A new flora from the Rio Bonito Formation (late Asselian) and its implications for the biostratigraphy of the southern Paraná Basin, Brazil

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A R T I C L E   I N F O

A B S T R A C T

The results of this contribution represent the first attempt regarding palynological and paleobotanical records from the municipality of Alfredo Wagner, Santa Catarina State, southern Brazil. The fossils were recovered in the top of the Siderópolis Member, upper portion of the Rio Bonito Formation, Paraná Basin. The palynological assemblage revealed a well-preserved assemblage composed of 28 spores and 24 pollen, mainly dominated by ferns and gymnosperms, correlated with the *Vittatina costabilis* Zone. Eight taxa are first records for this unit (*Granulatisporites varigranifer, Punctatisporites subvaricosus, Gondisporites serrulatus, Didecitriletes* sp, *Vitreisporites signatus, Alisporites ovatus, Pteruchipollenites indarraensis* and *Cycadopites cymbatus*), and three of them for the basin (*P. subvaricosus, Didecitriletes* sp. and *C. cymbatus*). The paleobotanical assemblage is mainly represented by *Glossopteris* (seven species), ferns (*Pecopteris* and *Sphenopteris*) and seeds (*Cornucarpus, Cordaicarpus* and *Samaropsis*), corresponding to the Gondwanan "*Glossopteris* Flora". Although *Cheirophyllum* and *Cornucarpus* would be typical and restricted to the underlying *Phyllotheca-Gangamopteris* Flora, their presence allows us to correlate the floristic deposits with the basal part of the *Glossopteris-Brasilodendron* Flora range. In addition, U–Pb zircon CA-TIMS datings obtained in nearby correlated sections allows the macro- and microfloras to be constrained to the latest Asselian age.

1. Introduction

Paleobotanical studies in the Paraná Basin from Brazil span some 140 years (for historical review see Iannuzzi, 2010). In fact, the initial interest in fossil plants was linked to prospecting and commercial exploitation of coal beds in the basin. Because of this, the better surveyed paleobotanical records correspond precisely to those regions where the main mines for the exploitation of this resource were located, namely: south and north-central of the state of Rio Grande do Sul, southermost of the state of Santa Catarina, north of the state of Paraná, and central-south of the state of São Paulo. In this context, the central region of the state of Santa Catarina did not receive attention by geologists and paleontologists despite having several exposures of rocks, sometimes relatively thick, of the Rio Bonito Formation. This was due to the recognition of non-economically exploitable coal beds in this portion of the basin with respect to other main coal measures found throughout

the basin. Therefore, the main goal of this contribution is to help fill this historical gap in the knowledge of the aforementioned region through the study of a new phytofossiliferous outcrop discovered in the countryside of the municipality of Alfredo Wagner, in Santa Catarina, southern Brazil, and of two other sections of surface and subsurface located in the municipalities of Alfredo Wagner and Anitápolis, respectively.

The new exposure containing plant macro- and microfossils, named the "Probst Outcrop", was fortuitously found by the first author (MR) many years ago during a trip he made to Brazil to visit his father. On this occasion, MR, together with the geologist J. Freitas (JF), collected samples containing fossil plants and also for palynological preparation, which proved to be fertile and herein analyzed (RN and MdP). Years later, JF returned to this same outcrop accompanied by paleobotanist R. Iannuzzi, during which more fossil plant material was collected. Finally, the geologist R. Alvarenga carried out the description and sedimentary

interpretation of the exposed sections. The results presented here represent the synthesis of all these field campaigns that have been conducted over the last few decades. High-precision radiometric datings were recently obtained from two sections close to the Probst Outcrop (Griffis et al., 2019), which made it possible to establish an approximate absolute age of the plants and palynomorphs associations through stratigraphic correlations. This fact stimulated the study and publication of the results referring to the Probst Outcrop, since very few fossiliferous associations could be calibrated by absolute dating in the basin until today.

2. Geological, stratigraphical and geochronological settings

2.1. The Paraná Basin

The Paraná Basin represents an intracratonic area in the south-west of Gondwana, between 15° and 34° South and 47° and 58° West (Almeida, 1969), occupying a total area of 1.700.000 km², of which 1.100.000 km² belongs to Brazil, 100.000 km² to Paraguay, 100.000 km² to Uruguay, and 400.000 km² to Argentina (Zalán et al., 1987). Stratigraphically divided into six supersequences, from the Ordovician-Silurian up to Late Cretaceous, bounded by significant regional unconformities (Milani, 1997; Milani and Zalán, 1997; Milani

et al., 2007): Rio Ivaí, Paraná, Gondwana I, Gondwana II, Gondwana III and Bauru (Fig. 1).

The supersequence Gondwana I, composed by Tubarão and Passa Dois supergroups, Carboniferous-Permian in age, is represented by a transgressive-regressive cycle in which two groups can be recognized: the Itararé Group (lowermost) and the Guatá Group (uppermost). The former represents the glacial sediment facies deposited during the Pennsylvanian-Early Permian, while the latter the post-glacial facies, Sakmarian-Artinskian in age, strongly marked by the deglaciation and consequent sea level elevation in the Paraná Basin (Milani et al., 2007).

The Guatá Group comprises two transgressive/regressive cycles, in which the lowermost Rio Bonito Formation is represented by transgressive cycles of sedimentation. In this context, extensive coal measures developed a very rich fossiliferous flora, being the subject of several palynological and paleobotanical contributions (Iannuzzi, 2010).

2.2. The Rio Bonito Formation

The term "Rio Bonito" comes from the expression "Beautiful Layers" used by I.C. White (1908) in reference to the sandstone, shale/musdstone and coal-layer packages observed in the type section described close to Lauro Müller, Guatá and São Joaquim, in the state of Santa Catarina (Krebs and Menezes Filho, 1984; Schneider et al., 1974). The
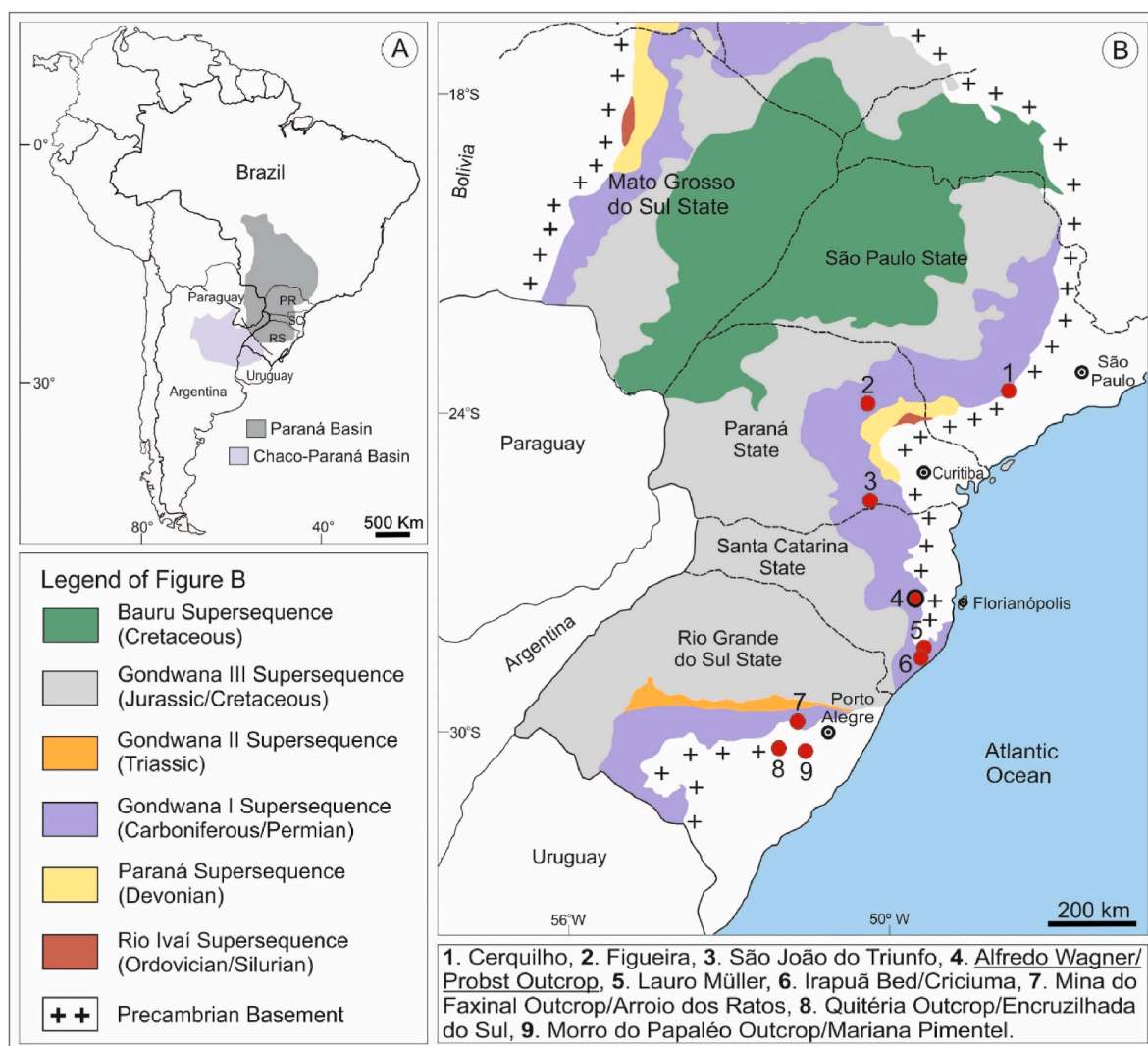

Fig. 1. A. Map of South America showing the position of the Paraná and Chaco-Paraná basins. **B.** Map of the south Brazilian region showing the position of Alfredo Wagner, Santa Catarina State, and the localities used for paleobotanical comparisons (map after Milani, 1997).

Rio Bonito Formation is characterized by a sedimentary package deposited above the Itararé Group consisting of quartz and arkose sandstones, siltites, carbonaceous siltites, carbonaceous shales and coal at the top of the section (Schneider et al., 1974). Some authors (Holz et al., 2006; Wildner et al., 2008; Maahs et al., 2019) suggest that the Rio Bonito Formation was deposited in estuarine, fluvial-deltaic, coastal and marine platform environments. At the top of the Rio Bonito Formation, Holz (2003) identified the transition from an estuarine system to a barrier lagoon, with the formation of lagoons behind barrier islands.

Schneider et al. (1974) proposed, to the eastern border of the Paraná Basin, the division of the Rio Bonito Formation into the members Triunfo, Paraguaçu and Siderópolis. The Triunfo Member, the most basal portion, presents in the base contact in concordant with the Rio do Sul Formation (uppermost Itararé Group) and has thicknesses greater than 100 m, being registered in the states of Paraná (PR) and Santa Catarina (SC). The Triunfo Member is characterized by the occurrence of fine to medium whitish sandstone, sometimes coarse, with sub-rounded and moderately sorted grains. Subsequently, conglomerates, very fine sandstones, siltstones, carbonaceous shales and charcoal lenses are present. In the sandstones, in general, planar, trough cross stratification and parallel lamination occur, and fossils such as plant remains and palynomorphs are commonly found. The upper contact of this unit usually occurs in concordant with the Paraguaçu Member (Schneider et al., 1974).

The Paraguaçu Member, middle portion of the Rio Bonito Formation, has a similar thickness to the underlying member. The outcrops extend from the south of Santa Catarina State to the mid-west of São Paulo State. This member is composed of gray to greenish parallel laminated siltstones and shales that alternate with cross-stratified fine sandstone that sometimes have bioturbation features that give the rock a massive character. Pelecypods, gastropods, brachiopods, echinoderms, plant remains and palynomorphs are the fossils recorded in this unit (Schneider et al., 1974). The upper contact between Paraguaçu and overlying Siderópolis Members is erosive or concordant and interdigitated, but sometimes occurs in direct contact with the Palermo Formation (Schneider et al., 1974).

Finally, the Siderópolis Member is characterized by fine to very fine sandstones interspersed with claystones, laminated carbonated shales and coal measures (more concentrated at the top). Medium to thick sandstones with high angle cross stratification are also observed. There is abundant record of plant and palynomorph fossils (Schneider et al., 1974; Iannuzzi, 2010; Bernardes-de-Oliveira et al., 2016a). The upper contact is transitional with the Palermo Formation.

2.3. Age of Rio Bonito Formation

Based on palynostratigraphy, the Rio Bonito Formation has always been considered to be Cisuralian in age, ranging from Asselian to Kungurian (Souza, 2006). This chronostratigraphic position has essentially been based on the fact that this unit is inserted in the *Vittatina costabilis* Zone (VcZ). Although the extension of VcZ to the end of the Carboniferous has recently been suggested, at first, this change does not affect the time span of the Rio Bonito Formation, as it was proposed with the basis of a U–Pb radiometric age obtained from deposits in the uppermost part of the Itararé Group that have been considered underlying the basalmost levels of the Rio Bonito unit (Souza et al., 2021).

Since the 2000s, U–Pb radiometric dates have been obtained from the different *tonstein* layers that occur intercalated in the famous coal measures present in the Rio Bonito Formation, commercially explored since the beginning of 20th century. These radiometric dates come from deposits in the state of Rio Grande do Sul, but have recently been also taken from volcaniclastic deposits located in the states of Santa Catarina and Paraná (synthesis in Souza et al., 2021). Different radiometric ages, using different analytical methods, have been released in the last two decades, some of which conflict with each other and are even contradictory, when compared with the expected time interval thought for this

unit. Only recently, these same *tonstein* layers were reanalyzed using a high-precision U–Pb radiometric method (ID-CA-TIMS) in a single laboratory, by Griffis and collaborators (Griffis et al., 2018, 2019), which allowed for an adjustment in ages attributed to the Rio Bonito Formation. These last results pointed to a time interval spanning from the early Asselian to the late Artinskian (according to Cohen et al., 2013, updated), taking into account the oldest (298.23 ± 0.31 Ma) and youngest ($285.42 + 1.2/-2.1$ Ma) ages obtained for those authors (Griffis et al., 2018, 2019), which is the accepted timeframe for the present contribution.

3. Biostratigraphy of the Rio Bonito Formation

Several biostratigraphic frameworks have been suggested and updated for the Late Paleozoic in the Paraná Basin since the pioneering contribution of Daemon and Quadros (1970). One of the remaining issues is the validity and applicability of these zones in the different parts of the basin due to its vast area of coverage and geologic complexity.

3.1. Plant stratigraphy

The first floristic zonation for the late Carboniferous-Permian interval of the Paraná Basin was proposed by Rösler (1978). This author subdivided the floristic succession of this time span into six informal "taphofloras" referred to by letters from the older (A) to the younger (E). Decades later, Iannuzzi and Souza (2005) proposed four successive developmental stages of the whole succession for late Carboniferous-early Permian interval of the Paraná Basin based on previous and unpublished studies. They are, in ascending order: Pre-*Glossopteris* (Pre-Gl), *Phyllotheca–Gangamopteris* (Phy-Ga), *Glossopteris–Brasilodendron* (Glo-Br) and *Polysolenoxylon–Glossopteris* (Po-Glo) floras. Besides that, Rohn and Rösler (2000) established formal plant zones for the middle-late Permian deposits applied to the whole basin. However, for the early Permian strata only few formal plant zones proposed decades ago were geographically restricted to northern (Millan, 1987 - updated by Bernardes-de-Oliveira et al., 2016b) and southern basin (Guerra-Sommer and Cazzulo-Klepzig, 1993 - updated by Iannuzzi et al., 2010), corresponding to outcrops distributed in São Paulo and Rio Grande do Sul states, respectively. For the state of Santa Catarina, no formal zonation has been proposed based on the paleobotanical record, and only the informal zonations by Rösler (1978) and Iannuzzi and Souza (2005) are considered valid to be applied in the early Permian age deposits of this state.

