
A synthesis of palynological data from the Lower Permian Cerro Pelado Formation (Paraná Basin, Uruguay): A record of warmer climate stages during Gondwana glaciations

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| A B S T R A C T |

This paper presents a synthesis of the palynological record in the Cerro Pelado Formation deposits (Lower Permian, Paraná basin, Cerro Largo Department, north-eastern Uruguay) based on pre-existing data and new findings. The successions studied in this formation consist mainly of non-marine to glacial-marine mudstones and sandy mudstones. The palynological assemblages yielded by 32 samples collected from two outcrops and thirty borehole samples demonstrate that not significant floral changes took place through the considered stratigraphic range. The correlation of these assemblages with biostratigraphic palynozones, proposed previously for the Paraná/Chacoparaná Basin of Brazil, Argentina and Uruguay point to their Early Permian age. The most widespread spore genera in these assemblages are *Punctatisporites*, *Lundbladispota*, *Vallatisporites* and *Granulatisporites*. Among pollen grains, *Caheniasaccites*, *Vittatina*, *Potonieisporites*, *Protohaploxylinus* and *Plicatipollenites* are the most representative. Palynomorphs assigned to Chlorophyta, Prasinophyta, and acritarchs indicate the development of brackish to fresh water lacustrine environments. The results from the facies and palynological analyses suggest that these deposits were formed during interglacial or postglacial warmer climatic episodes. This fact would agree well with the proposal that Gondwana glaciations were characterized by discrete glacial phases (with multiple glacial lobe advance-retreat phases) alternating with warmer climatic episodes. These episodes could be recognized thanks to sub-glacial and melt water related continental deposits that would bear characteristic palynological assemblages, like the recorded in the Cerro Pelado Fm. successions.

KEYWORDS | Lower Permian. Palynology. Interglacial-postglacial episodes. Gondwana. Uruguay

INTRODUCTION

During the Late Palaeozoic of Gondwana, an Ice Age characterized by short, discrete glacial events separated by periods of warmer climate occurred (Fielding et al., 2008).

Late Palaeozoic sedimentary sequences are well represented in the Paraná Basin in Uruguay and, as these strata probably record the moments of massive expansion of ice (Fielding et al., 2008), it is of interest to carry out palynological analyses and characterize the plant communities

that inhabited Western Gondwana by that time. This paper aims to present a synthesis of all available palynological data, complemented by new contributions, of the Cerro Pelado Formation (successions previously included in the San Gregorio Formation), which has been attributed to the Lower Permian (Gutiérrez et al., 2006).

The first palaeopalynological study of the Upper Palaeozoic in Uruguay was conducted by Martínez Macchiavello (1963), who analysed the San Gregorio and Tres Islas Formation. Later, Marques-Toigo (1970, 1972, 1973, and 1974) studied the palynological content of the San Gregorio Formation from a systematic standpoint, complemented by biostratigraphic observations. Subsequently, several additional publications have addressed the systematic palynology and biostratigraphy of the San Gregorio Formation (Beri and Daners, 1996; Beri and Goso, 1996, 1998; Beri et al., 2006; and Gutiérrez et al., 2006). However, these publications were based on single boreholes.

GEOLOGICAL SETTING

Three major basin types occurred in the Late Palaeozoic of South America: intracratonic or intraplate, arc-related, and retroarc. Intraplate basins (*i.e.*, Paraná, Chaco-Paraná, Sauce Grande-Colorado, and La Golondrina) are floored by continental or quasi-continental crust, with low or moderate subsidence rates and limited magmatic and tectonic activity (Limarino and Spalletti, 2006). The Paraná Basin is an intracratonic ramp basin of the South American platform formed in response to the geological stabilization that followed the Brasiliano cycle. This basin is filled by thick and widespread sedimentary sequences that cover approximately 1,700,000 km² in central-eastern South America, including present-day territories of Uruguay, Brazil, Paraguay and Argentina, where it is known as Chaco-Paraná Basin (Holtz et al., 2008) (Fig. 1). The south-eastern portion of the Paraná Basin extends into the northern Uruguay occupying an area of approximately 90,000 km² within the country where it is called the Northern Basin (de Santa Ana et al., 2006b). Palaeozoic outcrops are distributed throughout an area of 24,000 km² in the Cerro Largo, Tacuarembó, Rivera and Durazno Departments of Uruguay; while the rest of the sequence is covered by Lower Cretaceous extrusive rocks and younger sedimentary rocks (Andreis et al., 1996) (Fig. 1). According to de Santa Ana et al. (2006b), the beginning of the Neopalaeozoic sedimentation is characterised by extensive glacial, glacial-marine or glacial-influenced sedimentary records. The lithological formations corresponding to this time interval in Uruguay are, from bottom to top, San Gregorio, Cerro Pelado, Tres Islas, Frayle Muerto, Mangrullo, Yaguarí and Buena Vista (de Santa Ana et al., 2006a) (Fig. 2).

The Cerro Pelado Formation is a sedimentary succession of fine-grained rocks (mudstones, diamictites and fine-grained sandstones), which are greyish to blackish and brownish in colour. This formation records a transgressive event reported by de Santa Ana et al. (2006b). Previously, the successions of this formation were considered the upper sequences of the San Gregorio Formation (Caorsi and Goñi, 1958; Ferrando and Andreis, 1986) which in its turn can be correlated with the Itararé Group in Brazil (Petri and Fúlfaro, 1988). Two depositional cycles were identified for the San Gregorio Formation (de Santa Ana, 1989). The lower cycle, geographically restricted to the Río Negro Valley of Uruguay and adjacent areas, consists mainly of diamictites, conglomerates, sandstones and, to a lesser

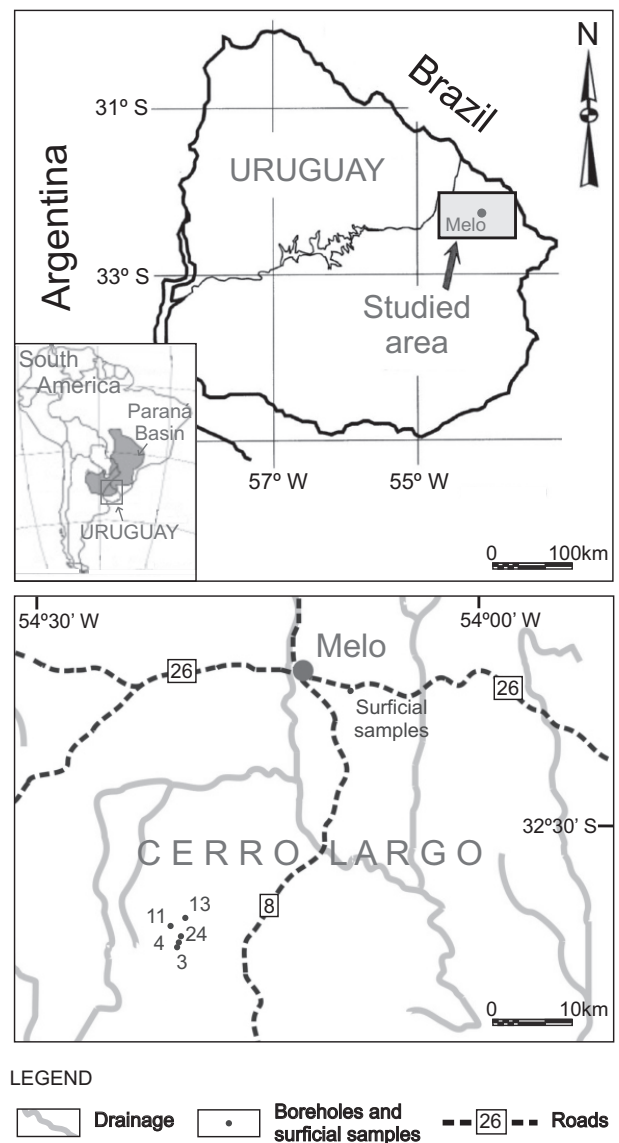


FIGURE 1 | Map of sample locations (modified from Goso, 1995; Souza et al., 2007).

