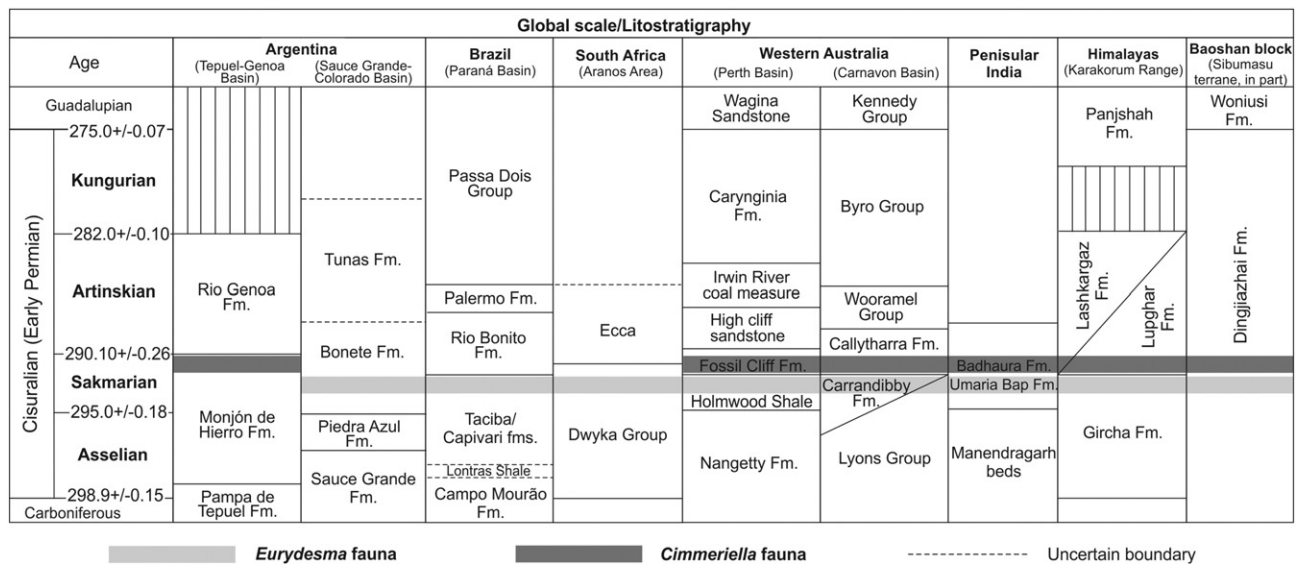
Global scale/Litostratigraphy									
Age	Argentina (Tepuel-Genoa Basin)	Argentina (Sauce Grande-Colorado Basin)	Brazil (Paraná Basin)	South Africa (Aranos Area)	Western Australia (Perth Basin)	Western Australia (Carnarvon Basin)	Penisular India	Himalayas (Karakorum Range)	Baoshan block (Sibumasu terrane, in part)
Guadalupian					Wagina Sandstone	Kennedy Group		Panjshah Fm.	Woniusi Fm.
—275.0+/-0.07—									
Kungurian		Tunas Fm.	Passa Dois Group		Carynginia Fm.	Byro Group		Lashkargaz Fm. / Lupghar Fm.	Dingjiazhai Fm.
—282.0+/-0.10—	Rio Genoa Fm.								
Artinskian			Palermo Fm.	Ecca	Irwin River coal measure / High cliff sandstone	Wooramel Group			
—290.10+/-0.26—		Bonete Fm.	Rio Bonito Fm.		Fossil Cliff Fm.	Callytharra Fm.	Badhaura Fm.		
Sakmarian	Monjón de Hierro Fm.	Piedra Azul Fm.	Taciba/ Capivari fms.	Dwyka Group	Holmwood Shale	Carrandibby Fm.	Umaria Bap Fm.	Gircha Fm.	
—295.0+/-0.18—							Manendragarh beds		
Asselian		Sauce Grande Fm.	Lontras Shale		Nangetty Fm.	Lyons Group			
—298.9+/-0.15—	Pampa de Tepuel Fm.		Campo Mourão Fm.						
Carboniferous									

Legend: ▭ *Eurydesma* fauna   ▬ *Cimmeriella* fauna   ------- Uncertain boundary

Fig. 6. Litostratigraphic correlation of the *Eurydesma* fauna across the W–E transgondwana marine connection.

transgression. Some authors have suggested this date as an important age calibration for the marked *Eurydesma* transgression reported Gondwana-wide, but this marine transgression continued upward in lower paleolatitudes, where glacial influence ceased earlier in more open marine basins (Bangert et al., 1999; Stollhofen et al., 2000, 2008). The *Eurydesma*-bearing Hardap shale Member is capped by the Deglaciation IV interval with a maximum thickness of 70 m and the top of the Dwyka Group in Namibia (Bangert et al., 1999; Stollhofen et al., 2000, 2008). The lower Gorge Tuff situated 1.6 m (basal Prince Albert Formation) above the Dwyka-Ecca boundary yielded a weighted mean ^{206}Pb/^{238}U age of 290.9 ± 1.7 Ma (Werner, 2006), constraining the top of the glacial-related DS IV to near the Sakmarian–Artinskian boundary. Another glacial-related horizon estimated to show a Sakmarian–Artinskian age was indicated in the upper part of the Mojón de Hierro Formation (Tepuel-Genoa Basin) in southern Patagonia, Argentina, but was located at subpolar paleolatitudes during the Late Paleozoic Ice Age (Taboada, 2010, Pagani and Taboada, 2011; Taboada and Shi, 2011; Isbell et al., 2013). An interval with a thickness of nearly 400 m underlies this glacial-related horizon and yields a fossil-rich *Cimmeriella* fauna (Taboada and Pagani, 2010), which shares common brachiopod genera (e.g., *Neilotreta*, *Spirelytha*, *Cimmeriella*, *Arctitreta*) with the Callytharra Formation, a unit that lies conformably above the Lyons Group/Carrandibby Formation in the Carnarvon Basin, Western Australia. This could constitute indirect evidence that the *Eurydesma*-bearing interval bounded by DS III and DS IV in Namibia (Aranos Basin) represents only a partial and slightly older *Eurydesma* record compared with those from South America and Western Australia.

In western Australia (eastern Gondwana), the *Eurydesma* fauna was recorded throughout the upper part of the glacial-related Lyons Group and the postglacial Carrandibby Formation (still with scattered glacial erratics: Mory and Haig, 2011), Carnarvon Basin, Western Australia. The age of this interval bearing the *Eurydesma* fauna is constrained by superpositional locations below the ammonoid *Juresanites jacksoni* (Etheridge, 1907) and *Uraloceras irwinense* (Teichert and Glenister, 1952) occurrences that are estimated to be late Sakmarian in age (Leonova, 1999, 2011; Archbold, 1999, 2001; Haig et al., 2014). The well-established transitional stratigraphic relationship (Hocking, 1990; Crostella, 1995; Mory and Backhouse, 1997; Mory et al., 2008) between the Carrandibby Formation (Byro Subbasin), bearing the uppermost *Eurydesma* occurrences, and the Callytharra Formation, with a relatively diversified fauna and incoming elements with Tethyan affinities (Dickins and Thomas, 1959), reinforces the above-suggested

diachronic condition with this youngest *Eurydesma* record and that from the Hardap shale Member in Namibia. Archbold (1993) proposed two brachiopod biozones characterizing the upper Lyons Group and Carrandibby Formation (formerly Stage A of Dickins, 1963, nearly 1500 m thick; Skwarko, 1993), referred to as the *Lyonia lyoni* and *Neilotreta occidentalis* (formerly *Trigonotreta occidentalis*; see Waterhouse, 2008; Taboada et al., 2015) zones. The *Lyonia lyoni* Zone grouped fossil localities from low and middle stratigraphic records of the Lyons Group. It is characterized by the brachiopods *Rhynchopora australassica* Archbold, 1995 (Rhynchonellacea gen. Indet. Dickins and Thomas, 1959; see also Archbold and Hogeboom, 2000), *Kiangsiella* sp. Thomas, 1958 (=*Kiangsiella* Dickins and Thomas, 1959), *Tomiopsis notoplicatus* Archbold and Thomas, 1986, *Punctocyrtella australis* (Thomas, 1971) (=*Pseudosyrinx* sp. Dickins and Thomas, 1959), *Trigonotreta lyonsensis* Archbold and Thomas, 1986 (=*Neospirifer* sp. and *Neospirifer* sp. Dickins and Thomas, 1959; see also Angiolini et al., 2005, 2009) and the bivalve *Deltopecten lyonsensis* Dickins, 1957 (see also Skwarko, 1993). The top of the *Lyonia lyoni* Zone was defined by the incoming of *Neilotreta occidentalis* and *Eurydesma playfordi* Dickins, 1957 (Archbold, 1993), although the exact stratigraphic position of their incoming is unknown (localities ML105-ML110 and T23-T27 in the upper part of the Lyons Group in the Lyndon River area: Dickins and Thomas, 1959). Most of the species (*Lyonia lyoni*, *Punctocyrtella australis*, *Trigonotreta lyonsensis*, *Tomiopsis notoplicatus* and *Deltopecten lyonsensis*) that were first recognized in the preceding biozone persist throughout the *Neilotreta occidentalis* Zone (Dickins, 1957; Dickins and Thomas, 1959; Archbold, 1993; Skwarko, 1993). Furthermore, numerous bivalves and gastropods are added in this biozone, such as *Schizodus crespinae* Dickins, 1957, *Astartila condoni* Dickins, 1957, *Peruvispira umariensis* (Reed, 1928), *Keenia carnarvonensis* Dickins, 1957, *Mourlonia* (*Mourlonia*) *lyndonensis* Dickins, 1957, *Stutchburia variabilis* Dickins, 1957, *Phestia lyonsensis* (Dickins, 1956), *Aviculopecten tenuicollis* (Dana, 1847), *Astartilla? oscura* Dickins, 1957, *Pachymyonia occidentalis* Dickins, 1957, *Praeundulomya elongata* Dickins, 1957, *Leiopteria? carrandibbiensis* Dickins, 1957, *Chaenomya? nuraensis* Dickins, 1963 and *Phestia darwini* (Koninck, 1877), among others (Dickins, 1956, 1957, 1963). This diversity of mollusks, specially bivalves, typifies the upper section of the *Neilotreta occidentalis* Zone as well as the younger terms of the *Eurydesma* fauna in Western Australia. An early Sakmarian or more likely an earliest Sakmarian age is here reinforced to the uppermost section of the Lyons Group and Carrandibby Formation, while an Asselian age can be expected for the lower faunal record in the *Lyonia lyoni* Zone, as indicated previously