Considering the Rio Bonito Formation, Rösler (1978) defined two taphofloras for this unit, namely Taphoflora B and Taphoflora C. In Tafoflora B, *Asterotheca*, *Pecopteris* spp. and *Annularia* are abundant elements, while *Paranocladus*, *Lycopodiopis* (=*Brasilodendron*) *pedroanus*, *Gangamopteris*, *Glossopteris* and *Sphenophyllum* are common. On the other hand, in Tafoflora C, *Gangamopteris* and *Glossopteris* become abundant and *Lycopodiopis* (=*Brasilodendron*) *pedroanus* and ferns (i.e. *Asterotheca* and *Pecopteris* spp.) become rare. Iannuzzi and Souza (2005) also considered that two floristic stages occur in the Rio Bonito Formation, one restricted to the base of this unit, i.e. *Phy-Ga* Flora, and another that would extend throughout the rest of this formation, corresponding to most of the paleobotanical records found in this unit, which would be *Glo-Bra* Flora. The *Phy-Ga* Flora is distinguished by the first appearance of glossopterids and by the abundance of *Gangamopteris*-type leaves and *Phyllotheca*-type sphenophytes. Among the typical taxa, Iannuzzi and Souza (2005) cite *Phyllotheca australis* (=*P. indica*), *Stephanophyllites sanpaulensis*, *Botrychiopsis plantiana*, *Rubidgea lanceolata*, *R. obovata*, *Gangamopteris angustifolia*, *G. obovata*, *G. buriadica*, *Glossopteris communis*, *G. indica*, *Chiropteris reniformis*, *Cheirophyllum speculare*, *Kawizophyllum* sp., *Buriadia isophylla*, *Cornucarpus patagonicus* and *Arberia minasica*. The overlying *Glo-Bra* Flora is characterized by the dominance of *Glossopteris*-type leaves, among the glossopterid elements, by the abundance of the *Glossopteris*,

Brasilodendron and *Cordaites* genera in the plant associations, and by the emergence of new elements, such as pecopterid ferns and sphenophyllaean sphenophytes. Taxa listed by Iannuzzi and Souza (2005) for this flora are: *Brasilodendron pedroanum, Phyllotheca griesbachi, Pecopteris pedrasica, Asterotheca* spp., *Sphenopteris lobifolia, S. ischavonensis, Neomariopteris* sp., *Botrychiopsis valida, Glossopteris occidentalis, G. taenioides, G. browniana, G. angustifolia, G. ampla, Gangamopteris intermedia, G. mosesii, Paranocladus dusenii, Arberia* spp., *Ottokaria* spp., *Plumsteadia sennes, Cordaicarpus zeillerii* and *Cornucarpus furcata*. Originally, neither Rösler (1978) nor Iannuzzi and Souza (2005) established any correspondence between their floristic units and members of the Rio Bonito Formation. However, Rösler's Taphoflora B was defined in the type-area of the Triunfo Member (i.e. São João do Triunfo, in Paraná state) while the taxa of Taphoflora C come from outcrops belonging to the Siderópolis Member, Santa Catarina state (Rösler, 1978). Recently, Iannuzzi (2021) pointed out that the stratigraphic range of *Phy-Ga* Flora would extend from the top of the Itararé Group to the Triunfo Member and the *Glo-Bra* Flora would be recorded along the entire Siderópolis Member.

3.2. Palynostratigaphy

The contribution of Daemon and Quadros (1970) was a landmark concerning the Carboniferous-Permian palynostratigraphy in the Paraná Basin, including strata from Mato Grosso to Rio Grande do Sul states. Based on the appearance and disappearance of species, Daemon and Quadros (1970) defined six informal intervals.

Currently, Souza et al. (2021) revised the *Vittatina costabilis* Zone (*VcZ*), from upper Itararé Group (Taciba Formation) to the Rio Bonito Formation, and invalidated the *Protohaploxypinus goraiensis* and the *Hamiapollenites karrooensis* subzones. In this new framework, the lower limit of *VcZ* is given by the appearance of the genus *Vittatina*, together *Illinites unicus, Converrucosisporites confluens, Protohaploxypinus goraiensis,* plus other monosaccate and taeniate bisaccate pollen grains, whereas the upper limit by the appearance of *Corisaccites alutas, Striatopodocarpites pantii, Lueckisporites stenotaeniatus, L. densicorpus, L. virkkiae, Staurosaccites cordubensis, Weylandites lucifer* and *Lunatisporites variesectus*. Furthermore, by radiometric dating, they positioned the *VcZ* as spanning from Gzhelian to Sakmarian/Artinskian (ca. 20 Ma - in Souza et al., 2021).

4. Materials and methods

4.1. Study area and stratigraphic analysis

The specimens described in this contribution were collected from an outcrop located in an unpaved secondary road connected with the BR-282 highway at the border between the municipalities of Alfredo Wagner and Rancho Queimado, in central region of state of Santa Catarina, southern Brazil (Fig. 1). The name "Probst Outcrop" is attributed to a small farm originally owned by Mr. Probst as its reference point. In addition, another section on the outskirts of the Alfredo Wagner city was described, as well as the 7RL-04-SC-02 borehole drilled (core) in the neighboring municipality of Anitápolis.

The description of facies associations, was based on lithostratigraphic data collected in the field for reconstruction of sedimentary paleoenvironments followed Miall (1996) within the hierarchy of depositional sequences, especially for 3rd order sequences (Catuneanu, 2006). For first and second order supersequences in the Paraná Basin see Milani et al. (2007).

4.2. Paleobotanical material

All examined fossils comprise specimens preserved as impressions and compressions recovered only from Probst Outcrop. The macroflora pictures were made with a Nikon D800e using a Meiji EMZ dissecting microscope (USA) and using a Canon EOS T3i camera with Sigma 70 mm

DG macro lens (Brazil). The specimens are stored at the Instituto de Geociências, Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul (IGeo/DPE/UFRGS), Laboratório de Paleobotânica, under the labels MP-Pb.

4.3. Palynological material

The palynological material analyzed herein was collected in shale/siltstone layers only from the above-mentioned Probst Outcrop. The 12 samples were processed at Global Geolab Limited, Alberta, Canada, applying standard methodologies (HCl, HF, HCl boiled and sieved using 25 μm meshes). The pollen and spore pictures were taken using a Motic BA 410 E compound light microscope with a Jenoptik Gryphax Series microscope camera (USA) and an Olympus CX 31 light microscope with Olympus Evolt E 330 microscope camera (Brazil). Sporomorph positions were annotated using England Finder. Slides are stored at the Instituto de Geociências, Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul (IG/DPE/UFRGS), at the Laboratório de Palinologia "Marleni Marques-Toigo", under the labels MP-P 14.904–14.913 and MP-P 15.030–15.031.

4.4. Statistical analysis

Several methodologies are available currently to compare paleontological data, thus allowing for a more accurate comparison among the phyto- and palyno assemblages beyond traditional analysis using qualitative methods. Two matrices were built and run to analyze their relationship with Brazilian and South American assemblages.

Hierarchical clustering analysis were performed using the software PAST (Hammer et al., 2001). Two hierarchical methods were applied and their dendograms depicted, one based on the concept of similarity of data, or on the distance between two data (Norušis, 2011). Hence, the Ward's method with Euclidian index was used to analyze similarity/dissimilarity regarding presence-absence of shared species, in which 0 represents no similarity and 1, equality/maximum association. On the other hand, the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) with Jaccard index was used to analyze the mathematical distance among data, in which every data contribute equally in the results, scoring absence of species as 0 and 1 as presence (Malhotra, 2006).

5. Results

5.1. Stratigraphic correlation of the Probst Outcrop

There are excellent and relatively thick exposures of rocks referring to the Rio Bonito Formation in the municipality of Alfredo Wagner as well as in the well 7RL-04-SC-02 – Anitápolis – SC, located c. a. 30 Km from the Probst Outcrop. Hence, this unit is represented by the three previously mentioned members erected by Schneider et al. (1974), i.e. Triunfo, Paraguaçu and Siderópolis.

Limited at the base by a subaerial unconformity seen in well 7RL-04-SC-02 -Anitápolis – SC (c.a. 332 m), the base of the Triunfo Member is represented by the deposition of sediments from fluvial channels, correlated with thick deltaic deposits in the Alfredo Wagner section (from 15 to 20 m), over a correlative conformity correlated to the subaerial unconformity of well core 7RL-04-SC-02 (Fig. 2). Sediments range from conglomerate to coarse sandstone with tangential cross bedding, unidirectional current ripples and fine upward to fluvial deposits. As for the deltaic deposits, there are layers of fine to coarse sandstones with low angle cross bedding, parallel planes, and climbing ripples ranging from subcritical to supercritical and sometimes massive. At the top of the deltaic deposits, a maximum regression surface is observed, and after that, the Paraguaçu Member deposits are installed (Fig. 2, Table 1).

The Paraguaçu Member is characterized by wave-dominated platform marine deposits with facies ranging from upper shoreface to offshore. These deposits range from pelites with plane-parallel
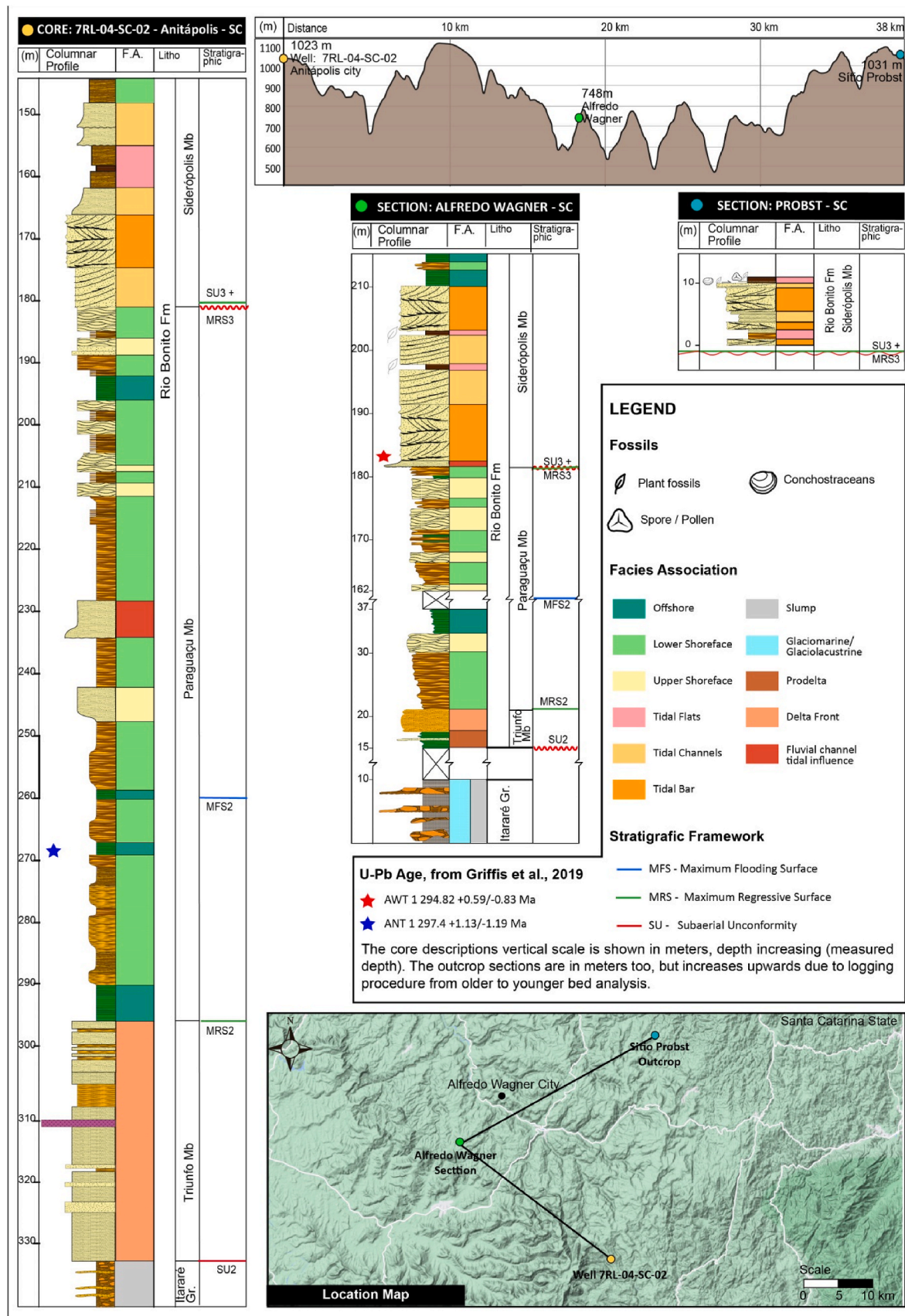
Fig. 2. Stratigraphical sections described in the municipalities of Anitápolis (well-core 7RL-04-SC-02) and Alfredo Wagner (Alfredo Wagner and Probst Outcrop), Santa Catarina State, showing the lithostratigraphic units and the limitrophe surfaces (MFS, MRS, SU) found out.

Table 1
Facies associations, descriptions and interpretations of sections analyzed in municipalities of Alfredo Wagner (Alfredo Wagner section and Probst Outcrop) and Anitápolis (well-core 7RL-04-SC-02), Santa Catarina State (SC), according to Miall (1996).

| Facies Association		Description	Interpretation
Glaciomarine or Glaciolacustrine	Slump	Diamictite with deformed lamination, irregular wavy and discontinuous bedding. Block-sized sandstone drip clasts, metric to centimeter lenses of fine sand occur	High density debris flow. Slumps and mudflows. Glacial deposits
Delta System	Prodelta	Laminated mudrocks	Distal deposits of deltaic lobes
	Delta front	Layers of fine to coarse sandstones with parallel, low-angle cross bedding, Climbing ripple cross-lamination (supercritical to subcritical) and sometimes massive	Progradation of sand bodies caused by unidirectional flows.
Estuarine System	Tidal flats	Siltstones with root marks	Overbank deposits with paleosols
	Tidal channels	Medium to coarse sandstone, with tangential and cross-bedding, cross-bedded strata and presence of mud (sometimes carbonaceous) between sets and foresets, grain thinning upward, and bed thinning upward	Bidirectional currents with a predominance of a preferential direction of higher energy. Formation of tidal channels
	Tidal bar	Coarse sandstone with large-scale cross-stratification and reverse ripples up to front face	Bidirectional sub-aqueous tractive flow, with a dominant flow separated by periods of fines decanting
	Fluvial channel with tidal influence	Medium sandstone with tangential cross-stratification with mud in the foresets, more common towards the top. The base of the succession is erosive and coarse-grained. Small ripple marks to the top of the succession opposite the stratification below	Unidirectional sub-aqueous tractive flows interspersed with fines decantation with the progressive drowning of the river valley
Marine Platform System	Offshore	Mudrocks with plane-parallel lamination and linsen bedding	Distal shelf deposits, located below the storm wave action level
	Lower Shoreface	Laminated mudrocks interbedded with fine to very fine sandstone with truncated wavy lamination. Interbedded wavy/linsen bedding. Hummocky stratification with wavy/flaser bedding	Deposits below normal wave action level and influenced by storm wave action level
	Upper Shoreface	Sandstones with truncated wavy lamination, parallel, low-angle cross-stratification. Small, medium and large wave ripples (swalley)	Deposits above the storm wave action level, formed at the normal wave action level
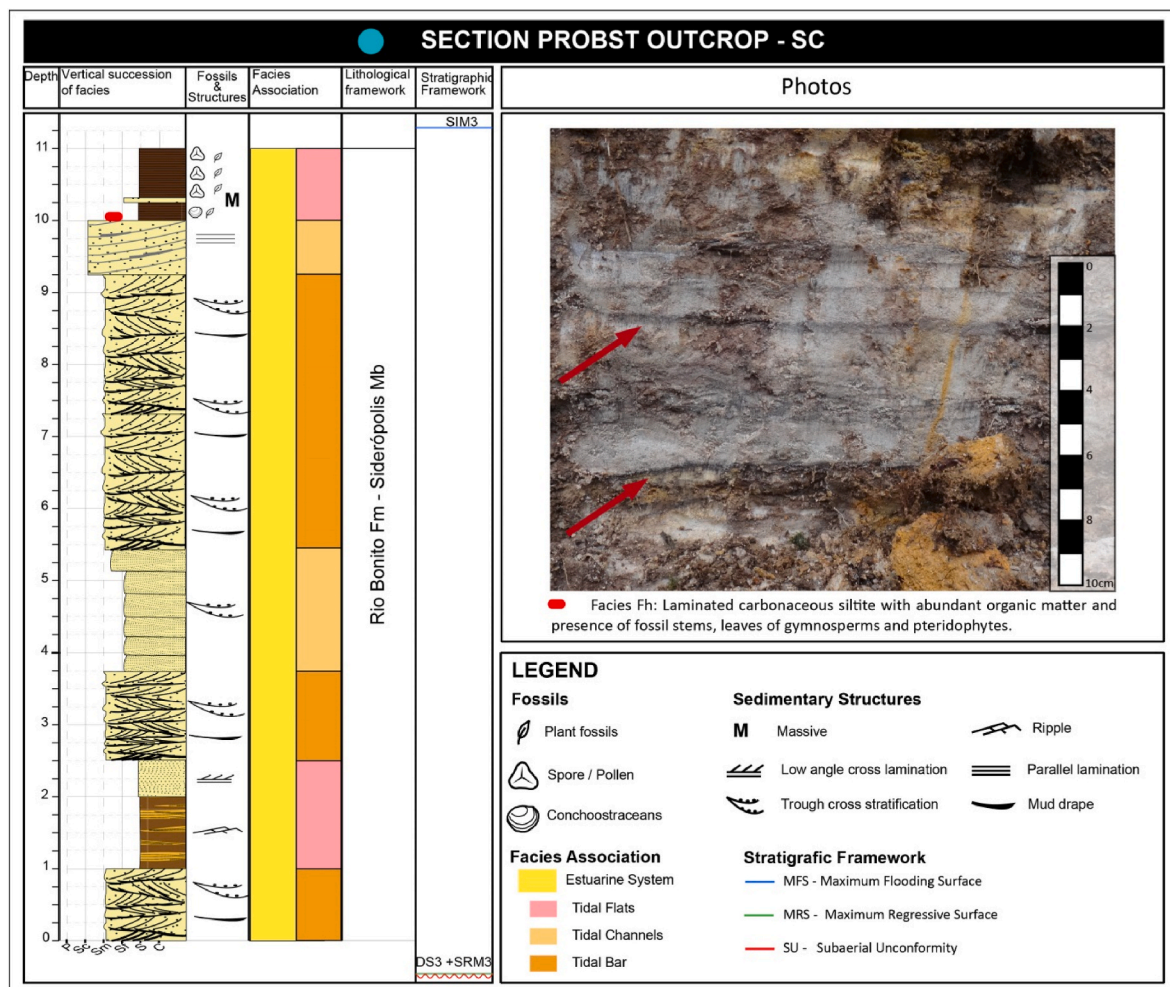
Fig. 3. Colunar section of the Probst Outcrop, in Santa Catarina State. To the right, the red arrows indicate the facies Fh.

lamination and linsen bedding to sandstones with plane-parallel bedding, low angle cross and truncated wavy lamination. Small, medium and large wave ripples (swalley) are sometimes observed (Fig. 2, Table 1).

