



Rare Carboniferous and Permian glacial and non-glacial bryophytes and associated lycophyte megaspores of the Paraná Basin, Brazil: A new occurrence and paleoenvironmental considerations



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ABSTRACT

Fossil bryophytes are rare because their preservation is compromised by the presence of a thin cuticle (if any) and a lack of lignin. Except for the occurrence of one bryophyte in the glacial Dwyka Group of the Karoo Basin, the other rare Late Paleozoic records in Gondwana are notably from the Paraná Basin in Southeast/South Brazil. Four bryophyte sites (including a newly discovered one) were found in the lower part of the thick Permo-Carboniferous glacial succession of the Itararé Group, and one was found in the Guadalupian Teresina Formation, which was roughly assigned to an epeiric sea (or “lake”) dominated by a warm, semi-arid climate. This study describes the fossils from the new occurrence from the Itararé Group and discusses the context in which the bryophyte beds originated in the basin. The new samples confirm that all of the bryophytes of the Itararé Group can be classified as *Dwykea araroi* Ricardi-Branco et al. (a possible pleurocarp) and are associated with the lycophyte megaspore *Sublagenicula brasiliensis* (Dijkstra) Dybová-Jachowicz. In the much younger Teresina Formation, the bryophytes are *Yguajemanus yucapirus* Cristiano-de-Souza et al. and *Capimirinus riopretensis* Cristiano-de-Souza et al., and abundant charophytes and rare dwarf lycophyte stems and bracts are present in the same layers. Although the two stratigraphic units represent distinct paleoenvironments and climates, they seem to share some characteristics: a) the bryophyte assemblages were transported very little; b) they were deposited in very calm environments; c) they were the main components (along with some lycophytes) of local or poorly diversified regional vegetation. The low number of species, which is characteristic of opportunistic communities, can be explained by local or regional conditions that would have been stressful for the vascular plants in other areas. During the deposition of the Itararé Group, the main control was probably the cold climate in addition to a relative (liquid) water deficit because the bryophyte vegetation may have belonged to a tundra biome in areas of retreating glaciers. For the Teresina Formation, it is possible that the control was scarce freshwater, an unstable environment and water-saturated soil in a scenario of bryophyte vegetation living around temporary ponds in a wide marginal area of the epeiric sea.

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1. Introduction

Mosses (Class Bryophyta), in contrast to tracheophytes, are small, fragile “non-vascular” plants, which are generally without conducting tissues and lack lignin (Taylor et al., 2009). A particularly distinctive characteristic of bryophytes is the dominance of the

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haploid (gametophyte) generation in their life cycle, including the possibility of an occasional sporophyte phase (Frey, 2009; Taylor et al., 2009). Acrocarpic specimens found in the Mississippian of Germany, which are related to ancestral forms, are traditionally believed to be the oldest fossil mosses (<http://www.amjbot.org/content/102/11/1883.full>Hübers and Kerp, 2012), and the earliest pleurocarpic mosses are evidenced in the Permian of Gondwana (Cristiano-de-Souza et al., 2012; Johnson et al., 2016). However, the Mesozoic moss record is more diverse than that of the Late Paleozoic (Shelton et al., 2015).

Some Devonian fossils are similar to bryophytes, but their affinities are uncertain, or they probably belong to other plant groups. One example is the Upper Devonian fossil that was first designated as *Hepaticites devonicus* Hueber (1961) and later moved to *Pallavicinites* (Goffinet et al., 2009). According to biophysical and morphological criteria as the size, Boyce (2008) suggested that Silurian-Early Devonian cooksonioid specimens may correspond to moss sporophytes, which may have been too small for sufficient aerated photosynthetic tissue. Gerrienne et al. (2006) proposed that the supposedly Eutracheophyta *Cooksonia paranaensis* from the Paraná Basin had a liverwort-like habit.

Bryophytes have been regarded as pioneer plants of deglaciated areas, but the preservation potential of these delicate plants in such sedimentary environments is very low. Therefore, the rare proglacial bryophyte fossils, such as those related to the Carboniferous-Permian Gondwanic glaciation, are very intriguing (Barclay et al., 2013).

The bryophytes described herein record, in part, a vegetation of a cold climatic context during the Late Paleozoic Ice Age (LPIA, Parrish et al., 1986; Fielding et al., 2008).

They were found in three previously known outcrops (Ricardi-Branco et al., 2013) and a new one of the Itararé Group in the northern portion of the Paraná Basin (State of São Paulo, southeastern Brazil, Western Gondwana). These elements were preserved in association with megaspores.

The only non-glacial bryophytes of the Paraná Basin are recorded in a single outcrop of the Guadalupian Teresina Formation (Cristiano-de-Souza et al., 2012).

2. Regional Geology and Paleontology

The Paraná Basin (*s.l.*) encloses a large intracratonic syncline in central-southern South America that was directly connected to the Chaco Basin (Argentina and Paraguay) and linked by seaways and/or continental environments to the Cape-Karoo Basin (South Africa) and the Huab Basin (Namibia) (Milani and DeWitt, 2008). The Ordovician to Cretaceous sedimentary fill is divided into six depositional sequences (Milani et al., 2007), of which the Carboniferous-Permian interval (Supersequence Gondwana I), 1.5–2.4 km thick, comprises the Itararé, Guatá and Passa Dois groups (Fig. 1) (Milani et al., 2007; Bocard et al., 2009). During this time, a probable clockwise rotation and northward movement of the Gondwana plate, as well as other global changes, caused a shift from a cold to a warm semi-arid climate in the Paraná Basin (Milani and DeWitt, 2008).

The Itararé Group encompasses one of the most expressive records of the Late Paleozoic Ice Age – LPIA in Southwestern Gondwana (Castro, 2004). According to palynological data (Souza, 2006; Souza et al., 2010) and the radiometric ages of overlying post-glacial strata (Rio Bonito Formation) (Souza, 2006; Holz et al., 2010), the deposition of the Itararé Group began in the Moscovian (Pennsylvanian) and ended in the Sakmarian (Cisuralian).

This unit is characterized by a great variety of lithofacies: claystones, sandstones, conglomerates, diamictites, varvites, turbidites, and thin coal seams, which formed in marine, coastal and

		Chronology	Lithostratigraphy			
TRIASSIC						
PERMIAN	Lopingian	Changhsingian	Passa Dois Group	Rio do Rasto Fm.		
		Wuchiapingian				
	Guadalupian	Capitanian			Guatá Group	Teresina Fm.
		Wordian				
		Roadian				
	Cisuralian	Kungurian			Tubarão Supergroup	Serra Alta Fm.
		Artinskian				
		Sakmarian				
		Asselian				
		Gzhelian				
PENNSYLVANIAN	Late	Kasimovian	Itararé Group	Irati Fm.		
		Moscovian				
	Middle	Moscovian			Palermo Fm.	
		Bashkirian				
Early	Bashkirian	Rio Bonito Fm.				
			Taciba Fm.			
			Campo Mourão Fm.			
			Lagoa Azul Fm.			

