

# Palynology of late Serpukhovian glacial and postglacial deposits from Paganzo Basin, northwestern Argentina

Valeria S. Perez Loinaze and Silvia N. Césari

Museo Argentino de Ciencias Naturales, "B. Rivadavia", Av. Ángel Gallardo 470, Buenos Aires, C1405DJR, Argentina  
email: loinazev@macn.gov.ar; scsari@macn.gov.ar

**ABSTRACT:** Palynological analysis is reported here for the first time from glacial and postglacial deposits of the lower-middle section of the Guandacol Formation at the Huaco area, central Paganzo Basin, Argentina. Forty-nine spore species are assigned to twenty-seven genera and twenty-one pollen species are assigned to ten genera, however few acritarchs were identified. Biostratigraphic ranges of species suggest an age no older than late Serpukhovian for the section studied. This age is also supported by radiometric data that indicate an early Bashkirian age at the top of the Guandacol Formation. The palynofloras consist mostly of endemic spore species, and provide new evidence for delimiting the Subzone A of the *Raistrickia densa-Convolutispora muriornata* Biozone in Argentina. Close correlation is suggested with palynological associations belonging to the widespread glaciation occurred during the Serpukhovian-early Bashkirian in South America and Australia.

## INTRODUCTION

The Late Paleozoic glaciation is considered as one of the most important in Earth history and it is often compared in magnitude to the Pleistocene glacial event (Crowley and Baum 1991). However, because the oldest glacial records in Gondwana belong to the Late Devonian and Early Mississippian of South America, while the youngest ones recognized in Australia, has been dated as early Late Permian in age (Fielding et al. 2008), it seems likely that these glaciations were neither continuous nor synchronous Gondwana (Veevers and Powell 1987; Isbell et al. 2003a). Several authors (Veevers and Powell 1987; López-Gamundí 1997; Isbell et al. 2003b) have proposed that the Gondwanan glaciation is composed of three major episodes dated as Frasnian–Tournaisian (Glacial I), Namurian-early Westphalian (Glacial II), and Stephanian–Sakmarian (Glacial III). In Argentina, the mid-Carboniferous glacial episode (Glacial II) was recorded in the Tarija, Calingasta–Uspallata, Paganzo, and Tepuel Basins (see Limarino and Spalletti 2006). The evidence of true tillites is very scarce (Marenssi et al. 2005). A Namurian age for the Glacial II event was originally proposed based on the presence of marine invertebrate fossils assigned to the *Levipustula* Biozone and megafloristic remains of the *Nothorhacopteris-Botrychiopsis-Ginkgophyllum* Biozone (NBG) Biozone (see Archangelsky et al. 1996). According to Isbell et al. (2003b) Glacial II deposits are only known from western South America, eastern Australia and southern Tibet. Jones and Truswell (1992) described palynological associations from the Joe Joe Group, considered by Jones and Fielding (2004) as the unique unequivocal record of the Namurian–Westphalian glaciation in Australia.

This paper describes rich palynological assemblages recovered from glacial sediments, resedimented diamictites, true tillites and postglacial deposits from the lower-middle section of the Guandacol Formation in the Los Pozuelos Creek in the Paganzo Basin, NW Argentina (text-fig. 1, 2). The assemblages obtained from the most basal levels of this unit contain one of the few records of palynological associations recovered from Serpuk-

hovian tillites. Thus, they provide palynological information in Gondwana for the Glacial II Episode identified by Isbell et al. (2003b).

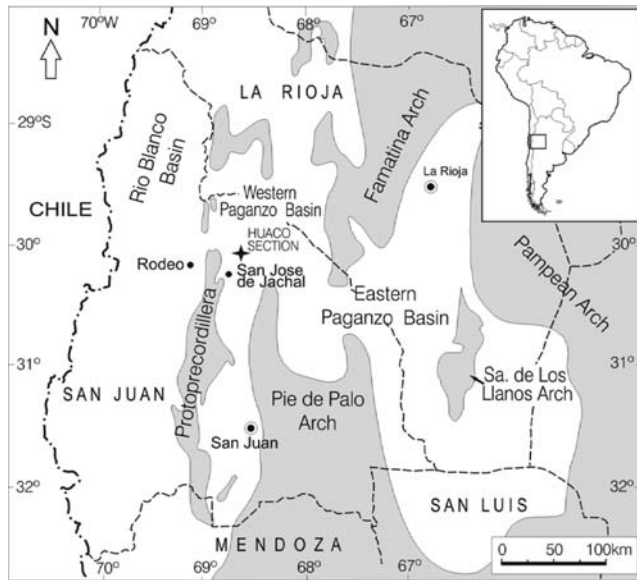
The time scale used in this paper follows the global Carboniferous chronostratigraphic time scale recently calibrated by Davydov et al. (2010). It must be emphasized that the time scale is being continually modified resulting in changes that make it difficult to relate with certainty the ages offered in the literature to an updated scale. Thus, the terms Namurian, Westphalian and Stephanian are used in the text, following the references of the original authors.

## GEOLOGICAL SETTING

The deposits studied here are located in the Paganzo Basin (northwestern Argentina) and included in the Guandacol Formation of the Paganzo Group (Azcuy and Morelli 1970) (text-fig. 1). The formation is composed of tillites and coarse grained conglomerates, shales and mudstones. The basal part of the formation has been interpreted as deposited in a fjord or shallow marine environment (Buatois and Mángano 1995; Limarino et al. 2002; Limarino et al. 2006) based on the presence of marine invertebrates and acritarchs (Ottone 1991; Martínez 1993).

Sampling was carried out in the Los Pozuelos creek area, located in the Anticlinal de Huaco area, approximately 6 km away from Huaco locality, 68° 33'W and 30° 07'S (text-figs. 1, 2). This interesting outcrop was described by Marenssi et al. (2002; 2005) who identified glaciomarine deposits, dominated by morainal bank accumulations. In this study, the section is divided into five facies associations (text-fig. 3): 1. basal diamictites (FA1), 2. shales with dropstones (FA2), 3. shales without dropstones (FA3), 4. large-scale cross-bedded sandstones (FA4) and 5. alternate sandstones and mudstones (FA5).

FA1 (50m thick) comprises matrix supported coarse-grained paraconglomerates, sandstones and thin levels of interlaminated very fine-grained sandstones and mudstones bearing small

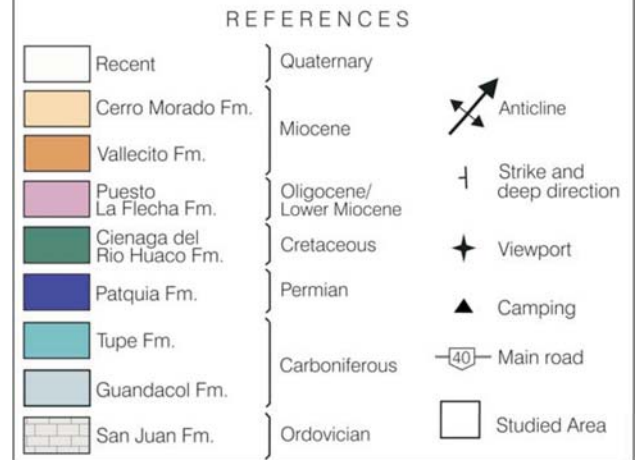
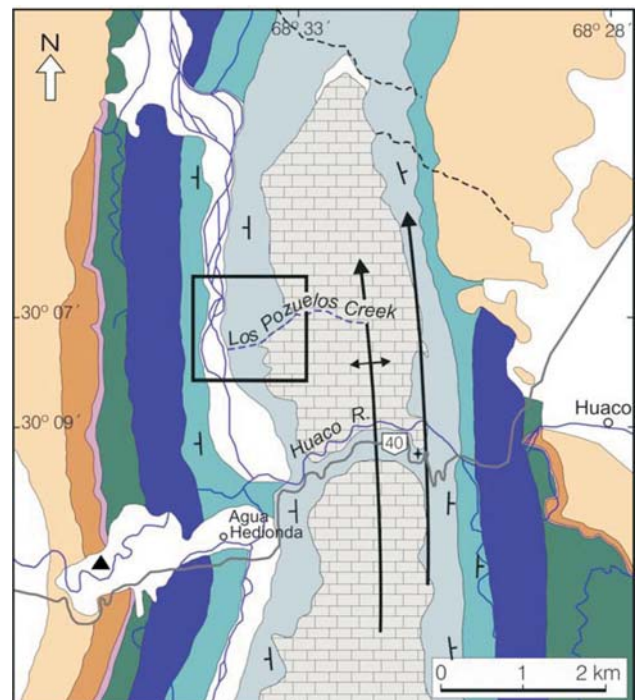


TEXT-FIGURE 1  
Palaeogeography of the Paganzo Basin during the Late Paleozoic. Start shows the fossiliferous area.

dropstones. Marensi et al. (2005) interpreted the depositional environment as a fjord filled by abundant resedimented diamictites (gravity flow deposits) and scarce glacial diamictites (lodgement till). FA2 (15m thick) is characterized by the presence of greenish-grey laminated shales with dropstones up to 0.30m in diameter, rounded and frequently showing pentagonal forms. Also, some thin sandstone beds occur. These deposits represent the melting of icebergs during the beginning of the post-glacial transgression (Marensi et al. 2005). FA3 (15m thick) is composed by laminated shales without dropstones, with frequent thin and very-thin sandstone beds, interpreted by Marensi et al. (2005) as deposited in the post glacial maximum flooding stage. FA4 reaches 10m in thickness, and is composed of large-scale yellowish grey cross-bedded fine or medium-grained sandstones in clusters up to 7m thick, deposited in an underwater estuary mouth bar (Marensi et al. 2005). Finally, FA5 (70m thick) consists of coarsened and thickened upward sequences of alternate sandstones and mudstones. The mudstones are more abundant in the lower part of the sequence, and containing poorly preserved plant remains. The sandstones are laminated, massive or with ripple lamination. The sequence was interpreted as resulting from deltaic progradation during the shallowing of the fjord environment (Perez Loinaze 2007a). All these facies associations have yielded palynological assemblages, with the exception of FA4.

#### PREVIOUS PALYNOLOGICAL STUDIES OF THE GUANDACOL FORMATION

The first palynological assemblages from the Guandacol Formation were described by Césari and Vázquez Nístico (1988). Those associations, recovered from the mid-upper part of the unit (=shales without dropstones), in the Huaco area (text-fig. 2) were referred to the late Westphalian-Stephanian based on the presence of *Vallatisporites ciliaris*, *Convolutispora muriorната*, *Crucisaccites monoletus* and *Potonieisporites magnus*. Later, Ottone and Azcuy (1989) analyzed one sample also from the mid-upper levels of the unit in the nearby La Delfina Creek.