by various authors (Dickins, 1957, 1963; Dickins and Thomas, 1959; Archbold, 1993; Stephenson, 2009; Taboada et al., 2015). Although a lower *Eurydesma* record is lacking within the *Lyonia lyoni* Zone, it can be expected.

4.2.1. The age of the long-lived Eurydesma fauna

The age of the whole *Eurydesma* fauna probably spans the earliest Asselian–Kungurian, but its older interglacial (SW Africa) or postglacial occurrences (South America and Western Australia towards the Cimmerian region) typified a mainly early Asselian–early Gondwana-wide transgression by a major postglacial eustatic rise in sea-level (Dickins and Thomas, 1959; Dickins, 1997), leading to the collapse of the mains Gondwana Ice Sheets (Veevers and Powell, 1987). Although only a transient retraction of the subpolar ice caps would be expected, (a) Sakmarian–Artinskian glacial-related horizon in South Africa, (b) striated lonestones in the lower Permian coal measures in Victoria Land, Antarctica, (c) ice-rafted debris and diamictites in eastern Australia and Tasmania (Isbell et al., 2013; and references therein), and (d) diamictites and ice-rafted debris in Patagonia are observed.

This early Permian *Eurydesma* transgression is well documented in Western Gondwana through the Bonete (Sauce Grande-Colorado Basin) and Taciba (Paraná Basin) formations in SE South America and the Hardap shale Member (Aranos Basin) in SW Africa, while in NE Gondwana, it is represented in the upper Lyons Group/Carrandibby Formation (Carnarvon Basin and correlatable units of neighboring basins) as well as peninsular India and beyond, toward the Cimmerian region (Dickins and Thomas, 1959; Archbold, 1998, 2000; among others). Moreover, *Eurydesma* developed successfully in eastern Australia, SE Gondwana, until Kungurian times due to persistent cold paleoclimatic conditions (Dickins, 1978).

4.3. The faunas preceding the Eurydesma fauna: the Lontras shale assemblage and correlatives

On the eastern border of the Paraná Basin, the diamictite interval (Chapéu do Sol Member by França and Potter, 1988) underlying the *Eurydesma* fauna covers the upper part of the Campo Mourão Formation or Lontras shale (Weinschutz and Castro, 2006). The >100 m-thick Lontras shale (Andrade, 2010) consists of thin varved shales with dropstones overlain by bioturbated siltstones, fossiliferous black shales with abundant concretions and shaly rhythmites at the top (Hamel, 2005). It yields a rich fossil metric interval (Campáleo outcrop) of immense significance for establishing a relative age constrained below the *Eurydesma* fauna. The main fossils consist of sponges, actinopterygian fishes, bivalves, coelacanth scales, coprolites, conodonts, brachiopods, insects, scolecodonts, shark teeth, and fragments of wood (Mouro et al., 2014; and references provided therein). Wilner (2014) assigned the conodont remains to *Mesogondelella* spp., a cold-water tolerant genus (Kozur, 1998; Henderson and Mei, 2000) that is also present in younger strata of the Canning Basin in Western Australia (Nicoll and Metcalfe, 1998; Haig et al., 2014). Although purely speculative at this time, a possible link to the short-lived warming spike thermal event reported from the latest Carboniferous in high paleolatitudes of Siberia and Gondwanic deposits of Timor should be investigated (Davydov et al., 2013; Davydov and Biakov, 2015). Among the fossil remains of the Lontras shale, the sponge *Microhemidiscia greinerti* Mouro et al. (2014) is of particular biochronological significance; this species is comparable to *Microhemidiscia ortmanni* Kling and Reif, 1969 from the San Gregorio Formation, southern Paraná Basin, Uruguay (Mouro et al., 2014). Based on Holz et al. (2010), these authors assigned an Asselian–Sakmarian age to the fossil assemblages of the Lontras shale, although these authors mixed the paleontological contents of the Lontras shale and the Taciba Formation, where the latter unit bears the *Eurydesma* fauna and provides the reason for this age. A preliminary revision of brachiopods from the Lontras shale indicates the presence of *Biconvexiella* sp., *Quinquenella* sp. and *Langella imbituvensis*, which are taxa that are also

recorded in the Taciba Formation; thus, a faunal affinity can be appreciated. Nevertheless, a record of the sponge *Microhemidiscia* in the San Gregorio Formation as well, among other fossil remains (summarized in Sprechmann et al., 2001) from shales of a marine intercalation between glacial deposits, suggests that its biocorrelation is more likely.

Furthermore, a probable counterpart of the Lontras shale/San Gregorio Formation is the Ganigobis shale Member of the Dwyka Group (Aranos Basin) in Namibia, southwest Africa (see also Werner, 2006). The 45 m-thick, black dropstone-bearing to dropstone-free Ganigobis shale also yields a diverse fauna (mostly non described) of bivalves, fishes, asteroideans, gastropods, brachiopods, sponges, echinoids, crinoids, foraminifera, radiolaria, and cephalopods (Stollhofen et al., 2000, and references provided therein). Tuffs interbedded in the Ganigobis shale Member dated via SHRIMP reveal ages of 302.3 ± 2.1 Ma, 302.0 ± 3.0 and 299.5 ± 3.1 Ma (Stollhofen et al., 2008), corresponding to the latest Gzhelian, close to the Carboniferous-Permian boundary. These ages coupled with the faunal assemblages from the Ganigobis shale Member as well as the Lontras shale constrain the younger *Eurydesma* fauna to post-Gzhelian times.

5. The paleobiogeographic scenario of the W–E trans-Gondwana transient marine connection

The western-eastern Gondwana *Eurydesma* faunas collectively exhibit Indoralian Paratinan/Westralian/Austrazean paleobiogeographical links (Archbold, 1983a, Shi and Archbold, 1993), as previously documented and reinforced herein based on new common taxa. Faunal exchange through shallow marine seaways between these regions (Dickins and Thomas, 1959; Shi and Archbold, 1993; Archbold et al., 1996) would have been possible, favored by a major glacio-eustatic sea-level rise (Dickins, 1997). Estimates of the magnitude of glacioeustasy during the late Paleozoic can vary sharply, although an average variation in sea level of ~120 m was suggested for the late Pennsylvanian–mid-Sakmarian span (Isbell et al., 2003; Rygel et al., 2008; Shi and Waterhouse, 2010), and a maximum fluctuation of 250 m could have occurred (Bates and Lyons, 2006). Within the Itararé Group, a 100 m sea-level fluctuation was documented in the so-called Lapa Sandstone in the southern Paraná Basin. The Lapa Sandstone has been interpreted as a channel-lobe system within a huge incised valley excavated during a sea-level lowstand at the end of the Carboniferous that was filled by sands from glacial outwashing during subsequent transgression (França et al., 1996; Holz et al., 2008). Nevertheless, even twice or three times this sea-level rise would appear to be insufficient to surpass thousands of kilometers of continental barriers (the landmass of Africa-India-Antarctica-Western Australia) intervening between the western and eastern Gondwana shorelines. An alternative mechanism must be coupled with the sea-level rise that allowed the *Eurydesma* fauna to be carried across the shallow seas of both the western and eastern sides of Gondwana.

