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The late Paleozoic palynological diversity in southernmost Paraná (Uruguay), Claromecó and Paganzo basins (Argentina), Western Gondwana

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ABSTRACT

This study explores the changes in palynoflora diversity of the late Paleozoic in boreholes DI.NA.MI.GE. 254 (26 samples) and DI.NA.MI.GE. 221 (14 samples) of the Paraná Basin in Uruguay and in 18 surface samples of the La Deheza Formation (Paganzo Basin) and 10 samples of borehole UTAL.CMM1.La Estrella.x-1 (Claromecó Basin) in Argentina. Possible relationships among biostratigraphic zones, diversity levels, facies and climatic evolution patterns in Western Gondwana are studied. Diversity curves of boreholes 221 and 254 and the La Deheza Formation outcrop exhibit similar diversity evolution patterns, i.e., an increase in lower strata diversity and a decrease in upper strata diversity. The disappearance events are determined to be more prominent in biozones of the Cisuralian to the Guadalupian age and less prominent in biozones of the early Cisuralian age. The number of genera raises from the glaciomarine facies, through the deltaic and the marine facies, up to the shallow marine or lagoon facies, in which the disappearance rates become more prominent. . The diversity of the lower part of the La Estrella borehole is lesser than that of the other sequences These diversity, disappearance and appearance behaviors may reflect post-glacial climatic amelioration patterns and the beginning of an arid phase.

1. Introduction

Significant late Paleozoic climatic changes in Western Gondwana are reflected in palynoflora observed in the region. Limarino et al. (2014) identified four phases of paleoclimatic evolution in the southern South American basins: 1, glacial (late Visean–early Bashkirian); 2, terminal glacial (Bashkirian–earliest Cisuralian); 3, postglacial (Cisuralian–early Guadalupian); and 4, arid–semiarid (late Guadalupian–Lopingian). Different climates and corresponding stratigraphical and faciological records follow various fossiliferous assemblage patterns (Limarino et al., 2014). Rather, major palynological assemblage changes, as a consequence of vegetation changes, are used for biostratigraphical purposes. Some Carboniferous and Permian Biozones of the Paraná Basin in Brazil and Uruguay and of the Paganzo and Claromecó basins in Argentina are defined based on changes in their palynological compositions (Beri et al., 2011; Césari and Gutiérrez, 2000; Gutiérrez et al., 2003; Souza and Marques-Toigo, 2003; Balarino, 2014). However, few studies have related climatic changes with palynological biozones and palynoflora diversity patterns. Goldberg (2004) and Beri et al. (2013a,b) studied diversity levels in Permian strata of the Paraná Basin and found relationships between biodiversity patterns and climate change trends. On the other hand, Venkatachala et al. (1995) observed distinct similarities among species related to Permian disappearance and climatic change in other regions of Gondwana.

We examine the changes of palynoflora diversity in late Paleozoic strata of Western Gondwana and relate observed patterns to paleoclimatic changes. Previously published data for the Paraná Basin in Uruguay are used (Gutiérrez et al., 2010; Beri et al., 2011, 2013b) in addition to La Deheza Formation data from the Paganzo Basin of Argentina (Correa and Gutiérrez, 2014; Balarino et al., 2015) and borehole data for the Claromecó Basin (Balarino, 2012, 2014) (Fig. 1).

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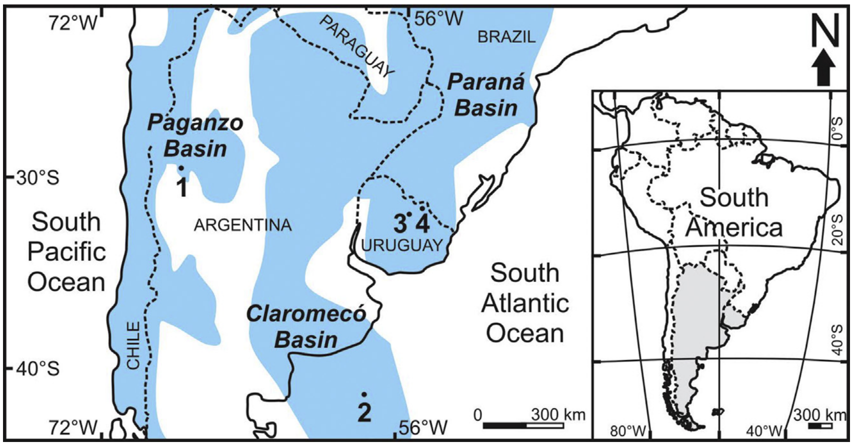

Fig. 1. Distribution of the locations of La Deheza Formation outcrop (1), La Estrella.x-1 borehole (2), 254 borehole (3) and 221 borehole (4).