The Siderópolis Member in the Alfredo Wagner section is well-characterized by fine to medium sandstones interspersed with flat-parallel lamination carbonaceous shales and coal lenses (more concentrated at the top section), high angle cross stratified coarse sandstones with mud drapes featuring sandy macroforms of bars and tidal channels. At the base of the interval, the contact between Paraguaçu and Siderópolis Members observed as an abrupt lithological change with erosive entry of tidal-influenced river channels followed by the installation of an estuarine system just above the wave-dominated platform (Fig. 2, Table 1).

Considering the description of the succession and interpretation of facies above (Table 1), and the identification of the main surfaces that represent the limits of stratigraphic sequences (i.e. MFS, MRS, SU), it was possible to establish a straight and reliable correlation between the Alfredo Wagner section and the well 7RL-04-SC-02 (Fig. 2).

The Probst Outcrop itself correspond to a relatively thin rocky exposure about 12 m thick and it is characterized by fine to medium sandstones interspersed with carbonaceous shales and very thin coal lenses (more concentrated at the top) with flat-parallel lamination, high angle and wavy stratification and mud drapes featuring sandy macroforms of tidal bars channels and tidal flats (Fig. 3, Table 1). However, these facies, facies association and architectural elements occurring in this outcrop are very similar to strata from the Siderópolis Member described in the Alfredo Wagner outcrop and the well-core 7RL-04-SC-02, that have been interpreted as a tidal-influenced estuarine system and were not assigned in the other two members described in the more complete sections of Alfredo Wagner and well-core 7RL-04-SC-02 (Fig. 2). Unfortunately, neither basal (contact with the Paraguaçu Member) or top (contact with the Palermo Formation) with other units outcrops in the vertical exposure was not observed (Figs. 2 and 3). Therefore, a correlation between Probst Outcrop and Siderópolis Member as defined in Alfredo Wagner area is proposed.

5.2. Paleobotany

Among the analyzed samples, compressions and impressions of different parts or organs of plants are preserved detached (isolated) and dispersed on the bedding planes of the fossiliferous layers at the Probst Outcrop. Among them, *Glossopteris* leaves are the more common and diversified whereas the remaining taxa mentioned below are represented by a single specimen each, except for lycopsids and ferns. Three distinct lycopsids remains (one type of microphyll and two of stems), two compound-leaves of ferns, an sphenopsid ilustrated for the first time for this portion of the basin (i.e., *Sphenophyllum* cf. *S. brasiliensis*), an specimen identified as *Gangamopteris* sp, seven species of *Glossopteris*, and reproductive portions associated with glossopterids, such as *Arberiopsis* sp. and *Fertiliger* sp, in addition to cordaitalean leaves (i.e., *Cordaites hislopii*) and allied forms as *Cheirophyllum* sp, and four types of seeds and a probably seedling were recovered (Figs. 4–6 and Table 2).

5.3. Palynology

The 12 palinological samples yielded well-to very well-preserved forms (Table 3), including 28 species of trilete spores (54% in the assemblage) and 24 pollen grains (46%) illustrated in Figs. 7–9. Taxonomic designations are based on numerous works from South America and elsewhere (e.g. Azcuy and di Pasquo, 2000; di Pasquo and Grader, 2012; di Pasquo et al., 2021, and references in those papers). In terms of diversity of botanical groups, spores document the presence of lycophytes (*Cristatisporites, Gondisporites, Lundbladispora*), sphenophytes (*Calamospora*) and ferns (*Brevitriletes, Convolutispora, Cyclogranisporites, Horriditriletes, Leiotriletes, Lophotriletes, Verrucosisporites*). Among pollen

grains of gymnosperms, cordaitalean and coniferalean are represented by 10 species of monosaccate (*Cannanoropollis, Caheniasaccites, Potonieisporites, Plicatipollenites*) whereas another 12 species of striate and non-striate bisaccate taxa (*Alisporites, Chordasporites, Illinites, Lunatisporites, Platysaccus, Protohaploxypinus Pteruchipollenites, Scheuringipollenites, Striatopodocarpites, Vittatina, Vitreisporites*) indicate coniferalean as well as glossopterids, corystosperms and peltasperms. Cycadophyta and Ginkgophyta complete the assemblages with monosulcoid non-taeniate pollen of *Cycadopites*. The most frequent forms are *Punctatiporites gretensis, Lundbladispora brazilienis, Alisporites ovatus, Vitreisporites signatus* and *Pteruchipollenites indarraensis*, in which the latest three are, together with *Cycadopites cymbatus, Punctatisporites subvaricosus, Gondisporites serrulatus, Didecitriletes* sp. and *Chordasporites* sp., registered for the first time in the Rio Bonito Formation, and because of this briefly described below. The paleoenvironmental importance of botanical groups is addressed in section 6.4 of Discussion.

6. Discussion

Several biostratigraphical frameworks have been suggested and updated for the late Paleozoic in the Paraná Basin. Once the analyzed material is characterized by very well-preserved and abundant palynomorphs and macrophytofossils, in which the majority of the specimens were classified in specific level, statistical methodologies were undertaken to establish a better comparison and correlation with selected phyto- and palyno assemblages of Brazil and elsewhere in South America. Estimated age of our flora obtained from recent radiometric datings of nearby sections is also addressed below.

6.1. U–Pb zircon age-constraints

An important age-constraint for our studied macro- and microfloras at Probst Outcrop, in Alfredo Wagner area, was provided by Griffis et al. (2019), who studied a volcaniclastic layer sample (see age marker 6 in their Fig. 1) between two fluvial sandstones at the lowermost part of the Siderópolis Member giving a minimum age of 294.82 + 0.59/-0.83 Ma (Fig. 2). However, Griffis et al. (2019) calculated an age of 294.77 + 0.72/-0.67 Ma, using the youngest zircon algorithm (only two reproduced early Permian ages). In addition, those authors reported a Bayesian model age of 294.82 + 0.59/-0.83 Ma, consistent with the latter age, which they interpret as the age of this deposit (Table A1 in Griffis et al., 2019). Therefore, due to the limited number of analysis from this sample as a result of limited sample material, this age should be used cautiously as younger grains may exist but may not be represented in the analyzed zircons. In southern Brazil, an erosional unconformity SB-3 separates offshore mudstones of the Paraguaçú Member from nearshore heterolithic mudstones, fluvial sandstones, and coals of the Siderópolis Member (Holz et al., 2006; Iannuzzi et al., 2010).

Other U–Pb zircon CA-TIMS obtained from volcaniclastic layers within the lowermost Paraguaçu Member (= Triunfo Member in Griffis et al., 2019) of the Rio Bonito Formation by Griffis et al. (2019) yielded ages of 297.4 + 1.13/-1.19 Ma (sample ANT1 from well 7RL-04-SC-02–Anitápolis; age marker 5 in their Fig. 1) (see Fig. 2). A regional sequence boundary SB-2 (and SB 1 + 2; Fig. 1 in Griffis et al., 2019) with the Taciba Formation (Itararé Group) confirmed a pre-Carboniferous-Permian Boundary deglaciation age (298.9 Ma) for all glacial deposits in the southern to southeastern Paraná Basin (Cagliari et al., 2016; Griffis et al., 2019). These volcaniclastics indicate that inferred base-level fall was synchronous across the south to southeastern Paraná Basin (Griffis et al., 2019).

Considering the U–Pb radiomeric age of 294.82 + 0.59/-0.83 Ma obtained in the most basal part of the Siderópolis Member by Griffis et al. (2019), the terrigenous nature of deposits, the thickness of only about 30–40 m of this unit in the Alfredo Wagner area (Fig. 2), and palynological data akin to the *Vc* Zone, which spans from the Gzhelian to Sakmarian/Artinskian (ca. 20 Ma - see Souza et al., 2021), the
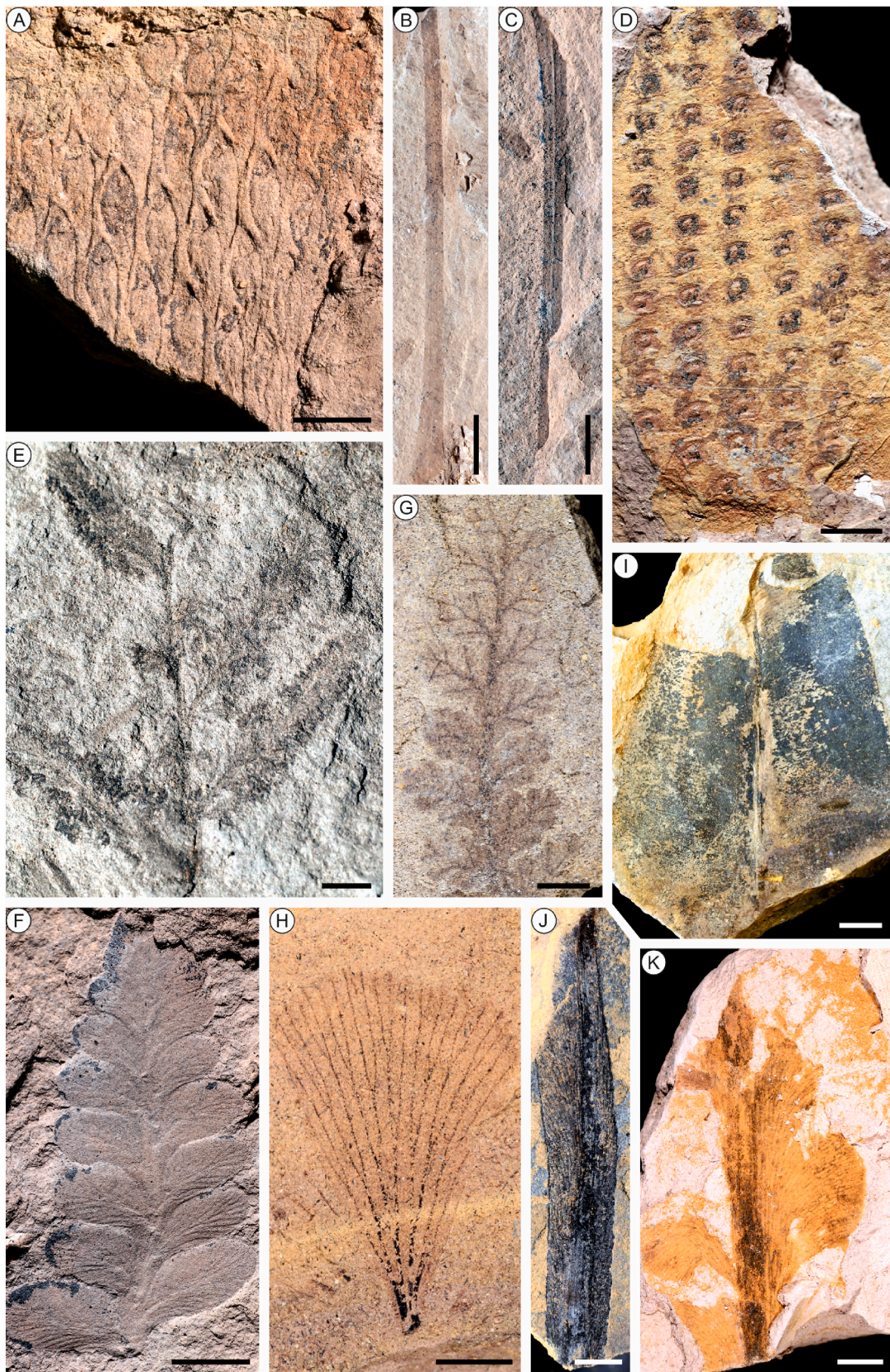
Fig. 4. A. *Brasilodendron* sp. MP-Pb 5512. Scale bar = 10 mm. **B.** Lycophyte microphyll. MP-Pb 5513. Scale bar = 5 mm. **C.** Lycophyte microphyll. MP-Pb 5514. Scale bar = 5 mm. **D.** *Lycopodiopsis* sp. MP-Pb 5515. Scale bar = 5 mm. **E.** *Pecopteris* cf. *pedrasica.* MP-Pb 5516. Scale bar = 5 mm; **F.** *Pecopteris pedrasica.* MP-Pb 5517. Scale bar = 5 mm. **G.** *Sphenopteris* sp. MP-Pb 5518. Scale bar = 2 mm. **H.** *Sphenophyllum* cf. *S. brasiliensis.* MP-Pb 5519. Scale bar = 5 mm. **I.** *Glossopteris occidentalis.* MP-Pb 5520. Scale bar = 10 mm. **J.** *Glossopteris angustifolia.* MP-Pb 5521. Scale bar = 5 mm. **K.** *Glossopteris browniana.* MP-Pb 5522. Scale bar = 5 mm.