TEXT-FIGURE 2  
Geological map of the Huaco area showing the location of the Los Pozuelos Creek.

This palynological assemblage was characterized by the abundance of monosaccate pollen and considered late Namurian-Westphalian in age (Ottone and Azcuy 1989). Ottone (1991) analyzed outcrops of the Guandacol Formation at the Esperanza mine (also in the Huaco area) and interpreted these levels of the Guandacol Formation as deposited in transitional marine environment by the presence the scarce marine forms related to green algae and the predominance of terrestrial palynomorphs. However, unfortunately the precise provenance of the samples was not mentioned by Ottone (1991). Finally, Césari and Limarino (2002) recovered rich palynological assemblages from shales with dropstones located in the basal to mid-section of the unit, deposited in the earlier stages of deglaciation, in the Cerro Bola area (La Rioja Province). These palynological assemblages contain abundant non taeniate pollen grains repre-



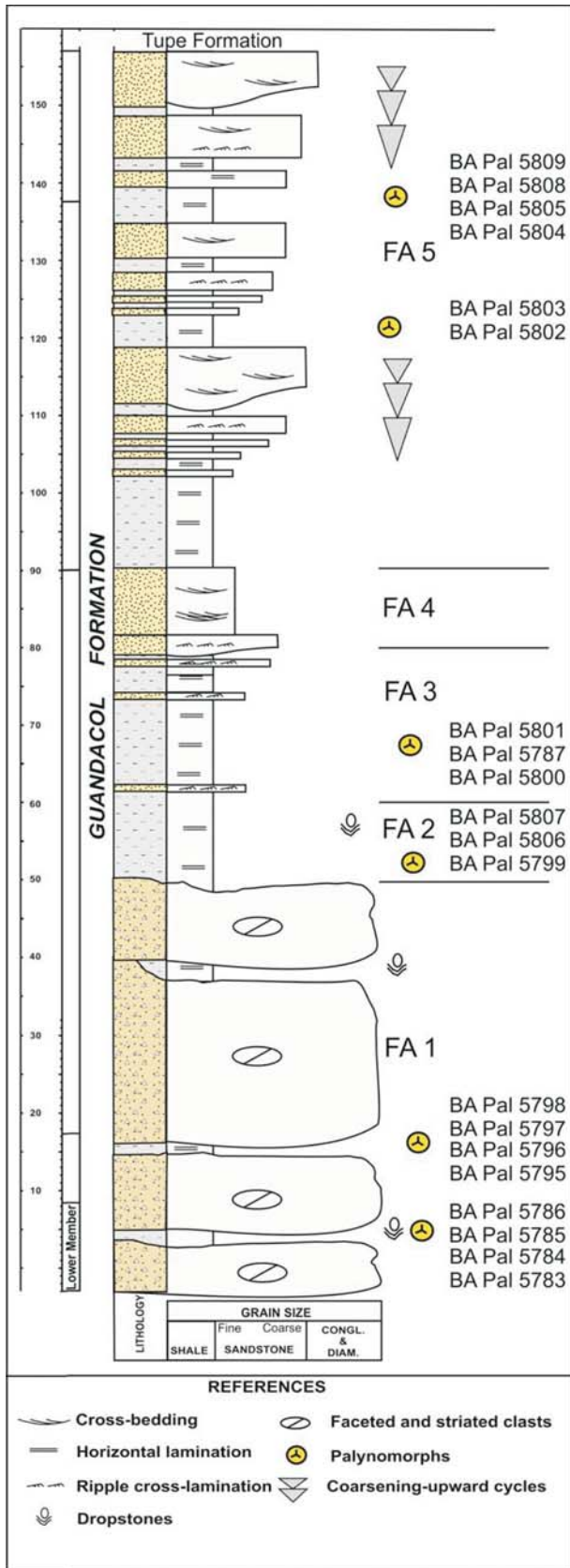
TABLE 1  
Palynomorph taxa from Guandacol Formation in Los Pozuelos Creek, listed in systematic order.

Spores		
<i>Anapiculatisporites concinnus</i> Playford 1962 (Plate 1.1)	<i>Reticulatisporites</i> sp. (Plate 2.18)	
<i>Apiculatasporites parviapiculatus</i> Azcuy 1975a (Plate 1.2)	<i>Retusotriletes</i> sp. (Plate 2.4)	
<i>Apiculatisporis</i> sp. (Plate 1.3)	<i>Spinozonotriletes hirsutus</i> Azcuy 1975b (Plate 2.6)	
<i>Apiculatisporis variornatus</i> di Pasquo, Azcuy and Souza 2003 (Plate 1.4)	<i>Tricidarispores gutii</i> Césari and Limarino 2002 (Plate 2.19)	
<i>Apiculiretusispora alonsoii</i> Ottone 1989 (Plate 1.5)	<i>Vallatisporites ciliaris</i> (Luber) Sullivan 1964 (Plate 2.7)	
<i>Asperispora</i> sp. cf. <i>A. reticulatispinosus</i> Jones and Truswell 1992 (Plate 1.6)	<i>Verrucosispores andersonii</i> (Anderson) Backhouse 1988 (Plate 2.8)	
<i>Brevitriletes cornutus</i> (Balme and Hennelly) Høeg and Bose 1960 (Plate 1.7)	<i>Verrucosispores menendezii</i> Archangelsky and Gamero 1979 (Plate 2.9)	
<i>Convolutispora clavata</i> (Ishchenko) Hughes and Playford 1961 (Plate 1.8)	<i>Verrucosispores</i> sp. cf. <i>V. quasigobbettii</i> Jones and Truswell 1992 (Plate 2.10)	
<i>Convolutispora muriornata</i> Menéndez 1965 (Plate 1.9)	Pollen	
<i>Convolutispora ordonezii</i> Archangelsky and Gamero 1979 (Plate 1.10)	<i>Caheniasaccites densus</i> Lele and Karin emend. Gutiérrez 1993 (Plate 3.9)	
<i>Cristatisporites chacoparanaensis</i> Ottone 1989 (Plate 1.22)	<i>Cannanoropollis densus</i> (Lele) Bose and Maheshwari 1968 (Plate 2.22)	
<i>Cristatisporites inconstans</i> Archangelsky and Gamero 1979 (Plate 1.12)	<i>Cannanoropollis janakii</i> Potonié and Sah 1960 (Plate 2.23)	
<i>Cristatisporites rollerii</i> Ottone 1989 (Plate 1.11)	<i>Cannanoropollis mehtae</i> (Lele) Bose and Maheshwari 1968 (Plate 2.24)	
<i>Cristatisporites stellatus</i> (Azcuy) Gutiérrez and Limarino 2001 (Plate 1.13)	<i>Circumplicatipollis plicatus</i> Ottone and Azcuy 1988 (Plate 3.5)	
<i>Cristatisporites</i> sp. (Plate 1.14)	<i>Colpisaccites granulatus</i> Archangelsky and Gamero 1979 (Plate 2.25)	
<i>Cyclogranisporites microgranus</i> Bharadwaj 1957 (Plate 1.17)	<i>Costatacycylus crenatus</i> Felix and Burbridge emend. Urban 1971 (Plate 2.29)	
<i>Cyclogranisporites rinconadensis</i> Césari and Limarino 2002 (Plate 1.16)	<i>Crucisaccites monoletus</i> Maithy 1965 (Plate 2.27)	
<i>Cyclogranisporites firmus</i> Jones and Truswell 1992 (Plate 1.15)	<i>Divarisaccus stringoplicatus</i> Ottone 1991 (Plate 3.10)	
<i>Dibolisporites disfacies</i> Jones and Truswell 1992 (Plate 1.18)	<i>Limitisporites rectus</i> Leschik 1956 (Plate 3.11)	
<i>Dictyotriletes cortaderensis</i> Césari and Limarino 1987 (Plate 1.19)	<i>Plicatipollenites gondwanensis</i> (Balme and Hennelly) Lele 1964 (Plate 2.20)	
<i>Ductilispora circularis</i> Perez Loinaze 2005 (Plate 1.20)	<i>Plicatipollenites malabarensis</i> (Potonié and Sah) Foster 1975 (Plate 2.26)	
<i>Endosporites</i> sp. (Plate 1.21)	<i>Plicatipollenites trigonalis</i> Lele 1964 (Plate 2.21)	
<i>Gondisporites serrulatus</i> Césari, Archangelsky and Seoane 1995 (Plate 1.25)	<i>Potonieisporites barrelii</i> Tiwari 1965 (Plate 3.1)	
<i>Grandispora</i> sp. (Plate 1.23)	<i>Potonieisporites brasiliensis</i> (Nahuys, Alpern and Ybert) Archangelsky and Gamero 1979 (Plate 2.28)	
<i>Granulatisporites austroamericanus</i> Archangelsky and Gamero 1979 (Plate 1.24)	<i>Potonieisporites densus</i> Maheshwari 1967 (Plate 3.2)	
<i>Leiotriletes directus</i> Balme and Hennelly 1956 (Plate 1.25)	<i>Potonieisporites lelei</i> Maheshwari 1967 (Plate 3.4)	
<i>Leiotriletes tenuis</i> Azcuy 1975a (Plate 1.28)	<i>Potonieisporites magnus</i> Lele and Karim 1971 (Plate 3.8)	
<i>Leiotriletes tiwarii</i> (Saxena) Saxena 1993 (Plate 1.27)	<i>Potonieisporites neglectus</i> Potonié and Lele 1961 (Plate 3.6)	
<i>Lundbladisporea brasiliensis</i> (Pant and Srivastava) Marques Toigo and Pons emend. Marques Toigo and Picarelli 1984 (Plate 1.30)	<i>Potonieisporites triangulatus</i> Tiwari 1965 (Plate 3.7)	
<i>Murospora torifera</i> Ybert 1975 (Plate 1.29)	<i>Potonieisporites</i> sp. cf. <i>P. balmeii</i> (Hart) Segroves 1969 (Plate 3.3)	
<i>Punctatisporites irrasus</i> Hacquebard 1957 (Plate 2.5)	Acritarcha	
<i>Punctatisporites priscus</i> Bharadwaj and Salujha 1965 (Plate 2.2)	<i>Gorgonisphaeridium</i> sp. (Plate 3.16)	
<i>Punctatisporites</i> sp. cf. <i>P. glaber</i> Playford 1962 (Plate 2.3)	<i>Micrhystridium</i> sp. (Plate 3.18)	
<i>Punctatisporites gretensis</i> Balme and Hennelly 1956 (Plate 2.1)	<i>Veryhachium (Veryhachium) reductum</i> (Deunff) Downie and Sarjeant emend. Stancliffe and Sarjeant 1994 (Plate 3.13)	
<i>Raistrickia densa</i> Menéndez 1965 (Plate 2.4)	<i>Veryhachium (V.)</i> sp. (Plate 3.14)	
<i>Raistrickia rotunda</i> Azcuy 1975a (Plate 2.12)	<i>Veryhachium (V.) triquetrum</i> Sarjeant emend. Stancliffe and Sarjeant 1994 (Plate 3.15)	
<i>Raistrickia</i> sp. (Plate 2.13)	<i>Veryhachium (V.) valensii</i> Downie and Sarjeant emend. Stancliffe and Sarjeant 1994 (Plate 3.17)	
<i>Reticulatisporites asperidictyus</i> Playford and Helby 1968 (Plate 2.14)	Algae	
<i>Reticulatisporites magnidictyus</i> Playford and Helby 1968 (Plate 2.15)	<i>Botryococcus</i> sp. (Plate 3.12)	
<i>Reticulatisporites papillatus</i> (Naumova) Playford 1971 (Plate 2.16)		
<i>Reticulatisporites passaspectus</i> Ottone 1991 (Plate 2.17)		