It has been suggested a V-shaped proto-rift system through two major axes of extensional basin development formed via a north-northwesterly trending axis paralleling the future South Atlantic and a broadly north-northeasterly trending line of separation related to the future Indian Ocean (Stollhofen et al., 2000, 2008) (see Fig. 7). Alongside the former axis, the Sauce Grande-Colorado Basin was located westward and the de Aranos Basin northeastward. In the middle, the recently characterized offshore Hesperides Basin connecting northward to the Paraná Basin and southward to the Kalahari and Karoo basins, among others, in a huge depositional area of near 3.000.000 km², with a Pennsylvanian–Triassic pile of up 7000 m in thickness (Pángaro and Ramos, 2015). Within this pile, facies of the *Eurydesma* transgression was seismically identified where the unconformity's amplitude reached minimum values, based on data from Argentinean offshore wells, extending southward until the Karro Basin (Pángaro and Ramos, 2015). The second axis coincides more closely with a tight continental fit between east Africa-India-west Antarctica-west Australia, with an
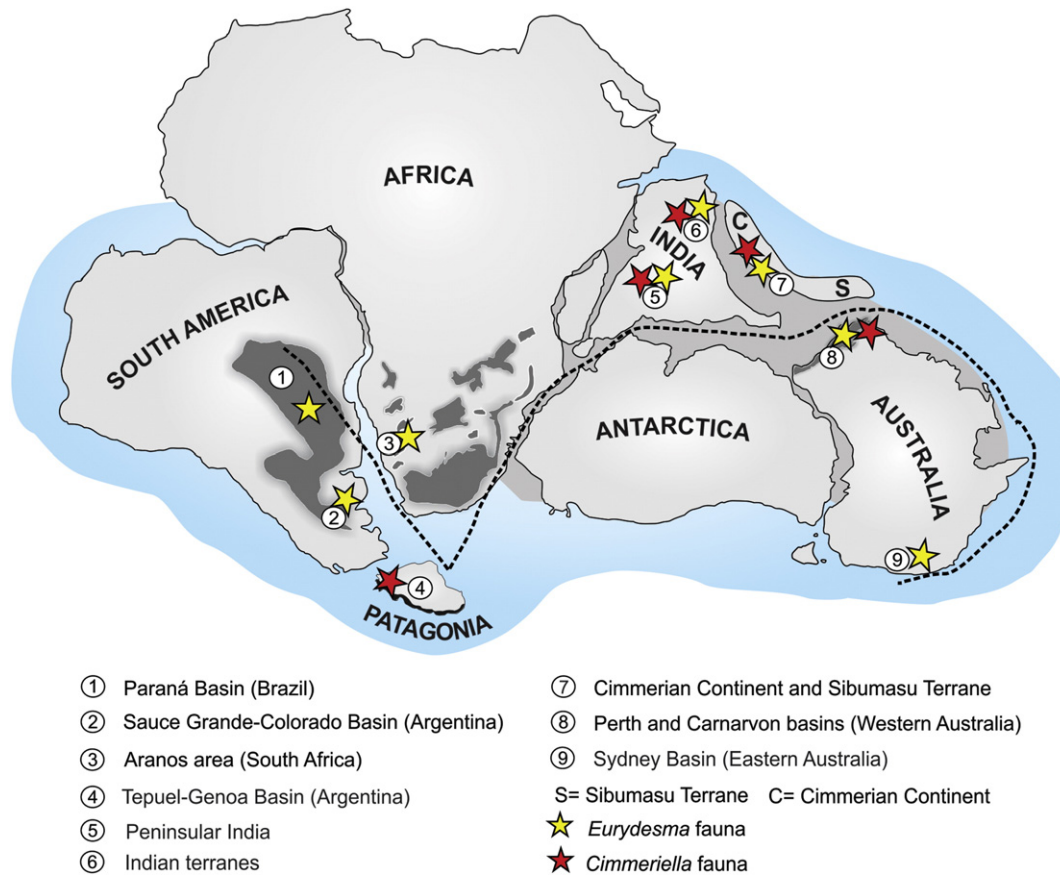
Fig. 7. Paleogeographic map showing the W–E transgondwanan marine connection. A V proto-rift system through two major axes of extensional basin development is suggested, formed by a north-northwesterly trending axis paralleling the future South Atlantic and a broadly north-northeasterly trending line of separation related to the future Indian Ocean.

accommodation zone consisting of a wide intracontinental rift that extended from Australia's Northwest Shelf, between India and Antarctica, to southern Africa (Harrowfield et al., 2005). This rift was compartmentalized over a length scale of ~650 km, corresponding to accommodation zones, margin-normal geophysical lineaments, and long-lived crustal weaknesses, collecting Gondwana's thick Permian–Triassic sedimentary deposits (Harrowfield et al., 2005), in a similar manner to the Hesperides Basin. The *Eurydesma* transgression would have progressed throughout this proto-rift system through a long narrow shallow seaway, allowing faunal exchange between east and west Gondwana. The vertex of this V-shaped proto-rift system and the seaway passage of the *Eurydesma* transgression would have been located between the South Africa-Malvinas/Falklands-Agulhas plateau and the Antarctic detached southern Patagonia (Deseado Massif) (Ramos and

Naipauer, 2014) before its collision with South Africa (Lindeque et al., 2011) and the pre-drifted Ellsworth mountain terrane (Elliot et al., 2014).

Central-eastern Peninsular India subsidiary linear rift basins, such as the Koel-Damodar, Son-Mahanadi, Pranhita-Godavari and Satpura basins (Casshyap and Tewari, 1987; Wopfner and Casshyap, 1997; Ghosh, 2003), to the eastern branch of the main proto-rift system would document the marine incursion of the *Eurydesma* transgression through this via. This Carboniferous-Permian intracontinental rift system continues northeastward to western Australia including the Perth, Carnarvon and Canning basins (Biswas, 1999; Cawood and Nemchin, 2000; Harrowfield et al., 2005), where early Permian marine faunas, particularly the *Eurydesma-Lyonia* fauna, occur profusely. As was mentioned above, the *Eurydesma-Lyonia* faunal affinities extend

Plate II. *Lyonia rochacamposi* sp. nov. A: holotype CP.I 769 I, composed mold in ventral view; B: CP. E 4396B, ventral valve exterior; C: CP.E 536, ventral valve exterior; D: detail of CP.I 769 I, showing hinge spines (arrow); E: paratype DZP 18913, mold exterior of dorsal valve, showing genicule (compressed) and minute hollows of dorsal spines; F: DZP 18906, ventral valve exterior; G: paratype DZP 19133B, dorsal valve interior, showing medium septum; H: CP.I 765, fragment ventral valve exterior; I: paratype CP.I 763, mold exterior of dorsal valve, showing minute hollows of dorsal spines; J: CP.I 755 II, composed mold in ventral view; K: CP.I 754, composed mold in ventral view; L: paratype CP.I 5011, dorsal valve interior, showing impression of cardinal process (arrow) and decorticate vestige of median septum; M: CP.I 2156, mold exterior of dorsal valve; N: CP.I 769 II, detail ornamentation of ventral valve; O: CP. I 753, detail ornamentation of ventral valve. Scale bar = 10 mm.

Plate III. A:? *Streptorhynchus* sp., DGM 4355, dorsal valve exterior; B–C: *Tomiopsis* sp. cf. *T. harringtoni* (Harrington), GP/1E 4364; B: ventral valve internal mould; C: detail of adminicula and muscle field; D–L: *Quinquenella rionegrensis* (Oliveira); D: GP/1E 4339a, external mold of ventral valve; E: cast of D; F: GP/1E 2056, dorsal valve interior; G: GP/1E 4339b, external mold of dorsal valve; H: cast of G; I: Missing sample of the IGc/USP; J: GP/1E 4402, external mold of ventral valve; K: cast of J; L: DZP 19139, dorsal valve internal mold; M: *Langella imbituvensis* (Oliveira), GP/1E 4439, dorsal valve external mold; N–P:? *Cyrtella* sp.; DZP 18829B, N, dorsal valve external mold; O, dorsal valve exterior; P, fragmentary ventral valve. Scale bar of A–H, N–P = 10 mm; scale bar J-M = 5 mm. (see on page 444)