Fig. 1. Cronostratigraphy of the Paraná Basin during Gondwana 1 Supersequence (Milani et al., 1998). Ages of the Tubarão Supergroup according to Holz et al. (2010) and Passa Dois Group by Ferreira-Oliveira and Rohn (2010). Gray-coloured lithostratigraphic units contain bryophyte records.

continental environments under glacial, proglacial, and interglacial conditions (Rocha-Campos et al., 2008). A different interpretation is that almost all of the deposits represent deglaciation sequences (ice-retreat depositional tracts in stratigraphic sequences), and only small intercalated intervals may correspond to ice-advances (Vesely and Assine, 2006). Several fossils, such as brachiopods, mollusks, foraminifers, insects, fishes, and plants, are recorded in the Itararé Group. The marine fossils indicate that the paleoenvironments were mostly marine (Vesely and Assine, 2006; Rocha-Campos et al., 2008), but the origin of some rocks remains controversial (Rocha Campos et al., 2008). The most important vascular plant occurrences are associated with coally beds in the states of Rio Grande do Sul and São Paulo, which are likely related to interglacial intervals (Bernardes-de-Oliveira et al., 2005). The youngest interglacial interval has the first elements of the *Glossopteris* Flora (Rösler, 1978; Rohn et al., 2000).

In the northeastern portion of the Paraná Basin (State of São Paulo), where the studied fossils were collected, the Itararé Group is exposed in a narrow NE-SW strip, although it reaches its greatest thicknesses in this region (approximately 1300 m; Vesely and Assine, 2006). The studied fossiliferous beds occur in the lower part of the group, only a few meters above the Precambrian basement, but the lower boundary of the unit is irregular because of glacial erosion. The depositional basin was a semi-isolated glacial inlet or estuary with salinity controlled by sea-level change (Rocha-

Campos et al., 2008). Bergamaschi et al. (2016) worked in the regions of Salto and Itu but was a little distant from the Salto 1 and Salto 2 outcrops, and no rhythmites or fossil plants were recorded.

The Guatá Group, which was deposited after the Itararé Group, has slightly thicker coal beds and more abundant and diversified plant fossils of the *Glossopteris* Flora, but no bryophytes had been found to date. The succession represents early Permian (Souza, 2006) fluvial, deltaic, coastal and marine environments in a predominantly deepening upward trend that were probably under the influence of humid and gradually warmer climates (see the revision in Holz et al., 2010).

The Passa Dois Group is divided into the Irati, Serra Alta, Teresina and Rio do Rasto formations, which roughly document the transition from a carbonatic-siliciclastic epeiric sea (with mesosaurs) to semiarid continental environments, probably from the Kungurian (Cisuralian) to the Wuchiapingian (Lopingian) (see the revision in Holz et al., 2010). Several plant megafossils are known in numerous locations, but bryophytes were only found in a single outcrop of the Teresina Formation in Rio Preto Quarry near Irati, State of Paraná (Cristiano-de-Souza et al., 2012). This formation is mainly characterized by interlaminated dark shales/argillites and very fine sandstones with flaser/wavy/lenticular bedding, bioturbation and, commonly, mud cracks. These predominantly pelitic facies are arranged in cyclic upward-coarsening successions (usually a few meters thick) including thin intercalations of coquinites, carbonate mudstones, grainstones (commonly oolitic), microbialite beds and fish bone beds. In general, the paleoenvironment was a large very shallow interior sea (i.e., epeiric sea) influenced by storms and climatic oscillations from humid to arid, presenting low to high water salinities, respectively (Rohn, 2001, 2007; Rohn and Fairchild, 2015).

3. Location of the outcrops, materials and methods

3.1. Fossiliferous outcrops and studied samples

Two bryophyte and megaspores occurrences of the Itararé Group are located in the Municipality of Campinas, and the other two are in the Municipality of Salto, approximately 34 km away, in the central region of the State of São Paulo (Figs. 2–4). Considering that the previously known outcrops are important for the descriptions, their locations are provided again. This information, as well as the location of the new bryophyte occurrence, namely, *Salto 2*, and the samples described here are as follows:

- *Salto 1* outcrop: km 101.7 of the SP-75, Prefeito H. Steffen Highway, Salto Municipality (47° 19' 28.74" W/23° 11' 49.34" S). Megaspore sample CP1/508
- *Salto 2* outcrop: near the Eucatex Industry, within the urban area of Salto (47° 17' 5.91" W/23° 12' 42.21"). Bryophyte samples CP1/440–449, 450–505; megaspore samples CP1/473, 496–500, 502–504.
- *Delta Landfill*, Campinas Municipality (47° 09' 00.57" W/22° 54' 47.22" S). Megaspore samples CP1/509 to 537, 539, 542, 546, 547, 550, 552, 555 to 559, 562 and 563.
- Km 96 of the *Bandeirantes Highway* (47° 07' 56.96" W/22° 55' 15.40" S), which now corresponds to km 6.5 of the Adalberto Panzan Highway, Campinas Municipality.

The samples are housed in the Repository of Paleontology of the Geosciences Institute of UNICAMP under their Paleobotanical Scientific Collection codes (CP1 code).

The Guadalupian bryophyte outcrop of the Paraná Basin is a quarry called *Rio Preto*, which is located at km 98 of the PR-364, 10 km south from the Irati urban center and 4 km north from Rio

Preto District (50° 44' 52.81" W/25° 31' 30.36" S).

3.2. Methods

Well-preserved carbonized megaspore exine of 28 samples from the Delta Landfill Outcrop was successfully recovered from the matrix after maceration in 50% HCl for one hour. Unfortunately, it was not possible to recover epidermis from carbonified gametophytes. Other megaspore and gametophyte samples are preserved as impressions.

The equipment used in this study was a Zeiss Stemi 2000-C stereoscopic microscope with a coupled digital camera and, for the bryophyte sample (CP1/416) of the Salto 1 outcrop, a scanning electron microscope (SEM) with energy dispersive spectroscopy (EDS) to determine the elemental composition at selected points on the gametophytes. The samples were reduced in size and coated laterally with an epoxy resin to form the efficient vacuum during the SEM and EDS analyses.

The taxonomic classification of the bryophytes was based on common criteria cited in the bibliography (e.g., Goffinet et al., 2009), such as the shape of the phyllids, the disposition around the stem and the relative dimensions. Intraspecific variations in megaspores, as noted by Trindade (1959, 1962), were noted through detailed descriptions and measurements of more than a hundred specimens. The plant kingdom classification scheme proposed by Frey (2009) was followed.

4. Results

4.1. Characterization of the bryophyte beds

In the Itararé Group, the bryophytes (mainly gametophytes) occur as small fragments and are associated with megaspores, dispersed cuticles, and unidentified phytoclasts, and the types of fossilization are carbonization (compression) or mold (impression). Ricardi-Branco et al. (2013) proposed the species *Dwykea araroi* for bryophytes from the *Salto 1*, *Bandeirantes Highway* (including aff. *Dwykea* sp. in Amaral et al., 2004) and *Delta Landfill* outcrops.

The *Delta Landfill* and *Bandeirantes Highway* outcrops expose massive and laminated mudstones, rhythmites, siltstones and shales. At the second outcrop, the rhythmites are 8 m thick, and the bryophytes and megaspores were observed along this succession. Thick, deformed sandstones are stacked on the top. The rhythmites were interpreted as distal facies of fans on marine slopes formed under the influence of meltwater inflows (Souza Filho, 1986) or in shallow water (Amaral and Ricardi-Branco, 2004).

Souza et al. (2006) suggested that the palynological content associated with the macrofossils at the *Bandeirantes Highway* outcrop is equivalent to that of the *Ahrensisporites cristatus* Interval Zone (Late Bashkirian to Moscovian, according to Souza, 2006 the oldest palynozone of the Itararé Group).