sented by the genera *Caheniasaccites*, *Cannanoropollis*, *Potonieisporites*, *Plicatipollenites*, and were referred to the Subzone A of the *Raistrickia densa* – *Convolutispora muriornata* (DM) Biozone (Césari and Gutiérrez 2001). This subzone recently constrained to the late Serpukhovian-early Bashkirian based on radiometric data (Césari et al. 2011) is characterized by the homonymous species, the presence of monosaccate pollen and the absence of taeniate pollen.

## MATERIAL AND METHODS

Twenty palynological samples were obtained from the different facies associations (FA) recognized in the Los Pozuelos creek, and the sample levels are marked in text-figure 3. Laboratory procedures for extraction and concentration of palynomorphs followed conventional practice (Phipps and Playford 1984), with carbonates and silicates removed by treatment with hydrochloric and hydrofluoric acids. The palynological residues were



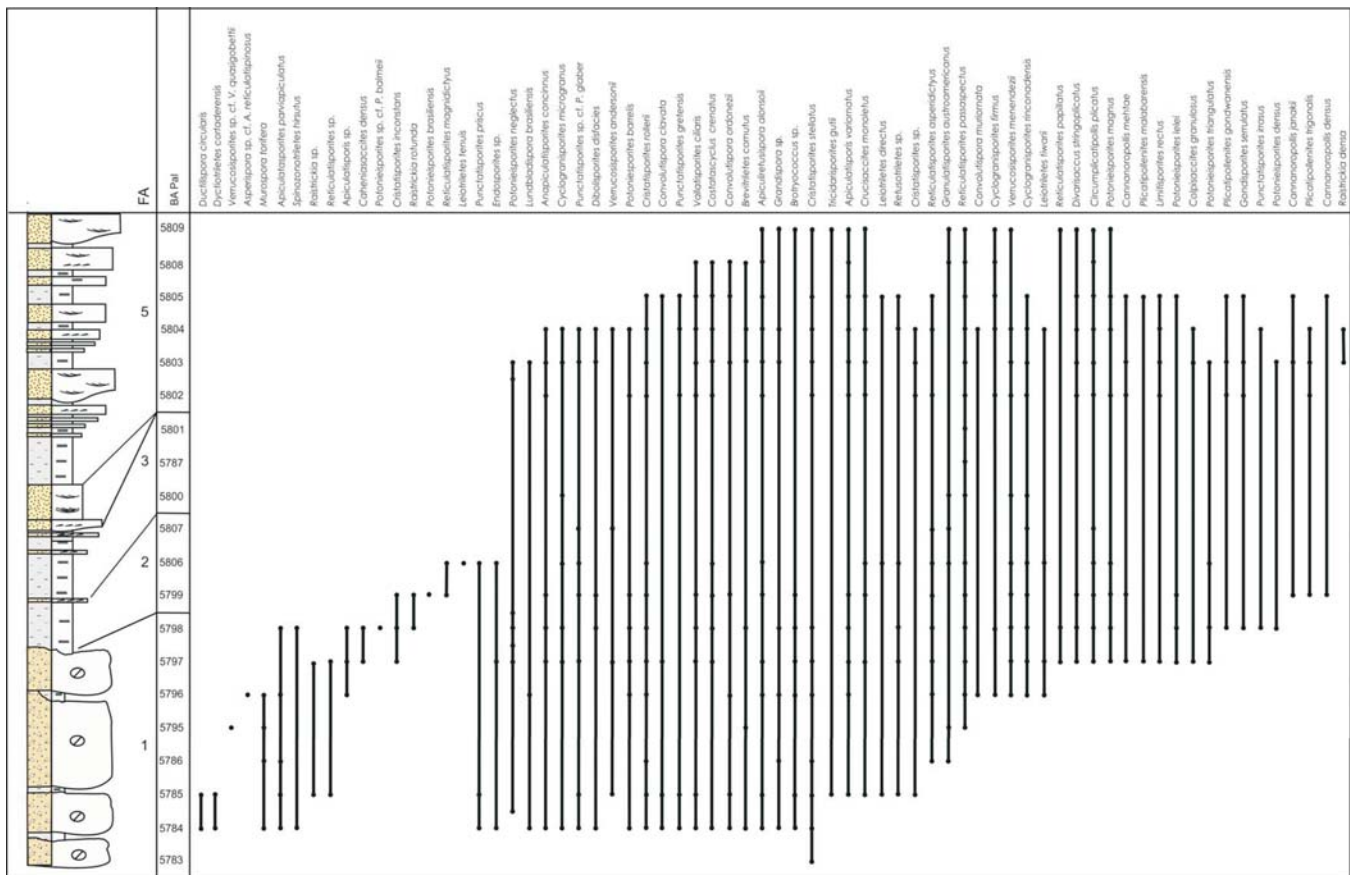
sieved on a 20µm mesh and mounted in unstained glycerin jelly. Counts of around 300 palynomorphs per sample were taken for quantitative analysis. The photographs were taken with a Nikon Coolpix 995 adapted to an Olympus BX 51 binocular microscope. All figured specimens are housed at the palynological Collection of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (BA Pal) and are identified with England Finder coordinates.

## RESULTS

Rich and very well-preserved palynological assemblages were recovered from the samples analyzed. Forty-nine species of spores and twenty-one of pollen were recorded from twenty samples of the lower-middle section of the Guandacol Formation. About fifty percent of these species are recorded for the first time in the unit. The identified palynomorphs (spores, pollen grains and algae) are listed in Table 1 and illustrations are given in Plates 1-3. The distribution of miospore taxa through the stratigraphic section is shown in text-figure 4.

A quantitative analysis of the palynological assemblages through the stratigraphic section reflects some important variations in diversity and percentage of pollen. Although the obtained values may be distorted by preservation issues, the results of the analysis can be interpreted as reflecting environmental variations.

As it can be observed in the text-figure 4 most of the samples of the FA1, have low diversity of species and scarce pollen content, represented by the lowermost percent (1, 5-3%) of the total (text-fig. 5). Spores are abundant components, especially *Anapiculatisporites concinnus*, *Apiculatisporites parviapiculatus*, *Apiculiretusispora alonsoii*, *Cristatisporites stellatus*, *Cyclogranisporites microgranus*, *Lundbladisporea braziliensis*, *Reticulatisporites passaspectus* and *Vallatisporites ciliaris*. An exception, inside this section, are the upper samples coming from shales interpreted as deposited in a glacialacustrine environment (BA Pal 5797 and 5798) which shows higher diversity and pollen content (18-25%). The appearance of the some species, i.e., *Cannanoropollis mehtae*, *Circumplicatipollis plicatus*, *Colpisaccites granulatus*, *Divarisaccus stringoplicatus*, *Limitisporites rectus*, *Plicatipollenites malabarensis*, *Potonieisporites magnus* and *Reticulatisporites papillatus* characterize these samples. In the FA2, a similar diversity and increase of pollen are observed (26-29%). Several species, i.e., *Cristatisporites inconstans*, *Raistrickia rotunda* and *Potonieisporites brasiliensis* are recorded for the last time in this interval; however they occur in upper levels of the Guandacol Formation in other localities (Ottone and Azcuy 1989; Ottone 1991). *Reticulatisporites magnidictyus* is only registered in the FA2. Unfortunately, the shales without dropstones (FA 3) provided scarce palynomorphs that are unable to carry out counts (text-fig. 5). The following section (FA 4), with large-scale cross-bedded sandstones, is characterized by lacking palynological assemblages. Finally, the upper assemblages of the FA 5 have a moderate diversity and a marked increase in the proportion of pollen (42-58%). *Raistrickia densa* has its first occurrence in this interval. Apart from the above land-derived components, few acritarchs are present in the basal levels of the unit (FA1), reinforcing the sedimentological interpretation of this sequence as fjord deposits (Marenssi et al. 2002), as was also suggested for other coeval stratigraphic sections in the basin (Ottone 1991; Martínez 1993; Gutiérrez and Limarino 2001).



TEXT-FIGURE 4  
The stratigraphic distribution of miospores in the Guadacol Formation in the Los Pozuelos Creek.

Reworked palynomorphs are apparently absent in the palynological assemblages. The only species that could be considered recycled because also have older records, are the long-ranging acritarchs identified in the most basal levels, *Reticulatisporites magnidictyus* from the FA2 and *Convolvutispora clavata* present in all the section. Since they are well-preserved and many of them have been registered in coeval Argentinian assemblages, we preliminarily interpret their presence as autochthonous.

**SYSTEMATIC PALEONTOLOGY**

Genus *Punctatisporites* (Ibrahim) Potonié and Kremp 1954

*Punctatisporites gretensis* Balme and Hennelly 1956  
Plate 2, figure 1

*Remarks:* *Punctatisporites* sp. 2 described from the Cortaderas Formation (Perez Loynaze 2008) is here considered conspecific with the specimens referred here to *P. gretensis*.

Genus *Raistrickia* (Schopf, Wilson and Bentall) Potonié and Kremp 1954

*Raistrickia* sp.  
Plate 2, figure 13

*Remarks:* Our specimens are sculptured comprehensively with a diversity of discrete clavae, bacula, grana and verrucae with truncate or rounded apices (2-3µm in basal width and height).