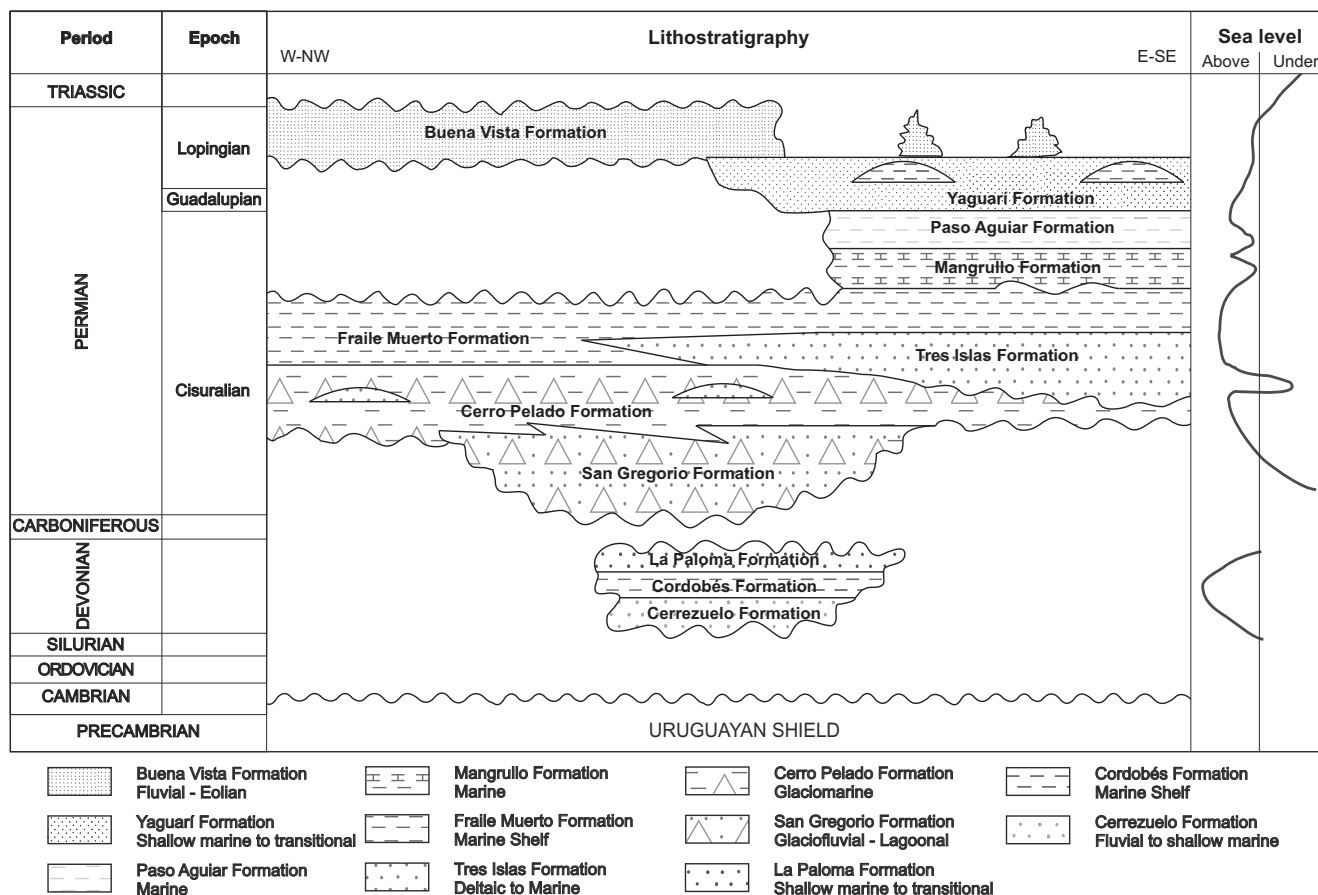


FIGURE 2 | Lithostratigraphy and chronostratigraphy of the Carboniferous-Permian basin fill units of the Paraná Basin in Uruguay and the regional model of sea level change (modified from de Santa Ana, 2004; de Santa Ana et al., 2006b).

extent, mudstones and rhythmites having greyish, reddish and yellowish colorations. The upper cycle, extensively developed in the northwest of the Paraná Basin, is predominantly composed of mudstones with lesser fine-grained diamictites and fine-grained sandstones (de Santa Ana, 1989). Andreis et al. (1996), using similar criteria, subdivided the San Gregorio Formation into two sequences: “glacial sequences” (or sub-glacial) as distinct from “glacial-marine sequences”. As a result of these considerations, de Santa Ana (2004) divided the San Gregorio Formation into two formations: San Gregorio and Cerro Pelado. The San Gregorio Formation corresponds to both the lower depositional cycle of de Santa Ana (1989) and the glacial sequences of Andreis et al. (1996) while the Cerro Pelado Formation corresponds to the upper cycle of de Santa Ana (1989) and the glacial-marine sequences of Andreis et al. (1996).

Cloos (1967) and Beltan (1977, 1981) dated the San Gregorio Formation as Late Carboniferous, based on the content of cephalopods and fishes found in concretions. However, as a result of palynological studies of those concretions, Marques-Toigo (1973) proposed an Early Permian age,

which was later supported by Beri and Daners (1996), Beri and Goso (1996) and Gutiérrez et al. (2006) for strata correlative with the Cerro Pelado Formation of the Cerro Guazunambí area.

MATERIALS AND METHODS

Two rock samples were taken from surface exposures and the remaining 30 are from boreholes made by Dirección Nacional de Minería y Geología (DI.NA.MI.GE.). The boreholes are located in the Cerro Guazunambí area, 35 km from Melo (Cerro Largo Department) and are designated as DCLS-3 (32°38' 1,2" S, 54°16' 43,1" W), 4 (32°37' 35,2" S, 54°16' 39,7" W), 11 (32°35' 55,1" S, 54°17' 27,4" W), 13 (32°35' 5,3" S, 54°15' 52,4" W) and 24 (32°37' 18,9" S, 54°16' 36,2" W). Surface samples were collected from outcrops located on Route 26, 7 km (S1) and 6.5 km (S2) east of Melo (Figs. 1, 3 and 4). Possible correlations considered in the present work are based on the presence of grey and black laminated claystones as described by Goso (1995), which represent events of maximum marine ingression into the basin (Fig. 3).

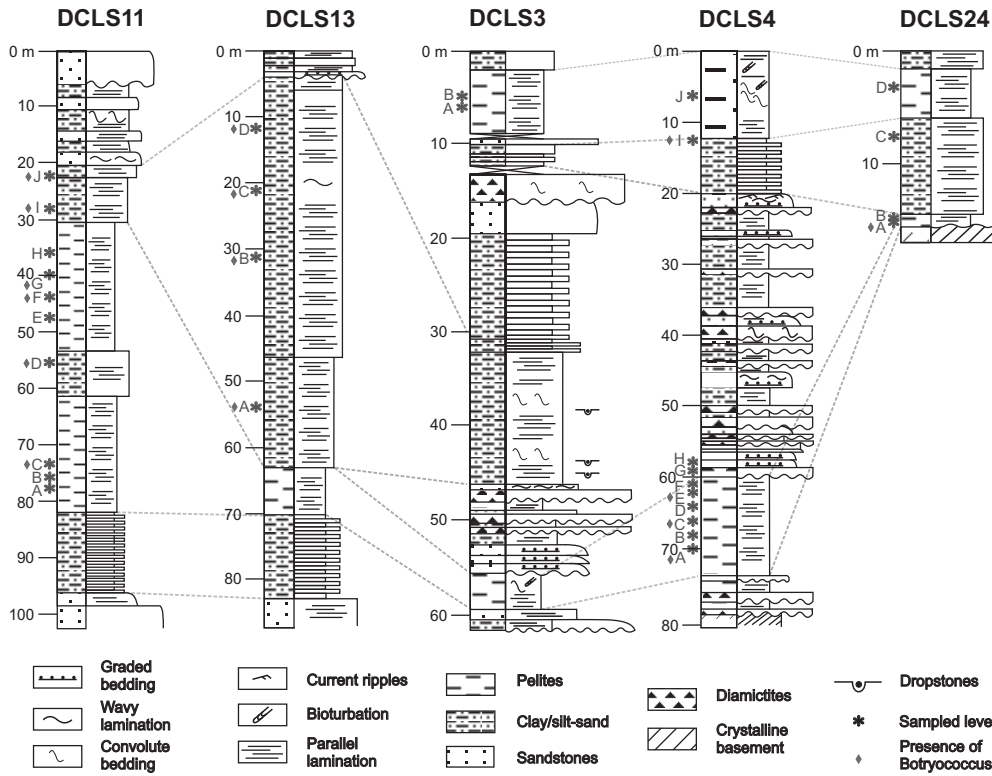


FIGURE 3 | Stratigraphic sections of the Cerro Pelado Formation corresponding to boreholes: DCLS-3, 4, 11, 13 and 24. Letters correspond to the levels mentioned in Appendix 2. Dashed line shows possible lithostratigraphic correlations. Depth in meters (m) (modified from Beri, 1997).