The *Salto 1* and *Salto 2* outcrops, which are now almost completely covered, present diamictites, sandstones, conglomerates, breccia and rhythmites (composed of 1–2 cm-thick pairs of very fine sandstones grading to dark shales). The rhythmite at *Salto 1*, which bears rare dropstones (Longhim et al., 2002), represents typical turbidites formed in a proglacial context, and its upper 0.5 m is in an inverse position (upside down) and brecciated close to its contact with an overlying massive, 8 m-thick sandstone. The inverted bed was certainly still plastic when a glacial thrust, or another glaciogenic process, folded it like an atectonic nappe. In addition to relatively abundant bryophytes and megaspores, the rhythmite at *Salto 1* contains a palynological assemblage of approximately 60 pollen and spore species that, unlike the premise, are partly indicative of not strictly cold climates (Longhim et al.,

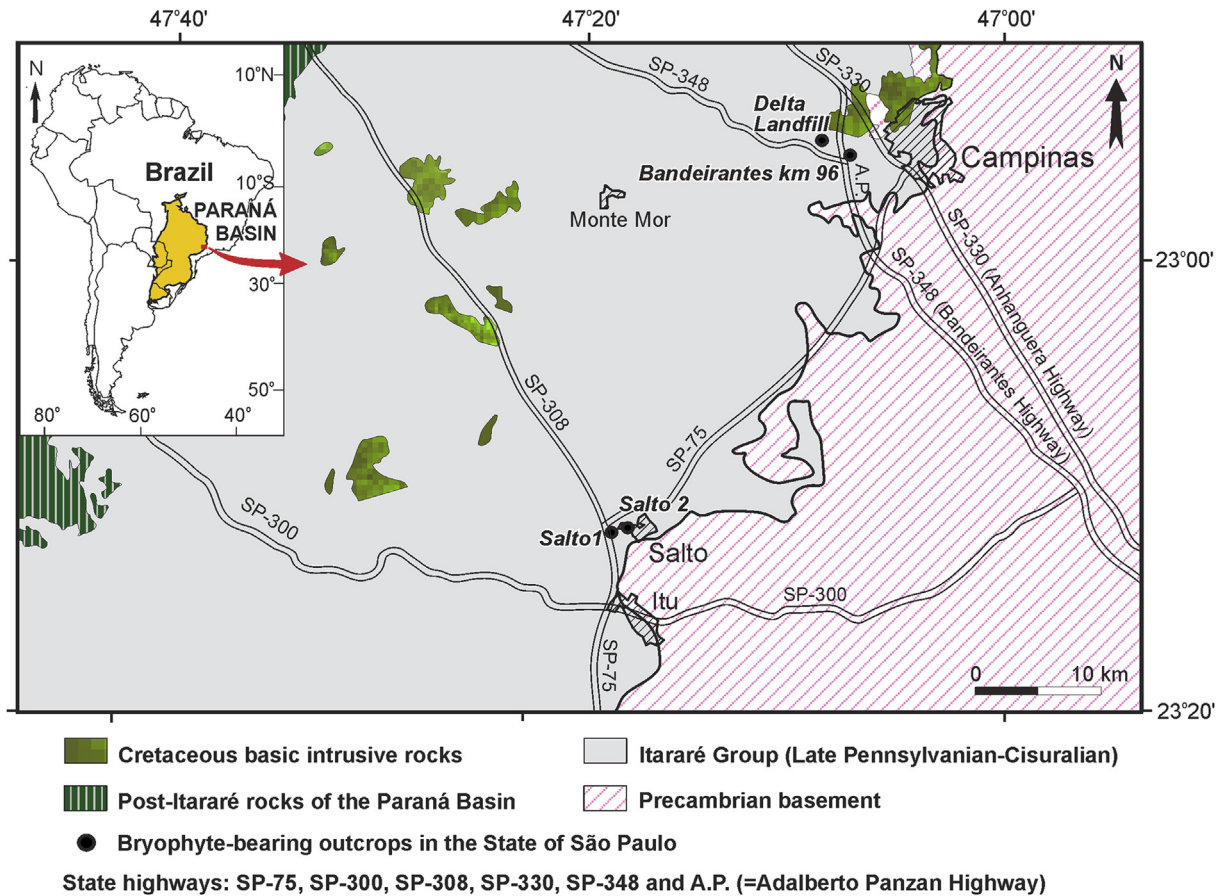


Fig. 2. Geologic map of the region of Campinas and Salto, State of São Paulo, Brazil (according to Almeida et al., 1981) and location of the fossiliferous outcrops.

2002). The palynoflora includes *Deusilites tenuistriatus* (whose affiliation is rather uncertain) and *Botryococcus* algae; no acritarchs were recognized (Longhim et al., 2002). It is consistent with the *Crucisaccites monoletus* Interval Zone, which is ascribed to the Moscovian-Kazimovian (Pennsylvanian) according to Souza (2006). At the *Salto 2* outcrop, reported here for the first time, the fossils occur in an approximately 0.5-m-thick, weathered, light yellow to gray pelite.

The bryophytes of the Teresina Formation of the Passa Dois Group, are restricted to a 1.8 m-thick, light gray, massive siltite above giant mud cracks at the base of the quarry (Neves et al., 2011), and the gametophytes commonly occur in close parallel orientation in several levels. Cristiano-de-Souza et al. (2012) proposed two bryophyte genera and species: *Capimirinus riopretensis* and *Yguajemanus yucapirus*, which are associated with abundant charophyte oogonia of the genus *Leonardosia* (Porocharaceae Family) described by Faria et al. (2013). Dispersed lycophyte stems identified as *Lycopodiopsis derbyi* and structures that are probably related to strobilus bracts were also found in the siltite (Faria et al., 2009). This bed is overlain by meter-thick coarsening-and-thickening upward successions of bioturbated heterolithic shales/very fine sandstones with wavy bedding. The siliciclastic rocks are interrupted by a few decimetric carbonates in the form of a 0.5 m-thick calcarenite composed of fragmented and complete bivalve mollusks, some allochthonous microstromatolites, other carbonate grains and silicified lycophyte microphylls (Neves et al., 2011).

Additional bryophytes in the Paraná Basin include *Tallites* sp., mentioned by Rigby (1968) and Mezzalira (1980) for the State of São Paulo. Because both species must be reviewed, they were not

considered in the final discussion of this work.

4.2. Chemical composition of the compressions

The targets of the EDS analyses were selected according to visual differences, such as in color and texture. The spectra generated from the three selected points are represented in Fig. 5, and based on the graphs and tables, the high content of carbon (C) in the fossils suggests a latent process of carbonification. The presence of barite, which can very often be an indicator of a reducing environment (Bonny and Jones, 2008), is also clear.

4.3. Systematic paleontology

4.3.1. Macrofossil remains

Class Bryophyta Schimper, 1879.

Genus *Dwykea* Anderson and Anderson, 1985.

Dwykea araroi Ricardi-Branco et al., 2013.

Figs. 6 and 7 (1, 2, 7 and 8).

Material. CP1/440, 441, 447–453, 455, 462, 469–472, 487–492, 496–498, 503 and 505.

Stratigraphic and geographic location. Itararé Group at the Salto 1, Salto 2 (not previously reported), Delta Landfill and Bandeirantes Highway outcrops.