*Raistrickia* sp. cf. *R. accinta* Gutiérrez and Limarino 2001 seems to be conspecific with the studied specimens, but this tentative assignment to *Raistrickia accinta* Playford and Helby 1968 is here rejected because the Australian species differs in having more prominent sculpture that is reduced on the proximal surface. *Raistrickia radiosa* Playford and Helby 1968 is distinguished in having more uniform sculpture of baculate elements diminish in size on the proximal face. *Raistrickia rotunda* possesses more prominent sculpture (Azcu 1975a).

Genus *Verrucosiporites* (Ibrahim) Smith and Butterworth 1967

*Verrucosiporites* sp. cf. *V. quasigobbettii* Jones and Truswell 1992  
Plate 2, figure 10

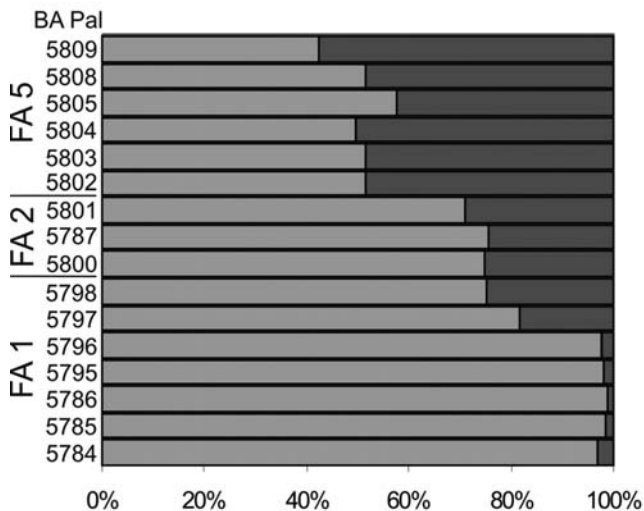
*Remarks:* The only specimen recognized is considered insufficient for a more confident identification.

**CORRELATION AND AGE**

**Age of the palynofloras**

Some of the species identified are frequently represented in Late Mississippian to Pennsylvanian palynological assemblages of Argentina and Brazil (Archangelsky et al. 1996; Souza et al. 2003): *Anapiculatisporites concinnus*, *Apiculatisporites variornatus*, *Apiculatisporites parviapiculatus*, *Apiculiretusispora alonsoi*, *Convolvutispora muriornata*, *Cyclogranisporites microgranus*, *Dytictotrites cortaderensis* and *Reticulati-*





TEXT-FIGURE 5  
Relative abundance of spores and pollen grains in the different facies associations of the Guandacol Formation in the Los Pozuelos Creek. Spores: gray shading; pollen: dark gray shading.

*sporites passaspectus*. Moreover, *Brevitriletes cornutus*, *Convolutispora ordonezii*, *Granulatisporites austro-americanus*, *Raistrickia densa* and *R. rotunda*, have been recognized in Pennsylvanian to Lower Permian sediments (Aceñalozza and Vergel 1987; Díaz Fabricio 1993; García 1995; Stephenson 2004; Beri et al. 2006). The spores *Verrucosisporites menendezii* and *Murospora torifera* have been previously recorded in Permian sediments (Archangelsky and Gamarro 1979; Ybert 1975; Beri et al. 2006). However, these species have been recently identified in late Serpukhovian-early Bashkirian palynofloras in Paganzo Basin, Argentina (Perez Loinaze et al. 2011).

Spore species with constrained biostratigraphic range are: *Reticulatisporites magnidictyus*, *R. papillatus* and *Convolutispora clavata*. According to Dino and Playford (2002), *Reticulatisporites magnidictyus* has an apparently near-synchronous late Viséan appearance in South America and Australia. Dino and Playford 2002 proposed a stratigraphic range late Viséan- early Serpukhovian in Australia with some reports in the Pennsylvanian of South America. Coincidentally in Argentina the first occurrence of this species is in the late Viséan *Reticulatisporites magnidictyus-Verrucosisporites quasigobettii* Biozone (Perez Loinaze 2007b) but has also been recognized in the overlying late Serpukhovian-early Bashkirian Subzone A of the DM Biozone (Ottone 1991; Gutiérrez and Barreda 2006; Perez Loinaze 2009).

*Reticulatisporites papillatus* has been recorded in late Viséan-early Namurian sediments of Australia, North America, Poland, Russia, Spitsbergen (see Playford 1971). *Convolutispora clavata* is constrained to the late Mississippian in Alaska, Australia, Russia and Canada (see Ravn 1991).

Many monosaccate pollen species recognized herein (e.g., *Plicatipollenites malabarensis*, *P. trigonalis*, *P. gondwanensis*, *Potontieisporites barreilis*, *P. brasiliensis*, *P. densus*, *P. magnus*, *P. neglectus*, *Circumplicatipollis plicatus* and *Crucisaccites monoletus*) are often found in Pennsylvanian-Permian palyno-

logical assemblages of Gondwana (Foster 1979; Gutiérrez 1993; di Pasquo et al. 2003). The presence of monosaccate pollen in the Guandacol Formation supports an age not older than Serpukhovian according to the first worldwide records of these palynomorphs (Brugman et al. 1985; Loboziak and Clayton 1988; Clayton et al. 1990; Zhu 1993; Clayton 1995). Also, bisaccate pollen, scarcely represented in the Guandacol Formation, was firstly recorded in Namurian sediments of China, and in Early Westphalian assemblages of Western Europe (Clayton et al. 1977; Zhu 1995).

According to the available palynological data, the studied assemblages from the Guandacol Formation can be interpreted as not older than Serpukhovian and probably late Serpukhovian in age by the abundance and diversity of monosaccate pollen (text-fig. 4, 5).

The absence of taeniate pollen grains in the studied assemblages can be also used as a time indicator. In Western Europe, Clayton et al. (1977) recognized the first record of taeniate pollen in the *Torispora secularis* – *Torispora laevigata* (SL) Biozone referred to Westphalian C. Arctic palynological assemblages contain the first taeniate pollen grains in the Westphalian or Late Bashkirian-Moscovian (Vigran et al. 1999; Lindström 2003).

In Australia, they occur in the upper part (Westphalian) of the *Spelaeotriletes ybertii* Assemblage Zone (Jones and Truswell 1992). Loboziak et al. (1997) pointed out that the first records of taeniate pollen are Westphalian in the Amazonas Basin and represented by a few isolated specimens. Zhu (1995) mentioned the apparently only known Namurian record of taeniate pollen (*Protohaploxypinus* sp.) represented by two specimens from the Hongtuwa Formation, northwest China. Recently, this stratigraphic unit was considered Bashkirian in age (Wang et al. 2004; Sun and Deng 2004).

Consequently, a pre- Bashkirian age, based on palynological species, may be suggested for the basal glacial deposits of the Guandacol Formation. Palynological assemblages from the upper section of the Guandacol Formation in La Delfina creek contain only one specimen of taeniate pollen described as *?Striatomonosaccites* sp. by Ottone and Azcuy (1989). Although extremely rare the presence of this taeniate pollen in strata overlying the deposits analyzed herein may be indicating the first incoming of this group in the palynological succession.

Recent  $^{206}\text{Pb}/^{238}\text{U}$  radiometric studies (Gulbranson et al. 2010) on samples collected at the top of the Guandacol Formation in the nearby Agua Hedionda locality yield an age of  $318.79 \pm 0.10$  Ma. In addition, coeval deposits of the Río del Peñón Formation have been dated in  $319.57 \pm 0.086$  Ma. Both datings confirm and constrain the palynological assemblages as not younger than early Bashkirian.

#### Correlation with other Argentinian palynologic assemblages

The Guandacol Formation was included in the late Serpukhovian-early Bashkirian Subzone A of the *Raistrickia densa* – *Convolutispora muriornata* Biozone (Césari and Gutiérrez 2001; Césari et al. 2011), and correlated with the lower section of the Agua Colorada, Malanzán, Jejenes and Lagares Formations from central-western of Argentina. None of these units contain taeniate pollen grains (text-fig. 6).

The basal glacial deposits of the Guandacol Formation represent the Glacial Episode II (Isbell et al. 2003b) in Argentina.

Age	Lithostratigraphic units					Biozones		
	Western Paganzo Basin			Eastern Paganzo Basin		Argentina	Brazil	Australia
Moscovian	Patquia Formation		Agua Colorada Formation	Loma Larga Formation	Lagares Formation	Subzone B	Ahrensisporites cristatus Biozone	Potonieisporites Assemblage
	Tupe Formation							
Bashkirian	*	Jejenes Formation		Malanzán Formation		Subzone A		Spelaeotriletes ybertii Biozone
	Guandacol Formation							
Late Serphukovian								

TEXT-FIGURE 6  
Correlation of some units of the Paganzo Basin and the main biozones of Argentina, Brazil and Australia (\*318.79 ± 0.10 Ma, Gulbranson et al. 2010).

These recovered assemblages are important for correlating the unit with others from Argentina, such as the Agua Colorada Formation, deposited at the western flank or the Famatina Arch (text-fig. 1). Palynological assemblages obtained from glaci-lacustrine sediments associated with continental diamictites of the Agua Colorada Formation were studied by Limarino and Gutiérrez (1990) from outcrops of Las Gredas creek (La Rioja Province). Both associations share species of monosaccate pollen grains and spores, such as: *Cannanoropollis densus*, *C. mehtae*, *Circumplicatipollis plicatus*, *Colpisaccites granulosus*, *Convolutispora murornata*, *C. ordonezii*, *Granulatisporites austroamericanus*, *Plicatipollenites gondwanensis*, *P. malabarensis*, *P. trigonalis*, *Potonieisporites barrelis*, *P. brasiliensis*, *P. magnus*, *P. neglectus* and *Crucisaccites monoletus*. The assemblages from the Agua Colorada Formation also contain a few species, e.g. *Apiculiretusispora multisetata* (Luber) Butterworth and Spinner, *Discernisporites micromanifestus* (Hacquebard) Sabry and Neves, *Asperispora acuta* (Kedo) van der Zwan, with older stratigraphic record but these taxonomic assignments should be revised, other possibility is that these specimens were reworked. *Reticulatisporites magnidictyus* and *R. asperidictyus*, recorded in both units (Guandacol Formation and lower section of the Agua Colorada Formation) are also present in the coeval Malanzán Formation, which share many species with the Guandacol Formation (Perez Loinaze 2009). Glacigenic deposits of the Malanzán Formation outcrop in the Sierra de los Llanos area (text-fig. 1).