2. Geological setting

The lithostratigraphic units correspond to the Paraná Basin in Uruguay and according to de Santa Ana et al. (2006), are arranged from oldest to youngest in the following order: San Gregorio-Cerro Pelado (maximum thickness, MT: 495 m), Tres Islas (MT: 160 m), Frayle Muerto (MT: 355 m), Mangrullo (MT: 35 m), Paso Aguiar (MT: 200 m), and Yaguarí (MT: 100 metros) formations. The San Gregorio-Cerro Pelado Formation primarily consists of diamictites and tillites and, to a lesser degree, conglomerates, claystones, siltstones and sandstones. These rocks were sedimented in marine-glacial and lacustrine-glacial environments. The Tres Islas Formation consists of fine to very coarse sandstones with varying proportions of grey shale and minor coals deposited in fluvial and deltaic environments. The Frayle Muerto Formation is composed of grey and black shale with parallel layering and of white and grey fine and very fine sandstones which were deposited in a marine platform environment. The Mangrullo Formation consists of sandy and dolomitic siltstone, dark grey and black oil shale, and micaceous shale deposited under restricted subaquatic conditions. The Paso Aguiar Formation is composed of gray micaceous shale with interbedded calcareous sandstone that grades into rhythmite via flaser, lenticular and wavy bedding deposited in marine shelf environments (Fig. 2).

The La Deheza Formation was deposited in the western area of the Paganzo Basin (SW of San Juan province), and more precisely of the Serpukhovian to late Cisuralian–early? Guadalupian (Correa and Gutiérrez, 2014). The 687-m-thick sequence (Correa and Gutiérrez, 2014) includes, in its lower levels, diamictites, conglomerates, sabulites, conglomeradic and fine sandstones, limestones, claystones and marlstones originating from environments associated with post-glacial Carboniferous transgression (165 m, facies I, II and III) and alternating mudstones and very fine sandstones (34 m, facies IV). The upper section includes coarse sandstones and conglomerates, fine sandstones with carbonate mudstone and thin layers of coal originating from a meandriform fluvial system (48 m, facies V). Overtop of this strata are sandstones, conglomerates, mudstones and marlstones corresponding to a new transgressive event deposited in marine coastal environments (80.4 m, facies VI). Overtop of this latter sequence, very fine sandstone and mudstone deposits of fluvial origin are found (102.6 m, facies VII). The upper segment of La Deheza Formation documents the youngest transgressive event (late Cisuralian–early? Guadalupian) in this area of the Paganzo Basin (238 m; facies VIII, IX and X). It includes fine and coarse sandstones and mudstones.

Late Paleozoic sedimentation in the Claromecó Basin in Argentina has occurred in the Pillahuincó Group (Harrington, 1947, 1970), which includes Sauce Grande, Piedra Azul, Bonete and Tunas formations (Andreis et al., 1987; Andreis and Japas, 1996). These formations reveal a sedimentary cycle of marine facies, marine shelf sediments and coastal to continental sequences (Lesta and Sylwan, 2005). The Sauce Grande Formation (Keidel, 1927; Varela, 1978; Massabie and Rossello, 1984) is comprised mainly of diamictites, sandstones, claystones and conglomerates, thus forming a shallow platform glaciomarine environment (Andreis et al., 1987, 1990; Andreis and Japas, 1996; Andreis and Torres- Ribeiro, 2003; Massabie et al., 2005; Gutiérrez et al., 2006). Throughout the following post-glacial transgressive phase (Andreis, 1984), offshore marine sediments (Lesta and Sylwan, 2005) and diamictites were gradually replaced by monotonous sequences of mudstone and fine-grained sandstones of the Piedra Azul Formation (López-Gamundí, 1989, 1997; Andreis and Japas, 1996). The Bonete Formation (195 m thick) is comprised mainly of fine and very fine sandstones and mudstones deposited in fluvial and deltaic environments (Andreis et al., 1987, 1990; Andreis and Japas, 1996), denoting the occurrence of a regressive phase. Finally, the lower section of the Tunas Formation (245 m thick) is composed of grey and black fine-grained sediments that were deposited during a subsequent transgressive phase in shallow, marine and tidally influenced environments (Andreis et al., 1987; Andreis and Japas, 1996; Zavala et al., 1993). However, the upper half is composed of tuffs with interbedded sandstone derived from volcanic eruptions that occurred in northern Patagonia during the Cisuralian–Lopingian (López-Gamundí et al., 1995).