Description. Gametophytes with erect stems greater than 5.8 mm in length and 0.27 to 1.12 mm in thickness. Erect-patent phyllides, with phyllotaxis in spiral, more tightly closed near the apex. Lanceolate phyllides with entire margins, amplexicaul bases, and acute tips. Average length of 2.81 mm and width at the base of

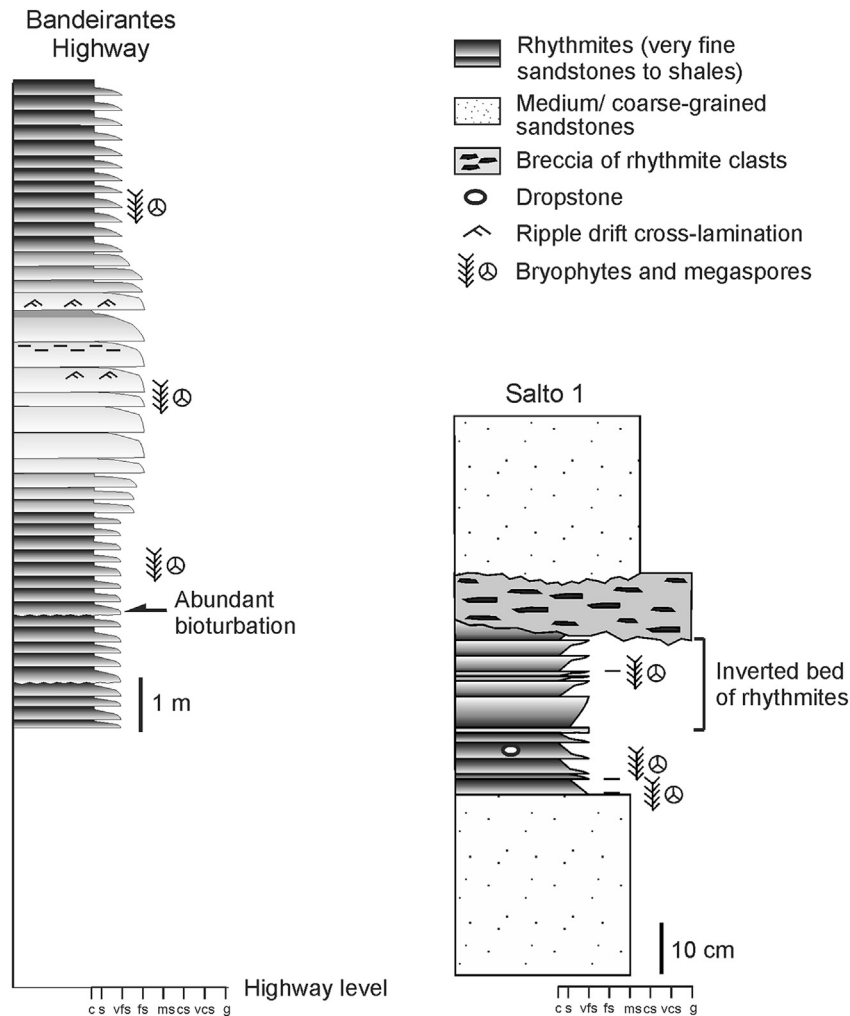


Fig. 3. Columnar sections of the most important fossiliferous outcrops: km 96 of the *Bandeirantes Highway* and *Salto 1*.

0.33 mm and 0.05 mm at the tip.

Discussion. All of the described gametophytes can be assigned to the Gondwanic genus *Dwykea* Anderson and Anderson 1985 that was established for specimens of the Dwyka Group (Karoo Basin, South Africa). The Dwyka Group, as with the Itararé Group, records Pennsylvanian to Cisuralian glacial and interglacial deposits (Milani and DeWitt, 2008). The studied gametophytes bear wider and shorter phyllides than *Dwykea goedehoopensis* from Africa (comparisons in Table 1), which reinforces the previous justification for the proposed species *D. araroi* Ricardi-Branco et al., 2013. The newly analyzed specimens present slightly wider phyllides than those in Ricardi-Branco et al. (2013) (0.3 mm instead of 0.2 mm), and the stems are generally more fragmented, not reaching half the length of some previously described specimens. The new fossil material does not include sporophytes.

The only possible pleurocarpic sporophyte belongs to the apparently immature specimen found in association with gametophytes from the *Bandeirantes Highway* outcrop, originally identified as aff. *Dwykea* sp. (Amaral et al., 2004) and synonymized with *D. araroi* in Ricardi-Branco et al. (2013), with a 0.6 mm-long and 0.04 mm-wide seta holding a 0.2 mm-long and 0.08 mm-wide capsule.

4.3.2. Microfossil remains

Anteturma *Sporites* Pant, 1962.

Turma *Triletes* (Reinsch) Potonié and Kremp, 1954.

Supraturma *Lagenotriletes* Potonié and Kremp, 1954.

Subturma *Gulati* Bharadwaj, 1957.

Genus *Sublagenicula* Dybová-Jachowicz et al., 1979.

Sublagenicula brasiliensis (Dijkstra, 1956) Dybová-Jachowicz et al., 1979

Fig. 7 (3, 4, 5, and 6).

Material. Lateral and proximal-distal compressions, one hundred thirteen (113) specimens in CP1/473, 496–500, 502–504, 508 to 537, 539, 542, 546, 547, 550, 552, 555 to 559, 562 and 563.

Stratigraphic and geographic location. Itararé Group, Salto 1 and 2 and Delta Landfill outcrops.

Description. Trilete, subgulate megaspores, prolate in lateral compression and oval in proximal-distal compression. Straight trilete rays. Well-defined arcuate ridges. Confluence of trilete rays with arcuate ridges sometimes marked by small triangular auriculae. Ornamentation of the psilate at contact area and psilate to scabrous in distal area.

Dimensions.

Polar view: Length 1060–1444 μm and width 854–1400 μm . Trilete ray 540–670 μm . Arcuate ridge 452–934 μm .

Equatorial view: Length 956–1180 μm and width 502–1553 μm . Trilete ray 489–801 μm . Arcuate ridge 322–1010 μm .

Discussion. The described specimens, according to their gula, trilete ray, distal area exine ornamentation, contact area, and dimensions, are similar to *Sublagenicula brasiliensis* recorded in monospecific megaspore assemblages, which is the most abundant