Palynological assemblages described from the Jejenes Formation (Césari and Bercowski 1998) in the south nearby area to San Juan city (text-figs. 1, 6) have many species in common with the associations described here: *Cannanoropollis densus*, *Circumplicatipollis plicatus*, *Convolutispora murornata*, *C. ordonezii*, *Indotriradites volkheimeri*, *Lundbladispota braziliensis*, *Plicatipollenites malabarensis*, *Raistrickia densa* and

*Reticulatisporites asperidictyus*. Other similar assemblages have been recovered from outcrops of the Lagares Formation in the eastern Paganzo Basin (Gutiérrez and Césari 1989) with species such as: *Anapiculatisporites concinnus*, *Cannanoropollis mehtae*, *Convolutispora murornata*, *C. ordonezii*, *Crucisaccites monoletus*, *Lundbladispota braziliensis*, *Plicatipollenites malabarensis*, *Potonieisporites neglectus*, *Raistrickia densa* and *Vallatisporites ciliaris*.

#### Comparisons with other Gondwanan palynologic assemblages

Comparisons with other Gondwanan assemblages can be established with coeval palynofloras from Brazil and Australia (text-fig. 6). The oldest biozone of the palynostratigraphic scheme of the Brazilian Paraná Basin (Souza 2006) is the *Ahrensisporites cristatus* Biozone, Bashkirian-Kasimovian in age, related to the lowermost glacial levels identified in the Itararé Group. Both palynological assemblages share many species (Souza 2006); however the Brazilian biozone differs in the presence of infrequent (< 5%) taeniate pollen. The current assemblages also differ from the records from the Brazilian Amazonas Basin because the *Spelaeotriletes triangulus* Assemblage Zone (Melo and Loboziak 2003) recorded there is characterized by the presence of taeniate and non-taeniate bisaccate pollen.

In Western Australia the lower part of the *Spelaeotriletes ybertii* Assemblage (Kemp et al. 1977) and the Opell-zone A of the *Spelaeotriletes queenslandensis* Superzone (Jones and Truswell 1992) of Eastern Australia are Serphukovian-Bashkirian in age, and are characterized by the incoming of monosaccate pollen. Both palynozones share with the associations studied here, the presence of abundant monosaccate pollen referred to the genera: *Potonieisporites*, *Cannanoropollis*, *Plicatipollenites* and spores *Cyclogranisporites firmus*, *Verrucosisporites quasigobettii* and *Anapiculatisporites concinnus*.

**PALEOBOTANICAL AND PALEOENVIRONMENT  
INFERENCES**

Carboniferous Gondwanan floras differ from the well-known flora of the Northern Hemisphere. Besides the endemic nature of the southern floras, one of the most outstanding differences is their lower abundance and diversity. In particular, Serpukhovian-early Bashkirian floras have few records in the Southern Hemisphere. Plant associations are mainly restricted to vegetative remains with scarce records of fertile organs in organic connection. The NBG flora characterizes the Late Serpukhovian-Late Moscovian sequences in Western Argentina (Archangelsky 1987; Césari et al. 2007; Césari et al. 2011). Lycophytes, sphenopsids, pteridosperms and cordaitales are the main groups identified represented by relatively few species in the macrofloristic records. To date, neither coniferous or fern remains have been recognized in these floras, however palynological associations show a broader diversity, including

morphogenera related to conifers and ferns. This discrepancy between the macro and microfloristic records may be the result of selective preservation (e.g. of the hinterland flora) or probably to the uncertain affinity of many gondwanic palynomorphs. It should be noted that plant affinities of nearly all the Carboniferous palynomorph taxa are known from fructifications found in the Northern Hemisphere.

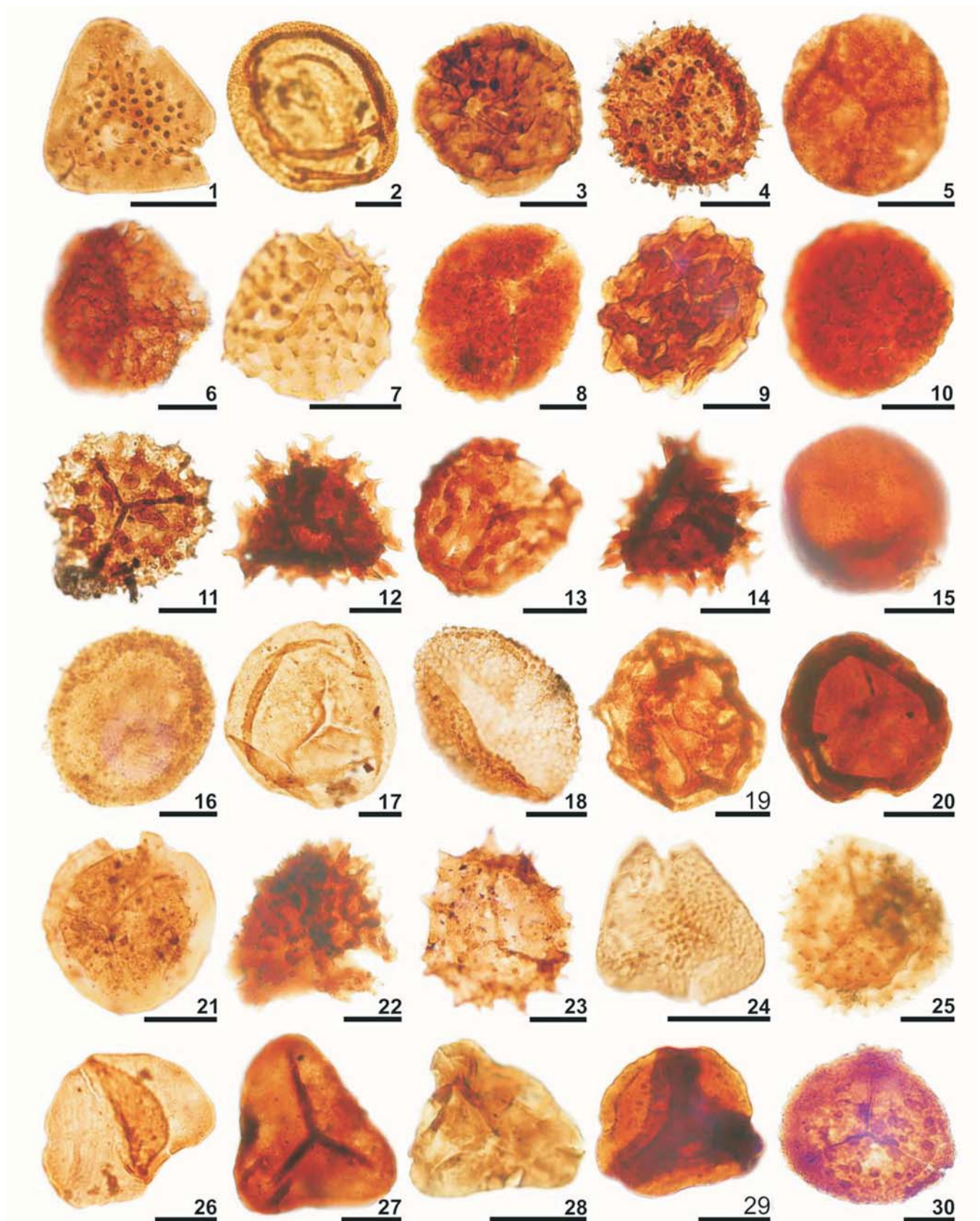
Among the palynomorphs, monosaccate pollen like *Potoniisporites* and *Plicatipollenites* are usually related to gymnosperms (mainly Coniferales and Pteridosperms). These pollen species have been considered pre-pollen (Poort and Veld 1997; Zaviolova and Stephenson 2006), found in association with walchian primitive conifers (Poort and Veld 1997; Hernández Castillo et al. 2001). In the same way, bilateral monosaccate pollen like *Florinites* was related to *Cordaites* (Renault 1879; Millay and Taylor 1974; Šimůnek et al. 2009). The almost syn-

**PLATE 1**

Scale bar : 20µm.

- |   |   |
|---|---|
| <p>1 <i>Anapiculatisporites concinnus</i> Playford BA 5798-2: L30/3;</p> <p>2 <i>Apiculatasporites parviapiculatus</i> Azcuy BA Pal 5798-3: T33/3;</p> <p>3 <i>Apiculatisporis</i> sp. BA Pal 5785-3: S53/2;</p> <p>4 <i>Apiculatisporis variornatus</i> di Pasquo et al. BA Pal 5704-1: K39/2;</p> <p>5 <i>Apiculiretusispora alonsoii</i> Ottone BA Pal 5796-1: P55/1;</p> <p>6 <i>Asperispora</i> sp. cf. <i>A. reticulatispinosus</i> Jones and Truswell BA Pal 5796-3: O48/4;</p> <p>7 <i>Brevitriletes cornutus</i> (Balme and Hennelly) Høeg and Bose BA Pal 5704-1: G45/3;</p> <p>8 <i>Convolutispora clavata</i> (Ishchenko) Hugues and Playford BA Pal 5784-3: M54/1;</p> <p>9 <i>Convolutispora muriornata</i> Menéndez BA Pal 5796-2: O26/1;</p> <p>10 <i>Convolutispora ordonenzii</i> Archangelsky and Gamero BA Pal 5799-2: Y47/2;</p> <p>11 <i>Cristatisporites rollerii</i> Ottone BA Pal 5799-1: R24/1;</p> <p>12 <i>Cristatisporites inconstans</i> Archangelsky and Gamero BA Pal 5798-1: E34/4;</p> <p>13 <i>Cristatisporites stellatus</i> (Azcuy) Gutiérrez and Limarino BA Pal 5796-1: Y40/3;</p> <p>14 <i>Cristatisporites</i> sp. BA Pal 5796-3: X30/2;</p> <p>15 <i>Cyclogranisporites firmus</i> Jones and Truswell BA Pal 5810-3: N30/0;</p> | <p>16 <i>Cyclogranisporites rinconadensis</i> Césari and Limarino BA Pal 5799-1: V21/4;</p> <p>17 <i>Cyclogranisporites microgranus</i> Bharadwaj BA Pal 5798-3: W28/4;</p> <p>18 <i>Dibolisporites disfacies</i> Jones and Truswell BA Pal 5803-1: Q31/3;</p> <p>19 <i>Dictyotriletes cortaderensis</i> Césari and Limarino BA Pal 5785-3: U25/4;</p> <p>20 <i>Ductilispora circularis</i> Pérez Loinaze BA Pal 5785-3: W49/1;</p> <p>21 <i>Endosporites</i> sp. BA Pal 5796-3: W30/4;</p> <p>22 <i>Cristatisporites chacoparanaensis</i> Ottone BA Pal 5786-2: M51/3;</p> <p>23 <i>Grandispora</i> sp. BA Pal 5803-1: N23/4;</p> <p>24 <i>Granulatisporites austroamericanus</i> Archangelsky and Gamero BA Pal 5787-1: Z43/3;</p> <p>25 <i>Gondisporites serrulatus</i> Césari et al. BA Pal 5803-1: F33/1;</p> <p>26 <i>Leiotriletes directus</i> Balme and Hennelly BA Pal 5804-3: Z42/0;</p> <p>27 <i>Leiotriletes tiwarii</i> (Saxena) Saxena 1993 BA Pal 5704-3: K41/2;</p> <p>28 <i>Leiotriletes tenuis</i> Azcuy BA Pal 5806-1: V26/2;</p> <p>29 <i>Murospora torifera</i> Ybert BA Pal 5796-2: X31/1;</p> <p>30 <i>Lundbladispota brasiliensis</i> (Pant and Srivastava) Marques Toigo and Pons emend. Marques Toigo and Picarelli BA Pal 5796-2: K34/4.</p> |
|---|---|