Plate IV. A-J: *Biconvexiella roxoi* (Oliveira); A: GP/1E 4367, ventral valve view; B: GP/1E 4437, butterflied ventral and dorsal internal molds; C: GP/1E 4373, butterflied ventral and dorsal internal molds; D: cast of A; E: butterflied ventral and dorsal casts of B; F: dorsal valve cast of C; G: lateral view of B; H–I: CP.E 7669, specimen of the Mafra Formation (Itararé Group), in the State of Santa Catarina, H: ventral valve internal mold, I: dorsal valve internal mold; J: GP/1E 4339, dorsal valve internal mold, specimen of the Capivari Formation (Itararé Group), in the State of São Paulo; K–M: *Crurithyris* sp. (formerly *Crurithyris roxoi* (Oliveira, 1936) Amos, 1958); K: LIEB-PI 417, latex mold of an articulate specimen in dorsal view; L: LIEB-PI 418, ventral valve internal mold; M: LIEB-PI 419, dorsal valve internal mold. Scale bar of A–F, H–M = 10 mm, scale bar of G = 5 mm. (see on page 445)
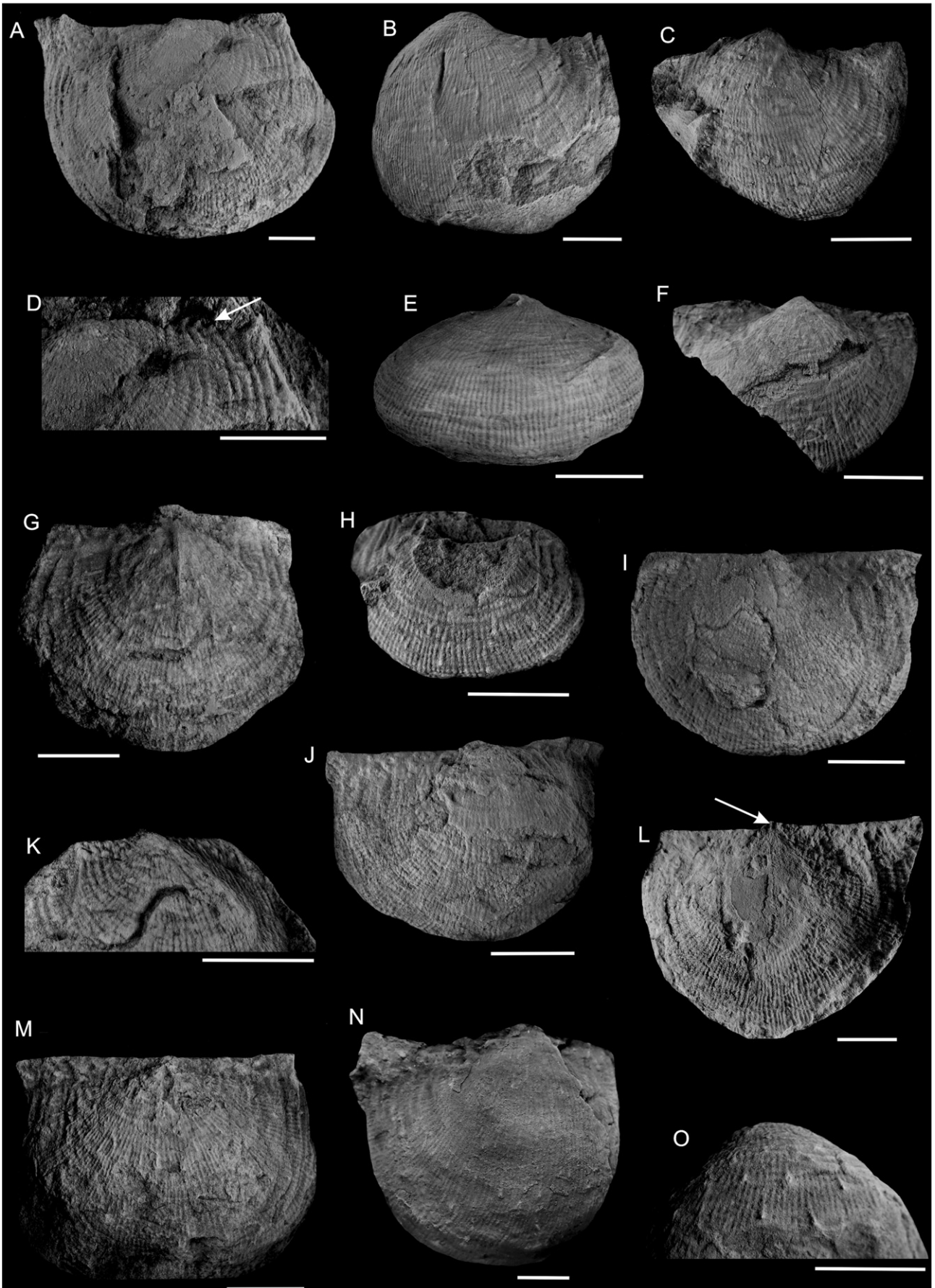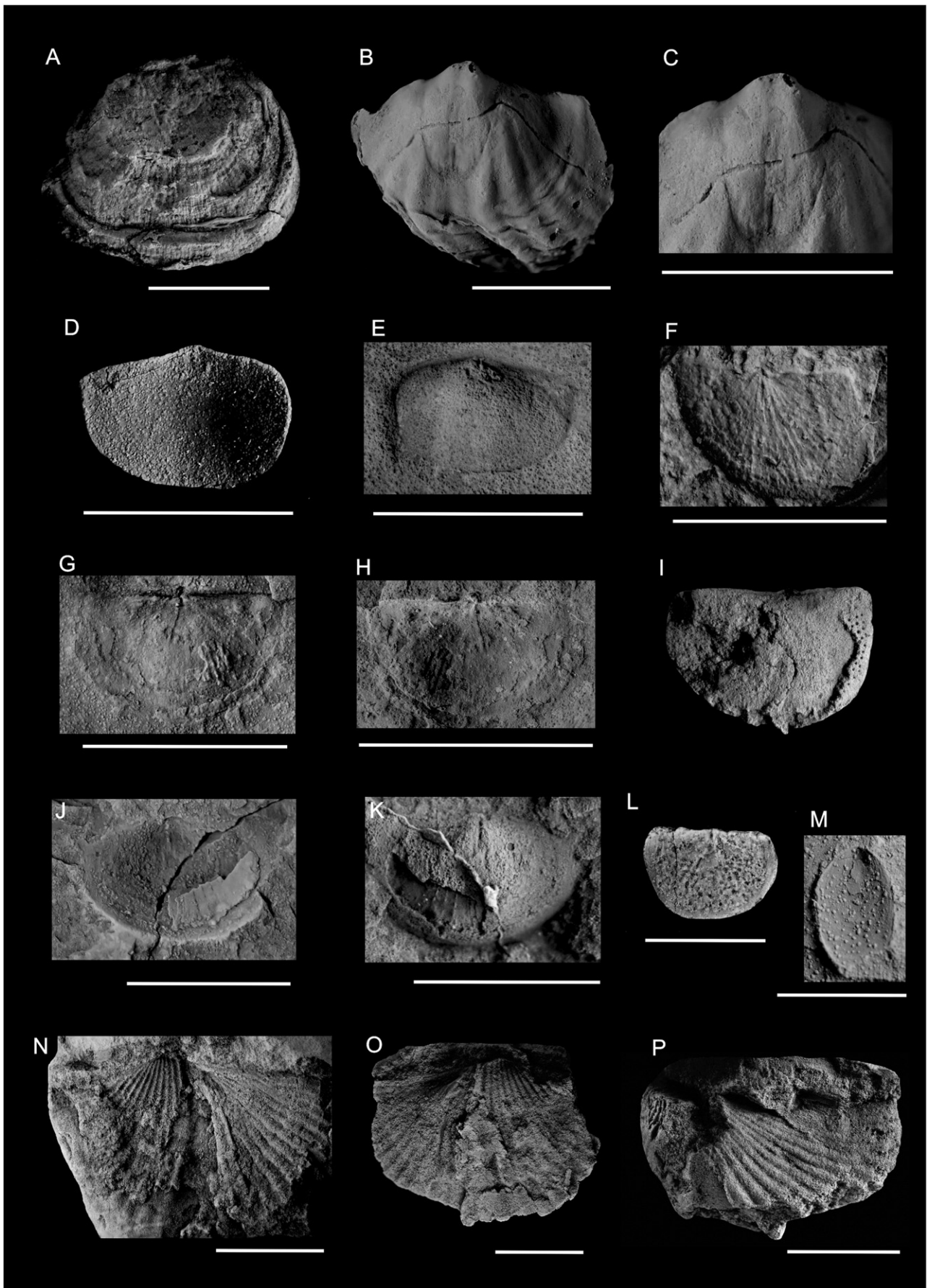
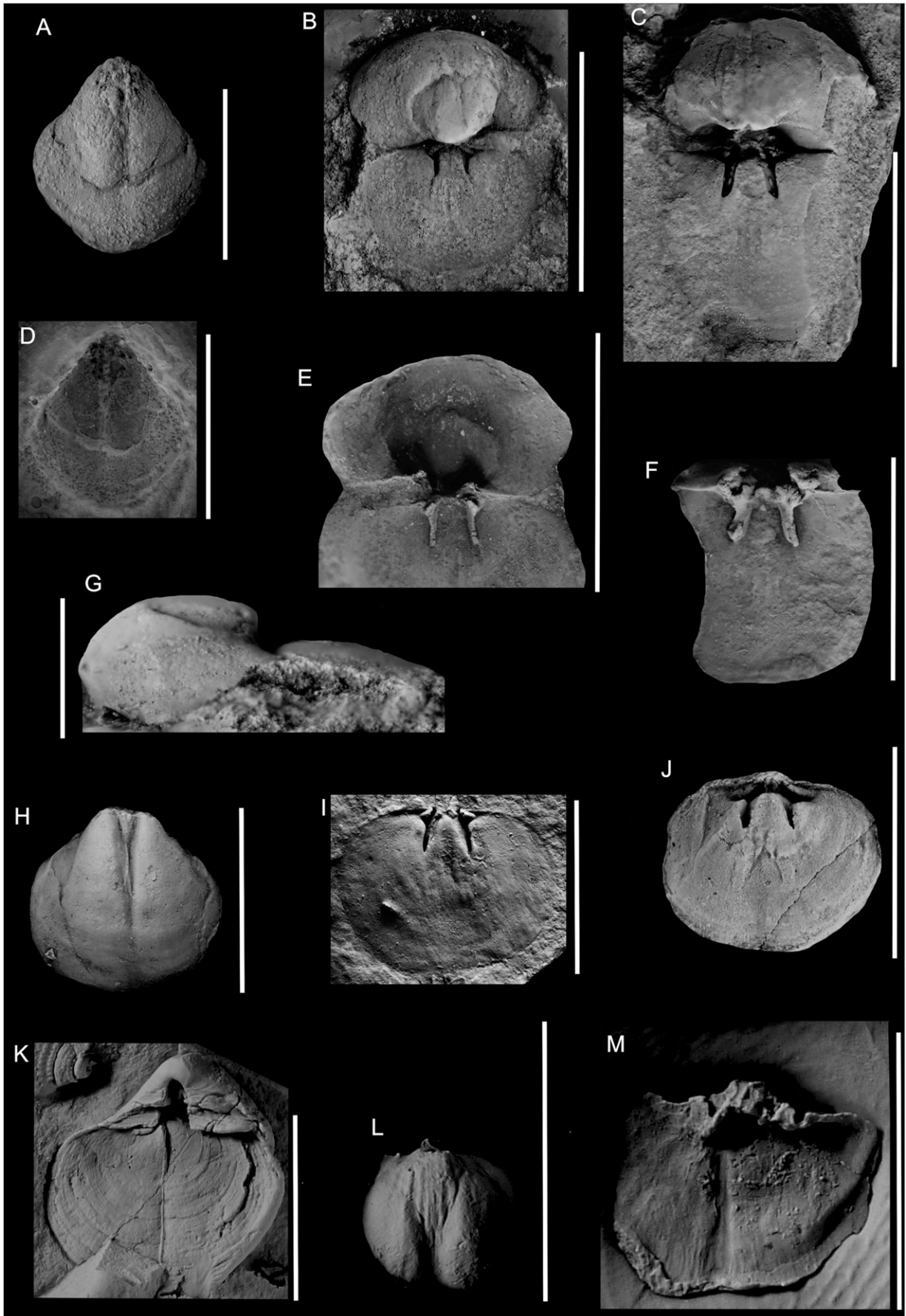**Plate II.**

Plate III (*caption on page 442*).