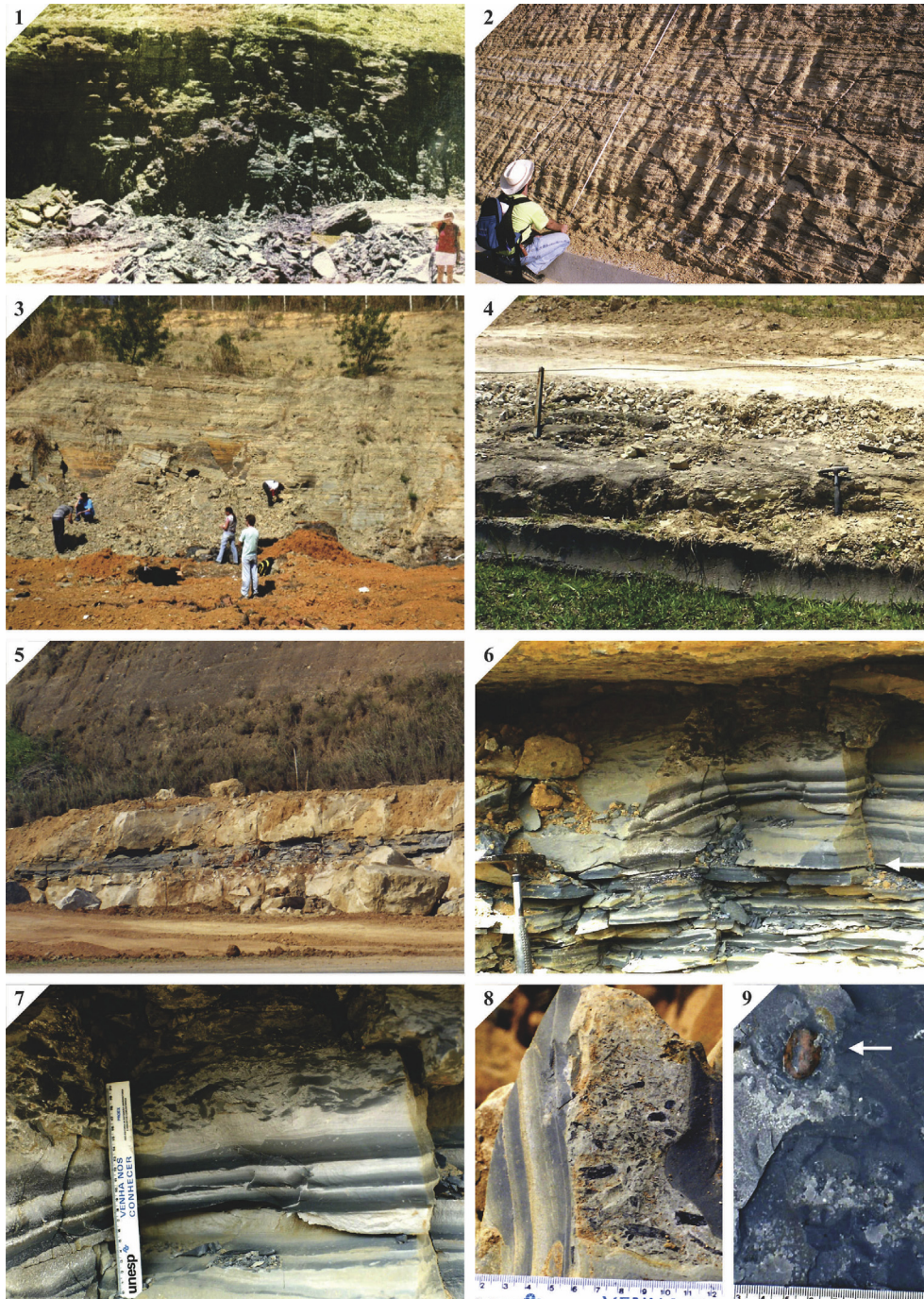


Fig. 4. Bryophyte and megaspore bearing outcrops of the Itararé Group. (1) and (2) Rhythmites exposed at a roadcut during works on the old km 96 of the Bandeirantes Highway (now km 6.5 of the Adalberto Panzan Highway). (3) Delta Landfill outcrop during works for a sanitary landfill, only 2 km apart from the first locality, presenting similar rhythmites, probably of the same stratigraphic interval. (4) Salto 2 outcrop, where the bryophytes occur in weathered very fine sandstones (more or less in the interval indicated by the hammer), Salto Municipality. (5) to (9) Salto 1 outcrop during works on the SP-75 Highway, highlighting the thin gray and white fossiliferous rhythmite intercalated between thick massive sandstones, with more sandstones further back (5). Details of the rhythmite bed (6 and 7), particularly of the upper inverted, slightly deformed and microfaulted part (above the arrow), erosionally overlain by a thin irregular breccia composed of not well lithified rhythmite clasts, passing up into the thick massive sandstone. In plan views, the rhythmite shows carbonized plant fragments (8) and a dropstone (9, arrow).

taxon of the Itararé Group in the State of São Paulo at Monte Mor, Buri and at km 96 of the Bandeirantes Highway Outcrop (Trindade, 1959, 1970; Amaral and Ricardi-Branco, 2004; Mune and Bernardes de Oliveira, 2007).

This species was also found in the states of Paraná (Arai and Rösler, 1984; Ricardi-Branco et al., 2002), Santa Catarina (Dijkstra, 1956; Trindade, 1959; Pant and Srivastava, 1962), and Rio Grande

do Sul (Dijkstra, 1956; Trindade, 1962, 1964, 1966; Pant and Srivastava, 1962; Cauduro and Zigano, 1965; Marques-Toigo et al., 1975; Bortoluzzi and Veiga, 1981).

Outside of the Paraná Basin, this species has been recorded in the Upper Carboniferous of Argentina (San Rafael and Paganzo Basins, Garcia, 1995) and the Permian strata of the Tepuel-Genoa Basin. On the African continent, it has been reported in the Lower

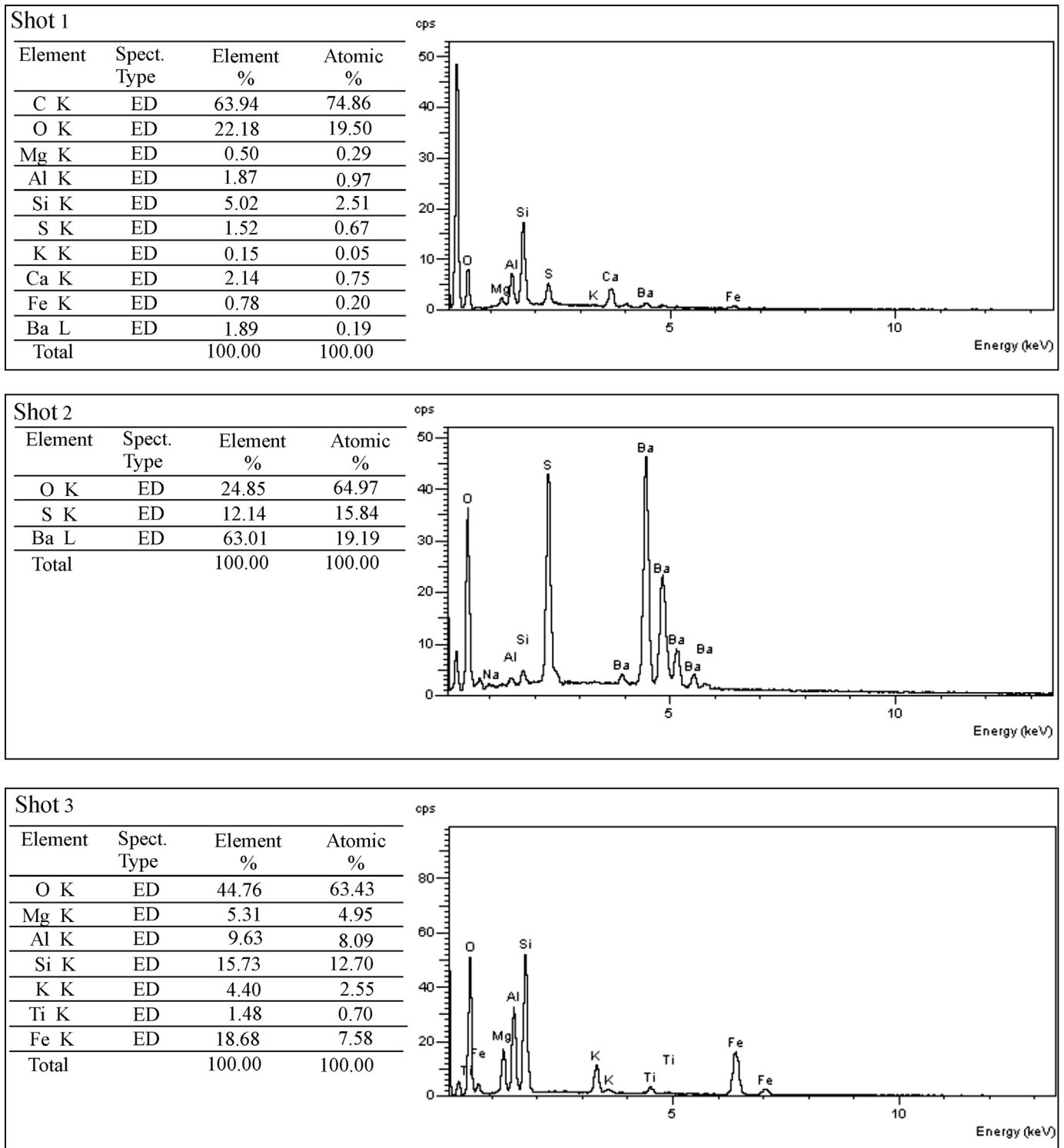


Fig. 5. SEM Result from gametophyte of *Dwykea arraroi*. Shot 1 shows the highest peak of Carbon (fossil carbonization). Shot 2 shows a high peak of barium, in a possibly reducing environment, and Shot 3 indicates the mineralogical composition of the rocky matrix.