chronous appearance, in the Serpukhovian, of monosaccate pollen grains and Cordaitales in Gondwana (Jones and Truswell 1992; Césari and Gutiérrez 2001) suggests a close relationship between them rather than with conifers in this area. This assumption seems true considering that conifers are registered later (late Pennsylvanian) in Gondwana (Archangelsky 1996; Césari et al. 2007).

The palynological succession within the Guandacol Formation allows identification of broad compositional changes within the basal records of the NBG flora. These changes occurred within the glacial-deglaciation interval referred to the paleoclimatic stage II and Substage IIIa (López Gamundi et al. 1992). Glacial conditions prevailed during the Stage II and the postglacial substage IIIa was characterized by humid cold to temperate climate.

Considering the uncertain affinities of many of the endemic spores identified, we grouped them as derived from lower vas-

cular plants characterizing the lowland vegetation. Cordaites are generally regarded as upland plants, but small cordaites are known to have flourished in marine influenced coastal habitat (Falcon-Lang 2005); therefore, monosaccate pollen is here interpreted as derived from extrabasinal vegetation.

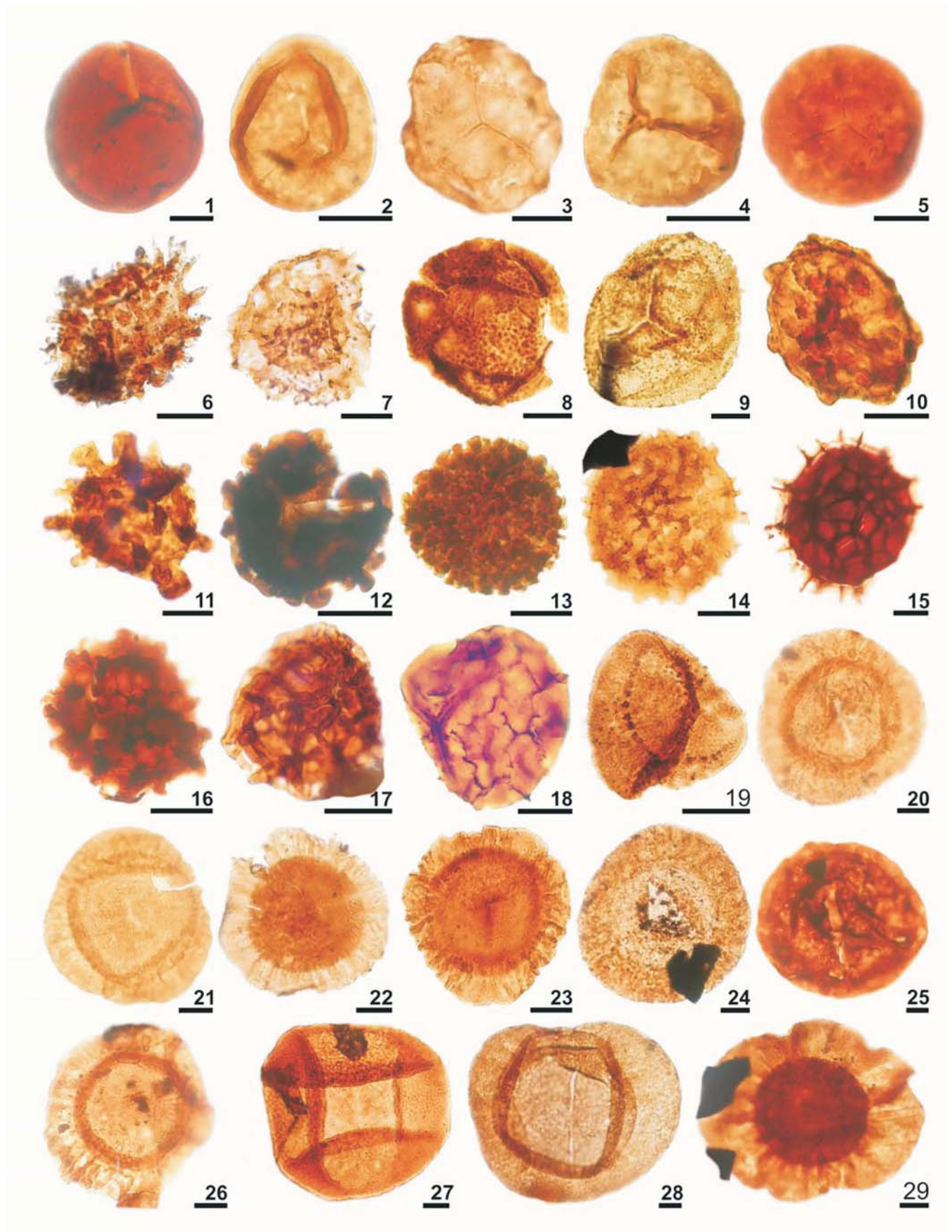
The lowest values of pollen (text-fig. 5), together with the low diversity, observed in the tillites (FA1), may mark a period of very cold conditions, not favorable for the development of vegetation. As reported in the Holocene (Tarasov et al. 2000; Vargas-Ramirez et al. 2008), low pollen concentration values document a poor vegetation cover and suggest cold climatic conditions. It is assumed that during these harsh conditions was developed a poorly diversified flora. The glacial marine deposits of the basal section may represent a temporary improvement of the environmental conditions, favouring the development of more diverse vegetation, reflected in a major number of species and higher percentages of pollen.

## PLATE 2

Scale bar: 20µm.

- |   |  |
|---|--|
| 1 <i>Punctatisporites gretensis</i> Balme and Hennelly BA Pal 5710-2 : V28/2;                         | 16 <i>Reticulatisporites papillatus</i> (Naumova) Playford BA Pal 5798-2: D45/2;                     |
| 2 <i>Punctatisporites priscus</i> Bharadwaj and Salujha BA Pal 2-4: 132.8/8.2;                        | 17 <i>Reticulatisporites passaspectus</i> Ottone BA Pal 5798-1:E30/3;                                |
| 3 <i>Punctatisporites</i> sp. cf. <i>P. glaber</i> Playford BA Pal 5784-3: V24/4;                     | 18 <i>Reticulatisporites</i> sp. BA Pal 5785-3: T33/2;   |
| 4 <i>Retusotriletes</i> sp. BA Pal 5805-2: L52/2;   | 19 <i>Tricidarisorites gutii</i> Césari and Limarino BA Pal 5784-3: C32/1;                           |
| 5 <i>Punctatisporites irrasus</i> Hacquebard BA Pal 5798-1: Q28/1;                                    | 20 <i>Plicatipollenites gondwanensis</i> (Balme and Hennelly) Lele BA Pal 5803-1: O30/3;             |
| 6 <i>Spinozonotriletes hirsutus</i> Azcuy BA Pal 5805-1: X33/4;                                       | 21 <i>Plicatipollenites trigonalis</i> Lele BA Pal 5799-2: Z25/1;                                    |
| 7 <i>Vallatisporites ciliaris</i> (Luber) Sullivan BA Pal 5804-2: G28/1;                              | 22 <i>Cannanoropolis densus</i> (Lele) Bose and Maheshwari BA Pal 5799-2: T22/0;                     |
| 8 <i>Verrucosisporites andersonii</i> (Anderson) Backhouse BA Pal 5785-3: K46/1;                      | 23 <i>Cannanoropolis janakii</i> Potonié and Sah BA Pal 5799-1: F25/1;                               |
| 9 <i>Verrucosisporites menendezii</i> Archangelsky and Gamero BA Pal 5799-1: M47/2;                   | 24 <i>Cannanoropolis mehtae</i> (Lele) Bose and Maheshwari BA Pal 5805-1: X30/3;                     |
| 10 <i>Verrucosisporites</i> sp. cf. <i>V. quasigobbettii</i> Jones and Truswell BA Pal 5787-1: U35/3; | 25 <i>Colpisaccites granulatus</i> Archangelsky and Gamero BA Pal 5803-1: H50/3;                     |
| 11 <i>Raistrickia densa</i> Ménendez BA Pal 5703-2: N22/3;  | 26 <i>Plicatipollenites malabarensis</i> (Potonié and Sah) Foster BA Pal 5797-1: U34/4;              |
| 12 <i>Raistrickia rotunda</i> Azcuy BA Pal 5798-1: L39/2;   | 27 <i>Crucisaccites monoletus</i> Maithy BA Pal 5803-2: Y52/2;                                       |
| 13 <i>Raistrickia</i> sp. BA Pal 5795-3: Z45/2;   | 28 <i>Potonieisorites brasiliensis</i> (Nahuys et al.) Archangelsky and Gamero BA Pal 5799-1: P38/1; |
| 14 <i>Reticulatisporites asperidictyus</i> Playford and Helby BA Pal 5799-1: D53/4;                   | 29 <i>Costatascyclus crenatus</i> Felix and Burbridge emend. Urban BA Pal 5799-1: F53/2.             |
| 15 <i>Reticulatisporites magnidictyus</i> Playford and Helby BA Pal 5809-2: P29/1;                    |  |







These shales with dropstones (FA2) represent a period of glacial retraction, reflecting more favorable conditions for the development of the vegetation in low areas (text-fig. 5). This period is accompanied by a higher participation of pollen derived from the upland flora. Finally, the upper assemblages have a moderate diversity and a marked increase in the proportion of pollen (42-58%). This uppermost section of alternate mudstones and sandstones (FA 5) represents deltaic deposits lacking evidence of glacial conditions. Under these more favorable environmental conditions more profuse vegetation developed, possibly with an increase in upland flora (represented by a higher percentage of pollen in the palynofloras).