3. Materials and methods

Palynological samples from the Paraná Basin in Uruguay corresponding to boreholes DI.NA.MI.GE. 254 (26 samples) and DI.NA.-MI.GE. 221 (14 samples) were examined. In addition, 18 surface samples from the La Deheza Formation (Paganzo Basin) and 10 samples from borehole UTAL.CMM1 and La Estrella.x-1 (Claromecó Basin) from Argentina were examined. These sections are described in greater detail in Beri et al. (2011) Balarino (2014), and Correa and Gutiérrez (2014).

To minimize bias due to likely differing classification criteria used by different researchers, genus level was chosen as the taxonomic unit of analysis. On the other hand, relationships between parataxonomical taxa of Paleozoic sporomorphs and biological taxa are, in many cases, uncertain, On occasion, different morphologies that had been assigned to different genera were later found in the

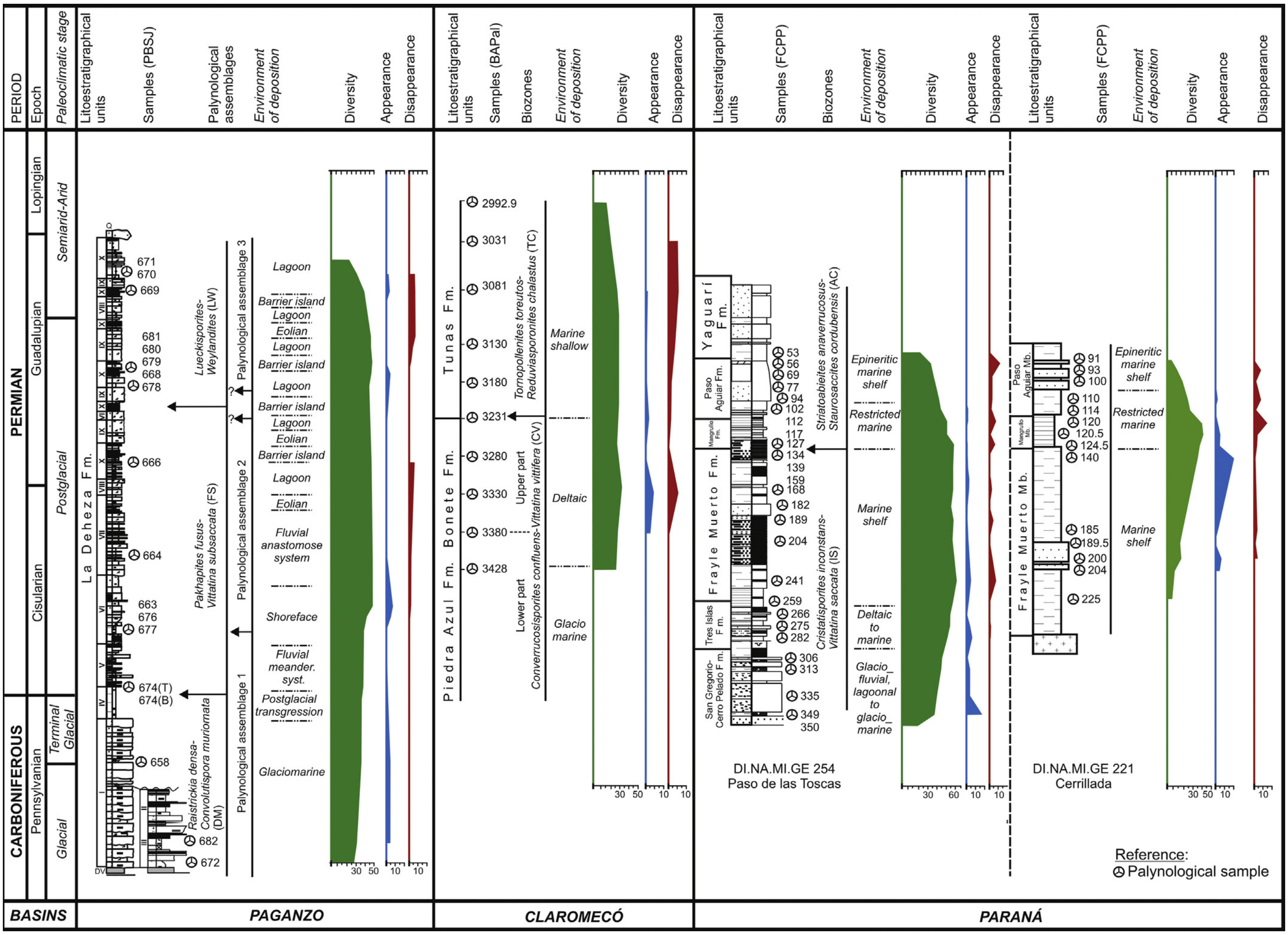

Fig. 2. Diversity, appearance and disappearance curves of genera for La Deheza Formation (Paganzo Basin) and boreholes La Estrella.x-1 (Claromecó Basin), 254 and 221 (Paraná Basin). The boreholes 254 and 221 share the palynological assemblages and the environment of deposition.

same cone (Lindström et al., 1997). Therefore, the lesser the taxonomic hierarchy, the larger the probability of introducing greater noise.

The term diversity refers to the number of sporomorph genera per sample. Data were processed using the PAST software program which employs range-through criteria. This method makes the range-through assumption, meaning that taxa are considered to have been present at all levels between the first and last appearance in any section (Hammer et al., 2001).

Appearance and disappearance ratio for each biozone were calculated by summing up the number of genera that developed or went extinct in all interval samples divided by the number of samples.