Carboniferous of Egypt and Chad, in the Viséan of Nigeria, and in the Namurian of Algeria and western Libya. It has also been found in the Lower Permian of the Democratic Republic of Congo (Dybová-Jachowicz et al., 1987; Glasspool, 2003) and South Africa (Glasspool, 2003).

5. Discussion of the results

Sousa Filho (1986) interpreted the fossiliferous rhythmites of the Itararé Group at the *Bandeirantes Highway* outcrop as turbidites that originated from glacial meltwater discharges and deposited in

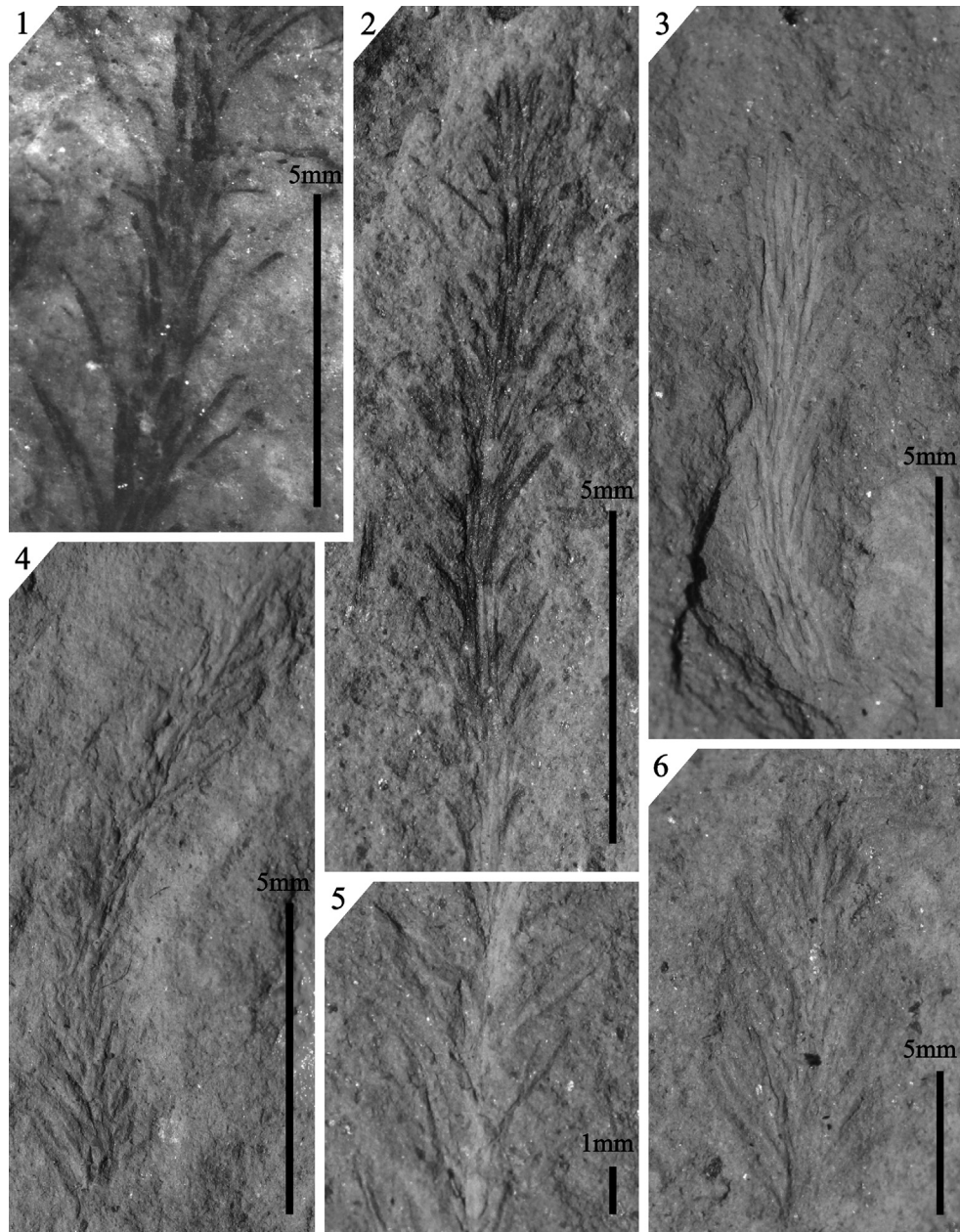


Fig. 6. Gametophytes of *Dwykea araroi*. (1), (2), (3), (4), and (6) Gametophytes with phyllotaxis in spiral, lanceolate phyllides, with amplexicaulis bases, and acute tips. Phyllides with phyllotaxis in spiral. Salto 1 Outcrop (1, CP1/244) and Salto 2 Outcrop (2, Sample CP1/244; 3, Sample CP1/447d, 4, Sample CP1/441; 5, Sample CP1/487, and 6, Sample CP1/440). (5) Note more condensed phyllides near the apex.

relatively deep and anoxic bathyal conditions. Vesely and Assine (2006) noted that the topographic gradients of the Paraná Basin were, in reality, low, but they also interpreted fine-grained particles, such as rhythmically laminated silt-clay couples, as representing “distal” glaciomarine environments during deglaciation and the gradual rise of the relative sea level. However, the high abundance of the bryophytes, their good preservation without strong fragmentation, the presence of a very fragile probable lateral sporophyte and the abundant megaspores evidence very proximal and shallow depositional settings instead (cf. bryophyte taphonomy in Bomfleur et al., 2014). The plants must have not been transported as bedload but in slow, fluctuating water flows and deposited in very calm conditions. Therefore, the term “distal” must here be considered to mean “not close” to outwash fans in front of

retreating glaciers and relatively near the plant community. The presence of dropstones in the rhythmite at *Salto 1* and the inverted position of the upper part of this bed indicate that icebergs and glaciers were penecontemporaneous to the bryophyte vegetation and reinforce the interpretation of a predominantly cold climate.

The presence of *Botryococcus* and the apparent lack of acritarchs in the rhythmite of *Salto 1* (Longhim et al., 2002) does not necessarily point to a lacustrine paleoenvironment; a palynofacies analysis is recommended.