Fig. 5. A. *Glossopteris communis.* MP-Pb 5523. Scale bar = 10 mm. **B**. *Glossopteris longicaulis.* MP-Pb 5524. Scale bar = 10 mm. **C**. *Glossopteris ampla.* MP-Pb 5525. Scale bar = 5 mm. **D**. *Glossopteris* ampla. MP-Pb 5526. Scale bar = 5 mm. **E**. *Glossopteris indica.* Arrows indicating herbivory marks. MP-Pb 5527. Scale bar = 5 mm. Scale bar = 10 mm. **F**. *Gangamopteris* sp. MP-Pb 5528. Scale bar = 5 mm.**G**. *Arberiopsis* sp. MP-Pb 5529. Scale bar = 5 mm.**H**. *Fertiliger* sp. MP-Pb 5530. Scale bar = 5 mm.
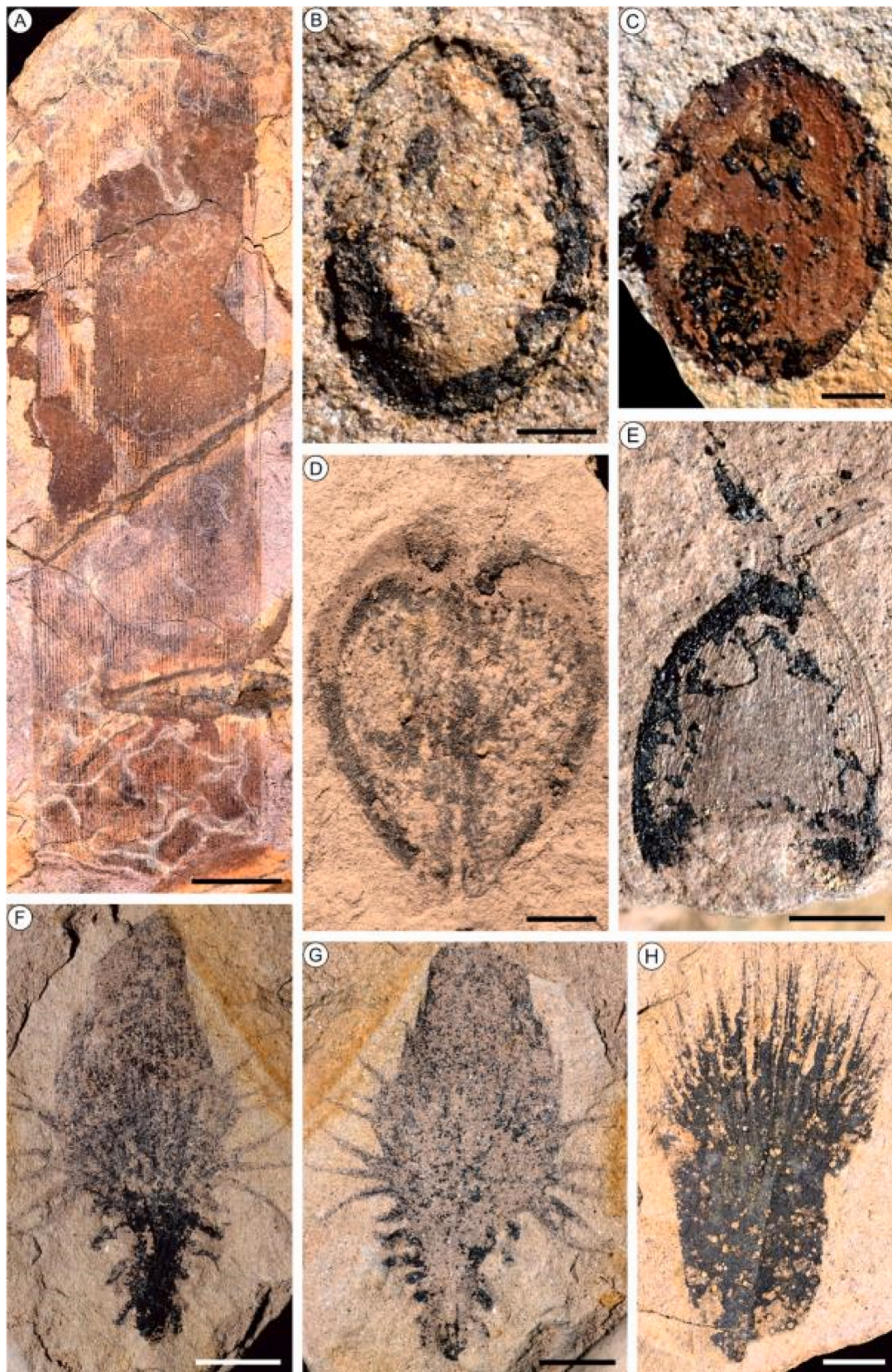
Fig. 6. A. Cordaites *hislopii*. MP-Pb 5531. Scale bar = 10 mm. **B**. *Cordaicarpus brasilianus*. MP-Pb 5532. Scale bar = 1 mm. **C**. *Cordaicarpus brasilianus*. MP-Pb 5533. Scale bar = 1 mm. **D**. *Cornucarpus patagonicus*. MP-Pb 5534. Scale bar = 5 mm. **E**. *Samaropsis mendesii*. MP-Pb 5535. Scale bar = 1 mm. **F**. Seedling. MP-Pb 5536. Scale bar = 5 mm.**F**. Seedling. MP-Pb 5537. Scale bar = 5 mm. **H**. *Cheirophyllum* sp. MP-Pb 5538. Scale bar = 5 mm.

Table 2

Plant taxa identified in the fossiliferous horizons of the Probst Outcrop, in municipality of Alfredo Wagner (SC).

Plant groups	
Lycopsida	***Brasilodendron*** cf. ***B. pedroanum*** Chaloner, Leistikow et Hill 1979 (Fig. 4, A)
	Lycopsid microphylls (Fig. 4, B–C)
	***Lycopodiopsis* sp.** (Fig. 4, D)
Filicopsida	***Pecopteris*** cf.***pedrasica*** (Fig. 4, E)
	Pecopteris pedrasica Read emend. Vieira, Iannuzzi et Guerra-Sommer 2007 (Fig. 4, F)
	***Sphenopteris* sp.** (Fig. 4, G)
Sphenopsida	***Sphenophyllum*** cf. ***S. brasiliensis*** Rösler 1974 (Fig. 4, G)
Glossopteridales	***Glossopteris occidentalis*** (White) emend. Tybusch et Iannuzzi (2010) (Fig. 4, I)
	Glossopteris angustifolia Brongniart 1828 (Fig. 4, J)
	Glossopteris browniana Brongniart 1828 (Fig. 4, K)
	Glossopteris communis Feistmantel 1876 (Fig. 5, A)
	Glossopteris longicaulis Feistmantel 1881 (Fig. 5, B)
	Glossopteris ampla Dana 1849 (Fig. 5, C-D)
	Glossopteris indica Schimper 1869 (Fig. 5, E)
	***Gangamopteris* sp.** (Fig. 5, F)
Cordaitales	***Cordaites hislopii*** Seward 1917 (Fig. 6, A)
Incertaesedis	***Cheirophyllum* sp.** (Fig. 6, H)
Reproductive organs	***Arberiopsis* sp.** (Fig. 5, G)
	***Fertiliger* sp.** (Fig. 5, H)
Seedsandalliens	***Cordaicarpus brasilianus*** Bernardes-de-Oliveira, Castro-Fernandes, Tewari et Ricardi-Branco 2007 (Fig. 6, B–C)
	Cornucarpus patagonicus (Feruglio) Correa da Silva et Arrondo 1977 (Fig. 6, D)
	Samaropsis mendesii Rigby emend. Marques-de-Souza et Iannuzzi 2016 (Fig. 6, E)
	Seedling (Fig. 6, F-G)

Siderópolis Member at Alfredo Wagner is attributed to the late Asselian. Accordingly, it is possible to suggest a latest Asselian age for the Probst Outcrop associations analyzed here, close to the Sakmarian age boundary (293.52 ± 0.17 Ma), as per the current Geological Time Scale (Cohen et al., 2013).

6.2. Phytostratigraphy

In terms of new occurrences, forms attributed to the genera *Lycopodiopsis* and *Cheirophyllum* are recorded for the first time in the Early Permian of the state of Santa Catarina. Compressed *Lycopodiopsis*-like stems are quite common in the Teresina Formation, Guadalupian of the Paraná Basin (Rohn and Rösler, 2000), but never have been recovered in deposits from the Cisuralian, despite the fact that one of the authors recognized its presence at the top of the Itararé Group towards the north of the basin, in the state of São Paulo (unpublished data, RI comm. pers.). *Cheirophyllum*-type laminated organs (leaves? bracts?) had been assigned only in the earliest Permian strata from the top of the Itararé Group, further south of the basin, in the state of Rio Grande do Sul, so far (Silva and Iannuzzi, 2000; Iannuzzi et al., 2007). This genus was also recognized in the earliest Permian strata from the Paganzo Basin (Bajo de Véliz), in northwestern Argentina (Césari and Cúneo, 1989).

Sphenopsid slender stems supporting *Sphenophyllum*-type leaves were previously recorded in (i) the Pennsylvanian strata of the Itararé Group, in São Paulo (Bernardes-de-Oliveira et al., 2016b), (ii) in the Cisuralian of the Rio Bonito Formation, in Paraná and Santa Catarina (Iannuzzi, 2010), and mainly (iii) in the Guadalupian deposits of the Rio do Rasto Formation, in Paraná and Santa Catarina states (Rohn and Rösler, 2000). Recently, *Sphenophyllum* leaves were found at the top of the Rio Bonito Formation (i.e. Siderópolis Member), in the extreme south of the state of Santa Catarina, but these fossils remain unpublished (RI comm. pers.). The specimen attributed to genus *Sphenophyllum* collected from the Probst Outcrop was preliminarily mentioned by Iannuzzi (2010, p. 240), but is being shown for the first time here named as *Sphenophyllum* cf. *S. brasiliensis* (Fig. 4H).

From the point of view of key species for biostratigraphy, there are

Table 3

Palino taxa identified in the fossiliferous horizons of the Probst Outcrop, in municipality of Alfredo Wagner (SC).

Palinomorphs	
Spores	***Brevitriletes cornutus*** (Balme et Hennelly) Backhouse 1991 (Fig. 7, A)
	Brevitriletes levis (Balme et Hennelly) Bharadwaj et Srivastava 1969 (Fig. 7, B)
	Calamospora liquida Kosanke 1950 (Fig. 7, C)
	Convolutispora ordonensis Archangelsky e tGamerro 1979 (Fig. 7, D)
	***Convolutispora* sp.** (Fig. 7, E)
	Cyclogranisporites gondwanensis (Leschik) Ybert 1975 (Fig. 7, F-G)
	Cyclogranisporites minutus Bharadwaj 1957 (Fig. 7, H)
	Cristatisporites morungavensis (Fig. 7, I)
	***Didecitriletes* sp.** (Fig. 7, J)
	This specimen is very similar to *Didecitrilete sericianus* presented by Foster (1979)
	Gondisporites serrulatus Césari, Archangelsky et Seoane 1995 (Fig. 7, K)
	Sub circular trilete spore, ornamented exine. Laesurae distinct, straight, thin, reaching the equator margin. Exine ornamented by granules approximately 1 μm in diameter, irregularly scattered.
	Gondisporites wilsoni Backhouse 1988 (Fig. 7, L)
	Granulatisporites varigranifer Menéndez et Azcuy 1971 (Fig. 7, M)
	Triangular trilete spore, straight sides, rounded apices, ornamented by granules 1–2 μm in diameter, densely and regularly scattered. Trilete mark almost reaching the equatorial margin. There is no record of this species in the Rio Bonito Formation.
	Granulatisporites austroamericanus Archangelsky et Gamerro 1979 (Fig. 7, N)
	Horriditriletes curvibaculosus Bharadwaj et Salujha 1964 (Fig. 7, O)
	Horriditriletes ramosus (Balme et Hennelly) Bharadwaj et Salujha 1964 (Fig. 7, P)
	Leiotriletesvirkii Tiwari 1965 (Fig. 7, Q)
	Lophotriletes rectus Bharadwaj et Salujha 1963 (Fig. 7, R)
	Lophotriletespseudo aculeatus Potonié et Kremp 1955 (Fig. 7, S)
	Lundbladispora areolata Césari, Archangelsky et Seoane 1995 (Fig. 7, T)
	Lundbladispora riobonitensis Marques-Toigo et Picarelli 1984 (Fig. 7, U)
	Lundbladispora brasiliensis (Pant et Srivastava) *emend.* Marques-Toigo & Pons 1976 (Fig. 8, A)
	Murospora bicingulata Ybert 1975 (Fig. 8, B)
	Punctatisporites gretensis Balme et Hennelly 1956 (Fig. 8, C)
	Punctatisporites subvaricosus Playford 1971 (Fig. 8, D-E)
	Circular trilete spore, laevigate exine. Laesurae very distinct, straight, very wide, of approximately 10 μm, reaching approximately 4/5 of the spore radius. There is no record of this species in the Rio Bonito Formation.
	Retusotriletes nigritellus (Lüber) Foster, 1979 (Fig. 8, F)
	Retusotriletes golatensis Staplin 1960 (Fig. 8, G)
	Secarisporites triangularis Gutiérrez, Zavattieri et Ezpeleta 2017 (Fig. 8, H)
	1995 *Granulatisporites absonus* Foster 1975 (auct. non); Quadros et al., p. 58.
	Triangular trilete spore, slight concave sides, rounded apices. Trilete mark reaching the equatorial diameter. This specimen is attributed to *Secarisporites* due to the separation of two walls (camerate), ornamentation composed of baculae (1–2 μm high, 1–1.5 μm wide) and verrucae (1–1.5 μm high, 2–3 μm wide), densely and regularly scattered. Few ornaments are present in the equator and are reduced proximally. Amb of exoexine and central body (intexine) are triangular. There is no previous records of this species in the Rio Bonito Formation, except by the illustrated specimen in Quadros et al. (1995, p.58), but without precise geo-stratigraphical information. Comparison. Our taxon is closely similar to *Secarisporites triangularis* Gutiérrez et al. (2017), a camerate spore having small verrucae (in general less than 2 μm in width), mainly spherical to globular in shape and polygonal in less proportion. There is no record of this species in the Paraná Basin.
	***Spelaeotriletes* sp.** (Fig. 8, I)
	Verrucosisporites verrucosus (Fig. 8, J)
Pollen	***Alisporites ovatus*** (Balme et Hennelly) Jansonius 1962 (Fig. 8, K-L)
	Bisaccate pollen grain, haploxylonoid to very slightly diploxilonoid, sulcate. Central body elliptical to rhomboidal vertically. Sacci semicircular, slightly greater them the central body, forming a

(continued on next page)

Table 3 (*continued*)

cappula parallel-sided, overlapping approx. 5/6 of central body. di Pasquo and Grader (2012) have considered Alisporites nuthalensis Clarke 1965 and *A. splendens* (Leschik) Foster (1979) as junior synonyms of *Alisporites ovatus*. This interpretation is followed here. There is no record of this species in the Rio Bonito Formation.
Cannanoropollis densus (Lele) Bose et Maheshwari 1968 (Fig. 8, M) Monosaccate pollen grain, central body circular, well defined and dense (very dark). Sacci folded, overlapping approximately 1/2 of central body and forming an elliptical cappa. Monolete mark straight, reaching 1/2 of the equatorial diameter. This species is smaller in comparison to *C. perfectus*and *C. janakii*.
Cannanoropollis perfectus (Bose et Maheshwari) emend. Dias-Fabrício 1981 (Fig. 8, N)
Cannanoropollis janakii (BharadwajetTiwari) Foster 1975 (Fig. 8, O)
Caheniasaccites elongatus Bose et Kar 1966 (Fig. 9, A)
Caheniasaccites flavatus Bose et Kar 1966 (Fig. 9, B–C)
***Chordasporites* sp.** (Fig. 9, D)
Cycadopites cymbatus (Balme et Hennelly) Hart (1965) (Fig. 9, E-F)
Monosulcate pollen grain, elliptical amb, laevigate exine. Sulcus extending full length, narrower medially. There is no record of this species in the Rio Bonito Formation.
Illinites unicus (Kosanke) emend. Jansonius et Hills 1976 (Fig. 9, G-H)
Lunatisporites variesectus Archangelsky et Gamerro 1979 (Fig. 9, I)
Platysaccus globosus (Leschik) Millsteed 1999 (Fig. 9, J)
Platysaccusles chikii Hart 1960 (Fig. 9, K)
Plicatipollenites malabarensis (Potonié et Sah) Foster 1975 (Fig. 9, L)
Plicatipollenites trigonalis Lele 1964 (Fig. 9, M)
Plicatipollenites gondwanensis (Balme et Hennelly) Lele 1964 (Fig. 9, N)
Potonieisporites lelei Maheshwari 1967 (Fig. 9, O–P)
Potonieisporite smethoris (Hart) Foster 1975 (Fig. 9, Q)
Protohaploxypinus perexiguus (Bharadwaj et Salujha) Foster (1979) (Fig. 9, R)
Protohaploxypinus perfectus (Naumova) Samoilovich 1953 (Fig. 9, S)
Pteruchipollenites indarraensis (Segroves) Foster (1979) (Fig. 9, T-U)
Bisaccate pollen grain, haploxylonoid, central body subcircular transversally. Saccisemi-circular, slightly greater them the central body forming a cappaparallel-sided, overlapping 3/4–2/3 of the central body. There is no record of this species in the Rio Bonito Formation.
Scheuringipollenites medius (Burjack) Dias-Fabrício 1981 (Fig. 9, V–W)
Striatopodocarpites fusus (Balme et Hennelly) Potonié 1958 (Fig. 9, X)
Vitreisporites signatus Leschik 1955 (Fig. 9, Y-Z) Bisaccate pollen grain, haploxylonoidto slightly diploxylonoid, central body circular to slightly subcircular. Sacci semicircular, slightly bigger them the central body, forming a concave cappa, overlapping 1/3–1/4 of central body. There is no record of this species in the Rio Bonito Formation.***Vittatina costabilis*** Wilson 1962 (Fig. 9, AA)

few taxa in the Probst Outcrop association that can be useful for this purpose, since most of them present relatively wide stratigraphic ranges, especially those of *Glossopteris* (Table 2). Among the helpful ones, *Sphenophyllum brasiliensis* occurs restricted to basal portions of the Rio Bonito Formation, i.e. Triunfo Member, in the state of Paraná (Iannuzzi, 2010), as well as *Pecopteris pedrasica*, which also appears more abundantly in these same deposits in Paraná. Although, the latter species was also recently identified at the top of the Siderópolis Member, upper third of the Rio Bonito Formation in southern Santa Catarina (Zardo, 2020). The species *Cornucarpus patagonicus* is restricted to the deposits from the top of the Itararé Group in the state of Rio Grande do Sul, probably earliest Permian in age (Iannuzzi et al., 2010). This seed species was also found in strata considered to be from the beginning of the Permian in the Argentinean Paganzo and Tepuel-Genoa basins (Archangelsky, 2000).