4. Results

Palynological assemblages in boreholes 221 and 254 and in the La Deheza outcrop are partially correlated. In boreholes 254 and 221, the following Biozones, listed from oldest to youngest, are found: *Cristatisporites inconstans-Vittatina saccata* and *Striatoabieites anaverrucosus-Sataurosaccites cordubensis*. The following Biozones, listed from oldest to youngest, are found in the Deheza Formation outcrop: *Raistrickia densa-Convolutispora muriornata, Pakhapites fusus-Vittatina subsaccata* and *Lueckisporites-Weylandites*; the latter two zones are correlated with those found in Uruguayan boreholes. The La Estrella borehole of the Claromecó Basin includes the *Converrucosisporites confluens-Vittatina vittifera* (lower part), *C. confluens-V. vittifera* (upper part) and *Tornopollenites toreutos-Reduviasporonites chalastus* zones, and the first two Biozones are correlated with the *C. inconstans-V. saccata* zone and are partially correlated with the *Pakhapites fusus—V. subsaccata* zone. The latter is correlated with the *S. anaverrucosus-S. cordubensis* zone and is partially correlated with the *Lueckisporites-Weylandites* zone (Fig. 2).

Proportions of genera that disappear and that appear in each biozone differ depending on whether samples were older or younger (Table 1). In the older biozones, (i.e., *Cristatisporites inconstans-V. saccata, C. confluens-Vittatina vittifera, and Raistrickia densa-Convolutispora muriornata*.and *Pakhapites fusus-V. subsaccata*) more appearance than disappearance events are found. In the younger biozones (i.e., *Lueckispotites-Weylandites, S. anaverrucosus-S. cordubensis* and *T. toreutos-R. chalastus*), the opposite holds, with the number of desappearances clearly higher than the number of appearences (Table 1).