Samples were processed by conventional palynological techniques, which involve treatment with hydrochloric and hydrofluoric acids (Volkheimer and Melendi, 1976). No oxidative treatment was performed. The residues were sieved through a 10 µm mesh screen to remove small particles. Palynological slides were prepared using glycerine jelly mounting medium. The samples were studied with an Olympus BH microscope. Photographs of palynomorphs were taken with Nikon “Coolpix P1” and “Coolpix P3” digital cameras. A permanent repository of the specimens is located at the Palynological Collection at the Facultad de Ciencias – UDELAR, with the abbreviation “FCPP”. Coordinates of specimens are denoted by England Finder (EF) coordinates.

The botanical affinities shown in the Appendix 1 (available in the electronic version of the paper at www.geologica-acta.com) are based on the determinations and inferred taxonomic level used by several authors. The quantitative analysis is based on 200 specimens, classified to the species level. However, for some samples species designations were not achieved due to the scarcity of the material.

This contribution integrates new observations with previously published data (Beri and Daners, 1996; Beri and Goso, 1996, 1998; Beri et al., 2006; and Gutiérrez et al., 2006). For this reason, the systematic treatment and photographic illustrations are exclusively from previously unpublished

palynological material (see Appendix 1 in the electronic version of the paper at www.geologica-acta.com).

RESULTS OF THE PALYNOLOGICAL ANALYSIS

The palynological content of the samples includes 63 genera and 131 species, 28 of which are new records for the Cerro Pelado Formation. Among species, 67 correspond to pollen grains, 52 to spores, four to Prasinophyta, three to Achritarcha, three to Chlorophyta, one to Fungi and one to *Incertae sedis* (see Appendix 1 in the electronic version of the paper at www.geologica-acta.com).

Assemblage analysis

The distribution of species in the different samples, ordered according to their probable stratigraphic correlation (Goso, 1995) show no significant changes through the considered stratigraphic range (Appendix 2 at www.geologica-acta.com). Apart from punctuated differences, no compositional turnover that persisted through time or that involved a significant number of taxa, enabling to establish distinct biohorizons, are observed. In addition, the genera that appear in a significant number of samples demonstrate the homogeneity of the assemblage compositions (Fig. 5). Among spore genera, the most frequent are *Lundbladispora*, *Punctatisporites*, *Vallatisporites*, *Cristatisporites*,

Converrucosisporites, *Horriditriletes*, *Granulatisporites*, *Calamospora*, *Leiotriletes* and *Brevitriletes* (Fig. 5), all of which are present in more than 10 samples (the median value). Based on the same criteria, the most frequent pollen genera are *Caheniasaccites*, *Vittatina*, *Potonieisporites*, *Plicatipollenites*, *Cannanoropollis* and *Protohaploxypinus*. At the same time, differences in relative abundance of taxa are observed. The assemblages are quantitatively dominated by spores. Pollen grains are abundant in four of the samples at the following depths: 64 m in borehole DCLS4; 56 m and 36 m in borehole DCLS11; and 54 m in borehole DCLS13.

DISCUSSION

This study shows that the palynofloras of the Cerro Pelado Formation have a homogeneous composition through the succession studied. This finding could indicate that, for the period of time analysed, there were no significant changes in the composition of paleoflora that produced the observed palynological material. Therefore, all samples are considered to pertain to a single assemblage in order to formulate biostratigraphic comparisons and palaeoenvironmental analysis.

Biostratigraphic considerations

The genera and species found are frequent in the entire Paraná Basin, including Brazil and Argentina (Russo et al., 1980; Césari et al., 2007; Gutiérrez et al., 2003; Souza and Marques-Toigo, 2003; Souza, 2006; Azcuy et al., 2007).

Although comparisons between palynological assemblages and regional biostratigraphic zones have been explored priorly (Beri and Daners, 1996; Beri and Goso, 1996; Beri et al., 2006 and Gutiérrez et al., 2006), this study presents the first synthesis of all the available data, complemented with the new findings for the Cerro Pelado Formation. As there is no formal biozonation scheme for Uruguay, the assemblages reported herein are correlated with palynostratigraphic biostratigraphy proposed for the same basin in other countries, that is the Chaco-Paraná Basin in Argentina (Russo et al., 1980; Vergel, 1993; Gutiérrez et al., 2003) and the Paraná Basin in Brazil (Souza and Marques-Toigo, 2003, 2005). Despite the lack of a formal biozonation scheme, the assemblages found in this study are also compared with those reported from Uruguay (Azcuy et al., 2007; Souza et al., 2007) (Fig. 6).

The analysed palynofloras show distinct similarities to those of the *Cristatisporites* Zone of the Chaco-Paraná Basin (Russo et al., 1980; Vergel, 1993; Gutiérrez et al., 2003). Due to the dominance of apiculate and cingulicavate trilete spores, as well as monosaccate and bisaccate pollen grains, an Asselian/Artinskian age was proposed for the Zone (Souza et al., 2007). The Cerro Pelado assemblages and this biostratigraphic Zone share the following species: *Vittatina saccata*, *Lundbladispora brazilensis*, *Converrucosisporites confluens*, *C. micronodosus*, *Hamiapollenites fusiformis*, *Protohaploxypinus limpidus*, *Marsupipollenites striatus*, *Calamospora liquida*, *Vallatisporites russoi*, *Mabuitasaccites crucistriatus*, *Lunatisporites variesectus*, *Convolutispora ordonezii*, *C. archangelskyi*, and *Horriditriletes uruguayensis*.

With regard to the zonation proposed by Souza and Marques-Toigo (2003, 2005) for the Paraná Basin in Brazil, the assemblages studied show several similarities with the *Protohaploxypinus goraiensis* Sub-zone of the *Vittatina costabilis* Zone. According to Souza et al. (2007), the age proposed for the Sub-zone is Asselian/Artinskian, based on the presence of such species as *Vittatina saccata*, *V. subsaccata*, *V. costabilis*, *V. vittifera*, *Protohaploxypinus goraiensis*, and *Hamiapollenites fusiformis*, *Granulatisporites austroamericanus* and *Converrucosisporites confluens*. However, differing from this biostratigraphic scheme, the palynoflora analysed in this study is generally dominated by spores.

Finally, in comparison with the Paraná Basin of Uruguay, the palynofloras studied clearly resemble the *Cristatisporites inconstans-Vittatina subsaccata* Zone of the Asselian to Artinskian age (Azcuy et al., 2007; Souza et al., 2007). This correlation is indicated by the presence of such species as *Converrucosisporites confluens*, *Converrucosisporites micronodosus*, *Brevitriletes levis*, *B. cornutus*, *Cristatisporites inconstans*, *C. lestai*, *C. microvacuolatus*,

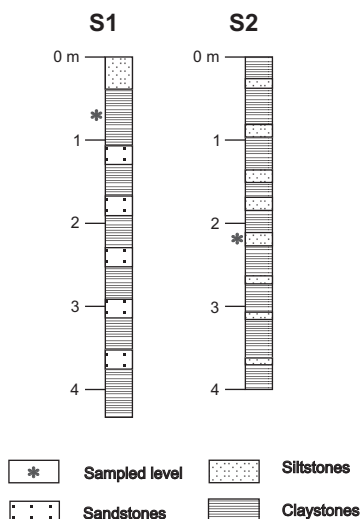


FIGURE 4 | Stratigraphic sections of the Cerro Pelado Formation corresponding to surficial samples S1 and S2. Thickness in meters (m). 0m corresponds to the top of the section.