In conclusion, the presence of *Cheirophyllum* sp. and *Cornucarpus patagonicus*, associated with *Sphenophyllum* cf. *S. brasiliensis* and *Pecopteris pedrasica*, suggest an intermediate biostratigraphic position of the Probst Outcrop plant association, in between those known from the top of the Itararé Group, in the state of Rio Grande do Sul, and those recovered mainly from the base of the Rio Bonito Formation, in the state of Paraná.

Using the most recent scheme by Iannuzzi and Souza (2005), in which the two mentioned taxa were already described, it can be seen that the abundance of *Glossopteris* leaves and the presence of pecopterid ferns and sphenophylls allow us to insert the association of the Probst Outcrop into the *Glossopteris-Brasilodendron* Flora. However, taxa such as *Cheirophyllum* and *Cornucarpus* would be typical and restricted to the underlying *Phyllotheca-Gangamopteris* Flora, as originally proposed by Iannuzzi and Souza (2005). Therefore, the occurrence of these two taxa indicates that we could be in the most basal portion of the *Glossopteris-Brasilodendron* Flora range.

6.2.1. Statistical correlations among paleofloras in Brazil

Considering the scarcity of taxa useful for biostratigraphy in the association of the Probst Outcrop, it was decided to use a cluster analysis, an approach that has been recurrently used in palynological studies to facilitate the comparison of palyno-associations among themselves, given that these are usually much richer than those composed of plant macro-remains. Hence, it is used for the first time here to compare this plant association with paleofloras from the Asselian-Artinskian interval of the Paraná Basin. To perform this analysis, paleofloras preserved as compression-impressions are chosen, to be comparable with the present association, which occur along the east margin of the basin being stratigraphically distributed from the upper portion of the Itararé Group to the top of the Rio Bonito Formation (Supplementary online material #1).

A cluster analyses using Unweighted Pair Group method with Arithmetic Mean (UPGMA) and Jaccard similarity index of 11 major paleofloras yielded a dendogram of three groups (clusters) consistent with the existing chronostratigraphic framework (Fig. 10) discussed below. The use of the UPGMA method and the Jaccard index are highly recommended in cases where the analyzed associations are constituted by few taxa, as in the present case, as they are simpler and more objective methods of analysis where binary data are used to compare finite sample sets (Legendre and Legendre, 2012). Futhermore, Jaccard index is less sensitive to taxa with high relative abundance in associations (Chao et al., 2005).

One of the clusters that stands out is basically constituted by three paleofloras positioned at the top of the Itararé Group, located in states of São Paulo and Rio Grande do Sul, i.e. Cerquilho, Morro do Papaléo (Itararé Gr, lower part) and Morro do Papaléo (Itararé Gr, upper part) (Fig. 10). This result is coherent, as they all supposedly occur within the same stratigraphic interval (Iannuzzi and Souza, 2005). The similarity between these floras is mainly based on the presence of *Stephanophyllites sanpaulensis*, *Arberia* sp. and some species of *Gangamopteris*, but also *Botrychiopsis plantiana*, *Cheirophyllum* sp. and *Kawizophyllum* sp, especially for the two floras of Morro do Papaléo, in south of the basin. Also positioned inside this cluster, it is the flora of Quitéria that belongs to the Rio Bonito Formation, in Rio Grande do Sul. Despite being somewhat dissimilar to the other three associations of the Group Itararé, there are elements in common such as *Botrychiopsis plantiana*, *Arberia* sp, *Arberiopsis* sp, *Rhodeopteridium* sp. and some species of *Gangamopteris*. Recent radiometric dating of the fossiliferous layers of the Quitéria outcrop yielded an age of $297 + 0.45/-0.72$ Ma (Griffis et al., 2018) corresponding to the early Asselian (according to Cohen et al., 2013, updated). This age was expected for the occurrence of the floras at the top of the Itararé Group and base of Rio Bonito Formation, according to palynological data (Holz et al., 2010). Therefore, these four paleofloras sharing the above-mentioned guide taxa would be considered chrono-correlated (Fig. 10).

The second cluster gathers our Probst Outcrop flora and another from the Rio Bonito Formation at the top of the Morro do Papaléo section (Fig. 10) due to sharing several taxa such as *Brasilodendron*,
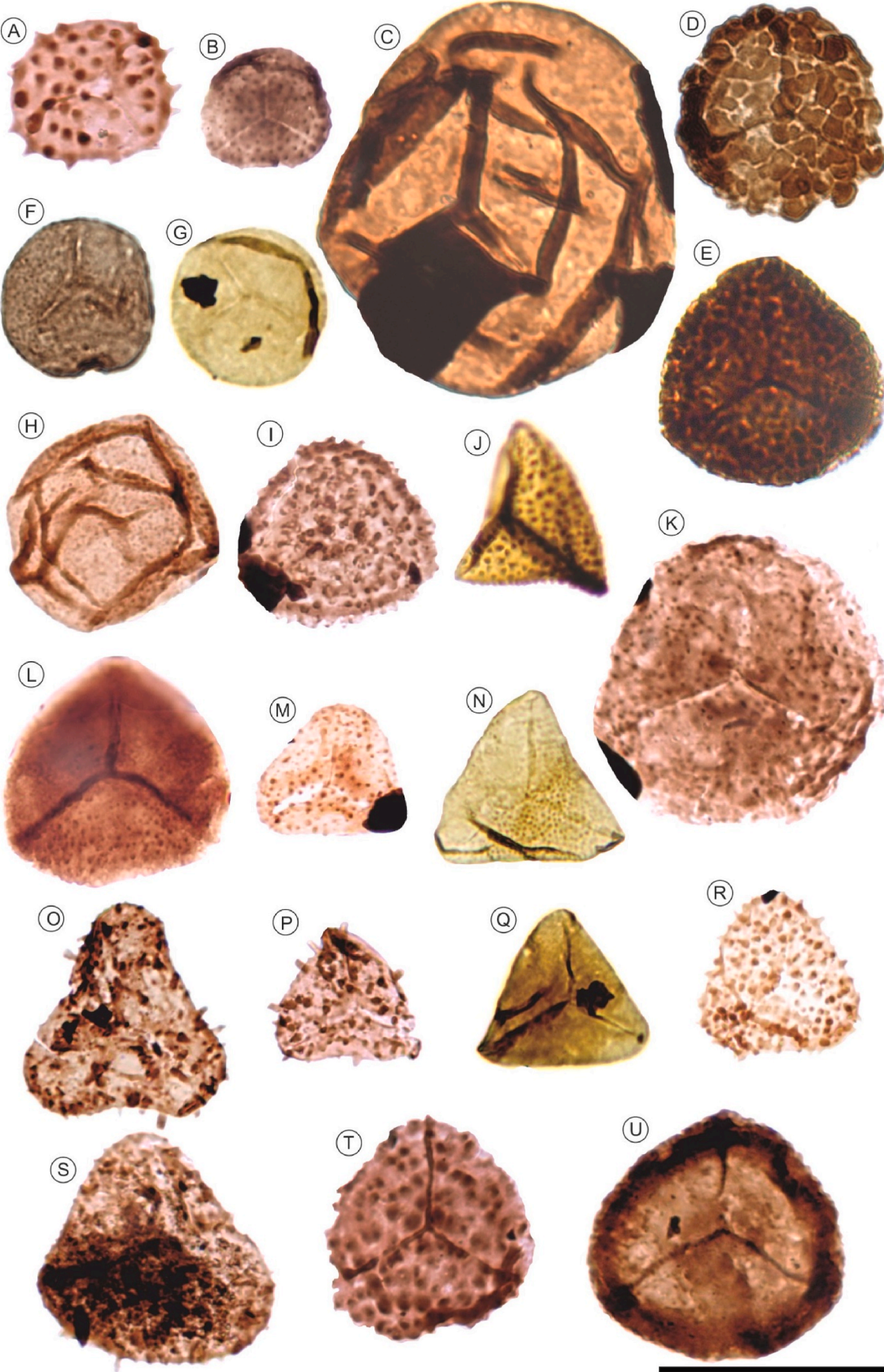
(caption on next page)

Fig. 7. **A**. *Brevitriletes cornutus*. Slide MP-P 14.909, EF X 25/3. **B**. *Brevitriletes levis*. Slide MP-P 14.911, EF S 17/4. **C**. *Calamospora liquida*. Slide MP-P 14.910, EF U 16/4. **D**. *Convolutispora ordonensis*. Slide MP-P 14.909, EF P 20/1. **E**. *Convolutispora* sp. Slide MP-P 14.907, EF M 16/4.**F**. *Cyclogranisporites gondwanensis*. Slide MP-P 14.911, EF W26/2. **G**. *Cyclogranisporites gondwanensis*. Slide MP-P 14.910, EFW 22/4. **H**. *Cyclogranisporites minutus*. Slide MP-P 14.909, EF J 17/4. **I**. *Cristatisporites morungavensis*. Slide MP-P 14.911, EF J 31/0.**J**. *Didecitriletes* sp. **K**. *Gondisporites serrulatus*. Slide MP-P 14.908, EF W 16/4. **M**. *Granulatisporites varigranifer*. Slide MP-P 14.908, EF F 31/0. **N**. *Granulatisporites austroamericanus*. Slide MP-P 14.909, EF J 24/2. **O**. *Horriditriletes curvibaculosus*. Slide MP-P 14.909, EF L 30/0. **P**. *Horriditriletes ramosus*. Slide MP-P 14.908, EF J 16/3. **Q**. *Leiotriletes virkkii*. Slide MP-P 14.908, EF U 22/3. **R**. *Lophotriletes rectus*. Slide MP-P 14.909, EF E 33/0. **S**. *Lophotriletes pseudoaculeatus*. Slide MP-P 14.908, EF K 28/0.**T**. *Lundbladispora areolata*. Slide MP-P 14.911, EF T 31/1.**U**. *Lundbladispora riobonitensis*. Slide MP-P 14.908, EF W22/0. **Scale bar** = 50 μm.

Pecopteris pedrasica, *Sphenopteris*, *Glossopteris indica*, *G. occidentalis*, *Cordaicarpus brasilianus* and *Samaropsis mendesii*. Interestingly, none of those taxa are exclusive to these two floras nor can they be considered as guide taxa, as they have wide stratigraphic range and extend either to the floras positioned below or above them. Despite this, the latest Asselian age attributed to the paleoflora of the Probst Outcrop is in agreement with the age of the Rio Bonito Formation at the top of Morro do Papaléo.

The last cluster (Fig. 10) is composed of four paleofloras belonging to the Rio Bonito Formation, namely: Figueira and São João do Triunfo (Paraná state), and Irapuá and Lauro Müller (Santa Catarina state). The main reason they are grouped is due to sharing the following taxa: *Pecopteris pedrasica*, *Glossopteris browniana*, *Buriadia* sp, and mainly *Paracalamites australis* and *Sphenopteris lobifolia*. The last taxon is exclusive of the cluster, and furthermore, there are two well-defined subgroups in this cluster, one formed by Figueira and São João do Triunfo floras, and another one by Irapuá and Lauro Müller. The former is characterized by the presence of *Annularia* spp. and *Sphenophyllum brasiliensis*, while the latter by the co-occurrence of *Phyllotheca griesbachii*. Still, Irapuá and Lauro Müller share some other taxa that are commonly documented in other paleofloras, such as *Glossopteris ampla*, *G. occidentalis*, *Arberia* sp, *Cordaites* spp. and *Samaropsis mendesii*. Among the paleofloras in this cluster, only Figueira has a radiometric age of 286 ± 3 Ma obtained from an underlying tonstein of this flora (Jurigan et al., 2019), equivalent to middle Artinskian according to Cohen et al. (2013). Based on that, an approximately similar age, i.e. middle Artinskian can be suggested for the other paleofloras present in this group (Fig. 10).

Finally, the paleoflora of Mina do Faxinal is the most dissimilar among the analyzed floras, as it shares very few taxa with the others, except for the presence of a few species of *Glossopteris*, such as *G. communis*, *G. indica* and *G. occidentalis*, and other extremely common genera such as *Ottokaria*, *Cordaicarpus* and *Cordaites* (see supplementary online material #1). On the other hand, this flora has several exclusive taxa, such as ovulate-fructification *Plumnstedia* and *Glossopteris* species based on cuticular anatomy, which are not comparable to others (and therefore not included in the data matrix). In this way, this flora appears in a separate branch like being an outgroup in the cluster analysis (Fig. 10). Interestingly, from the fossiliferous *tonstein* layer an age of 285.4 + 1.2/-2.1 Ma (ID-TIMS) was obtained by Griffis et al. (2018), which corresponds to the youngest ever recorded for the Rio Bonito Formation (= late Artinskian, according to Cohen et al., 2013 updated), and supports the taxonomic difference in relation to the others analyzed herein.

6.2.2. Stratigraphical considerations

Schneider et al. (1974) when defining the tripartite division into members of the Rio Bonito Formation did not extend it to the deposits of the state of Rio Grande Sul, where the strata of this formation remain undivided until today (Iannuzzi, 2010; Holz et al., 2010). Thus, any proposed correlations between the phytofosilliferous sections belonging to the Rio Bonito Formation found in Rio Grande do Sul (i.e. Morro do Papaléo, Quitéria and Faxinal Mine) and those present in other states, such as Santa Catarina and Paraná, do not need to be justified from the point of view of stratigraphic distribution or lateral extent of one of the members established by Schneider et al. (1974), as they were not delimited in the southernmost Brazilian portion of the basin.

However, when analyzing the results obtained between the

phytofosiliferous sections of the states of Santa Catarina and Paraná (Fig. 10), it is noticed that there is a certain incongruity between the stratigraphic positioning of the plant fossil-containing horizons based on the tradicional distribution of the three members of the Rio Bonito Formation and the one proposed based on (i) the recent radiometric dating obtained (Griffis et al., 2019; Jurigan et al., 2019) and (ii) the cluster analysis carried out here (Fig. 10). According to those ages, the Triunfo Member in the state of Paraná, dated as middle Artinskian by Jurigan et al. (2019), should be considered a younger-age rock deposit when compared to strata designated as Triunfo Member in the Alfredo Wagner area (present study), which inevitably, has an early (or older) Asselian age, based on the two radiometric ages obtained from overlying deposits by Griffis et al. (2019). The differences in the floristic composition (Table 2) and the grouping into different groups in the cluster analysis (Fig. 10) would reinforce this difference in the ages of this same member between the states of Paraná and Santa Catarina (central portion). In conclusion, it appears that despite being tripartite in the different sections analyzed in the two mentioned states, the Rio Bonito Formation and/or its members are not necessarily chronocorrelated with each other along the different portions of the basin in which they occur.