Diversity curves of the 221 and 254 boreholes and La Deheza Formation outcrop show similar diversity patterns, i.e., an increase in lower strata diversity and a decrease in upper strata diversity (Fig. 2). On the other hand, genera appearances tend to be more prominent in the lowest stratigraphic areas, whereas disappearances predominate in the highest stratigraphic levels (Table 2). In

Table 1
Disappearance (D.) and appearance (A.) ratios in each analyzed unit. Zone AC: *Cristatisporites inconstans-Vittatina saccata* Zone. Zone IS: *Striatoabieites anaverrucosus-Sataurosaccites cordubensis* Zone. Zone LW:*Lueckisporites-Weylandites* Zone. Zone CS: *Pakhapites fusus-Vittatina subsaccata* Zone. Zone DM: *Raistrickia densa-Convolutispora muriornata*, Zone. Zone TC: *Tornopollenites toreutos-Reduviasporonites chalastus* Zone. Zone CV: *Converrucosisporites confluens-Vittatina vittifera* (upper and lower part) Zone.

	221	254	La Deheza		La Estrella	
Zone AC	**D. 5.8**	**D. 4.8**	**Zone LW**	**D. 2.5**	**Zone TC**	**D. 3.7**
	A. 1.6	A. 0.3		A. 1.3		A. 0.6
Zone IS	D. 1.1	D. 1	**Zone CS**	D. 1.6	**Zone CV**	D. 1.2
	A. 6.6	A. **3.4**		**A. 2.4**		**A. 2**
			Zone DM	D. 0		
				A.**1.8**		

Boldface means the highest value found.

borehole 221, disappearance rates reach a maximum of 35.0% (sample 120), and appearance rates reach a maximum of 57.1% (sample 140). In borehole 254, disappearance rates reach a maximum of 36.6% (sample 56), while for the appearance rates, the maximum is 47.2% (sample 349). In the La Deheza outcrop, on the other hand, turnover rates are more gradual: disappearance rates only reach 17.3% (sample 681), and appearance rates only reach 14.5% (sample 663).

The La Estrella borehole includes younger strata than the other examined units. The diversity curve shows small oscillations in the lower strata and a decline in diversity in the upper strata; disappearance rates reach a maximum of 25.0% (sample 3031), and appearance rates reach a maximum of 12.9%. (sample 3330) (Fig. 2; Table 2).

The facies of the analyzed units are also comparable (Fig. 2). Generally speaking, the number of genera increases from glaciomarine facies, through deltaic and marine facies. Most prominent disappearance events are observed in lagoon facies in boreholes 221 and 254 and at the beginning of the levels that correspond to lagoon facies in La Deheza outcrop and in the marine shallow facies in La Estrella borehole.

The data were analyzed following the paleoclimatic scheme proposed by Limarino et al. (2014). For the sequence studied here, it can be identified in the intraplate basins (Paraná and Claromecó) and in the Paganzo retroarc basin, although each basin may show different stratigraphical expressions. The Glacial stage (late Visean—early Bashkirian) is identifiable at the base of the La Deheza Formation (Association of Facies I— IV, Correa and Gutiérrez, 2014 which is not considered in this study. The late Bashkirian-early Cisuralian Terminal Glacial stage is found in the La Deheza Formation (Association of Facies V and VI; Palynological assemblages 1, Correa and Gutiérrez, 2014) in the Sauce Grande Formation (which is not considered in this study), and in borehole 254 (San Gregorio-Cerro Pelado Formation). The Postglacial stage (Cisuralian late—early Guadalupian) is found in the La Deheza Formation (Association of Facies VII-IX; Palynological assemblage 2) Piedra Azul and Bonete formations. Terminal stages are also likely found in San Gregorio-Cerro Pelado, Tres Islas, Frayle Muerto, Mangrullo and Paso Aguiar formations (borehole 254 and partially in borehole 221). The Semiarid-Arid stage (late Guadalupian—Lopingian) is present in Associations of Facies IX and X (Palynological assemblage 3, La Deheza) and in the upper segments of the Bonete and Tunas formations (Claromecó Basin).

Table 2
Number of genera diversity, appearance and disappearance in each sample analyzed.