Plate IV (*caption on page 442*).

the transgondwanan marine connection to geographical areas that were adjacent or close to western Australia- Peninsular India during Asselian–early Sakmarian times. During this time interval, a narrow and elongate continental assembled microcontinents grouped into the Cimmerian Continent (Sengör, 1979) was close to northern Gondwana (Fig. 7). The Cimmerian Continent was composed of small pieces of continental fragments distributed from present-day Turkey to Sumatra through Transcaucasia, Central Iran, South Afghanistan, South Pamir, Karakoram, Tibet, West Yunnan, the Shan State of Burma, western and Peninsular Thailand, and western Peninsular Malaysia (Sengör, 1979, 1984; Metcalfe, 1996, 1999, 2002; Ueno, 2003; Angiolini et al., 2013; Zhang et al., 2013). Close Gondwana faunal affinities based on brachiopods from some blocks of the Cimmerian Continent such as the Sibumasu terrane, as well as others from independent blocks such as Lhasa, Bijni tectonic unit, south and central Tibet ("Himalayan terranes"), and Peninsular India and Carnarvon Basin, among others, allowed recognize the Indolarian faunal province by Shi and Archbold (1993, 1996) (see also Shen et al., 2013). The Indolarian faunal province was possibly over 50°-60° S, as indicated by low taxonomy diversity, a characteristic coldwater bivalve fauna (*Eurydesma* and *Deltopecten*, among others), and glacial deposits. Furthermore, Shi and Archbold (1993) anticipated the assignation of the *Eurydesma* fauna from the Paraná (Brazil) and Sauce Grande basins (Argentina) within the Indolarian province. The central-eastern Indolarian fauna (Asselian–early Sakmarian) characterized the domain of the Khsir Sagar sea, limited northward by the eastern Cimmerian Continent (Sibumasu block), westward by the Paleotethys ocean and stretching southward to Peninsular India (Kapoor and Maheshwari, 1991; see also Kapoor et al., 1992 and Dickins, 2000) and western Gondwana through the narrow rift-system net. The Khsir Sagar sea domain expanded with the incoming of the *Cimmeriella* fauna (formerly *Stepanoviella* or *Globiella* faunas) during the late Sakmarian (Kapoor and Maheshwari, 1991). This expansion linked to a widespread record of the brachiopod *Cimmeriella*, being recognized in Western Australia, India and the Cimmerian Continent, sometimes coupled with the *Eurydesma* fauna. This fauna was interpreted as evidence of a cold-temperate faunal association linked to a general trend towards paleoclimatic amelioration (Waterhouse, 1970; Archbold et al., 1993; Dickins et al., 1993; Shi and Archbold, 1993, 1996). A complete analysis of Gondwanan, early Permian correlations of this time interval was offered by Archbold (2000, 2001, 2002) and Foster and Archbold (2001). The *Cimmeriella* fauna recognized in the Mojón de Hierro Formation in southern Patagonia, among others common brachiopod genera with eastern Gondwana such *Neilotreta*, *Arctictreta*, *Quinquenella*, *Spirelhyta* and *Neochonetes* (Taboada and Pagani, 2010; Pagani and Taboada, 2011) reinforced the transgondwanan marine connection throughout the proto V-shaped rift system transient (Asseliann-Sakmarian) marine corridor, connecting the eastern Khisr Sagar and western Terra Australis seas (Taboada et al., 2013). The Khsir Sagar sea end (Kapoor and Maheshwari, 1991) or would became in the Meso-Tethys ocean (Metcalfe, 1995, 2009), after rifting and northward drifting of the Cimmerian Continent and associated Terranes, now stretching from the Middle East to Southeast Asia, before have consumed the Paleotethys ocean (Sengör, 1979).

The Indolarian/Austrazean faunal province was recognized in eastern Australia (Shi and Archbold, 1993; Shen et al., 2013; Cisterna and Shi, 2014) where a number of brachiopods (*Nambuccalinus*, *Tomiopsis*, *Biconvexiella*, *Quinquenella*, *Trigonotreta*) and bivalves genera (*Eurydesma*, *Deltopecten*) possibly migrated or evolved from western Australia-India-Cimmerian Continent, including the faunal imput from western Gondwana trough the W–E trans-gondwanan connection (see also Waterhouse, 2011). Conversely, a reverse migration pattern from eastern to western Gondwana appeared to be documented by the *Cimmeriella* fauna in southern Patagonia.

6. Conclusions

The biocorrelation of the marine invertebrate fauna recorded in the post-glacial succession of the uppermost portion of the Late Paleozoic Itararé Group (Taciba Formation), Paraná Basin, Brazil, is firmly constrained with other well-dated Gondwanan assemblages, and a latest Asselian–early Sakmarian age is suggested. Seven species were identified and illustrated: *Lyonia rochacamposi* sp. nov. (Butiá assemblage), *Langella imbituvensis* (Oliveira),? *Streptorhynchus* sp.,? *Cyrtella* sp., *Tomiopsis* sp. cf. *T. harringtoni* Archbold and Thomas, *Quinquenella rionegrensis* (Oliveira) and *Biconvexiella roxoi* Oliveira (Teixeira Soares assemblages).

The presence of *Tomiopsis* sp. cf. *T. harringtoni* and the bivalve *Atomodesma* (*Aphanaia*) *orbirugata* in the Teixeira Soares beds and the associated bivalves *Myonia argentinensis* and *Heteropecten paranaensis*, both recorded in deposits at Teixeira Soares and Mafra (Butiá), suggest a biocorrelation with the *Eurydesma* fauna from the Bonete Formation, Sauce Grande-Colorado Basin, Argentina. The *Myonia argentinensis-Atomodesma* (*Aphanaia*) *orbirugata-Heteropectenparanaensis* association (MAH) assemblage is proposed here to recognize a regional stratigraphic interval, or Subzone, within the Biozone of *Eurydesma*. The MAH interbasinal assemblage is recorded in the Sauce Grande and Paraná basins, including faunas of the Capivari Formation, northernmost Paraná Basin.

The faunal assemblages of the Lontras and its correlatives, coupled with radiometric ages from the Ganigobis shale Member, constrain the younger *Eurydesma* fauna to post-Gzhelian times.

A V-shaped proto-rift system through two major axes of extensional basin development, formed by a north-northwesterly trending axis paralleling the future South Atlantic and a broadly north-northeasterly trending line of separation related to the future Indian Ocean, coupled with a sea-level rise of at least 100 m, favored the establishment of a long narrow shallow seaway allowing faunal exchange between eastern and western Gondwana.

A general W–E Gondwanan *Eurydesma-Lyonia* faunal migration pattern trend is suggested during Asselian–early Sakmarian times but reversed in the late Sakmarian with the incoming of the *Cimmeriella* fauna in southern Patagonia.

Appendix A. Systematic paleontology

Phylum Brachiopoda Duméril, 1806
Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Linoproductidina Waterhouse, 2013
Superfamily Proboscidelloidea Muir-Wood & Cooper, 1960
Family Auriculispinidae Waterhouse, 1986
Subfamily Lyoniinae Waterhouse, 2001
Tribe Lyoniini Waterhouse, 2001
Genus *Lyonia* Archbold, 1983b

Type species: *Linoproductus* (*Cancrinella*) *cancriniformis* var. *lyoni* Prendergast, 1943, from Lyons Group (Lower Permian), Carnarvon Basin, Western Australia.

Discussion: Closer genera to *Lyonia* are *Nambuccalinus* Waterhouse, 2001 and *Bandoproductus* Jin and Sun, 1981. When compared to *Nambuccalinus* (type species *Lyonia bourkei* Briggs, 1998) *Lyonia* has only one row of cardinal spines, far fewer dorsal spines, and numerous pits over the dorsal exterior (Briggs, 1998; Waterhouse, 2001). *Lyonia* differs from *Bandoproductus* by the presence of dorsal spines, lower cardinal process and longer median septum (Archbold, 1983b).

Lyonia rochacamposi sp. nov.
Plate II, Figs. A–O
1969 *Cancrinella* sp. Rocha Campos, p. 105, pl. X, figs. 1-5, 8.
1969 *Linoproductus* sp. Rocha Campos, p. 106, pl. X, figs. 6-7.

Material: One hundred seven specimens among internal and external moulds of ventral and dorsal valves. Holotype: CP.I 769 I. Paratypes: CP.I 763, 5011, DZP 18913, 19133B. Other material: CP.I 750-757, 759–760, 762, 764–767, 769 II, 781, 2153–2158, 2162; CP.E 536, 3682–3697, 4392–4396 A and B, 5003–5009, 5014–5015; DZP 18821, 18,885–18,896, 18,898-18903a and b, 18,904–18,907, 18,909–18,917, 18,969–18,977, 18,981–18,983; 18,913, 19,133 A.