Another result obtained from the cluster analysis corroborates this framework of diachronous occurrences of the Rio Bonito unit in the basin. The grouping of the floras of Figueira and São João do Triunfo, included in the Triunfo Member in Paraná, together with the floras of Lauro Müller and Irapuá bed, positioned at the top of the Siderópolis Member in the south of Santa Catarina, suggests that these floras would have existed within a same time interval, tentatively attributed here to the mean Artinskian (Fig. 10) from the U–Pb radiometric dating obtained in Figueira (Jurigan et al., 2019). In this context, the coal deposits of Paraná, located in the basal portion of the Rio Bonito Formation, would be approximately chronocorrelated with those of the coalfields of southern Santa Catarina (Carboniferous Region of Criciúma), positioned at the top of this unit. However, the lack of radiometric ages in the deposits that contain the coal seams in Santa Catarina so far prevents the confirmation of this hypothesis.

6.3. Palynostratigraphy

Due to the importance of the biostratigraphic chart proposed by Daemon and Quadros (1970), the material from Alfredo Wagner was firstly compared with this contribution.

As exposed previously, the intervals G, H_1 and H_2 of Daemon and Quadros (1970) are characterized by monosaccate pollen grains of the genera *Cannanoropolis*, *Potonieisporites* and *Plicatipollenites*, whereas the sub-interval H_3, beyond these forms, is marked by the first appearance of the genus *Vittatina*, and species such as *V. saccata*, *V. subsaccata*, *V. costabilis* and *V. vittifera*. Since *Vittatina costabilis* found in our samples together with the absence of *Corisaccites alutas*, *Striatopodocarpites pantii*, *Lueckisporites stenotaeniatus*, *L. densicorpus*, *L. virkkiae*, *Staurosaccites cordubensis*, *Weylandites lucifer,* the material from Alfredo Wagner is likely attributed to the H_3 interval.

In the resulting palynozonation after Marques-Toigo (1988, 1991), Souza and Marques-Toigo (2001, 2003, 2005) and Souza (2006), the presence of *Vittatina* and other forms such as *Converrucosisporites confluens*, *Caheniasaccites*, *Scheuringipollenites*, *Protohaploxypinus* and *Illinites unicus* supports the affiliation of our material with the *Vittatina costabilis*
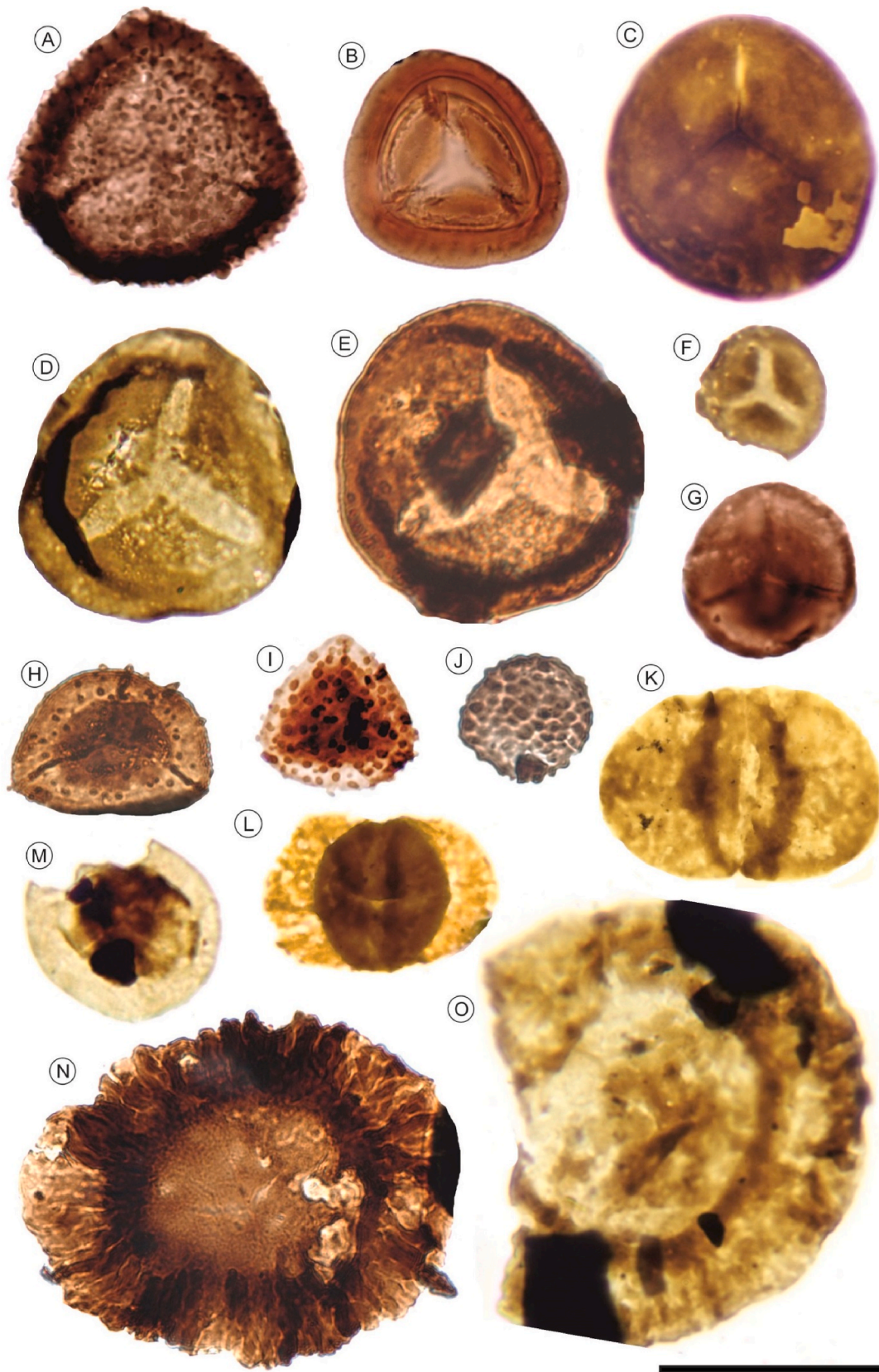
Fig. 8. A. *Lundbladispora braziliensis*. Slide MP-P 14.908, EF U 29/2. **B**. *Murospora bicingulata*. Slide MP-P 15.030, EF G 34/0. **C**. *Punctatisporites gretensis*. Slide MP-P 14.909, EF H 14/3. **D**. *Punctatisporites subvaricosus*. Slide MP-P 14.909, EF U 28/1. **E**. *Punctatisporites subvaricosus*. Slide MP-P 14.911, EF L23/2. **F**. *Retusotriletes nigritellus*. Slide MP-P 14.910, EF T 24/0. **G**. *Retusotriletes golatensis*. Slide MP-P 14.909, EF J 28/0. **H**. *Secarisporites triangularis*. Slide MP-P 14.908, EF V 21/4. **I**. *Spelaeotriletes* sp. Slide MP-P 14.909, EF J 16/0. **J**. *Verrucosisporites verrucosus*. Slide MP-P 14.911, EF R 25/3. **K**. *Alisporites ovatus*. Slide MP-P 14.910, EFO18/4. **L**. *Alisporites ovatus*. Slide MP-P 14.910, EF R 17/3. **M**. *Cannanoropollis densus*. Slide MP-P 14.908, EF L 29/1. **N**. *Cannanoropollis perfectus*. Slide MP-P 14.908, EF W 19/4. **O**. *Cannanoropollis janakii*. Slide MP-P 14.908, EF Q 27/2. **Scale bar** = 50 μm.
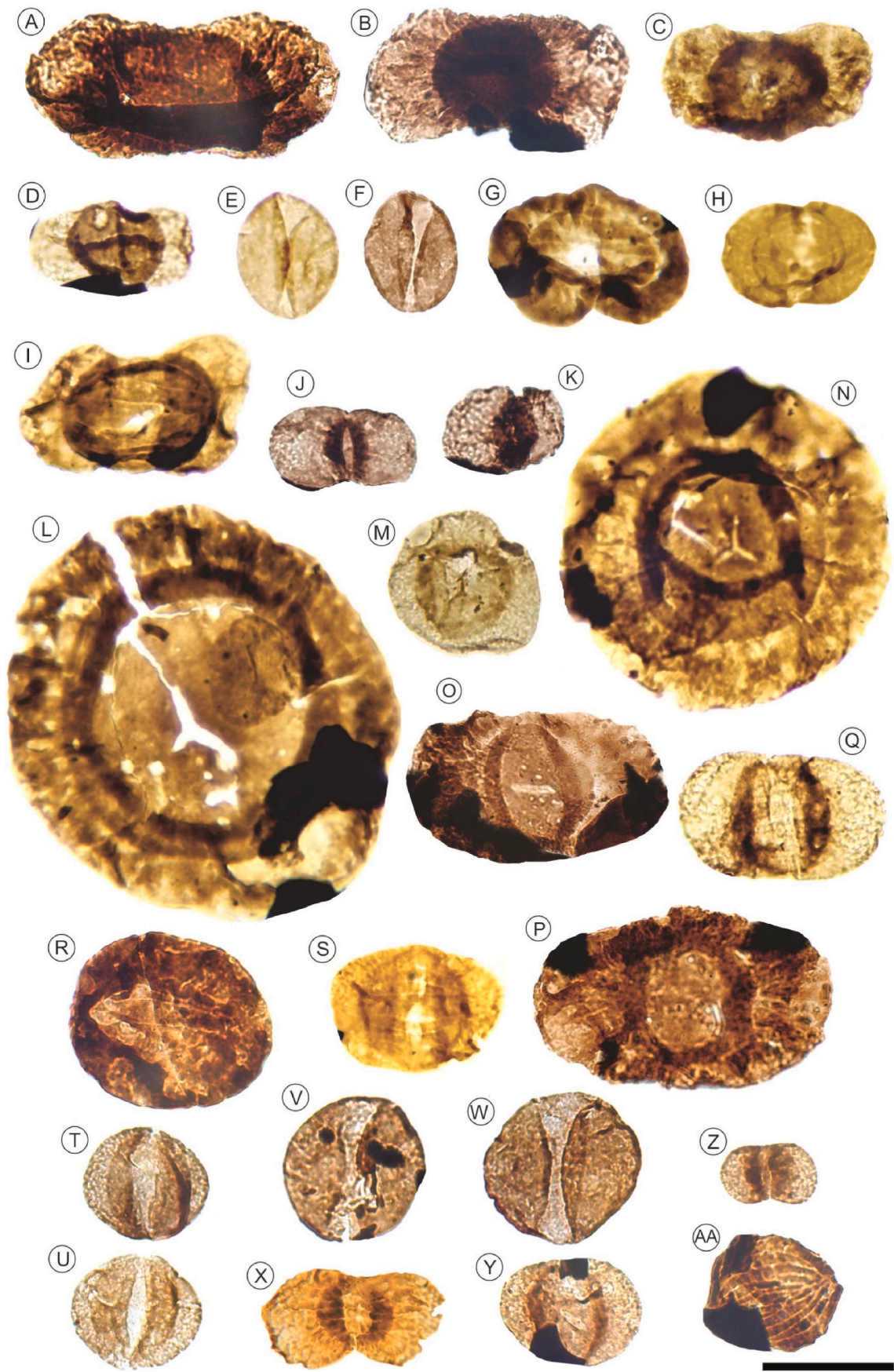
(caption on next page)

Fig. 9. A. *Caheniasaccites elongatus.* Slide MP-P 14.911, EF C 24/2. **B.** *Caheniasaccites flavatus.* Slide MP-P 14.910, EF R 21/4. **C.** *Caheniasaccites flavatus.* Slide MP-P 14.908, EF J 27/3. **D.** *Chordasporites* sp. Slide MP-P 14.908, EF P 14/4. **E.** *Cycadopites cymbatus.* Slide MP-P 14.905, EF R 20/1. **F.** *Cycadopites cymbatus.* Slide MP-P 14.909, EF D 16/0.**G.** *Illinites unicus.* Slide MP-P 14.908, EF O 27/1. **H.** *Illinites unicus.* Slide MP-P 14.910, EF V 22/1. **I.** *Lunatisporites variesectus.* Slide MP-P 14.909, EF N 31/0. **J.** *Platysaccus globosus.* MP-P 14.909, EF J 15/0.**K.** *Platysaccus leschikii.* Slide MP-P 14.910, EF T 18/2. **L.** *Plicatipollenites malabarensis.* Slide MP-P 14.908, EF M 30/2. **M.** *Plicatipollenites trigonalis.* Slide MP-P 14.908, EF N 24/3. **N.** *Plicatipollenites gondwanensis.* Slide MP-P 14.911, EF M 20/0. **O.** *Potonieisporites lelei.* Slide MP-P 14.911, EF O 27/0.**P.** *Potonieisporites lelei.* SlideMP-P 14.909, EF K 26/0. **Q.** *Potonieisporites methoris.* Slide MP-P 14.909, EFD 17/34. **R.** *Protohaploxypinus perexiguus* (=*P. rugatus*by di Pasquo et al., 2021). Slide MP-P 14.910, EF D 34/0. **S.** *Protohaploxypinus perfectus* (=*P. jacobii*by di Pasquo et al., 2021). Slide MP-P 14.909, EF T 24/3. **T.** *Pteruchipollenites indarraensis.* Slide MP-P 14.907, EF T 21/3. **U.** *Pteruchipollenites indarraensis.* Slide MP-P 14.905, EF W 19/0. **V.** *Scheuringipollenites medius.* Slide MP-P 14.908, EF R25/4.**W.** *Scheuringipollenites medius.* Slide MP-P 14.908, EFX 22/3.**X.** *Striatopodocarpites fusus.* Slide MP-P 14.910, EF R 28/0.**Y.** *Vitreisporites signatus.* Slide MP-P 14.908, EF W 20/2. **Z.** *Vitreisporites signatus.* Slide MP-P 14.904, EF J 22/4. **AA.** *Vittatina costabilis.* Slide MP-P 14.908, EF M 27/4. **Scale bar** = 50 μm.

Fig. 10. Hierarchical clustering using algorithm Paired group (UPGMA) and Jaccard similarity index comparing our paleobotanical data with previous described floras from Paraná to Rio Grande do Sul states in early Permian units. Flora used in the matrix based on: Faxinal Mine/RS: Boardman et al. (2012b); Irapuá Bed/SC: Iannuzzi (2010); Lauro Müller/SC: Rigby (1972); São João do Triunfo/PR: Iannuzzi (2010); Figueira/PR: Iannuzzi (2010); Morro do Papaléo/RS-Rio Bonito Fm, Iannuzzi (2010), Iannuzzi et al. (2007, 2010); Quitéria/RS: Iannuzzi (2010), Boardman et al. (2012a); Morro do Papaléo/RS-lowerpart: Iannuzzi et al. (2007, 2010); Cerquilho/SP: Bernardes-de-Oliveira et al. (2016b); Morro do Papaléo/RS-upperpart: Iannuzzi et al. (2007, 2010); Alfredo Wagner/SC: this study (supplementary online material # 1). Radiometric U–Pb ages based on: Faxinal Mine/RS: Griffis et al. (2018); Quitéria/RS: Griffis et al. (2018); Figueira/PR: Jurigan et al. (2019); Alfredo Wagner/SC: Griffis et al. (2019).

Zone (*VcZ*), currently interpreted as Ghzelian to early Artinskian in age (Souza et al., 2021). Within the *VcZ*, the presence of *Protohaploxypinus goraiensis* and *Illinites unicus* (stratigraphically restricted to the *Protohaploxypinus goraiensis* Subzone), and the absence of *Hamiapollenites karrooensis*, the material from Alfredo Wagner can be correlated with the *Protohaploxypinus goraiensis* Subzone. Except for few species such as *Punctatisporites subvaricosus, Vitreisporites signatus, Alisporites ovatus, Pteruchipollenites indarraensis* and *Cycadopites cymbatus*, the remaining recovered sporomorphs are relatively common in the Rio Bonito Formation. This microfloral zone broadly documented in the Rio Bonito Formation assigned to the Asselian-Artinskian (Iannuzzi, 2013; Souza et al., 2021), characterized by the highest appearance rates of spore and pollen taxa with striate forms in common with Upper Paleozoic successions of Brazil and Uruguay (see Beri et al., 2018, 2019).

Therefore, the studied palynological interval constrained to a meter claystone layer with a thin siltstone layer embedded of the Siderópolis Member, is likely akin to the upper *VcZ* of latest Asselian-earliest Sakmarian age. Earliest appearances of *Glossopteris* occur in the *Phyllotheca-Gangamopteris* Flora within the upper Itararé Group bearing palynologic associations assigned to the latest Pennsylvanian lower *VcZ* (Souza et al., 2021). Although, our plant fossil assemblage found in the same package of the palynoflora is more congruent with the *Glossopteris-Brasilodendron* Flora (*Glo-Br* Flora) of Iannuzzi and Souza (2005), in which the genus *Glossopteris* is dominant together with lycophytes and new floral elements (pecopterids, sphenophylls, among others).