	Sample	Sample#	Diversity	Appearance	Disappearance		Sample	Sample#	Diversity	Appearance	Disappearance
LA DEHEZA	672	1	28	0	0	**LA ESTRELLA**	3428	1	25	0	0
	682	2	31	3	0		3380	2	27	2	0
	658	3	35	4	0		3330	3	31	4	5
	674B	4	36	1	0		3280	4	26	0	0
	674T	5	37	1	0		3231	5	28	2	1
	677	6	37	0	0		3180	6	28	1	1
	676	7	41	4	0		3130	7	28	1	4
	663	8	48	7	1		3081	8	25	1	5
	664	9	48	1	2		3031	9	20	0	5
	666	10	46	0	5		2992.9	10	15	0	0
	678	11	44	3	0	**254 BOREHOLE**	350	1	19	0	0
	668	12	48	4	0		349	2	36	17	0
	679	13	48	0	2		335	3	40	4	0
	680	14	46	0	3		313	4	44	4	0
	681	15	46	3	8		306	5	45	1	0
	669	16	39	1	7		282	6	51	6	1
	670	17	32	0	7		275	7	54	4	1
	671	18	25	0	0		266	8	54	1	0
221 BOREHOLE	225	1	8	0	0		259	9	57	3	1
	204	2	11	3	0		241	10	61	5	7
	200	3	18	7	2		204	11	56	2	0
	189.5	4	16	0	1		189	12	57	1	4
	185	5	18	3	3		182	13	54	1	0
	140	6	35	20	1		168	14	56	2	2
	124.5	7	38	4	2		159	15	56	2	1
	120.5	8	41	5	4		139	16	56	1	0
	120	9	40	3	14		134	17	57	1	0
	114	10	26	0	3		127	18	58	1	7
	110	11	24	1	7		117	19	51	0	1
	100	12	17	0	4		112	20	51	1	8
	93	13	13	0	7		102	21	44	1	2
	91	14	6	0	0		94	22	42	0	3
							77	23	39	0	3
							69	24	36	0	3
							56	25	33	0	12
							53	26	21	0	0

Although this study was performed at a generic level for the aforementioned reasons, a number of species-level changes are found during the Glacial and Terminal Glacial stages. In the La Deheza Formation, for instance, according to Balarino et al. (2015), the most predominant species are *Cristatisporites stellatus, C. rollerii, C. incoinstans, C. longispinosus, C. sacbiosus, C. menendezi, C. chacoparanaensis, C.* cf. *spinosus, Punctatisporites* cf. *gretensis, Leiotriletes directus, L. virkkii, L.* cf. *corius, Lundbladispora riobonitensis, L. brasiliensis, Kraeuselisporites* spp., *Retusotriletes diversiformis, Cyclogranisporites* spp., *Brevitriletes cornutus, Brevitriletes parmatus, Brevitriletes levis, Anapiculatisporites.* spp., *Vallatisporites arcuatus, V. russoi, Granulatisporites austroamericanus, Spelaeotriletes* spp., *Grossusporites microgranulatus, Verrucosisporites* spp., and *Apiculatasporites* spp.

In the Terminal Glacial stage of La Deheza formation appearance events continued at generic level and the first desappearance events occurred at species level, whereby trilete spores such as *Cristatisporites menendezii*, *Brevitriletes cornutus*, *B. parmatus*, *Retusotriletes simplex* disappeared as other spores (*Calamospora breviradiata*, *Horriditriletes ramosus*, etc.) Monosaccate and bisaccate pollen grains (*Cannanorpollis methae*, *Pteruchipollenites gracilis*, etc.) and plicates (*Vittatina subsaccata)* appeared .

The Terminal Glacial stage also ocurrs in the San Gregorio Formation, although it is represented by only three samples. According to Beri et al. (2011), some of the most typical species are *Lundbladispora riobonitensis*, *L. areloata*, *Spelaeotriletes ybertii*, *Mabuitasaccites crucistriatus* and others started to appear as *Verrucosisporites menendezii* and *Caheniasaccites ovatus* disappeared.

The Postglacial stage was found in all stratigraphic sections examined. For this phase, maximum diversity levels are found for all of the curves, with both disappearance events and genera appearance events identified. In the La Deheza Formation, this stage is, characterized by trilete spores such as *Dibolisporites* cf. *disfacies*, *Grossusporites microgranulatus*, *Cristatisporites longispinosus,* while *C. scabiosus*, among others, disappear and *Alisporites australis*, and *Falcisporites similis* appear for the first time. In the Piedra Azul and Bonete formations (lower sequence) of the Claromecó Basin, *B. cornutus*, *Kraeuselisporites punctatus*, *Diatomozonotriletes subbaculiferus* and others disappear. During this period, *Striatopodocarpites gondwanensis*, *Lueckisporites singraulensis*, *Protohaploxypinus microcorpus* striate pollen grains and *Pakhapites ovatus* and *Preacolpatites sinuosus* plicates diversify, though smooth bisaccate pollen grains dominate the spectrum at roughly 51.6–55.6% and 50.0–55.0%, respectively. At the end of the postglacial stage, disappearance rates in boreholes 254 and 221 grow more prominent than appearance rates, as in the case of *Brevitriletes parmatus*, *Converrucosisporites micronodosus* and *Cristatisporites chacoparanensis* spores. However, bisaccate striated (*Lueckisporites balmei*, *L. virkkiae*, *L.* sp., *Striatopodocarpites rarus*, etc.) and plicate (*Vittatina ovalis*) pollen grains appear.