Bomfleur et al. (2014) emphasized that the preservation of bryophytes usually requires rapid burial to inhibit chemical decay and destruction by organisms, but this premise can only partly be extrapolated to the Itararé Group. Firstly, it is necessary to bear in mind that plants lying on the floor of cold water environments are

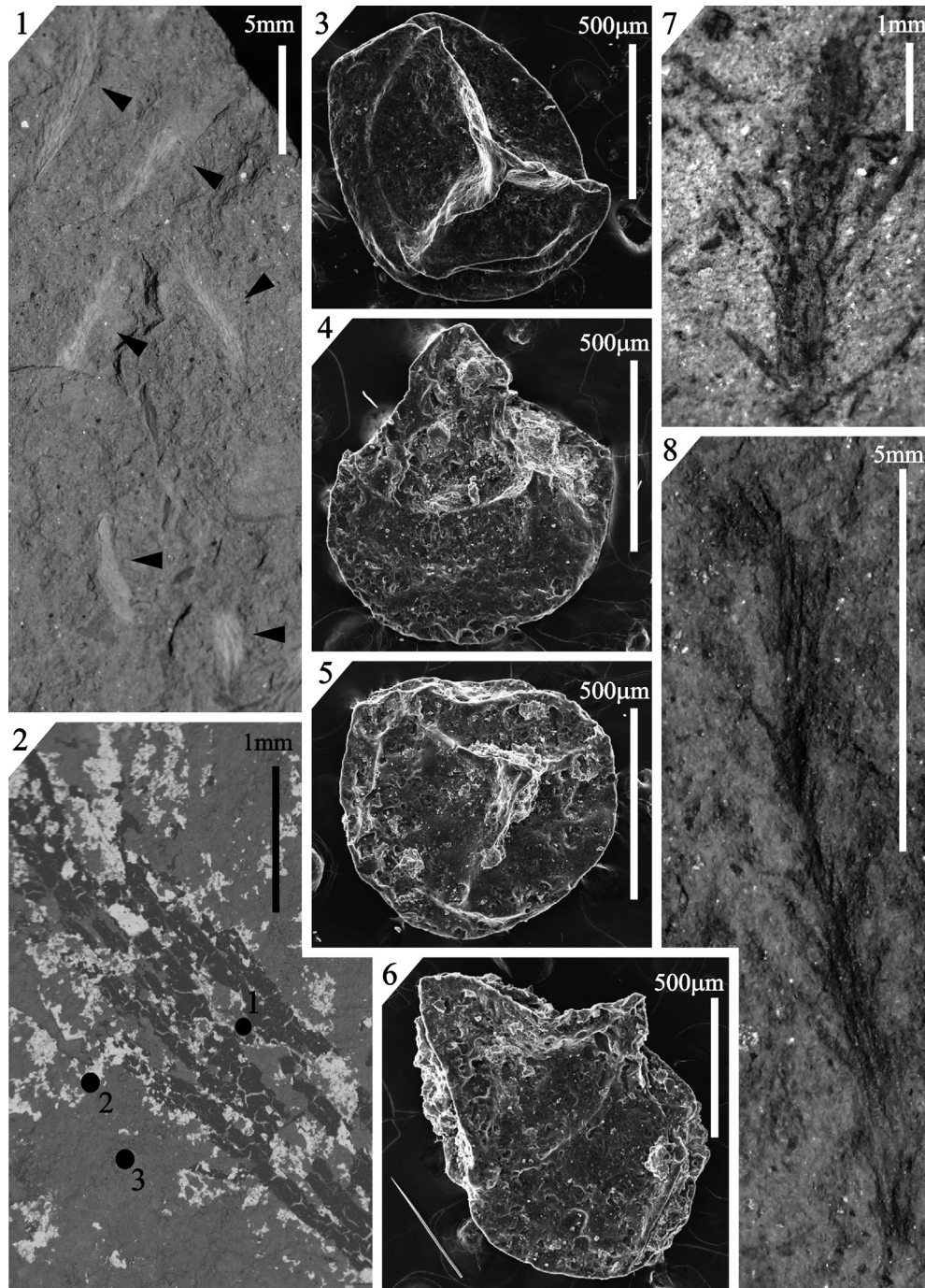


Fig. 7. *Dwykea araroi* and *Sublagenicula brasiliensis*. (1) Gametophytes of *Dwykea araroi* (CP1/496), Salto 2 Outcrop. (2) Gametophytes of *Dwykea araroi* (CP1/416) in a SEM with highlighted shots, Salto 1 Outcrop. (3) *Sublagenicula brasiliensis* (CP1/510) polar view, Delta Landfill Outcrop. (4) *Sublagenicula brasiliensis* (CP1/515) equatorial view, Delta Landfill Outcrop. (5) *Sublagenicula brasiliensis* (CP1/510) polar view, Delta Landfill Outcrop. (6) *Sublagenicula brasiliensis* (CP1/515) equatorial view, Delta Landfill Outcrop. (7) *Dwykea araroi* (CP1/556), Delta Landfill Outcrop. (8) *Dwykea araroi* (CP1/497), Salto 2 Outcrop.

less prone to destruction or degradation by scavengers and decomposers because these organisms are less active at low temperatures. If the water of the depositional environment had been warm, the presence of carbon and barite in the studied fossils, or simply the compressions *per se*, would attest to depleted dissolved oxygen in the lower part of the water column. However, under cold conditions, the produced organic matter could have been insufficient to cause anoxic conditions, so the water circulation (controlling the dissolved oxygen) was possibly more effective depending

on the temperatures of the inflowing melt-water, salinity, etc. The coalification of macrodetritus does not necessarily indicate depleted oxygen in the depositional site but rather a low percolation rate of oxygenated waters in the plant-bearing deposit (as argillaceous muds), thus preventing plant degradation (Gastaldo, 1988). Therefore, the preservation of the bryophytes in the Itararé Group must have been enhanced by low temperatures and a more or less rapid, but not quite catastrophic, burial (compare with the statement of Bomfleur et al., 2014 about rapidly buried bryophytes

Table 1Comparison of the described samples of *Dwykea araroi* and *Dwykea* Anderson and Anderson (1985).

Morphological features	<i>Dwykea</i> in Dwyka group, South Africa	<i>Dwykea araroi</i> of the Itararé group (this study)
Stem length	>25 mm	>5.8 mm
Leaves length × width)	5.0 mm × 0.15 mm	3.0 mm × 0.3 mm
Leaf Apex	Acute	Acute
Phyllotaxis		Helicoidally
Costa		
Gametophyte	Preserved	Preserved
Sporophyte		Pleurocarpic?

in a fluvial depositional system). The rhythmite at least evidence repetitive (periodic?) embedding events of the plants.

Taking into account the likely gentle taphonomic factors in the origin of the bryophyte beds (such as the low transport of the plants, almost no selection by floatage, etc.), the monotonous associations of *Dwykea araroi* along with the monospecific (*Salto 1–2* and *Delta Landfill* outcrops) or poorly diversified megaspore assemblages (*Bandeirantes Highway* outcrop) reflect low plant diversities in the source vegetations. The most important controlling factor of the small number of species must have been the cold climate.

It is important to note that the palynological assemblage of the *Salto 1* rhythmite may be assigned to the flora of a warmer climate (Longhim et al., 2002), but wind or water (or even glaciers, in part) may have easily transported or reworked spores and pollen grains from distant warmer source areas to the depositional site.

The bryophyte communities represented in the Itararé Group could have belonged to tundra-like biomes in coastal environments, so the subsoil (a few decimeters below the surface) may have been permanently frozen, as in the typical tundra biomes of Antarctica where bryophytes have been the dominant vegetation components since the Miocene (Lewis et al., 2008; Ochyra et al., 2008; Désamoré et al., 2012). As typical opportunistic elements, this vegetation could have immediately colonized exposed areas after the retreat of glaciers. The true interglacial successions, formed at times of considerable climate amelioration, include much richer plant beds as well as coal (Bernardes-de-Oliveira et al., 2005).

The presumed cold climate probably implied low (liquid) water availability for the bryophyte beds, at least during the winter. The poikilohydry and the tolerance to desiccation of bryophyte gametophytes (Mishler and Kelch, 2009) meant a survival advantage

under water deficit (Fig. 8).