Among the spores, *Verrucosisporites verrucosus* and *Granulatisporites varigranifer* are identified in several Pennsylvanian deposits in the western Argentina (Azcuy, 1975 a,b) and elsewhere in Argentina, Bolivia and Brazil (e.g. Césari and Gutiérrez, 2001; di Pasquo, 2003), without records elsewhere in Gondwana. *Punctatisporites subvaricosus* is registered for the first time in the Paraná Basin, being worldwide distributed since Early Carboniferous up to Late Asselian in Australia (Playford, 1990; Foster and Waterhouse, 1988); in Brazil, it represents an index species of the *Grandispora maculosa* Zone at the Roncador Creek

(Poti Formation, Parnaíba Basin), latest Visean in age (di Pasquo and Iannuzzi, 2014). *Gondisporites serrulatus* identified from Late Carboniferous up to Early Permian in Argentina (Césari et al., 1995) and in the Early Permian of Uruguay (Mautino et al., 1998).

Among the pollen, *Vitreisporites pallidus/signatus* is relatively common in Pennsylvanian-Permian of Gondwana and worldwide, from Permian to Cretaceous (Raine et al., 2011). *Alisporites ovatus* was mostly registered in Cisuralian of South America up to middle Triassic of Argentina (Jain, 1968). *Pteruchipollenites indarraensis* was registered in the Itararé Group of the Paraná Basin, Early Permian in age (Souza and Callegari, 2004), in the late Early Permian to early Late Permian of Paraguay (Muff et al., 1999), and worldwide since the Late Carboniferous (Wood, 1984) up to Middle Permian in Australia (Foster, 1979; McMinn, 1987). *Cycadopites cymbatus*, also registered for the first time in the Paraná Basin, is common in Permian/Sakmarian-Kungurian in Australia (Hart, 1965; Segroves, 1970), and worldwide from Permian to Cretaceous (Raine et al., 2011). Despite none of the newest species helped in any biostratigraphic refinement of the Siderópolis Member, some approaches derived from the selected cluster analyses are addressed herein below.

6.3.1. Statistical correlations among palynozones in Brazil and South America

The palynoflora here studied (Table 3) is composed of 52 species and was merged into the matrix proposed by di Pasquo et al. (2017 - see supplementary online material #3) for a comparison with Ghezelian-Artinskian palynoassemblages from South America. For a more accurate comparison, older and younger localities than the cited interval and species occurring in a single locality were removed from the resulted matrix based on our palynotaxa list (Table 3, and supplementary online material #2). Some taxonomic proposals, such as *Caheniasaccites ovatus* and *Caheniasaccites densus* considered as synonymies of *Caheniasaccites flavatus* (senior species), *Potonieisporites barrelis* as a senior species of *Potonieisporites jayantiensis* are followed herein to
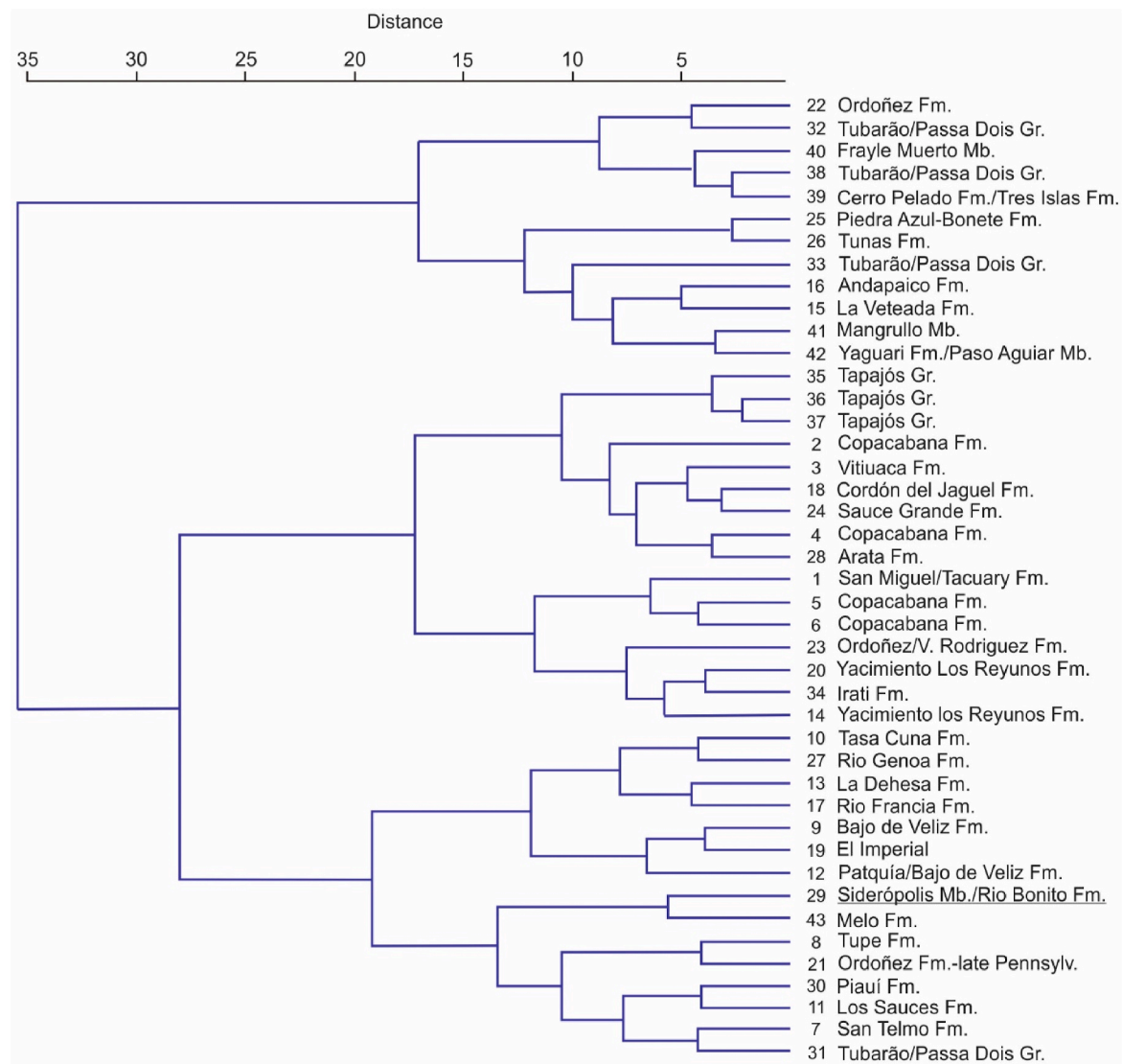
Fig. 11. Hierarchical clustering analysis using Ward's method algorithm with Euclidian similarity index (cophenetical correlation 0.66) comparing our studied palynoflora with South American assemblages. Numbers before the locations/formations indicate their position in the Past's analysis (supplementary online material # 2).

complete the matrix (see Azcuy and di Pasquo, 2000).

The hierarchical clustering using Ward's methodology and Euclidian similarity index (cophenetical correlation = 0.66, Fig. 11) gathered our palynoflora with the number 43 IS Zone of Melo Formation, sharing 24 species, in which some of them are diagnostic, like *Vittatina costabilis* along with *Gondisporites serrulatus, Converrucosisporites micronodosus, Lunatisporites variesectus, Scheuringipollenites ovatus*. On the contrary, the absence of *Lueckisporites* species in our samples did not prevent their grouping. A closer correlation with several palynofloras attributed to the *Pakhapites fusus-Vittatina subsaccata* Zone of Argentina (Tasa Cuna, Dehesa, Bajo de Veliz, El Imperial, Río Genoa, and Tupe/Patquía formations) is established by sharing some of those mentioned species among other exclusive ones of *Vittatina, Pakhapites, Weylandites, Mabuitasaccites* and spores (*Converrucosisporites confluens*). Another closer group is composed of mostly late Pennsylvanian palynofloras of Argentina (*Raistrickia densa-Convolutispora muriornata* Subzone of Tupe Fm, *Potonieisporites-Lundbladispora* Zone of Ordoñez Fm, *Marsupipollenites triradiatus–Lundbladispora braziliensis* Zone of San Telmo Fm, lower *Pakhapites fusus-Vittatina subsaccata* Zone of Sauces Fm), and *Crucisaccites monoletus* Zone of Itararé Group from Brazil. They share long-ranging taxa from Pennsylvanian to Cisuralian mostly monosaccate

and few other pollen grains (e.g. *Cycadopites, Protohaploxypinus, Platysaccus*) and spores of genera like *Lundbladispora, Cristatisporites*. Although, the absence of striate pollen grains especially those of *Vittatina*, prevents their correlation with those of *Vittatina costabilis* Zone and equivalents.

In the same way, the hierarchical clustering using Unweighted Pair Group method with Arithmetic Mean (UPGMA) and Jaccard similarity index (cophenetical correlation 0.87, Fig. 12) yielded similar arrangements of correlation of similar age-zones with few exceptions, in which the main difference is that the number 43 *Cristatisporites inconstans-Vittatina subsaccata* Zone of Melo Formation is quite distant from our palynoflora.

It is interesting to note that there are some diachronisms in the appearance of species such as *Barakarites rotatus* and *Mabuitasaccites crucistriatus*, even not present in our palynoflora, they are documented in *Pakhapites fusus-Vittatina subsaccata* Zone and other Cisuralian palynofloras of South America. Instead, they appear in the late Pennsylvanian assemblages of the Amazonas Basin (Playford & Dino, 2000 a,b), together with other long-ranging taxa such as *Horriditriletes gondwanensis, Illinites unicus, Polarisaccites bilateralis, Striatosporites heylerii, Striatopodocarpidites fusus*. Instead, they are not recorded in the
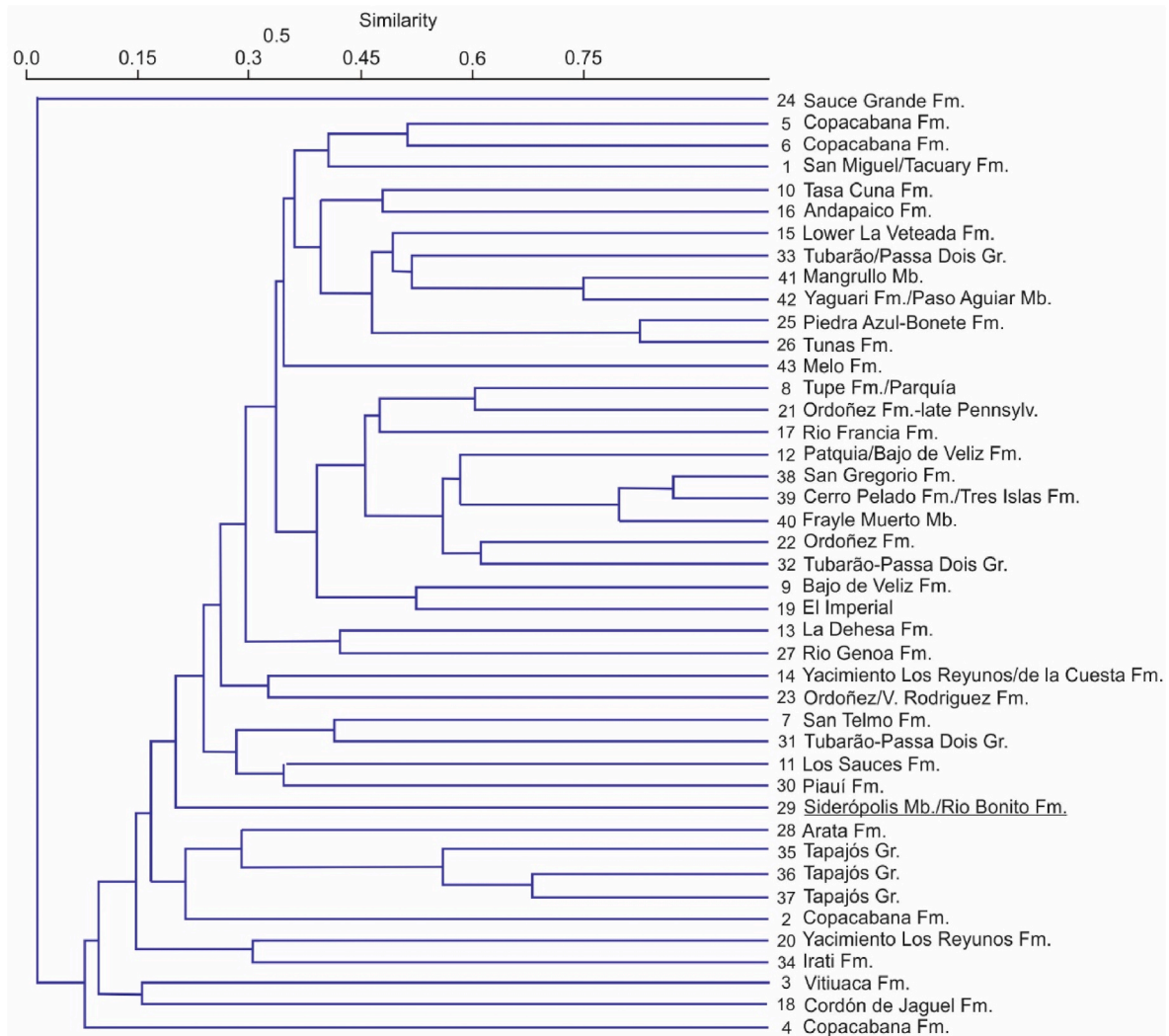
Fig. 12. Hierarchical clustering using algorithm Paired Group (UPGMA) and Jaccard similarity index (cophenetical correlation 0.87) comparing our studied palynoflora with South American assemblages. Numbers before the locations/formations indicate their position in the Past's analysis (supplementary online material # 2).

overlying Cisuralian *Vittatina* zones of the Amazonas Basin (Supplementary online material #2).

These results allow us to notice that there is a small number of species with short ranges, useful to constrain zones and the need of doing taxonomic revisions and synonymizations to reduce superfluous taxa and maintained diagnostic taxa. Hence, more accurate correlations are established combining different fossil groups along with sedimentologic and stratigraphic data, and much better if isotopic data can be obtained from same layers/outcrops. In our case, a minimum age of 294.82 + 0.59/−0.83 Ma given by Griffis et al. (2019), improved the age of our palynoflora akin to a long time-interval of the *Vittatina costabilis* Zone and *Glossopteris-Brasilodendron* Flora.

6.4. Botanical affinities of the palynotaxa and environmental implications

Following the botanical affinities mainly proposed by Azcuy (1978) and Quadros et al. (1995) for the Gondwanan strata, the vegetation characterized by the spores revealed a very high predominance of pteridophytes; lycophytes are represented by only few species such as *Lundbladispora, Gondisporites* and *Cristatisporites*, and sphenophytes by one, *Calamospora*. *Brevitriletes* does not present a botanical affinity following the above authors, neither by Balme (1995) or Traverse (2007), as showed in Table 4.

Cristatisporites is generically associated to the lycophytes (Azcuy, 1978; Traverse, 2007), but more precisely within the Family Chaloreniaceae by Balme (1995). However, gametophytes of *Chaloneria cormosa* were interpreted as the mother plant of *Valvisisporites* and *Endosporites* (Pigg and Rothwell, 1983), and *Sporangiostrobus* as the mother plant of *Cristatisporites* by Traverse (2007) and of *Densosporites* by Chaloner (1962). Although both gametophytes are not present in the Paraná Basin, *Cristatisporites* should be considered as related to lycophytes. *Retusotriletes* has been assigned to the primitive plants, such as the psilophytes, rhyniophytes and zosterophylls (Azcuy, 1978; Traverse, 2007), representing an important genera during the Devonian (Traverse, 2007). Although, it was reported *in situ* in *Cheirostrobus*, a sphenophyte cone (Neregato and Hilton, 2019).

In terms of pollen, many are associated to conifers (*Cannanoropollis, Caheniasaccites, Illinites, Platysaccus, Lunatisporites*) and glossopterids (*Protohaploxypinus* and *Striatopodocarpites*); *Chordasporites* is the only one assigned to the gymnosperms without a more specific botanical affinity following any above authors.