During the Semiarid-Arid stage, diversity rates decrease considerably; disappearance processes tend to be more prominent than those of appearance. In the La Deheza Formation, *Cristatisporites* spp. (*C. stellatus, C. rolleri, C. inconstans*), *Krauselisporites apiculatus, Speleotriletes ybertii, C. confluens, Brevitriletes levis, Granulatisporites austroamericanus* and *Leiotriletes corius* trilete spores disappear. In the Claromecó Basin, *C. confluens*, *Triadispora epigona*, *Protohaploxypinus bharadwakii* and *Vittatina corrugata* are not found anymore. The palynological assemblage is conformed with a predominance of bisaccate pollen grains (74.3–88.9%), while the remaining groups remain relictual (spores: 2.4–10.9%, striated pollen grains: 3.4–9.4%, plicate: 0.2–4.3%, monosaccate: 0.7–3.0%, monosulcate: 0–0.9%). Boreholes 221 and 254 do not undergo this phase.

These higher strata disappearance phenomena contrasts with very few new appearances, resulting in the impoverishment of palynoflora in the upper strata, which are essentially represented by striated and bisaccate pollen grains.

5. Discussion

According to Servais and Wellman (2004), Paleozoic pollen grains and spores can contribute to assess patterns of diversity, biogeography and evolution. However, pollen analyses for the examination of vegetation dynamics present numerous limitations (e.g., variations in pollen and spore production and dispersion and in the preservational potential of different species). Biases can also be introduced through the use of basin size and type variables, the categorization of pollen and spores, and through the study of various vegetation structures. These factors complicate the viability of using pollen richness as an indicator floristic richness (Birks and Line, 1992). An additional problem arises from the fact that little is known of the environmental requirements of plants that originated in Paleozoic sporomorphs, but that have no modern counterparts. In numerous cases, organic relations are not known, or one morphotype can be produced by numerous plants (Lindström et al., 1997). However, in some cases, data on organic relationships between megafossils and sporomorphs (Balme, 1995; among others) allow us to make paleoecological proposals.

Despite the limitations noted above some trends can be observed. For instance, there appears to be a relationship between diversity and different types of facies as a consequence of environments and climates. Diversity trends found in boreholes 221 and 254 and in the La Deheza Formation suggest that taxa appearance rates increase in facies associated with glacial, glaciofluvial, fluvial and coal-rich deltaic environments. For all lagoon and superficial marine facies, maximum diversity rates are followed by significant disappearance events and by limited rates of appearance. This phenomenon was also found by Beri et al. (2013a) in their examination of Cisuralian sediments of the southernmost Paraná Basin in Brazil and Uruguay, wherein diversity levels rise in lower stratigraphic levels and decrease in upper strata, confirming widespread diversity decline in western Gondwana. However, it cannot be ruled out that this could be due to differential preservation of some morphological types and, therefore, this decrease in the number of genera could be in fact the result of a taphonomical bias.