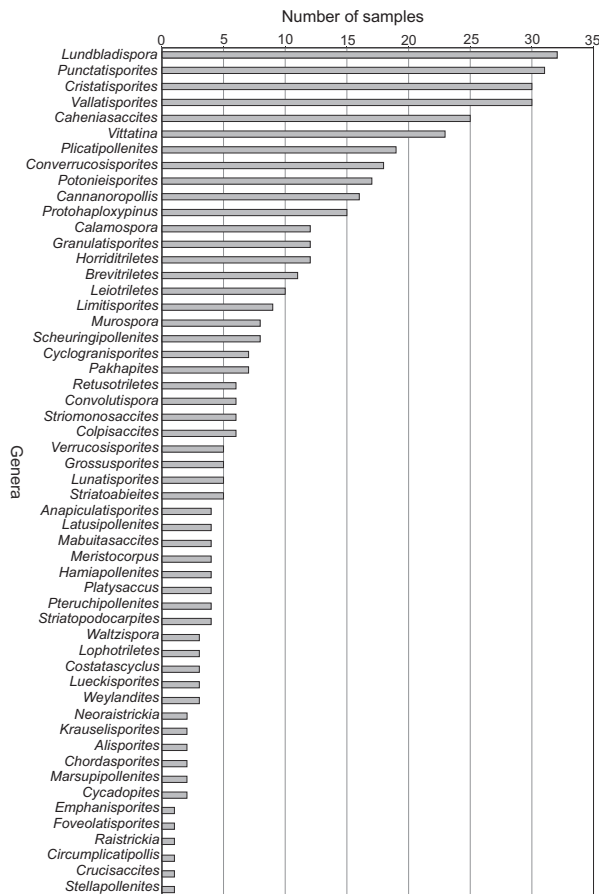


FIGURE 5 | Frequency of the genera found in the studied samples.

C. morungavensis, *Krauselisporites spinosus*, *Latusipollenites quadrisaccatus*, *Murospora bicingulata* and *Vallatisporites russoi*, as well as by the dominance of trilete (especially cingulicavate) spores and the presence of bisaccate and striate-plicate pollen grains.

It is relevant to point out that the assemblages studied here include the genera *Lueckisporites*, *Weylandites*, *Striatoabieites*, *Lunatisporites* and *Marsupipollenites*, which are characteristic of younger biozones, such as Striatites Zone (Chaco-Paraná Basin, Argentina) and *Lueckisporites* Zone (Paraná Basin, Brazil). Nonetheless, these genera occur in only a few samples and are scantily represented therein (Fig. 5).

Palaeoenvironmental and palaeoclimatic conditions

As previously mentioned, the sediments analysed in this study have been considered of glacial-marine origin by Beri and Goso (1998) and de Santa Ana et al. (2006b). However, the remaining microplankton species found,

such as chlorophyte algae (*Botryococcus braunii*, *Tetraporina punctata* and *Quadrisporites horridus*), prasinophytes (*Leiosphaeridia* spp. and *Deusilites tenuistriatus*), and acritarchs (*Brazilea* spp.), indicate freshwater to brackish water bodies (see Appendix 3 in the electronic version of the paper at www.geologica-acta.com). The only genus of palaeomicroplankton that could be possibly associated with marine conditions is *Micrhystridium* sp., which appeared exclusively in sample 24 B (Appendix 3 at www.geologica-acta.com). The distribution of palaeomicroplankton along the stratigraphic record studied indicates a constant salinity range, and thus suggests that no significant environmental changes took place.

The evidence for low-saline to fresh water non-marine environments, as indicated by the minimal contribution of marine palynomorphs, could be explained by freshwater influxes coupled with sea level variation (Beri and Goso, 1998). This environmental condition are also coherent with regional paleoclimatic models proposed by Rocha-Campos et al. (2008) for the Paraná Basin in Brazil, suggesting the existence of multiple advance-retreat phases of glacial lobes that left a carpet of subglacial and meltwater deposits. In addition, palaeoclimatic models for the Late Palaeozoic glaciation also suggest discrete glacial events separated by warmer climate periods (Fielding et al., 2008). Therefore, the low salinity lacustrine environments might result from a significant increase of freshwater input from melting glaciers, which would also explain the presence of brackish to fresh water characteristic palaeomicroplankton.

Considering the depositional conditions of sediments in periglacial environments, the possibility of reworking of palynological material should not be rejected. However, the only clear evidence of species whose biochron does not extend up to the Permian is the Devonian species *Emphanisporites rotatus*, which is present in only one surface sample. In support of *in situ* deposition, the presence of tetrads corresponding to the genus *Lundbladispora* was detected in 16 samples, suggesting proximity to the mother plant. Nevertheless, Visscher et al. (2004) proposed that the presence of such tetrads could be related also to mutations in the mother plant as a product of environmental change. Therefore, in spite of the fact that these tetrads refer to strata corresponding with the Permo-Triassic boundary, the potential influence of mutations in the mother plant may question the role of tetrads as an indicator of localized transport of spores.

Despite the above mentioned taphonomic aspects related to deposition of strata, it is possible to make some generalizations regarding the vegetation represented by the palynofloras. According to Balme (1995), the botanical affinities of the most frequent spore genera found here correspond fundamentally to Lycopsida (*Lundbladispora*, *Cristatis-*

porites and *Vallatisporites*). The remaining spore genera found in high frequency do not have a clear botanical affinity as they are associated with diverse groups of “Pteridophytes” and Gymnosperms, except for the case of genus *Horriditriteles*, which is related to Filicopsida and Ginkgoopsida. Among pollen grains, the most frequent correspond to Coniferales, Glossopteridales and pteridosperms (Ginkgoopsida according to Balme, 1995) represented by *Vittatina*, *Plicatipollenites*, *Potonieisporites*, *Cannanoropollis* and *Protohaploxypinus* (Balme, 1995; Archangelsky and Cúneo, 1987).

No megaflora remains have been found in the succession studied. The palaeofloristic assemblages in corresponding to comparable glacio-continental sediments of the Itararé Group of the Paraná Basin in Brazil (Fig. 6) have been described (Cazzulo-Kleipzig and Guerra-Sommer, 1983; Guerra-Sommer et al., 2001) and record a floristic turnover near the Permian-Carboniferous boundary identified by the

presence of *Glossopteris* in the South American Gondwana. This palaeoflora is dominated by seed-bearing Glossopteridales and *Botrychiopsis plantiana*, which is the taxon second in abundance. Cordaitals, Conifers and Ginkgoals are complementary elements and herbaceous forms are very rare, represented by few specimens of *Phyllothea* sp. (Guerra-Sommer et al., 2001). Iannuzzi and Souza (2005) described for the same age the *Phyllothea-Gangamopteris* flora, characterized by the first appearance of glossopterid elements and by the abundance of *Phyllothea*-like sphenophytes. This flora represents the interval during the transition between deglaciation and postglacial depositional sequences. Moreover, similar assemblages occur elsewhere in the lowest Lower Gondwana strata, such as in Australia, India, South Africa and southern America (Iannuzzi and Souza 2005).

In order to explain the composition of palynological assemblages, where palynomorphs associated with Gymnosperms