Vitreisporites and *Pteruchipollenites*, two very common genera in the samples, do not present a precise affinity according to Azcuy (1978) and Quadros et al. (1995), being associated to several groups. The former could be associated to Caytoniales or Peltaspermales (Balme, 1995; Traverse, 2007), whereas *Pteruchipollenites* has botanical affinity with

Table 4

Table presenting the palino taxa species found at Probst Outcrop, in munici-
pality of Alfredo Wagner (SC) and their botanical affinities taking in consider-
ation the generic level. Possible dispersal ways based on Slater and Wellman
(2015). In the left, the light blue represents the spores and the light red the
pollen grains.

Genus	Botanical affinity	Possible dispersal way
Brevitriletes levis	Ferns ? (Raine et al., 2011)	–
Brevitriletes cornutus		–
Calamospora liquida	Sphenophytes (Azcuy, 1978; Quadros et al., 1995)	wind
Convolutispora ordonezii	Ferns (Azcuy, 1978; Quadros et al., 1995)	mostly wind
Convolutispora sp.		
Cristatisporites morungavensis	Lycophyte (Azcuy, 1978)	
Cyclogranisporites minutus	Ferns (Azcuy, 1978; Quadros et al., 1995)	
Cyclogranisporites gondwanensis		
Didecitriletes sp.	Ferns? (Raine et al., 2011)	–
Granulatisporites austroamericanus	Ferns (Azcuy, 1978; Quadros et al., 1995)	mostly wind
Granulatisporites varigranifer		
Gondisporites serrulatus	Lycophyte (Traverse, 2007)	
Gosdisporites wilsoni		
Horriditriletes ramosus	Ferns (Quadros et al., 1995)	
Horriditriletes curvibaculosus		
Leiotriletes virkkii	Ferns (Azcuy, 1978; Quadros et al., 1995)	
Lophotriletes pseudoaculeatus		
Lophotriletes rectus	–	
Lundbladispora areolata	Lycophyte (Quadros et al., 1995)	
Lundbladispora brasiliensis		
Lundbladispora riobonitensis		
Murospora bicingulata	Ferns (Quadros et al., 1995)	
Punctatisporites subvaricosus	Ferns (Azcuy, 1978; Quadros et al., 1995)	
Punctatisporites gretensis		
Retusotriletes golatensis	Psilophytes (Azcuy, 1978), ferns (Quadros et al., 1995)	mostly wind (?)
Retusotriletes nigritellus		
Secarisporites triangularis	–	–
Verrucosisporites verrucosus	Ferns (Azcuy, 1978; Quadros et al., 1995)	mostly wind
Alisporites ovatus	*Glossopteris* or pteridosperm (Quadros et al., 1995)	mostly wind, potentially insect
Caheniasaccites elongatus	Conifer? (Azcuy, 1978);	wind?
Caheniasaccites flavatus		
Cannanoropollis janakii	Conifer or cordaitophyte (Quadros et al., 1995)	wind
Cannanoropollis perfectus		
Cannanoropollis densus		
Chordasporites sp.	–	–
Cycadopites cymbatus	Gymnosperm? (Quadros et al., 1995)	wind and insect
Illinites unicus	Conifer (Traverse, 2007)	wind
Lunatisporites variesectus	Conifer (Quadros et al., 1995)	
Platysaccus cf. *leschikii*	Gymnosperm (Quadros et al., 1995)	
Platysaccus cf. *globosus*		
Plicatipollenites trigonalis	Conifer, cordaitophyte or pteridospermophyte (Quadros et al., 1995)	
Plicatipollenites gondwanensis		
Plicatipollenites malabarensis		
Potonieisporites lelei	Gymnosperm? (Quadros et al., 1995), conifer (Traverse, 2007)	

Table 4 (*continued*)

Genus	Botanical affinity	Possible dispersal way
Potonieisporites methoris		
Pteruchipollenites indarraensis	*Pteruchus* (Traverse, 2007)	–
Protohaploxypinus perexiguus	*Glossopteris* (Azcuy, 1978; Quadros et al., 1995)	wind
Protohaploxypinus perfectus		
Scheuringipollenites medius	Gymnosperm? (Quadros et al., 1995)	–
Striatopodocarpites fusus	*Glossopteris* (Quadros et al., 1995)	wind
Vitreisporites signatus	Caytoniales, Peltaspermales (Balme, 1995); *Caytonanthus, Harrisiothecium* (Traverse, 2007)	wind and insect (?)
Vittatina costabilis	Conifer or pteridosperm (Quadros et al., 1995)	Mostly wind, potentially insect

Pteruchus (Traverse, 2007), a corystosperm pollen organ. However,
Pteruchus is also found in the Triassic from Antarctica (Yao et al., 1995)
and Argentina (Taylor et al., 1984), and considered as the mother plant
of *Alisporites*-type. Nevertheless, none of these plants has been found in
the Paraná Basin. *Cycadopites*, represented by some specimens in the
samples, has been, doubtfully, assigned to the gymnosperm by Quadros
et al. (1995), whereas Balme (1995) reported several species assigned to
the cycadophytes within the orders Cycadales and Bennettitales. *Vitta-
tina*, a very important guide species, widely spread in several Permian
strata in the Paraná Basin (Marques-Toigo, 1988; Neregato et al., 2008;
Souza et al., 2003; Souza, 2006; Boardman et al., 2012a,b; Mori and
Souza, 2012). According to Quadros et al. (1995), the genus has prob-
able affinity to conifers or pteridosperms; whereas, Balme (1995) and
Traverse (2007) summarized records assigned to the Peltaspermales,
although this plant group is not present in the Permian of the Paraná
Basin (Table 4).

Taphonomically, the dispersal methods of spores and pollen depends
on their size, weight, sculpture and atmospheric conditions, in which
large miospores can settle down on rivers, estuaries, deltas or shallow
shelf, whereas small forms in outer shelf and oceanic areas (Armstrong
and Brasier, 2005), as usually, spores and pollen are deposited as
silt-sized particles (Traverse, 2007). In the Late Paleozoic, the dispersal
way of the majority of the sporomorphs is mainly associated to the wind
and rivers.

As previously discussed, the sediments from Rio Bonito Formation
have been considered as deposited in estuarine, fluvial-deltaic, coastal
and marine platform environments containing carbonaceous shales and
shoreline and supratidal facies (Holz et al., 2006; Wildner et al., 2008;
Maahs et al., 2019), or even under a transition from an estuarine system
to a barrier lagoon, with the formation of lagoons behind barrier islands
(Holz, 2003). There is no evidence of acritarchs in the samples from
Alfredo Wagner to corroborate any marine influence. On the other hand,
a horizon containing conchostracans is positioned just in between the
fossiliferous levels studied herein (Fig. 3), indicating a freshwater in-
fluence on this depositional site and corroborating the palynologic
interpretation. Locally, some facies indicate the fossiliferous beds
correspond to tidal flats into an estuarine system (see above items 5.1.
and 5.2.), clearly dominated by the input of terrestrial material proved
by paleontologic groups (i.e., sporomorphs and conchostracans).
Finally, the different parts/organs of the plants in the studied layers are
found detached and isolated, some fragmented as well, and represent
different groups, without apparently showing any type of selection
(either by group or by type of organ - stems, leaves, reproductive
structures, seeds). These are taphonomic features commonly seen in
allochthonous associations, recorded in tidal flats, in estuaries, and
interdistributary bays in deltas (Gastaldo et al., 1995), where there is a

short transport (for short distances/for a short time) of the remains by weak currents, with a subsequent random deposition of the remains when the stream energy of the water bodies decreases and/or the waterlogging and sinking of the parts or organs occurs.

6.5. Floristic succession and climate change

In view of the probable age of the flora study, it is possible that Probst Outcrop record represents the oldest Permian record in the basin of pecopterid ferns (*Pecopteris* spp.) and sphenophylls (*Sphenophyllum* spp.). From the point of view of floristic succession and climatic evolution, the forthcoming of these two plant groups may indicate a significant climatic amelioration after the end of the main glacial episode (Late Paleozoic Ice Age - LPIA) in the basin (Holz et al., 2010; Griffis et al., 2019), as they would have migrated from surrounding areas (sedimentary basins) in Argentina, where climatic conditions were already free of glacial influence since the latest Carboniferous (Iannuzzi, 2010; Césari et al., 2011). Actually, pecopterid ferns and sphenophylls are, in turn, considered to be taxa with a northern hemisphere alliance (Rösler, 1978; Archangelsky et al., 1996; Iannuzzi, 2010) that would have rapidly colonized Gondwanan terrains after the end of the main glacial phase in the earliest Permian (Gastaldo et al., 1996; Montañez et al., 2007), coming from low-latitude areas (= tropics).

However, in the Paraná Basin, the appearance of those two groups (i. e. pecopterids and sphenophylls) is preceded by the installation of a flora dominated by *Gangamopteris* leaf-bearing glossopterids with an herbaceous-shrubby sphenophytes bearing *Phyllotheca*-type leaflets that appear in the record just above the last diamictites (Holz et al., 2010). This flora normally recorded at the top of the Itararé Group, but which can also reach the lower portions of the Rio Bonito Formation, named *Phyllotheca-Gangamopteris* Flora by Iannuzzi and Souza (2005). It is only in strata above these records that a flora dominated by *Glossopteris*-type leaves appears, in which pecopterid ferns and sphenophylls arise for the first time in the basin. This floristic stage corresponds to the Flora *Brasilodendron-Glossopteris* by Iannuzzi and Souza (2005). Therefore, although the interval that extends from the top of the Itararé Group to the base of the Rio Bonito Formation represents a post-glacial phase of milder climatic conditions (=warm temperate), with a likely progressive increase in average temperatures and humidity (Iannuzzi, 2013), from the point of view of the floristic succession, this climatic transition took place in two stages. The first one represents the vegetation that colonized the lowlands immediately after the end of the glacial event, represented by the Flora *Phyllotheca-Gangamopteris* that contains the record of new groups, such as the first glossopterids, but also shows the occurrence of relict elements from the Carboniferous times, i.e. *Botrychiopsis*, which flourished in the interglacial intervals during the main Carboniferous phase of the Gondwanan glaciation (=LPIA) (Pinheiro et al., 2015). The second stage already shows a diversification of glossopterids, with an increase in the number of *Glossopteris* species, the arrival of immigrant elements from surrounding areas, such as pecopterid ferns, sphenophylls and sphenophytes bearing *Annullaria*-type leaf, as well as the increase of lycophytes and peat-accumulating environments, and the last remaining elements of the Ice Age disappear (Iannuzzi, 2010, 2013). In this phase, the elements of the typical *Glossopteris* Flora associated with coal deposits throughout Gondwana are installed (Iannuzzi and Souza, 2005; Iannuzzi, 2010) as favorable climatic and tectono-sedimentary conditions arise for the generation of peat accumulating environments along the coastal plains on the eastern rim of the basin.

In summary, the transition from an Ice-House to a Green-House world that took place from the end of the Carboniferous to the beginning of the Permian (Montañez et al., 2007; Montañez, 2021) occurred, from a floristic point of view, in a transitional way in the Basin from Paraná, through the succession of a "Pre-*Glossopteris* Flora" to a "*Phyllotheca-Gangamopteris* Flora" and from this latter to a "*Glossopteris-Brasilodendron* Flora", according to the scheme established by Iannuzzi

and Souza (2005). In this context, the flora of the Probst Outcrop may represent the initial record of the last portion of this transitional phase when the typical flora (=*Glossopteris-Brasilodendron* Flora) of the post-glacial interval emerged.

This type of analysis corroborates that the slow and gradual change of floras (ecosystems) in a floristic region or kingdom is more frequent in the geological record, largely defined by the interaction of palaeoenvironment (soil, type of vegetation), geographic (orography, latitude), climatic (humidity, temperature) and tectonic factors triggering the evolution of taxa and migrations (e.g. Montañez and Poulsen, 2013). However, floristic changes of great magnitude are registered mainly from catastrophic events or changes that generated the extinction of large number of taxa such as at the Devonian-Carboniferous, Permian-Triassic and Cretaceous-Paleocene (e.g. Montañez and Poulsen, 2013; Wilson et al., 2017; Beri et al., 2019).

7. Conclusions

The main results obtained, which constitute an effective contribution of this article to the knowledge of the Cisuralian paleofloras of the Paraná Basin, can be summarized in this way:

- The inedit association of macro- and microfossils of plants from the Probst Outcrop, despite not being so diverse, proved to be distinct, with a unique combination of plant taxa and some novelties in terms of sporomorphs for the Rio Bonito Formation and/or the Paraná Basin;

- Two key taxa for phytostratigraphy in the basin according to Iannuzzi and Souza (2005), i.e. *Cheirophyllum* sp. and *Cornucarpus patagonicus*, are recorded for the first time in the Rio Bonito Formation, which previously had their occurrence in the basin restricted to the top of the Itararé Group in the state of Rio Grande do Sul (Silva and Iannuzzi, 2000; Iannuzzi et al., 2007);

- A few sporomorphs had their stratigraphic range extended to the Rio Bonito Formation, while three forms (i.e. *Punctatisporites subvaricosus, Didecitriletes* sp, *Vitreisporites*, *Cycadopites cymbatus*) were recorded for the first time, with their geographic occurrence extended to the Paraná Basin from previous records existing in the Pennsylvanian of Argentina and elsewhere in South America;

- Species of *Vittatina* indicate a correlation with the Gzhelian – early Artinskian *Vittatina costabilis* Zone of the Paraná Basin, and their correlative zones in South America while the absence of *Lueckisporites* and other exclusive taxa of the overlying *L. virkkiae* Zone in the Paraná Basin (see Souza, 2006) confirmed this correlation;

- This distinct composition of the macro- and microfloristic associations of the Probst Outcrop should reflect (i) the geographic position, situated in a gap of information in the phytofossilliferous record for the Lower Permian strata of the basin, as well as (ii) the intermediate position in floristic succession of the basin, supported by the results obtained from correlations established with the main macro- and microflora of the Paraná Basin and surrounding areas, through qualitative and quantitative cluster analysis (Figs. 10–12);

- The absolute ages obtained in two stratigraphic sections located close to the Probst Outcrop suggested a late Asselian age for this paleoflora, a different age from the vast majority of paleofloras from the Rio Bonito Formation radiometrically dated so far in the basin (Fig. 10), which are concentrated in the early Asselian, as is the case of the floras from the Candiota region and in the Quitéria Outcrop (Griffis et al., 2018), in the state of Rio Grande do Sul, or in the middle-to-late Artinskian, as for instance, seen in the floras of Mina do Faxinal (Griffis et al., 2018), in Rio Grande do Sul, and Figueira (Jurigan et al., 2019), in the state of Paraná;

- According to previous U–Pb radiometric ages published (Griffis et al., 2018, 2019; Jurigan et al., 2019), the Rio Bonito Formation and/or its members are not necessarily chronocorrelated with each other along the different portions of the basin, which is reinforce by the differences in the composition of floras analized (Table 2) and the groupings resulting from the cluster analysis carried out here (Fig. 10);

- In view of the intermediate chronostratigraphic position of the paleoflora of the Probst Outcrop, it is possible that it represents the oldest Permian record in the basin of pecopterid ferns (*Pecopteris* spp.) and sphenophylls (*Sphenophyllum* spp.), perhaps, together with the flora of the top of Morro do Papaléo, considered close to the one studied herein, according to the cluster analysis performed (Fig. 10);

- From a climatic point of view, the paleoflora of the Probst Outcrop may represent the first record of the last step of transition from a glacial to a post-glacial phase in the Paraná Basin, in which the *Glossopteris-Brasilodendron* Flora emerged without the survival of any Carboniferous relictual elements (i.e. *Botrychiopsis*) and showing the appearence of typical post-glacial elements, such as pecopterid ferns and sphenophylls.

Since the paleoflora of the Probst Outcrop is one of the most accurately dated in chronostratigraphic terms, it fills a temporal and spatial gap in the floristic distribution of the early Permian deposits in the Paraná Basin, thus contributing significantly to the understanding of floristic succession in the LPIA of western Gondwana.

CRediT authorship contribution statement

M. Rischbieter: Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **R. Neregato:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **R. Iannuzzi:** Investigation, Conceptualization, Data curation, Formal analysis, Funding acquisition, Writing - original draft, Writing - review & editing. **M.M. di Pasquo:** Writing – original draft, Investigation, Formal analysis. **R. Alvarenga:** Writing – original draft, Formal analysis. **J. Freitas:** Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2022.104010.

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