The observed diversity, disappearances and appearances reflect possible post-glacial climatic amelioration and the start of an arid phase. Indeed, both regional and global paleoclimatic reconstructions suggest that in western Gondwana, following Carboniferous glaciation, climatic amelioration enabled accumulation of coal deposits (Limarino et al., 1996, 2014). Thereafter, during significant postglacial events characterized by temperate cold and humid climates, conditions must have been suitable for coal formation and *Glossopteris* flora expansion (Limarino et al., 1996; Limarino and Spalletti, 2006; Benedetto, 2010). For the sequences examined here, postglacial facies are associated with an increase in diversity as a consequence of numerous new genera appearances and limited disappearances. By the end of the postglacial phase, an increase in disappearance rates and an absence genera development was observed in boreholes 254 and 221 and in the La Deheza Fm outcrop. This can be interpreted as an early sign of a climatic phase that developed during the middle or late Cisuralian. This remarkable late Permian trend evolved into extreme global patterns of aridization (Limarino et al., 1996, 2014; Limarino and Spalletti, 2006), whereby diversity decline is common in arid environments (Huenneke and Noble, 1996). Vegetation represented in the samples that correspond to this phase is dominated by mesophilic and xerophylic (striate and bisaccate pollen grains) plants, which is congruent with the environmental conditions. It is noteworthy that no new genera appear, denoting the establishment of new arid-adapted vegetation. By contrast, impoverished palynoflora begin to characterize genera that survive in older strata. This phenomenon is comparable to that described by DiMichele et al. (2009) in reference to Paleozoic vegetation in equatorial latitudes, as mesophilic and xerophylic communities developed in extrabasin habitats and, when environmental conditions became more arid, intrabasin hydrophilous vegetation was replaced by communities that inhabited higher elevation zones. Though this is especially true of the Pennsylvanian Coal Age, wherein climates alternated between dry and wet conditions according to DiMichele (2014), vegetation dynamics may be similar for the region studied here.

Regional climatic processes are not entirely synchronous in all basins of Western Gondwana, as the area covers a variety of paleolatitudinal features. For example, the occurrence of coals that indicate a rather humid climate with only short dry seasons. (Roscher et al 2008) would show a Cisuralian age in the Paraná basin. On the otherhand, in the basins of the NW of the Argentinian territory would be od Carboniferous-Permian age (Limarino et al., 2014). For the examined sequences, boreholes 254 and 221 and La Estrella correspond with the Eastern intraplate basins, and the La Deheza outcrop is found in a Western retroarc basin (Limarino et al., 2014). Taking into account these diachronisms, it is remarkable that palynological diversity patterns are similar in different facies, suggesting that vegetation may have responded in the same way to climatic processes at different times.

Observations of megafossils show that vegetation evolved in ways that are consistent with palynological data. According to Jasper et al. (2013), by the mid-Cisuralian (Sakmarian), Gondwana showed ameliorated climatic conditions, and a significant increase in macrofloral diversity was detected in predominantly glacial-influenced post-glacial strata. By the end of the Cisuralian, eastern-western major Gondwana paleofloristic differentiation persisted. Western South America (Brazil and northwestern Argentina) formed part of a temperate belt with cold winters and warm summers. Diversified plant associations can be inferred from the presence of glossopterids, cordaitaleans, conifers, early ginkgophytes, subarborescent lycopsids, ferns, equisetaleans and sphenophylls. From the start of the Guadalupian, there was a decline in the number of plant assemblages and in taxonomic diversity levels, denoting climate deterioration due to drier conditions.

Vegetation changes due to regional climatic changes are reflected in the palynological content of sediments, and despite the biases noted above, there is congruence between the climatic stages examined and the composition of palynoassemblages that compose different biostratigraphic zones.

6. Conclusions

The boreholes 221, 254 and La Estrella Formation and the La Deheza outcrop exhibit similar diversity patterns. The oldest palynological associations include numerous taxa. Conversely, disappearance processes are more significant in the younger biozones while appearance processes are scarcer, resulting in a decline in diversity levels.

Generally speaking, while different facies deposit in different basins during the same climatic phase, the number of genera increases from glaciomarine facies, through deltaic and marine facies, and until facies of shallow marine or lagoon environments, in which disappearance rates increase as diversity rates decrease.

Despite limitations that may complicate the relationship between palynological assemblages and vegetation that produce them; diversity, disappearances and appearances are consistent with potential post-glacial climatic amelioration and the start of an arid phase. For the La Estrella borehole and the La Deheza outcrop, we found an increase in disappearance rates during the semiarid period, and for boreholes 221 and 254, this trend was observed at the end of the postglacial period, as they do not represent semiarid periods.

While further studies with more numerous samples will shed light on some details, overall trends are found that are consistent with the results of other studies. It is thus necessary to continue conducting similar analyses to assess whether diversity evolution patterns observed in this study apply to the rest of Gondwana and to other geographic areas.

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