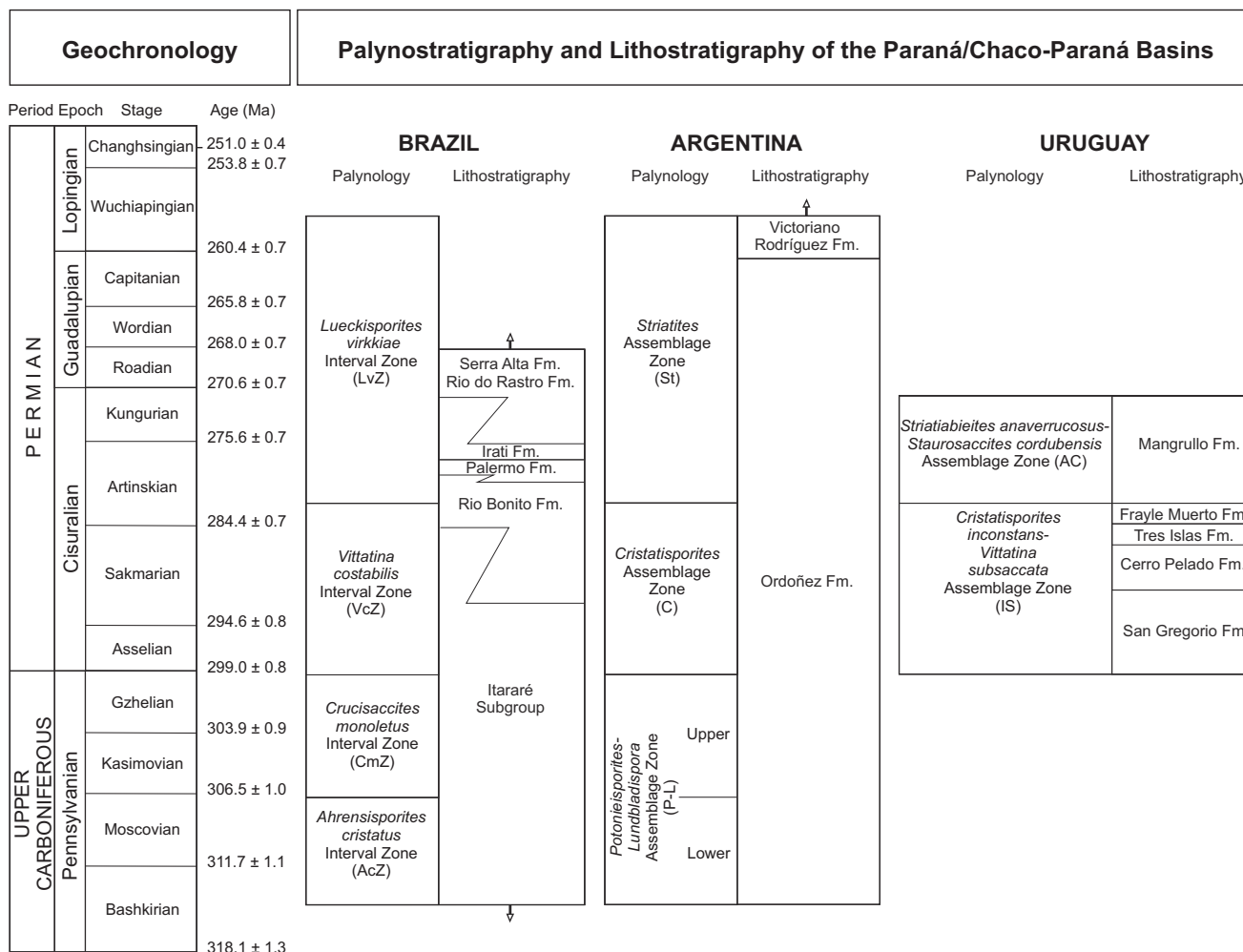


FIGURE 6 | Correlation of chrono-, litho- and palynostratigraphy data for the Upper Carboniferous – Permian interval of the Paraná and Chaco-Paraná basins (modified from Azcuy et al., 2007; Iannuzzi & Souza, 2005; Souza et al., 2007).

(e.g., Conifers), characteristic of dry land vegetation, and Pteridophytes, characteristic of wetland vegetation, appear together in the same assemblage, the general context of sea level change related to glacial advance and retreat should be considered. In that context, models proposed by Dimichele et al. (2009) for the Late Palaeozoic in Equatorial Pangea could be applied. Such models suggest that basinal lowlands or their margins were home to vegetation of an entirely different taxonomic composition. The diverse vegetation types occupied the basin at different times in the covariant ice/sea-level/climate cycles. Dry vegetation types eventually became prominent in the basin lowland. However, Cúneo (1983) proposed that some Gymnosperms in the Southern Hemisphere could have had a wider range of environmental requirements than previously thought. These Gymnosperms could have been associated either with hydrophilous communities or with environments developed at varying distances from water bodies. Therefore, it could be suggested that the gymnosperms that produced the pollen grains found in the analysed associations were not markedly distant from the deposition zone.

From a paleoclimatic point of view, a model of climatic evolution has been proposed for the Late Palaeozoic in the Basins of Western Argentina (López-Gamundí et al., 1992; Limarino et al., 1996). According to this model, there were two phases with glacial influence; phase II and phase IIIa, which would be coeval to the studied record. Phase II corresponds to an important glacial event developed over much of Gondwana. This glaciation had an important effect on sedimentation in continental as well as marine areas, primarily resulting in an extensive formation of diamictites. Phase IIIa corresponds to wet and cold finiglacial conditions. In continental areas this phase is represented by widespread formation of lacustrine deposits containing carbonaceous shales, frequent turbidites and dropstones. Marine areas correspond to diamictite deposits that are resedimented by gravity flows, and interpreted as responses to glacioeustatic sea level changes. These deposits are covered by clastic facies of open sea that probably corresponds to a postglacial transgressive phase (Limarino et al., 1996). Such facies are the same as those represented in the Cerro Pelado Formation, indicating that generation of these deposits is coherent with regional context of postglacial conditions.

This palaeoclimatic scenario is congruent with a palaeogeographical model characterized by transgressive post- or interglacial events (Scotese et al., 1999) that corresponds to the so-called Stage 3, established for South America by Limarino and Spalletti (2006). According to these authors, Stage 3 (Late Pennsylvanian–Early Cisuralian), is characterised by maximum extension of glacial–postglacial sediments in the Paraná Basin (intraplate region), where fluvial deposits interfingering with thin intervals of shallow marine sediments.

The palynological assemblages founded in the Cerro Pelado Formation do not present significant compositional changes. They are abundant and have a relatively high diversity (63 genera). The presence of pollen grains belonging to groups such as Coniferales, Glossopteridales and pteridosperms in association with Lycopsida and Filicopsida suggests that communities characteristic of milder climates could have developed at the time of deposition of these rocks (Guerra-Sommer et al., 2001). Although it has been proposed that ice sheets had their maximum extent during the Asselian to early Sakmariano in Gondwana (Fielding et al., 2008), the age of the studied sediments, the facies and palynoflora analyses carried out in the Cerro Pelado Formation indicate episodes of climatic amelioration. According to these interpretations, these sediments were deposited during interglacial–postglacial periods. The palynological content found in these strata represents a palaeoflora that, due to its environmental requirements, does not seem to have developed under extreme cold climatic conditions.

CONCLUSIONS

The currently available palynological database from the glacial-related deposits of the lower Permian Cerro Pelado Formation demonstrates that the composition of the palaeofloral assemblages analysed was relatively homogeneous through the whole stratigraphic range studied. In other words, plant palaeocommunity composition during the period of time recorded by these strata was relatively stable. These assemblages consist primarily of laevigate and cingulicavate triletes spores, together with monosaccate and plicate pollen grains. Acritarchs, algae, prasinophytes, Fungi and *Incertae sedis* forms also occur. Although pollen grains account for a higher number of species, spores are more abundant.

The Cerro Pelado Fm. assemblages can be correlated with the *Cristatisporites* Zone of the Chaco-Paraná Basin in Argentina; with the *Protohaploxylinus goraiensis* Sub-zone of the *Vittatina costabilis* Zone of the Paraná Basin in Brazil; and with the *Cristatisporites inconstans-Vittatina subsaccata* Zone of the Paraná Basin in Uruguay. According to the ages proposed for these palynozones, the Cerro Pelado Fm. successions are considered Early Permian (Asselian/Artinskian) in age, which is coherent with the previously proposed chronostratigraphy for these sediments.

Many of the palynomorph bearing strata were accumulated in brackish to fresh water lacustrine bodies, and alternated with rock intervals deposited under higher salinity, marine conditions. This fact would be coherent with the regional and general palaeoclimatic models that propose glacial phases characterized by multiple glacial lobe advance-

retreat stages that resulted in the interbedding of glacial deposits (that led to the generation of subglacial and melt water-related deposits) and interglacial-postglacial sediments formed during milder warmer climatic episodes.

Although general palaeoclimatic models propose a massive expansion of glaciers in the Late Palaeozoic southern hemisphere, the plant communities that contributed to the palynoflora found in the Cerro Pelado Formation suggest an early Permian climatic amelioration in this Western Gondwana region.

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ELECTRONIC APPENDIX I

SYSTEMATICS OF THE PALYNOLOGICAL RECORD IN THE LOWER PERMIAN CERRO PELADO FORMATION (PARANA BASIN, URUGUAY)

Anteturma PROXIMEGERMINANTES R. Potonié 1970
 Turma TRILETE Reinsch emend. Dettmann 1963
 Suprasubturma ACAVATITRILETES Dettmann 1963
 Subturma AZONOTRILETES Luber emend. Dettmann 1963
 Infraturma LAEVIGATI Bennie & Kidston emend. R. Potonié 1956

Genus *Calamospora* Schopf, Wilson & Bentall 1944

Type species. *Calamospora hartungiana* Schopf in Schopf, Wilson & Bentall, 1944.