## CONCLUSIONS

Palynological assemblages recovered from glacial and postglacial deposits of the Guandacol Formation, represented by true tillites and resedimented diamictites, represent one of the few palynological records of Serpukhovian glacial deposits in Gondwana, and add new evidence for elucidating the Upper Paleozoic glacial history in the region. The study of 20 samples from the lower-middle section of the Guandacol Formation in the Pozuelos Creek allowed the recognition of 49 species of spores and 21 of pollen grains, which suggest a Serpukhovian, and probably Late Serpukhovian age. Recent U-Pb radiometric studies confirm this age (Gulbranson et al. 2010). These assemblages are the most complete South American palynological record from deposits related with the Glacial II Episode proposed by Isbell et al. (2003b), and the glacial interval C2 recognized by Fielding et al. (2008) in Australia, which have been referred to the Late Serpukhovian.

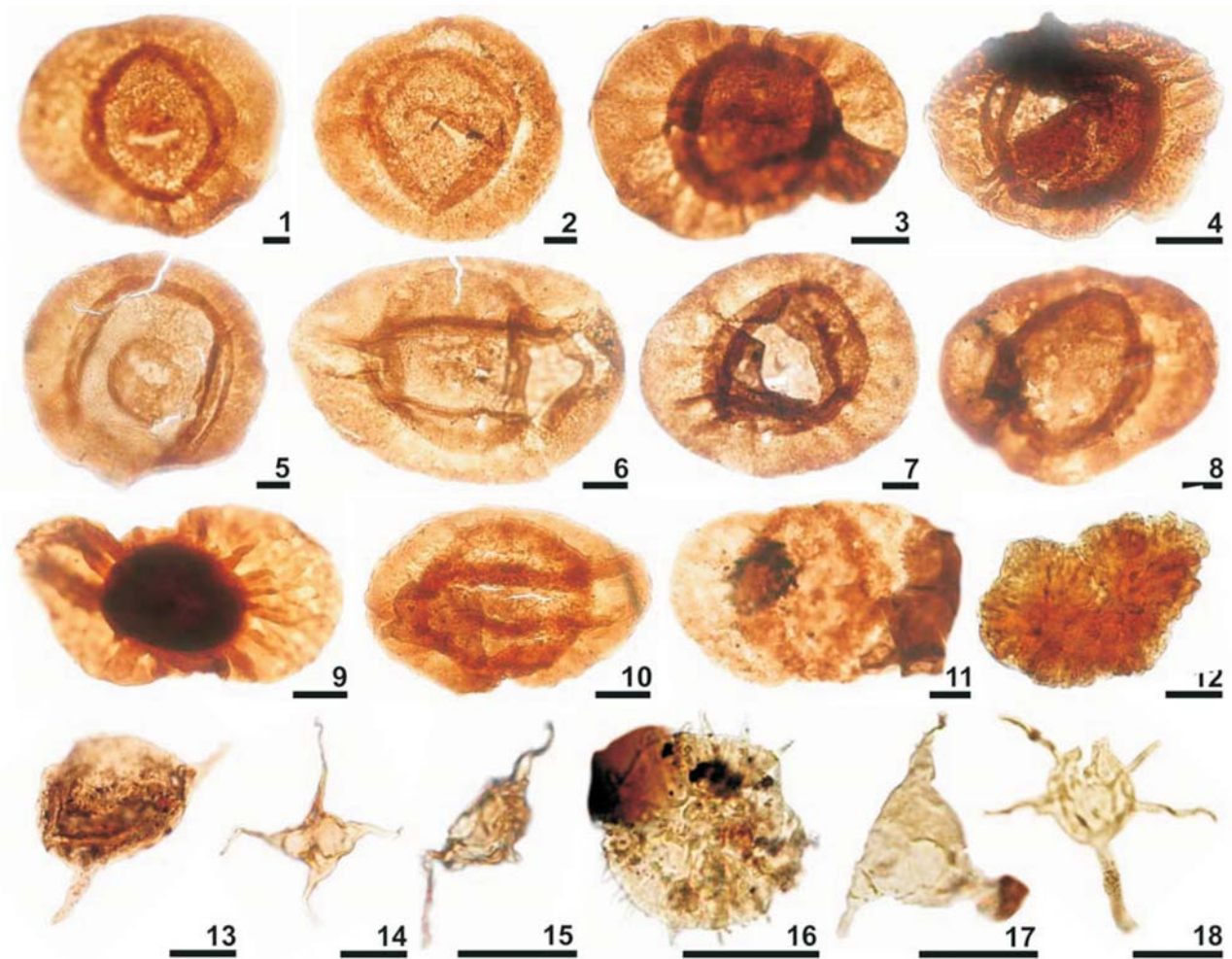
Additionally, these assemblages promote a more precise characterization of the Subzone A of the *Raistrickia densa-Convolutispora muriornata* Biozone. Paleontological and lithological evidence suggests that the Guandacol Formation was deposited in a glacial marine environment.

## ACKNOWLEDGMENTS

Magalí Yáñez Calderón and John Graham are thanked for their help with English grammar. Thanks are extended to Oscar Limarino for his valuable help on geological aspects. This research was funded by grants from the Agencia Nacional de Promoción Científica y Tecnológica (PICT 20752, PICT 1650, and PICT 1499). Parts of this work belong to the Ph.D. Thesis research made by Valeria Perez Loinaze.

## REFERENCES

- ACEÑOLAZA, F. G. and VERGEL, M. M., 1987. Hallazgo del Pérmico Superior fosilífero en el Sistema de Famatina. In: Asociación Geológica Argentina, Eds., *10th Congreso Geológico Argentino, Tucumán, Actas*, 3, 125–129. San Miguel de Tucumán: Asociación Geológica Argentina.
- ARCHANGELSKY, S., 1996. Aspects of Gondwana paleobotany: gymnosperms of the Paleozoic–Mesozoic transition. *Review of Palaeobotany and Palynology*, 90: 287–302.
- ARCHANGELSKY, S. and GAMERRO, J. C., 1979. Palinología del Paleozoico superior en el subsuelo de la Cuenca Chacoparanense, República Argentina. I. Estudio sistemático de los palinomorfos de tres perforaciones de la provincia de Córdoba. *Revista Española de Micropaleontología*, 11: 417–478.
- ARCHANGELSKY, S., AZCUY, C. L., CÉSARI, S., GONZÁLEZ, C., HÜNICKEN, M., MAZZONI, A., and SABATTINI, N., 1996. Correlación y edad de las biozonas. In: Archangelsky, S., Ed., *El Sistema Pérmico en la República Argentina y en la República Oriental del Uruguay*, 203–226. Córdoba: Academia Nacional de Ciencias Córdoba.
- AZCUY, C. L., 1975a. Miosporas del Namuriano y Westfaliano de la comarca Malanzán–Loma Larga, provincia de La Rioja, Argentina. I. Localización geográfica y geológica de la comarca y descripción es sistemáticas. *Ameghiniana*, 12: 1–69.
- , 1975b. Miosporas del Namuriano y Westfaliano de la comarca Malanzán–Loma Larga, provincia de La Rioja, Argentina. II. Descripciones sistemáticas y significado estratigráfico de las microfloras. *Ameghiniana*, 12: 113–163.
- AZCUY, C. L. and DI PASQUO, M. M., 2006. Early Carboniferous palynoflora from the Ambo Formation, Pongo de Mainique, Peru. *Review of Palaeobotany and Palynology*, 134: 153–184.
- AZCUY, C. L. and MORELLI, J. R., 1970. Geología de la Comarca de Paganzo–Amaná. El Grupo Paganzo, formaciones que lo componen y sus relaciones. *Revista de la Asociación Geológica Argentina*, 25: 405–429.
- BACKHOUSE, J., 1988. Permian trilete spores from the Collie Basin, Western Australia. *Memoirs of the Association of Australasian Palaeontologists*, 5: 53–72.
- BALME, B. E., 1980. Palynology and the Carboniferous–Permian Boundary in Australia and other Gondwana continents. *Palynology*, 4: 43–55.
- BALME, B. E. and HENNELLY, J. P. F., 1956. Trilete sporomorphs from Australian Permian Sediments. *Australian Journal of Botany*, 4: 241–260.
- BERI, A., GUTIÉRREZ, P. R., CERNUSCHI, F. and BALARINO, M. L., 2006. Palinología del Pérmico Inferior en la Perforación DCL5–24 (Formación San Gregorio), Departamento de Cerro Largo, Uruguay. Parte I: Esporas, algas prasinofitas y acritarcas. *Ameghiniana*, 43: 227–244.
- BHARDWAJ, D. C., 1957. The spore flora of the Velener Schichten (Lower Westphalian D) in the Ruhr Coal Measures. *Palaeontographica Abteilung B*, 102: 110–138.
- BHARDWAJ, D. C. and SALUJHA, S. K., 1965. A sporological study of seam VII (Jote Dhem Colliere) in the Raniganj Coalfield, Bihar (India). *The Palaeobotanist*, 13: 30–41.
- BODENBENDER, G., 1912. Parte meridional de la provincia de La Rioja y regiones limítrofes, constitución geológica y productos minerales. *Anales del Ministerio de Agricultura, Secretaría de Geología y Minería, Buenos Aires, Argentina*, 7: 1–161.
- BOSE, M. N. and MAHESHWARI, H. K., 1968. Palaeozoic Sporeae dispersae from Congo. VII – Coal measures near lake Tanganyika, South of Albertville. *Annales de Musée royal de l'Afrique centrale, serie 8, sciences géologiques*, 60: 1–116.
- BRUGMAN, W. A., EGGINK, J. W., LOBOZIAK, S. and VISSCHER, H., 1985. Late Carboniferous–Early Permian (Ghzelian–Artinskian) palynomorphs. *Journal of Micropalaeontology*, 4: 93–106.
- BUATOIS, L. A. and MÁNGANO, M. G., 1995. Sedimentary dynamics and Evolutionary History of a Late Carboniferous Gondwanic Lake in North–Western Argentina. *Sedimentology*, 42: 415–436.
- CÉSARI, S. and BERCOWSKI, F., 1998. Palinología de la Formación Jejenes (Carbonífero) en la quebrada de Las Lajas, provincia de San



## PLATE 3

Scale bar: 20µm.