Megaspores assigned to the genus *Sublagenicula* were probably produced by lycophytes (e.g., *Brasilodendron*; see Glasspool, 2003), but considering that this genus, particularly *S. brasiliensis*, has a large stratigraphic range (Pennsylvanian – Cisuralian) and apparently lived in distinct paleoclimates (from cold to temperate) and diverse paleoenvironments (marginal swamps, flood plains, etc.), it is difficult to interpret the characteristics of the mother plant. Similar megaspores were perhaps produced by distinct lycophytes. In the idealized community reconstruction in Fig. 8, the producing *Sublagenicula brasiliensis* plant is represented by an herbaceous lycophyte, which is consistent with rapid growth during the milder seasons of a cold climate context. Mishler and Kelch (2009) commented that Lycophyta also included tolerant species with respect to hydrological constraints, and this interpretation can be extended to the producing plant of *Sublagenicula brasiliensis*.

In terms of the paleogeographic and temporal/stratigraphic distribution of the bryophytes, Catuneanu et al. (2005) commented that *Dwykea* occurs in association with proglacial conditions in the Karoo Basin. Hence, this genus was at least successful at dispersing in the immense Western Gondwana proglacial terrains during the Pennsylvanian. Although the known bryophyte occurrences are still few, the low diversity and the large geographic distribution (and also, apparently, the ample stratigraphic range) corroborate the interpretation that *Dwykea* was an opportunistic element.

The megaspore *Sublagenicula* occurs from Argentina to South Africa in the Pennsylvanian – Cisuralian. Based on the spatial and temporal distribution of *S. brasiliensis*, Piérart (1975, 1981; 1984) noted the possibility that this species has been one of the “transgressive megaspores”, along with *Setosisporites furcatus*, that were typical of the marginal areas of glaciers during the Carboniferous and that established in coastal environments with the *Glossopteris* Flora during the Permian under inter- or post-glacial transgressive conditions. According to the *Sublagenicula* record in the coal-bearing Rio Bonito Formation of the Paraná Basin, the respective lycophytes were relatively flexible plants with respect to the climate, from cold and dry glacial conditions to temperate/warm and humid conditions. However, they supposedly have not reached the Northern Floras, perhaps because they were not able to invade areas with ecologically similar plants in addition to possible geographic (e.g., Hercynian Mountain Range) and climatic barriers (e.g., an arid belt in low latitudes; Capretz and Rohn, 2013). *Sublagenicula* have also not been recorded in younger stratigraphic levels of the Paraná Basin, which are related to warmer and dryer climates. However, this absence can be absolutely taphonomic considering that small lycophyte stems and microphylls are common in the Teresina Formation (Faria et al., 2009; Faria and Ricardi-Branco, 2010), and some not-yet-studied but reported megaspores have been found in this formation in the Western part of the basin (Dharani Sundaran, Federal University of Mato Grosso, oral communication).

Similarly, the lack of bryophytes in the Rio Bonito Formation may be a taphonomic artifact. Mosses were surely abundant and



Fig. 8. Reconstruction of the landscape where the bryophytes and lycophytes lived according to the studied fossils of the Itararé Group at Campinas and Salto, State of São Paulo.

diversified in the shaded, warm and humid areas of the understory of the *Glossopteris* vegetation, but they must have been destroyed by exposure to chemical and microbial decay as well as during transport and mixing with more resistant vascular plants. For example, Bomfleur et al. (2014) found only very small bryophyte fragments (<1 cm long) mixed with other fossil phyllids in Triassic floodplain and crevasse-splay deposits in Antarctica and commented that other probable bryophytes occur as abundant but unrecognizable very small organic fragments.

In the stratigraphic succession of the Paraná Basin, it is significant that bryophytes reappear in one bed of the Teresina Formation, and the fact that the bryophyte genera of this formation are distinct from *Dwykea* is not surprising because they were separated by a long time span and lived under different climate conditions. The discovery of these bryophytes was made possible by the good exposure of the rock in a quarry, but luck during a fieldtrip could not have been the only favorable factor. The bryophytes, which were associated with one species of carophyte oogons as well as very rare, small but also monospecific lycophyte stems and not-yet-described rare strobili bracts, were probably deposited in a very proximal and calm environment, such as a temporary pond, without the input of vascular plants that should have masked or hidden the delicate bryophytes. According to this hypothesis, the fossil assemblage was derived from a vegetation mostly composed of bryophytes and rare lycophytes that was perhaps controlled by a water-saturated soil, very unstable environmental conditions and/or scarce freshwater, and this, in turn, could have been controlled by low pluviosity. The lycophytes and bryophytes, like modern mangroves, were probably hydro-hygrophyllous and tolerant to slightly saline water (Garbary et al., 2008; Faria et al., 2009). According to the epeiric sea model interpreted for the Teresina Formation (Rohn and Fairchild, 2015), the very low floor gradients of the basin defined a huge and wide marginal area that was sometimes totally exposed and sometimes totally flooded. At times of exposition, the slightly depressed parts of the floor were transformed into tiny temporary ponds, which could have been fringed by the bryophyte and lycophyte vegetation and colonized by charophyte algae. The vascular plants of the true terrestrial regions with normal soils lived far from the bryophytes and thus are only scarcely represented in the formation. As in the glacial Itararé Group, the bryophyte vegetation recorded in the Teresina Formation can be classified as an opportunistic community.

6. Conclusions

As shown here, Permo-Carboniferous bryophytes are rare fossils, and nearly all records in Gondwana are limited to the Paraná Basin and were the result of recent research. The present study increased the number of bryophyte occurrences in the Itararé Group to four, and palynological analyses positioned the fossil beds in distinct stratigraphic intervals within the Carboniferous part of this unit. The fossil assemblage of the new outcrop, as with those in earlier studies, is composed of the single bryophyte species *Dwykea araroi* Ricardi-Branco et al. and the megaspore *Sublagenicula brasiliensis* (Dijkstra) Dybová-Jachowicz. The bryophytes are probably the oldest representatives of the Core Pleurocarps *sensu* Bell et al. (2007). *S. brasiliensis* was most certainly produced by lycophytes, and only the *Bandeirantes Highway* outcrop yielded other rare megaspores.

Based on the abundance and preservation of the fossils, their low diversity cannot be ascribed to taphonomic selection but probably to an original low-diversity tundra vegetation that was installed in coastal areas during glacier retreat in early interglacial intervals. *Dwykea* and the *Sublagenicula* producing plants were certainly opportunistic and not only tolerated the cold climate but

also a relative (liquid) water deficit. In the Karoo Basin, where the genus *Dwykea* was proposed, these proglacial conditions were probably very similar. Bryophytes were not recognized in the more diversified plant assemblages that formed during the warmer inter- and post-glacial intervals, but this absence may be related to the low preservation potential of these plants. In contrast, *Sublagenicula* is represented in a greater stratigraphic range and in wider Gondwanic areas, which suggests that the respective lycophytes tolerated a broader scale of climates.

In the higher stratigraphic levels of the Paraná Basin as well as throughout Gondwana, the only preserved bryophytes were found in a single bed of the Guadalupian Teresina Formation and designated as *Yguajemanus yucapirus* and *Capimirinus riopretensis* by Cristiano-de-Souza et al. (2012). As the older glacial bryophytes, those of the Teresina Formation may also indicate a poorly diversified, opportunistic local vegetation, including monotonous hydro-hygrophyllous dwarf lycophytes, that probably fringed small shallow ponds across the wide marginal areas of an epeiric sea.

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