Botanical affinity. Rhyniopsida (Trimerophytales), Zosterophylloids, Barinophytoids (Barinophytales), Lycopsidea (Selaginellales?), Equisetopsida (Bowmaniales, Calamostachyales, Equisetales), Progymnospermopsida (Noeggerathiales) (cf. Balme, 1995).

Calamospora microrugosa (Ibrahim) Schopf, Wilson & Bentall, 1944.
 Figure A1.1, A.

Dimensions (1 specimen). Equatorial diameter, 37 μm ; exine thickness, 1 μm .

Infraturma APICULATI Bennie & Kidston emend. R. Potonié 1956
 Subinfraturma GRANULATI Dybová & Jachowicz 1957

Genus *Cyclogranisporites* R. Potonié & Kremp 1954

Type species. *Cyclogranisporites leopoldi* (Kremp) R. Potonié & Kremp, 1954.

Botanical affinity. ? Bryophyta (Sporogonites), Lycopsidea (Order uncertain, Angarodendron), Filicopsida (? Botryopteridales, Zygopteridales, Marattiales), Progymnospermopsida (Aneurophytales, Noeggerathiales), Cycadopsida (Lagenostomales, Trigonocarpales) (cf. Balme, 1995).

Cyclogranisporites gondwanensis Bharadwaj & Salhuja 1964
 Figure A1.1, B.

Dimensions (9 specimens). Equatorial diameter, 28 (31.2) 41 μm ; exine thickness, 1 (1.6) 2 μm .

Subinfraturma VERRUCATI Dybová & Jachowicz 1957

Genus *Verrucosisporites* Ibrahim emend. Smith & Butterworth 1967

Type species. *Verrucosisporites verrucosus* (Ibrahim) Ibrahim, 1933.

Botanical affinity. Lycopsidea (Isoetales), Filicopsida (Botryopteridales, Zygopteridales, Marattiales), Cycadopsida (Lagenostomales, Trigonocarpales) (cf. Balme, 1995).

Verrucosisporites verrucosus (Ibrahim) Ibrahim 1933
 Figure A1.1, F.

Dimensions (1 specimen). Equatorial diameter, 36 μm .

Verrucosisporites sp. cf. *V. verrucosus* (Ibrahim) Ibrahim 1933

Dimensions (1 specimen). Equatorial diameter, 28 μm .

Remarks. The specimen here identified is smaller than the specimens described by Ibrahim (1933).

Subinfraturma BACULATI Dybová & Jachowicz 1957

Genus *Raistrickia* Schopf, Wilson & Bentall 1944-emend. R. Potonié & Kremp 1954

Type species. *Raistrickia grovensis* Schopf, Wilson & Bentall, 1944.

Botanical affinity. Filicopsida (Botryopteridales, Zygopteridales) (cf. Balme, 1995).

Raistrickia sp. cf. *R. rotunda* Azcuy 1975
 Figure A1.1, E.

Dimensions (1 specimen). Equatorial diameter, 47 μm ; exine thickness, 3 μm ; bacula, 1.5-6 μm wide and 1.5-4 μm long.

Remarks. This specimen differs from *Raistrickia rotunda* Azcuy (1975) in bacula size.

Infraturma MURORNATI R. Potonié & Kremp 1954

Genus *Convolutispora* Hoffmeister, Staplin & Malloy 1955

Type species. *Convolutispora florida* Hoffmeister, Staplin & Malloy, 1955.

Botanical affinity. Filicopsida (Botryopteridales, Zygopteridales, Marattiales, Filicales Order uncertain) & Cycadopsida (Lagenostomales) (cf. Balme, 1995).

Convolutispora archangelskii Playford & Dino 2002
Figure A1.1, D.

Dimensions (1 specimen). Equatorial diameter, 37 μm .

Genus *Emphanisporites* McGregor 1961

Type species. *Emphanisporites rotatus* McGregor, 1961.

Botanical affinity. Rhyniophyta (cf. Balme, 1995).

Emphanisporites rotatus McGregor 1961 emend.
McGregor 1973
Figure A1.1, C.

Dimensions (1 specimen). Equatorial diameter, 26 μm .

Suprasubturma LAMINATITRILETES Smith &
Butterworth 1967

Subturma ZONOLAMINATITRILETES Smith &
Butterworth 1967

Infraturma CINGULICAVATI Smith & Butterworth 1967

Genus *Cristatisporites* R. Potonié & Kremp 1954

Type species. *Cristatisporites indignabundus* (Loose) R. Potonié & Kremp, 1954.

Botanical affinity. Lycopsidea (Chaloneriaceae) (cf. Balme, 1995).

Cristatisporites sp. cf. *C. saltitensis* Ottone 1989
Figure A1.1, G.

Dimensions (1 specimen). Equatorial diameter, 46 μm ; cingulum, 6 μm wide.

Remarks. The poor preservation of the specimen disallows more precise specific assignation.

Anteturma VARIEGERMINANTES R. Potonié 1970
Turma SACCITES Erdtman 1947

Subturma MONOSACCITES Chitaley emend.
R. Potonié & Kremp 1954

Infraturma DIPOLSACCITI Hart emend. Dibner 1971
Subinfraturma APERTTACORPINI Dibner 1971

Genus *Plicatipollenites* Lele 1964

Type species. *Plicatipollenites malabarensis* (Potonié & Sah) Foster, 1975.

Botanical affinity. Pteridospermophyta, Coniferophyta,

Cordaitophyta (cf. Quadros et al., 1996).

Plicatipollenites gondwanensis (Balme & Hennelly) Lele
1964

Figure A1.1, I.

Dimensions (2 specimens). Overall equatorial diameter, 94–112 μm ; corpus diameter, 67–88 μm ; saccus, 15 μm wide.

Genus *Potonieisporites* Bharadwaj emend. Bharadwaj
1964

Type species. *Potonieisporites novicus* Bharadwaj 1964.

Botanical affinity. Coniferopsida (Emporiaceae, Ruffloriaceae, Utrechtiaceae) (cf. Balme, 1995).

Potonieisporites marleniae Playford & Dino 2000
Figure A1.1, J.

Dimensions (1 specimen). Overall length, 80 μm ; overall breadth, 150 μm ; corpus length, 77 μm ; corpus breadth, 85 μm .

Potonieisporites sp. cf. *P. marleniae* Playford & Dino 2000

Dimensions (1 specimen). Overall length, 45 μm ; overall breadth, 89 μm .

Remarks. The specimen lacks a corpus and hence is only tentatively identified.

Potonieisporites methoris (Hart) Foster 1975
Figure A1.1, K.

Dimensions (10 specimens). Overall length, 49(61.2)73 μm ; overall breadth, 100(120.6)180 μm ; corpus length, 48(58.4)67 μm ; corpus breadth 48(55.8)65 μm .

Potonieisporites sp. cf. *P. methoris* (Hart) Foster 1975

Dimensions (1 specimen). Overall length, 63 μm ; overall breadth, 97 μm ; corpus length, 51 μm ; corpus breadth, 55 μm .

Remarks. A more precise specific identification is not possible owing to the specimen's deficient preservation.

Genus *Circumplicatipollis* Ottone & Azcuy 1988

Type species. *Circumplicatipollis plicatus* Ottone & Azcuy, 1988.

Botanical affinity. Uncertain.

Circumplicatipollis stigmatus (Lele & Karim)
Ottone & Azcuy 1988
Figure A1.1, H.

Dimensions (1 specimen). Overall horizontal diameter, 112 μm ; overall vertical diameter, 85 μm ; saccus, 15 μm wide.

Remarks. The poor preservation of the material inhibits a more precise specific assignation.

Infraturma STRIASACCTI Bharadwaj 1962

Genus *Striomonosaccites* Bharadwaj 1962

Type species. *Striomonosaccites ovatus* Bharadwaj, 1962.

Botanical affinity. Glossopteridales (cf. Lindström *et al.*, 1997).

Striomonosaccites sp. cf. *S. ovatus* Bharadwaj 1962
Figure A1.2, A.

Dimensions (1 specimen). Overall diameter, 79 μm ; corpus diameter, 50 μm ; approximately 20 taeniae.

Remarks. The specimen features more taeniae than those described by Bharadwaj (1962).

Subturma DISACCITES Cookson 1947
Infraturma DISACCITRILETI Leschik emend.
R. Potonié 1958

Genus *Alisporites* Daugherty emend. Jansonius 1971

Type species. *Alisporites opii* Daugherty, 1941.