Locality, unit and age: Fossil site 3, Pedreira (Quarry) Butiá, Bela Vista do Sul district, Mafra County, state of Santa Catarina State, Brazil. Butiá siltstone, uppermost portion of the Taciba Formation, Paraná Basin. Latest Asselian–earliest Sakmarian.

Etymology: In honor of its discoverer and outstanding Brazilian paleontologist and geologist Antonio Carlos Rocha-Campos, Institute of Geosciences, University of São Paulo.

Diagnosis: Average-sized *Lyonia*, subelliptical transverse outline and gently concave-moderate convex profile. Maximum ventral valve width equal or close to hinge line, with maximum dimensions up to 50 mm width, 40 mm length, and width/length ratio between 1.13/1.25. Ornamentation of fine radial costellae (8–12/5 mm on the venter) and ventral spine bases in roughly quincuncial to uneven arrangement. Dorsal valve flat to gently concave with strong genicule. Geniculation beginning at 50° angle and reaching up 100° toward end of short trail. Thin median septum half of valve length.

Description: Average-sized *Lyonia*, subelliptical transverse outline and gently concave-moderate convex profile. Maximum ventral valve width equal or close to hinge line, with maximum dimensions up to 50 mm wide, 32 mm long, and width/length ratio between 1.30/1.56. Ventral valve moderate convex to subglobose, with largeflatten ears (rarely preserved), cardinal ends at right angles and not distinct trail. Ornamentation of fine radial costellae (the number of costellae per milimeter varies between 8 and 12 but most specimens have 9–10 costellae per 5 mm on the venter), weak rugae on venter slightly stronger on ears. Costellae number increasing by splitting into two ribs anteriorly from a slightly swollen minute spine bases in roughly quincuncial to uneven arrangement. A single row of spines, coarser than those on the venter on hinge line, occasionally with one or two extra hinge spines (not a second row), although this character is not well preserved. Internal ornament reflects external ornament being other internal characters imperceptibles.

Dorsal valve flat to gently concave with strong genicule. Geniculation beginning at 50° angle and reaching up 100° toward end ofshort trail. Rugae and costellae similar to ventral valve, slightly elongate small dimples variably arranged and minute erect spines scattered anteriorly half of dorsal valve length, more densely grouped toward genicule.Thin median septum half of valve length. Cardinal process small and bilobed, subelliptical outline (not well preserved) apparently without continuity with the median septum. Internal ornament reflects external ornament.

Discussion: The studied specimens exhibit moderately large size, gently concave-convex profile, transverse outline, large flattened ears, single row of hinge spines, distinct costellae, ventral and dorsal spines, and thin long dorsal median septum, allowing its assignment to *Lyonia* Archbold, 1983b. The type species *Lyonia lyoni* (Prendergast, 1943) from the Lyons Group (Early Permian), Carnarvon Basin, Western Australia (Archbold, 1983b; Skwarko, 1993; Waterhouse, 2011) resembles *Lyonia rochacamposi* sp. nov. in morphology, ornamentation and internal characters. Nevertheless, the Brazilian species is more transverse, has finer costellae and exhibit stronger geniculation at higher angle. Other overseas species assigned to *Lyonia* such as *L. lyoni* by Lapparent et al. (1971), early Permian of Afghanistan, and *L.* sp. by Angiolini (1995), early Permian of Pakistan, lack both dorsal valves preventing detailed comparisons. *Lyonia rochamposi* sp. nov. was originally described (but not published) as *Cancrinella* sp. by Rocha Campos (1969), a tentative assignation based on limited (6) topotypic ventral valves. Rocha Campos' specimens share all ventral valve diagnostic features of *Lyonia rochacamposi* sp. nov. Likewise, *Linoproductus* sp. of Rocha Campos (1969) grouped two compressed less spinous specimens from the same type locality (fossil site 3, Butiá quarry) which are interpreted representing intraspecific variations and included here in *Lyonia rochacamposi* sp. nov.

Order Orthotetida Waagen, 1884
Suborder Orthotetidina Waagen, 1884
Superfamily Orthotetoidea Waagen, 1884
Family Schichertellidae Williams, 1953
Subfamily Steptorhynchinae Stehli, 1954
Genus *Streptorhynchus* King, 1850
Type species: *Terebratulites pelargonatus* Schlotheim, 1816, from the Middle Permian of Gera, Germany.

?*Streptorhynchus* sp.
Plate III, Fig. A
Locality, unit and age: Fossil site 2, Texeira Soares County, state of Paraná, Brazil. Baitaca siltstone, uppermost portion of the Taciba Formation. Latest Asselian–earliest Sakmarian.

Comments: One illustrated exterior of dorsal valve (DGM 4355) suggests the presence of *Streptorhynchus* or and allied genus in the Taciba Formation. It is gently convex of subquadrate outline, 17 mm width and 14.5 mm length, with its maximum width at 2/3 of valve length. Ornamentation of fine costellae (3/mm at the anterior margin), fine growth lines (6–7/mm) and few marked constrictions anteriorly. Rocha Campos (1969) indicated this same specimen evenly to *Streptorhynchus* or *Kiangsella* Grabau (in Chao, 1927). *Kiangsiella* exhibits stronger costellae or two order sizes although more marked in younger representatives of the genus (Angiolini et al., 2005). Scarcity and deficient preservation of available material do not allow an accurate generic identification. Previously, *Streptorhynchus* sp. was indicated (not described or published) by Beurlen (in Lange, 1954) for these same unit (formerly Teixeira Soares Formation in Lange, 1954).

Order Spiriferinida Cooper and Grant, 1976
Suborder Spiriferinidina Ivanova, 1972
Superfamily Syringothyridoidea Fredericks, 1926
Family Syringothyrididae Fredericks, 1926
Subfamily Permasyrinxinae Waterhouse, 1986
Genus *Cyrtella* Fredericks, 1924
Type species: *Cyrtia kulikiana* Fredericks, 1916, from Cisuralian of northern Russia, by original designation.

?*Cyrtella* sp.
Plate III, Figs. N-P
Material: Two internal molds of dorsal valves, one of them with its counterpart, one internal mold of a broken posteriorly ventral valve. DZP 18829B, DZP 19134.
Locality, unit and age: Fossil site 2, Texeira Soares County, state of Paraná, Brazil. Baitaca siltstone, uppermost portion of the Taciba Formation. Latest Asselian–earliest Sakmarian.

Comments: The material exhibits spiriferiform outline with estimated 34 mm width and 24 mm length with 1.41 W/L ratio, smooth sulcus, furrowed fold on posterior half –length and 10 simple rounded plica on each flank. It recalls *Cyrtella* Fredericks, 1927 or an allied genus, although without available interareas, interior features and microornamentation, generic assignation remains dubious.

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Martinoidea Waagen, 1883
Family Ingelarellidae Campbell, 1959
Subfamily Ingelarellinae Campbell, 1959
Genus *Tomiopsis* Benediktova, 1956
Type species: *Brachthyris kumpani* Yanishevskiy, 1935 from the Early Carboniferous of Kuznetsk Basin, Russia.

Tomiopsis sp. cf. *T. harringtoni* Archbold and Thomas, 1986
Plate III, Figs. B-C
Material: A single distorted mold of ventral valve interior, GP/1E 4364.
Locality, unit and age: Fossil site 2, Texeira Soares County, state of Paraná, Brazil. Baitaca siltstone, uppermost portion of the Taciba Formation. Latest Asselian–earliest Sakmarian.
Description: Small-sized *Tomiopsis* of rounded transverse outline, 15 mm width and 10 mm length (estimated), gently lamellose anteriorly. Umbo distinct, hinge length shorter than maximum width, which is located at two-thirds of valve length. Sulcus rounded, lateral slopes with 4 low rounded plicae less stronger posteriorly. Adminicula slightly divergent (≈15°) and gently curved enclosing a wide subelliptical muscle field with a thin shallow myophragm-like median septum anteriorly. Muscle scars indistinct.
Discussion: The specimen shares size, shape, number and nature of plicae with the closest species *Tomiopsis harringtoni* Archbold and Thomas, 1986 (= *Notospirifer darwini* (Morris) Harrington, 1955) (see also Amos, 1979) from the Bonete Formation (early Permian), Sauce Grande-Colorado Basin, Argentina. The Brazilian specimen exhibits adminicula slightly less diverging and a thin myophragm-like median septum when compared to *T. harringtoni*. These subtle differences and scarcity of material prevent its assignation to *T. harringtoni*. Other comparable species is *Tomiopsis notoplicatus* Archbold and Thomas, 1986 (see also Skwarko, 1993), from the Lyons Group and Carrandiby Formation (early Permian), particularly to the specimen CPC 24242 (from the lowest fossil-bearing horizon of Lyons Group), Carnarvon Basin, Western Australia. This oldest specimen of *T. notoplicatus* has weaker plicae such as those present in *Tomiopsis* sp. cf. *T. harringtoni*, although the former is distinguished by its straight and shorter adminicula. *Tomiopsis* sp. cf. *T. harringtoni* (Harrington) was previously assigned (unpublished) to *Notospirifer* sp. by Rocha Campos (1969) and compared with Argentine specimens assigned to *Notospirifer darwini* (Morris) by Harrington (1955), currently *Tomiopsis harringtoni* Archbold and Thomas, 1986.

Superfamily Ambocoelioidea George, 1931
Family Ambocoeliidae George, 1931
Subfamily Ambocoeliinae George, 1931
Genus *Biconvexiella* Waterhouse, 1983
Type species: *Attenuatella convexa* Armstrong, 1968, from the Tiverton Formation (early Permian), Bowen Basin, Queensland, Australia.