Botanical affinity. Ginkgoopsida (Peltaspermales), Coniferopsida (Podocarpaceae, Ulmanniaceae, Voltziales s.l.) (cf. Balme, 1995).

Alisporites australis de Jersey 1962
Figure A1.2, B.

Dimensions (1 specimen). Corpus breath, 50 μm ; corpus length, 41 μm ; saccus, 25 μm wide.

Genus *Scheuringipollenites* Tiwari 1973

Type species. *Scheuringipollenites maximus* (Hart) Tiwari, 1973.

Botanical affinity. Uncertain.

Scheuringipollenites sp. cf. *S. ovatus* (Balme & Hennelly) Foster 1976.

Dimensions (1 specimen). Overall length, 38 μm ; overall breadth, 36 μm .

Remarks. Due to the poor preservation of the specimen, it is not possible to make a more precise assignation.

Infraturma STRIATITI Pant 1954

Genus *Protohaploxypinus* Samoilovich emend. Morbey 1975

Type species. *Protohaploxypinus latissimus* (Luber) Samoilovich, 1953.

Botanical affinity. Ginkgoopsida (Glossopteridales, Peltaspermales) (cf. Balme, 1995).

Protohaploxypinus amplus (Balme & Hennelly) Hart 1964

Dimensions (2 specimens). Overall breadth, 67-120 μm ; corpus diameter, 72 μm ; saccus, 50 μm wide; number of taeniae, 9 and 12.

Protohaploxypinus paucitaeniatus Césari, Archangelsky & Seoane 1995
Figure A1.2, C.

Dimensions (1 specimen). Overall length, 36 μm ; corpus length, 20 μm ; corpus breath, 24 μm .

Turma PLICATES Naumova emend. R. Potonié 1960
Subturma COSTATES R. Potonié 1970
Infraturma COSTATI Jansonius 1962

Genus *Vittatina* Luber emend. Wilson 1962

Type species. *Vittatina subsaccata* Samoilovich, 1953.

Botanical affinity. Ginkgoopsida (Peltaspermales) (cf. Balme, 1995).

Vittatina corrugata Marques-Toigo 1974
Figure A1.2, E.

Dimensions (8 specimens). Overall length, 39(62.3)82 μm ; overall breadth, 26(56.4)102 μm ; number of taeniae, 13(16)19.

Vittatina saccata (Hart) Playford & Dino 2000
Figure A1.2, F.

Dimensions (2 specimens). Overall length, 52-54 μm ; overall breadth, 73-79 μm ; saccus, 32-33 μm wide; 9-13 taeniae, 2-4 μm wide.

Vittatina saccifer Jansonius 1962
Figure A1.2, G.

Dimensions (2 specimens). Overall length, 27-45 μm ; overall breadth, 39-42 μm ; 8-9 taeniae, 2-3 μm wide.

Vittatina vittifera (Luber & Waltz) Samoilovich 1953
Figure A1.2, D.

Dimensions (9 specimens). Overall length, 24(52.2)80 μm ; overall breadth, 35(54)77 μm ; 9-16 taeniae, 1.5-4 μm wide.

Vittatina sp. cf. *V. vittifera* (Luber & Waltz) Samoilovich 1953

Dimensions (1 specimen). Overall length 55 μm ; number of taeniae, 8.

Remarks. The poor preservation of the specimen negates accurate taxonomic assignation.

Turma MONOCOLPATES Iverson & Troels Smith 1950

Genus *Cycadopites* Woodhouse 1933

Type species. *Cycadopites follicularis* Wilson & Webster, 1946.

Botanical affinity. Cycadopsida (Bennettiales, Cycadales) Ginkgoopsida (Ginkgoales, Gnetales, Peltaspermales, Pentoxylales) (cf. Balme, 1995).

Cycadopites caperatus (Luber & Waltz) Hart 1965
Figure A1.2, H

Dimensions (8 specimens). Overall length, 30(45.4)63 μm ; overall breadth, 22(30.5)47 μm ; colpus, 2-6 μm ; granules, 0.5 μm .

Division CLOROPHYTA Pacher 1914

Genus *Quadrisporites* Hennelly emend. R. Potonié & Lele 1961

Type species. *Quadrisporites horridus* Hennelly ex R. Potonié & Lele, 1961.

Quadrisporites horridus (Hennelly) R. Potonié & Lele 1961
Figure A1.2, I.

Dimensions (1 specimen). Diameter of each specimen, 20 μm .

Division PRASINOPHYTA Round 1971

Genus *Leiosphaeridia* Eisenack emend. Downie & Sarjeant 1963

Type species. *Leiosphaeridia baltica* Eisenack, 1958.

Leiosphaeridia minutissima (Naumova) Jankauskas 1989
Figure A1.2, J.

Dimensions (13 specimens). Equatorial diameter, 24(30)35 μm ; exine thickness, 0.5(1)2 μm .

Leiosphaeridia tenuissima Eisenack 1958
Figure A1.2, K.

Dimensions (10 specimens). Diameter, 79(104.8)119 μm ; exine thickness, 0.5 μm .