Biconvexiella roxoi (Oliveira, 1936)
Plate IV, Figs. A-G
1936 *Ambocoelia roxoi* Oliveira, p. 9–10, figs. 1-3
1952 *Crurithyris roxoi* (Oliveira, 1936), Lange, p. 86-88, pl. 1, figs. 4-5
1969 *Attenuatella roxoi* (Oliveira, 1936), Rocha Campos, p. 113-–114, pl. XI, figs. 16, 18

Material: Available topotypic material are one ventral valve internal mold labeled GP/1E 4367 (= DGP 3 666 in Rocha Campos, 1969).

Other material are two butterflied ventral and dorsal internal molds, GP/1E 4373 or RG9A (= URS 9 A in Rocha Campos, 1969) and GP/1E4437 (= P235 and "hypotype" of Lange, 1952). Others three ventral valve internal molds (not revised) are DGM E 378 (in Rocha Campos, 1969), DGM 3232 and 3233 (in Oliveira, 1936), this last one dessignated as holotype by Lange (1952).
Locality, unit and age: Fossil site 2 (Baitaca stream margins), Texeira Soares County, state of Paraná, Brazil. Baitaca siltstone (GP/1E 4373 or RG9A) and Passinho shale (GP/1E 4367, DGM E 378, DGM 3232-3233). Fossil site 1, Restinga (Imbituva), Texeira Soares County, state of Paraná, Brazil. Passinho shale (GP/1E 4437). Uppermost portion of the Taciba Formation. Latest Asselian–earliest Sakmarian.
Description: Average-sized *Biconvexiella* of plane-strong convex profile, subcircular anterior outline and broad convex posteriorly, subequal in width and length. Maximum width up 9 mm, maximum length up 11 mm with an W/L ratio varying between 0.73–0.82 and W/L average of 0.78, with slightly transverse dorsal valve (W/L average of 1.2) and hinge line shorter than maximum width which is located nearly valve midlenght. Ventral valve strongly convex with its stronger convexity in the umbonal region. Median sinus very shallow and narrow. Umbo rounded slightly incurved over hinge line not concealing the delthyrium. Umbonal angle of 75°. Interior of ventral valve with, in nearly 1 mm width, a well developed long (2/3 ventral valve length), narrow median adductor ridge bounded by two narrow elongate depressed diductor scars. Dorsal valve flat to slightly concave of subcircular to subelipticall transverse outline. Crural plates short, straight to slightly divergent. Small subrectangular (0.8 mm width, 2 mm length) posterior adductor scars separated by a short (2.5 mm lenght) thin median ridge. Anterior diductor scars not discernible. Cardinal process tuberculate.
Discussion: The material described here was originally referred to *Ambocoelia* Hall, 1860 (Oliveira, 1936), later to *Crurithyris* George, 1931 (Lange, 1952) and *Attenuatella* Stehli, 1954 (Rocha Campos, 1969, 1970), all of them with similar external spinose microornamentation. *Ambocoelia* is characterized by a hinge-line equal to its greatest width, a moderate to strong incurved umbo, a bifid cardinal process, and a dorsal musculature consisting of four equal-sized quadrate adductors (Hall, 1860; He et al., 2007; Zambito and Schemm-Gregory, 2013). The Brazilian specimens possess a slightly incurved umbo, the hinge-line shorter than maximum width and a minute tuberculate cardinal process, unlike *Ambocoelia*. *Crurithyris* is characterized by a subrounded to transversely ovate shell outline, a hinge-line shorter than maximum width, a moderately to strong incurved ventral umbo, a pair of centrally depressed ventral adductor scars bisected by a thin ridge or absent, a pair of laterally depressed diductor scars, which are separated from their adjacent adductor scars by ridges, and a pair of dorsal adductors scars bisected by a median ridge (George, 1931; Stehli, 1954; He et al., 2007, 2012). The Brazilian specimens although very close to *Crurithyris* have a more longitudinally elongate outline, a less incurved ventral umbo and a well-developed ventral median ridge. *Attenuatella* Stehli, 1954 is distinguished from the Brazilian specimens by its unique attenuated outline, a stronger convex ventral valve and umbo strongly incurved (up 180°) concealing the apical part of the delthyrium, as well as different arrangement and proportions of muscle scars (Stehli, 1954; Waterhouse, 1964; Landis and Waterhouse, 1966; Shi and Waterhouse, 1996; He et al., 2007, 2012). *Attenuatella convexa* Armstrong, 1968, type species of *Biconvenxiella* Waterhouse, 1983, shares with the Brazilian ambocoelids, shell shape, slightly incurved umbo, strong ventral median ridge supporting muscle scars and a dorsal thin median ridge separating adductors scars, that collectively allow consider to be both forms congeneric. *Biconvexiella convexa* (Armstrong) from the Tiverton Formation (Sakmarian), Bowen Basin, Queensland, Australia, also present in the Farley Formation, Sydney Basin, New South Wales, Australia (Armstrong and Telford, 1970), possess a gently convex dorsal valve and two pairs of adductors scars, being the posterior pair scars smaller than anterior pair scars (Shi and Waterhouse, 1996; He et al., 2007). These last both features

although lacking in the Brazilian specimens, which exhibit a flat dorsal valve and the anterior pair of adductor scars are not discernible, do not prevent its assignation to *Biconvexiella* Waterhouse, 1983. Furthermore, a flat dorsal valve was indicated to *Biconvexiella* aff. *B. elgae* (Besnossova in Besnossova et al., 1968) from the Kokpekten Complex (Ghzelian–Asselian) of Kazakhstan by Shi and Waterhouse (1996). *Biconvexiella* spp. (formerly *Crurithyris roxoi/Crurithyris* aff. *C. planoconvexa* Shumard/ *Attenuatella* sp. in Mendes, 1952; Rocha Campos, 1970; Rocha Campos and Rösler, 1978; Mezzalira, 1989, and others) occur profusely in units close stratigraphically to the Taciba Formation, such as Mafra Formation and Lontras shales and the Capivari Formation, showing the two pairs of adductors scars being the posterior pair scars smaller than anterior pair scars (Plate IV, figures H-J).

Amos (1958; see also Amos, 1979) attributed specimens from the upper part of the "Tepuel System" (more precisely base of LS9 member of Las Salinas Formation of González, 1972; roughly Kasimovian in age), Tepuel-Geona Basin, Chubut Province, Argentina, to *Crurithyris roxoi* (Oliveira). This assignation was questioned by Rocha Campos (1969) who indicated the absence of a well-developed ventral median ridge in the Patagonian specimens, unlike its presence in *Biconvenxiella roxoi* (Oliveira). Patagonian topotypic material collected (Plate IV, Figs. K-M) 2 km SSW of the Nazer store (="boliche and estafeta Las Salinas" in Amos, 1958) by the first author, show a ventral interior with a wide subelliptical depressed muscle field, narrow elongate aductor scars bisected by a thin median ridge and subelliptical diductors separated from the adductor scars by thin short ridges. Dorsal valve gently concave with strong median ridge separating a single pair of relatively large subrectangular adductor scars. Externally they exhibit a gently concave-moderately convex profile with a narrow shallow sinus, a slightly transverse outline, hinge line shorter than maximum width, the umbo moderately incurved, gently lamellose with spinose microornamentation of one order in concentric arrangement. When compared to *Biconvexiella roxoi* (Oliveira) the Patagonian specimens have up twice the size of the Brazilian species and a different profile, more transverse outline, distinct ventral and dorsal muscle scars, thinner ventral median ridge and stronger dorsal median ridge. The assignment of the Amos' Patagonian species to *Crurithyris* George, 1931 is confirmed here but not its previous co-specific condition with *B. roxoi* (Oliveira).

Order Chonetida Nalivkin, 1979
Suborder Chonetidina Muir-Wood, 1955
Superfamily Chonetoidea Bronn, 1862
Family Rugosochonetidae Muir-Wood, 1962
Subfamily Quinquenellinae Archbold, 1981
Genus *Quinquenella* Waterhouse, 1975
Type species: *Quinquenella glabra* Waterhouse, 1975 from the Nambdo Member of the Senja Formation (Late Permian), east Jumla City, northwest Nepal, by original designation.

Quinquenella rionegrensis (Oliveira, 1930)
Plate III, Figs. D-L
1930 *Chonetes rionegrensis* Oliveira, p. 19, unnumbered figure

Material: Four dorsal valves (exteriors and interiors), one fragmentary ventral valve interior and one external mold of ventral valve. Lectotype by present designation, GP/1E 4439b; Paralectotypes by present designation, GP/1E 4439a, 2056, 4402; Other material, DZP 19139 and a missing sample of the IGc/USP (Plate III, figure I).
Locality, unit and age: Fossil site 2, Texeira Soares County, state of Paraná, Brazil. Baitaca siltstone (DZP 19139) and Passinho shale (GP/1E 2056; 4439a, b; 4402), uppermost portion of the Taciba Formation. Latest Asselian–earliest Sakmarian.
Diagnosis: Average-sized *Quinquenella* of subelliptical transverse outline of gentle concave-convex profile and maximum width at hinge line. *Maximum* width up 10 mm, maximum length up 7 mm with an

W/L ratio varying between 1.43–1.60 and W/L average of 1.53. Ventral valve moderately concave, smooth with umbonal angle nearly 150°, ortomorph oblique hinge spines and short ventral median septum. Dorsal valve smooth, gentle concave on visceral disk, flattened towards auricles and flanks, auricles poorly differentiated with its margins at right angles. Dorsal interior with short lateral septa (?), thin long accessory septa, ill-defined median septum, fused posteriorly into low platform surrounding a small, circular shallow alveolus.