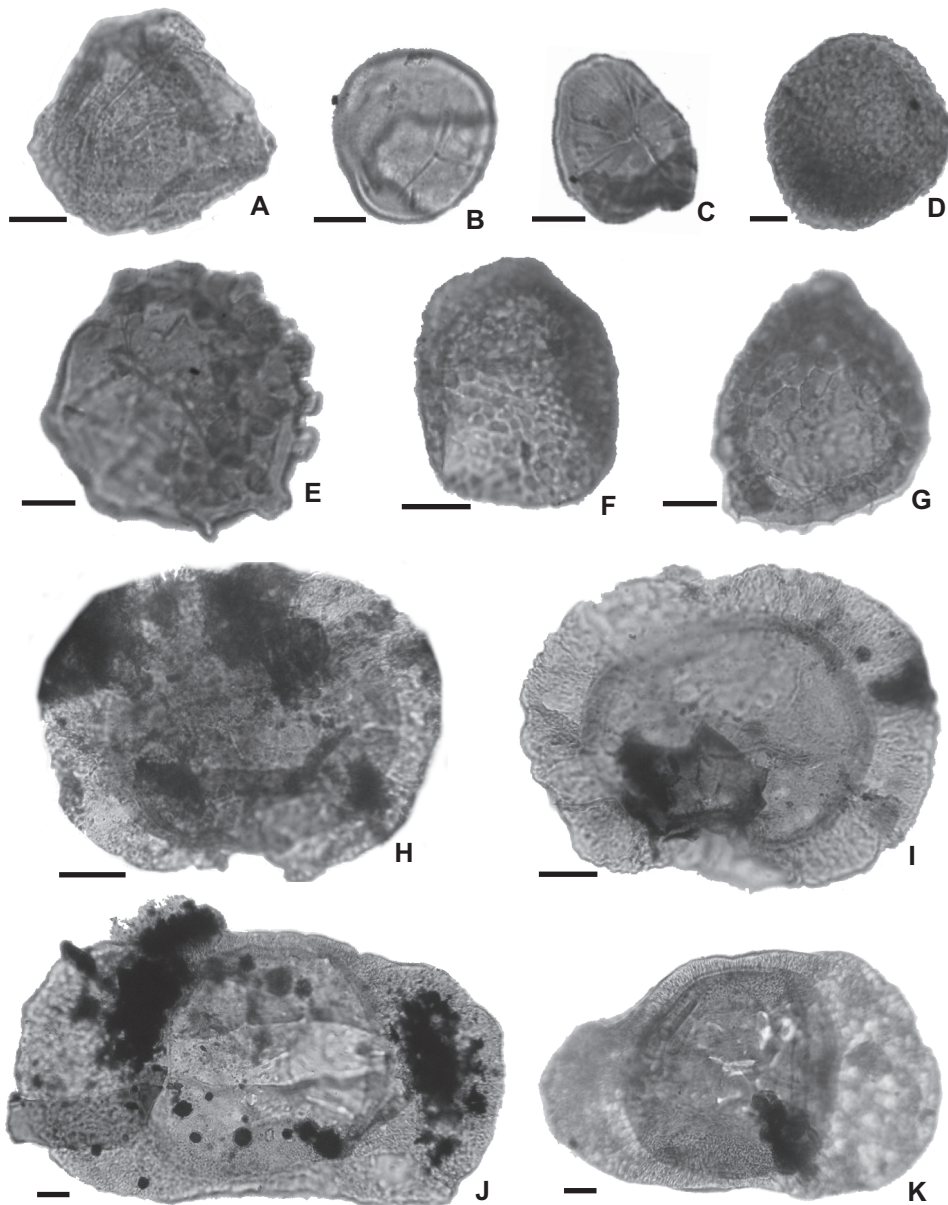


FIGURE A11 | A) *Calamospora microrugosa* (Ibrahim) Schopf, Wilson & Bentall, FCPP 337 030/4. B) *Cyclogranisporites gondwanensis* Bharadwaj & Salhuja, FCPP 338 M41/3. C) *Emphanisporites rotatus* McGregor, FCPP 337 M44/4. D) *Convolutispora archangelskii* Playford & Dino, FCPP 351 E29/2. E) *Raistrickia* sp. cf. *R. rotunda* Azcuy, FCPP 337 R39/3. F) *Verrucosisporites verrucosus* Ibrahim, FCPP 338 J31/4. G) *Cristatisporites* sp. cf. *C. saltitensis* Ottone, FCPP 337 S15/2. H) *Circumplicatipollis stigmatus* (Lele & Karim) Ottone & Azcuy, FCPP 354 F38/1. I) *Plicatipollenites gondwanensis* (Balme & Hennesly) Lele, FCPP 351 E26/4. J) *Potonieisporites marleniae* Playford & Dino, FCPP 345 M14/3. K) *Potonieisporites methoris* (Hart) Foster, FCPP 345 U21/1. Scale bar, 10 μ m.

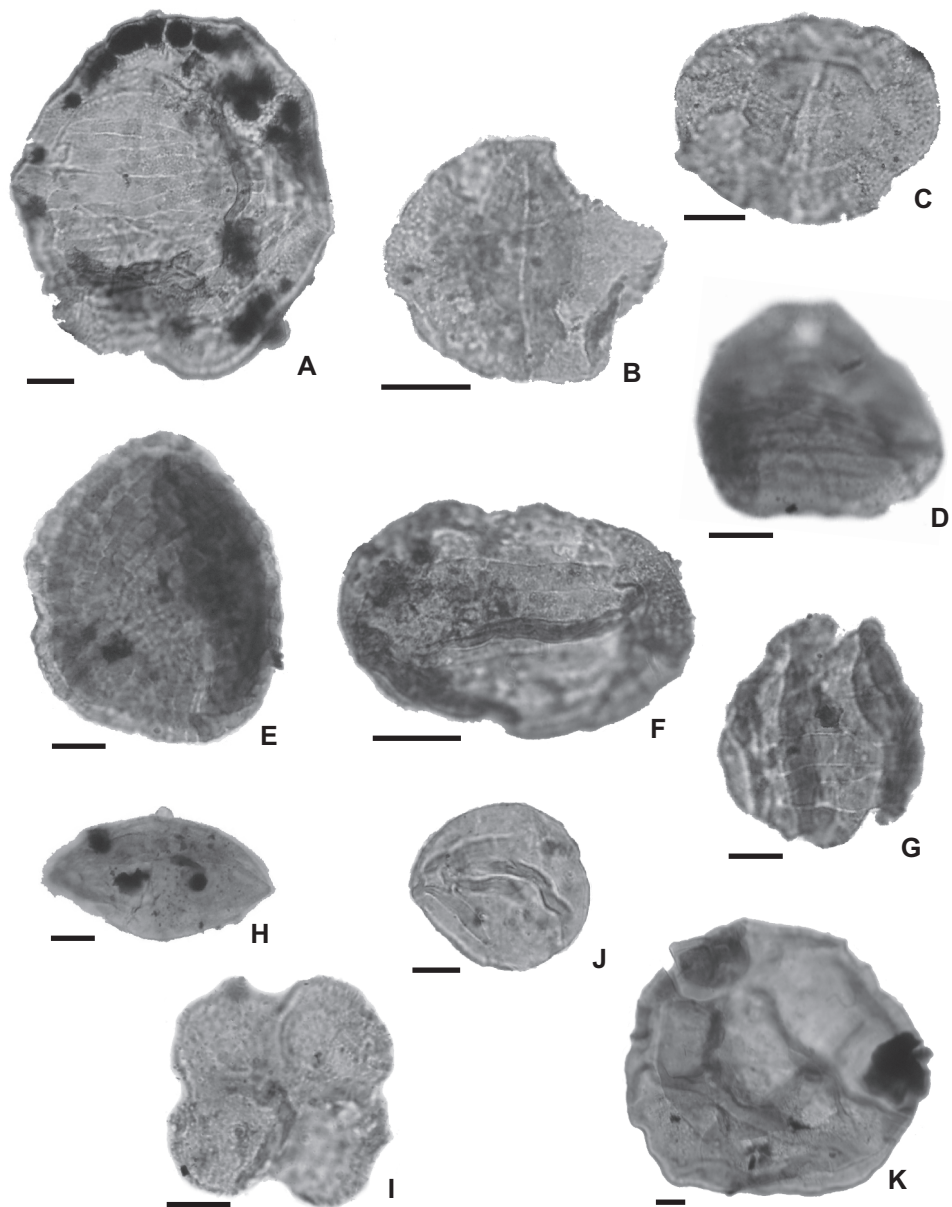


FIGURE A12 | A) *Striomonosaccites* sp. cf. *S. ovatus* Bharadwaj, FCPP 345 M22/4. B) *Alisporites australis* de Jersey, FCPP 351 015/3. C) *Protohaploxypinus paucitaeniatus* Césari, Archangelsky & Seoane, FCPP 345 R27/1. D) *Vittatina vittifera* (Luber & Waltz) Samoilovich, FCPP 337 K18/1. E) *Vittatina corrugata* Marques-Toigo, FCPP 345 L17/1. F) *Vittatina saccata* (Hart) Playford & Dino, FCPP 353 P37/4. G) *Vittatina saccifer* Jansonius, FCPP 345 H17/4. H) *Cycadopites caperatus* (Luber & Waltz) Hart, FCPP 345 F13/2. I) *Quadrисporites horridus* (Hennelly) R. Potonié & Lele, FCPP 337 N24/3. J) *Leiosphaeridia minutissima* (Naumova) Jankauskas, FCPP 345 H12/2. K) *Leiosphaeridia tenuissima* Eisenack, FCPP 337 K42/1. Scale bar, 10 μ m.

ELECTRONIC APPENDIX II

SYSTEMATICS OF THE PALYNOLOGICAL RECORD IN THE LOWER PERMIAN CERRO PELADO FORMATION (PARANA BASIN, URUGUAY)

Palynomorph taxa present in the boreholes DCLS-3, 4, 11, 13 and 24, and in surficial samples S1 and S2

(* indicates taxa not previously recorded from the Cerro Pelado Formation).

P3 (Borehole DCLS-3): A, 6,20m; B: 4,70m. P4 (Borehole DCLS-4): A, 70m; B, 68m; C, 66m; D, 64m; E, 62m; F, 61m; G, 59m; H, 58m; I, 12m; J, 7m. P11 (Borehole DCLS-11): A, 77m; B, 76m; C, 74m; D, 56m; E, 48m; F, 44m; G, 40m; H, 36m; I, 28m; J, 22m. P13 (Borehole DCLS-13): A, 54m; B, 31,10m; C, 21,30m; D, 12m. P24 (Borehole DCLS-24): A, 14,90m; B, 14,80m; C, 7,8m; D, 3,5m. S: Surficial samples S1 and S2.

ELECTRONIC APPENDIX III

Palynomorph taxa as palaeoenvironmental indicators in the boreholes DCLS-3, 4, 11, 13 and 24, and in surficial samples S1 and S2

(* indicates taxa not previously recorded from the Cerro Pelado Formation).

P3 (Borehole DCLS-3): A, 6,20m; B, 4,70m. P4 (Borehole DCLS-4): A, 70m; B, 68m; C, 66m; D, 64m; E, 62m; F, 61m; G, 59m; H, 58m; I, 12m; J, 7m. P11 (Borehole DCLS-11): A, 77m; B, 76m; C, 74m; D, 56m; E, 48m; F, 44m; G, 40m; H, 36m; I, 28m; J, 22m. P13 (Borehole DCLS-13): A, 54m; B, 31,10m; C, 21,30m; D, 12m. P24 (Borehole DCLS-24): A, 14,90m; B, 14,80m; C, 7,8m; D, 3,5m. S: Surficial samples S1 and S2.