Description: Average-sized *Quinquenella* of subelliptical transverse outline of gentle concave-convex profile and maximum width at hinge line. *Maximum* width up 10 mm, maximum length up 7 mm with an W/L ratio varying between 1.43–1.60 and W/L average of 1.53. Ventral valve moderately concave, smooth with umbonal angle nearly 150°, ortomorph oblique hinge spines (few preserved) and internally with a short (≈ 1 mm) median septum. Dorsal valve smooth, gentle concave on visceral disk, flattened towards auricles and flanks, auricles poorly differentiated with its margins at right angles and apparently gentle concave longitudinally striated interarea. Dorsal interior with short lateral septa (?), thin long accessory septa, ill-defined median septum, fused posteriorly into low platform surrounding a small, circular shallow alveolus. Lines of pustules radially aligned, less densely grouped toward lateral margins. Muscle scars and brachial field inconspicuous. Cardinal process apparently bilobed externally.

Discussion: Oliveira (1930, p. 19) described briefly the Texeira Soares' chonetids having "small size (7.5 mm width/4.25 mm length), semicircular transverse outline, ornamented with radial striae and ventral hinge spines". A single specimen and holotype (supposedly a ventral valve) was illustrated (sketch) in an unnumbered figure (Oliveira, 1930) (Text-Fig. 1). The holotype lacks collection register number, therefore it does not fulfils the 73C.6 recommendation of the ICZN on holotype data.
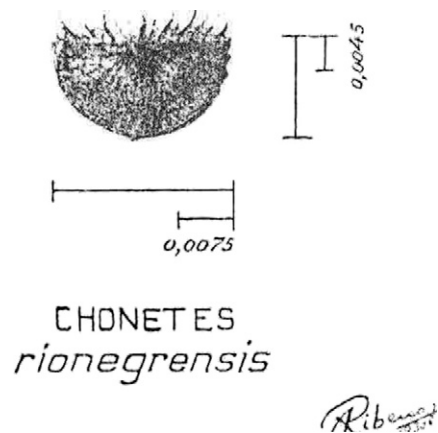
Text-Fig. 1: Original illustration of "*Chonetes*" *rionegrensis* Oliveira, 1930.

A collection label of some available specimens (housed in the Seção de Paleontologia da Divisão de Geologia e Mineralogia, Departamento Nacional da Produção Mineral, Rio de Janeiro State, Brazil, numbered GP/1E 4439a, 4439b and 4402), indicates its provenance, collector and date as follow: from the Texeira Soares locality, collected by Dr. Euzébio de Oliveira, in 1908. Consequently, they appear to be the syntype series on which Oliveira (1930) based his study. These and other topotypic specimens are herein figured (Plate III, Figures D-L), although unfortunately none of them matches exactly with the illustrated specimen named *Chonetes rionegrensis* by Oliveira (1930) (see Text-Fig. 1), being this denomination a possible *nomen dubium*. On the other hand, Rocha Campos (1970) examined the above mentioned syntype series and reassigned *Chonetes rionegrenis* to the smooth chonetid *Lissochonetes* Dunbar and Condra, 1932, in agreement to the

description herein offered. Possibly, the sketch of *Chonetes rionegrensis* of Oliveira (1930) (Fig. 4) represents an idealized composition of main characters observed by Oliveira, although confusing the external radial ornament with the internal radial dorsal accessory septa, also exaggerating number and dimensions of hinge spines. Furthermore, the supposed ventral valve drew in Oliveira (1930) did not exhibits a moderate convexity, but it matches in shape, size and gentle convexity flattened towards auricles and margins, to the specimen GP/1E 4439b (a dorsal valve mould) of the syntype series. This specimen is here selected as lectoype by inference of holotype, supporting *rionegrensis* as an available and valid name.

Archbold (1983a) based in Oliveira's illustration interpreted *Chonetes rionegrensis* as an endemic genus, possessing an external radial ornament and numerous and large ventral hinge spines, unlike any other known chonetacean. According to the description herein provided, the chonetids from Texeira Soares show smooth exterior, low concave-moderate convex profile, tranverse outline, ventral median septum, oblique hinge spines and long thin accessory septa that collectively suggest its inclusion in *Quinquenella* Waterhouse, 1975, more than in *Lissochonetes* Dunbar and Condra, 1932 as suggested by Rocha Campos (1970) or such as Archbold (1983a) indicated in a new endemic genus. *Lissochonetes* exhibits well developed dorsal median septum and lacks accessory septa unlike *Quinquenella*.

Quinquenella rionegrensis (Oliveira) is close to the type species *Quinquenella glabra* Waterhouse, 1975 (see also Waterhouse, 1978) from the Nambdo Member of the Senja Formation (Late Permian), northwest Nepal (also recorded in the Juripu Formation of southern Tibet by Shi et al., 2003), sharing comparable size and outline, but the late can be differentiated from the Brazilian species by its more inflated ventral valve and stronger developed internal characters. *Quinquenella australis* Archbold, 1981 (see also Skwarko, 1993) from the Cunlego Formation (late Artinskian) of the Carnarvon Basin, Western Australia, is larger, has subquadrate less transverse outline, longer ventral median septum and stronger internal characters of dorsal valve when compared to *Q.rionegrensis* (Oliveira). *Quinquenella kuwanensis* (Waterhouse, 1978) (Shen et al., 2001) from the Kuwa Member of the Senja Formation (late Permian) of northwest Nepal, exhibits similar transverse outline with *Q. rionegrensis* (Oliveira), although the former has smaller average-size, almost flat dorsal valve, longer ventral valve median septum and well impressed dorsal muscle scars. *Quinquenella planoconvexa* Abramov and Grigorjewa, 1988, as well as *Quinquenella pseudobrama* (Zavodowsky, 1960) (Abramov, 1970; Abramov and Grigorjewa, 1988; Klets, 2005a,b), from the Khorokytian and Echian Horizons (Asselian–Artinskian) of Verchojan region, northeast Asia, have subquadrate to subcircular outlines, inflated ventral valves, dorsal valves flat, long ventral median septum and strong accessory septa, unlike *Q. rionegrensis* (Oliveira). *Quinquenella*? sp. Archbold, 1999, from the Phuket/Kaeng Krachan Group (late Asselian–Sakmarian), Thailand, is a small species with unknown dorsal valve, preventing accurate comparison. *Quinquenella* sp. by Taboada and Shi (2009) (formerly *Tornquistia* sp. of Amos, 1960; *Yagonia* sp. of Roberts in Roberts et al., 1976, Amos, 1979; Archangelsky, 1987; Cúneo and Sabattini, 1987; *Lissochonetes jachalensis* of Simanauskas, 1991, in part) from the Mojón de Hierro (late Sakmarian) and Río Genoa (early Artinskian) formations, Tepuel-Genoa Basin, Patagonia Argentina, exhibits hinge margin shorter than maximum width, subcircular outline, longer ventral septum and shorter accessory septa that distinguish it from *Q. rionegrensis* (Oliveira).

Subphylum Linguliformea Williams, Carlson, Brunton, Holmer and Popov, 1996

Class Lingulata Gorjansky and Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Genus *Langella* Mendes, 1961

Type species: *Lingula imbituvensis* de Oliveira, 1930 from the Passinho drill core (120 m depth), Passinho Creek, 15 km from Texeira Soares City, Paraná State, Brazil. Passinho Shale, uppermost Taciba Formation, late Pennsylvanian–early Sakmarian.

Langella imbituvensis (Oliveira, 1930)

Plate III, Fig. M

1930 *Lingula imbituvensis* Oliveira, p. 18–22, fig. 1

1948 *Lingula budoensis* Martins, p. 237, figs. 1-2

1949 *Lingula* sp. Pinto, p. 3, figs. 2a-2b

1952 *Barroisella imbituvensis* (Oliveira) Lange, p. 83–86, Pl. 4, figs.1-8.

1961 *Langella imbituvensis* (Oliveira) Mendes, 3–5, Pl. 1, Figs. 1–2, Pl. 2, Figs. 1–3, Text-Fig. 1–3.

Locality, unit and age: Fossil site 2, Texeira Soares County, state of Paraná, Brazil. Passinho shale, uppermost portion of the Taciba Formation. Latest Asselian–earliest Sakmarian.

Comments: One figured dorsal valve external mold (GP/IE 4439) of longitudinally oval outline, ornamented with feebly concentric growth lines, 5.0 mm in length, 3.0 mm in width and L/W ratio of 1.67, suggests *Langella imbituvensis* (Oliveira, 1930). Holotype (dorsal valve DGM 386) exhibits 6.5 mm in width, 4.25 mm in width and a L/W ratio of 1.53, while Lange (1952) reports maximum size of dorsal valves of 6.53 mm in length, 3.82 mm in width, with L/W ratio of 1.71. Despite having in hand only one specimen, dimensions are shared with previous description of Oliveira species from the same stratigraphic interval. Furthermore, no other lingulid is known from the Itararé succession where this brachiopod occurs profusely in numbers like no other one.

Langella sp. Sun and Baliński, 2008 (= *Lingula* sp. of Baliński, 1999) from the Muhua Formation (Tournaisian) of the Gizhou Province, south China, is comparable in size and outline with *L. imbituvensis*, but its fragmentary record prevent accurate comparison.

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