- |   |   |    |  |
|---|---|----|--|
| 1 | <i>Potonieisporites barrelis</i> Tiwari BA Pal 5797-2: E38/1;                           | 9  | <i>Caheniasaccites densus</i> Lele and Karin emend. Gutiérrez BA Pal 5804-1: Z40/1;  |
| 2 | <i>Potonieisporites densus</i> Maheshwari BA Pal 5803-2: B24/3;                         | 10 | <i>Divarisaccus stringoplicatus</i> Ottone BA Pal 5803-4: I52/4;   |
| 3 | <i>Potonieisporites</i> sp. cf. <i>P. balmeii</i> (Hart) Segroves BA Pal 5803-1: O30/3; | 11 | <i>Limitisporites rectus</i> Leschik BA Pal 5805-2: Z39/3;   |
| 4 | <i>Potonieisporites lelei</i> Maheshwari BA Pal 5797-1: W34/3;                          | 12 | <i>Botryococcus</i> sp. BA Pal 5797-1: F55/3;  |
| 5 | <i>Circumplicatipollis plicatus</i> Ottone and Azcuy BA Pal 5797-3: V31/3;              | 13 | <i>Veryhachium</i> ( <i>V.</i> ) <i>reductum</i> (Deunff) Downie and Sarjeant emend. Stancliffe and Sarjeant BA Pal 5809-1: Z35/0; |
| 6 | <i>Potonieisporites neglectus</i> Potonié and Lele BA Pal 5798-2: S30/3;                | 14 | <i>Veryhachium</i> ( <i>V.</i> ) sp. BA Pal 5796-1: K50/3;   |
| 7 | <i>Potonieisporites triangulatus</i> Tiwari BA Pal 5798-1: W47/3;                       | 15 | <i>Veryhachium</i> ( <i>V.</i> ) <i>triqueter</i> Sarjeant emend. Stancliffe and Sarjeant BA Pal 5804-2: D42/2;                    |
| 8 | <i>Potonieisporites magnus</i> Lele and Karim BA Pal 5798-1: S36/3;                     | 16 | <i>Gorgonisphaeridium</i> sp. BA Pal 5785-3: T41/3;  |
|   |   | 17 | <i>Veryhachium</i> ( <i>V.</i> ) <i>valensii</i> Downie and Sarjeant emend. Sarjeant BA Pal 5808-1: N28/2;                         |
|   |   | 18 | <i>Micrhystridium</i> sp. BA Pal 5784-2: O24/4.  |

- Juan, Argentina. Nuevas inferencias paleoambientales. *Ameghiniana*, 34: 497–510.
- CÉSARI, S. and GUTIÉRREZ, P. R., 2001. Palynostratigraphy of Upper Paleozoic sequences in Central–Western Argentina. *Palynology*, 24: 113–146.
- CÉSARI, S. and LIMARINO, C. O., 1987. Análisis estratigráfico del perfil de la quebrada de La Cortadera (Carbonífero), Sierra de Maz, La Rioja, Argentina. In: Philippe, J., Ed., *4th Congreso Latinoamericano de Paleontología y Bioestratigrafía, Bolivia, Memorias I*, 315–330. Santa Cruz de la Sierra.
- , 2002. Palynology of glacial sediments from the Guandacol Formation (Middle Carboniferous) in the Cerro Bola area, Paganzo Basin, Argentina. *Alcheringa*, 26: 159–176.
- CÉSARI, S. and VÁZQUEZ-NÍSTICO, B., 1988. Palinología de la Formación Guandacol (Carbonífero), provincia de San Juan, República Argentina. *Revista Española de Micropaleontología*, 20: 39–58.
- CÉSARI, S., ARCHANGELSKY, S. and SEOANE, L. V. de., 1995. Palinología del Paleozoico Superior de la perforación Las Mochas, provincia de Santa Fe, Argentina. *Ameghiniana*, 32: 73–106.
- CÉSARI, S., GUTIÉRREZ, P. R., SABATTINI, N. et al., 2007. Paleozoico Superior de Argentina: un registro fosilífero integral para el Gondwana occidental. *Publicación Especial de la Asociación Paleontológica Argentina*, 11: 35–54.
- CLAYTON, G., 1995. Carboniferous miospore and pollen assemblages from the Kingdom of Saudi Arabia. *Review of Paleobotany and Palynology*, 89: 115–123.
- CLAYTON, G., COQUEL, R., DOUBINGER, J., GUEINN, K. J., LOBOZIAK, S., OWENS, B., STREEL, M., 1977. Carboniferous miospores of western Europe: illustration and zonation. *Mededelingen Rijks Geologische Dienst*, 29: 1–71.
- CLAYTON, G., LOBOZIAK, S., STREEL, M., TURNAU, E., UTTING, J., 1990. Palynological events in the Mississippian (Lower Carboniferous) of Europe, North Africa and North America. *Courier Forschungs institut Senckenberg*, 130: 79–84.
- CROWLEY, T.J. and BAUM, S. K., 1991. Estimating Carboniferous sea-level fluctuations from Gondwanan ice extent. *Geology*, 19: 975–977.
- DAVYDOV, V. I., CROWLEY, J. L., SCHMITZ, M. D., and POLETAEV, V. I., 2010. High-precision U–Pb zircon age calibration of the global Carboniferous time scale and Milankovitch–band cyclicity in the Donets Basin, eastern Ukraine: Geochemistry Geophysics Geosystems, 11, Q0AA04, doi:10.1029/2009GC002736.
- DI PASQUO, M., AZCUY, C. and SOUZA, P., 2003. Palinología del Carbonífero Superior del Subgrupo Itararé en Ita poronga, Cuenca Paraná, Estado de São Paulo, Brasil. Parte 1: sistemática de esporas y paleofitoplancton. *Ameghiniana*, 40: 277–296.
- DÍAZ FABRÍCIO, M. E. R., 1993. Palinología do Grupo Itararé na Porção Centro–Sul do Rio Grande do Sul, Permiano da Bacia do Paraná, Brazil. *Pesquisas*, 20: 119–131.
- DINO, R. and PLAYFORD, G., 2002. Miospores common to South American and Australian Carboniferous sequences: stratigraphic and phytogeographic implications. In: Hills, L. V., Henderson C. M., Bamber E. W., Eds., *Carboniferous and Permian of the World: XIV ICCP Proceedings*, 336–359. Calgary: Canadian Society of Petroleum Geologist, Memoir, 19.
- FALCON–LANG, H. J., 2005. Small cordaitalean trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia. *Journal of the Geological Society*, 162: 485–500.
- , 2006. Vegetation ecology of Early Pennsylvanian alluvial fan and piedmont environments in southern New Brunswick, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 233: 34–50.
- FASOLO, Z., VERGEL, M. M., OLLER, J. and AZCUY, C., 2006. Nuevos datos palinológicos de la Formación Kaka (Viseano – Serpukhoviano) en la Encañada de Beu, Subandino Norte de Bolivia. *Revista Brasileira de Paleontología*, 9: 53–62.
- FELIX, C. J. and BURBRIDGE, P. P., 1967. Palynology of the Springer Formation of Southern Oklahoma, U.S.A. *Palaeontology* 10: 349–425.
- FIELDING, C. R., FRANK, T. D., BIERGENHEIER, L. P., RYSEL, M. C., JONES, A. T. and ROBERTS, J., 2008. Stratigraphy record and facies associations of the late Paleozoic ice age in eastern Australia (New South Wales and Queensland). In: Fielding, C.R., Frank, T.D., Isbell, J.L., (Ed., *Resolving the Late Paleozoic Ice Age in Time and Space*, 41–57. Geological Society of America Special Paper 441.
- FOSTER, C. B., 1975. Permian plant microfossils from the Blair Athol Coal Measures, Central Queensland, Australia. *Palaeontographica Abteilung B*, 154: 121–171.
- GARCÍA, G. B., 1995. Palinología de la Formación El Imperial, Paleozoico Superior, Cuenca San Rafael, Argentina. Parte I: esporas. *Ameghiniana*, 32: 315–339.
- GULBRANSON, E. L., MONTAÑEZ, I. P., SCHMITZ, M.D., LIMARINO, C. O., ISBELL, J. L., MARENSSI, S. A. and CROWLEY, J. L., 2010. High-precision U–Pb calibration of Carboniferous glaciation and climate history, Paganzo Group, NW Argentina. *Geological Society of America Bulletin*, 122: 1480–1498.
- GUTIÉRREZ, P. R., 1993. Palinología de la Formación Agua Colorada (Carbonífero Superior), sierra de Famatina, provincia de La Rioja, Argentina. I. Granos de polen. *Ameghiniana*, 30: 163–212.
- GUTIÉRREZ, P. R. and BARREDA, V. D., 2006. Palinología de la Formación El Trampeadero (Carbonífero Superior), La Rioja, Argentina: significado bioestratigráfico. *Ameghiniana*, 43: 71–84.
- GUTIÉRREZ, P. R. and CÉSARI, S. N. 1989. Nuevas microfloras de la Formación Lagares (Carbonífero), provincia de La Rioja, República Argentina. *Ameghiniana*, 25: 85–96.
- GUTIÉRREZ, P. R. and LIMARINO, C. O., 2001. Palinología de la Formación Malanzán (Carbonífero Superior), La Rioja, Argentina: nuevos datos y consideraciones paleoambientales. *Ameghiniana*, 38: 99118.
- HACQUEBARD, P. A., 1957. Plant spores in coal from the Horton Group (Mississippian) of Nova Scotia. *Micropaleontology*, 3: 301–324.
- HERNÁNDEZ CASTILLO, G. R., ROTHWELL, G. W. and MAPES, G., 2001. Compound pollen cone in a Paleozoic conifer. *American Journal of Botany*, 88: 1139–1142.
- HØEG, C. A. and BOSE, M. N., 1960. The *Glossopteris* flora of the Belgian Congo with a note on some fossil plants from the Zambesi basin (Mozambique). *Annales de Musée Royal de l’Afrique Centrale, serie 8, sciences géologiques*, 32 : 1–107.
- HUGHES, N. F. and PLAYFORD, G., 1961. Palynological reconnaissance of the Lower Carboniferous of Spitsbergen. *Micropaleontology*, 7: 27–44.



- ISBELL, J. L., LENAHER, P. A., ASKIN, R. A., MILLER, M. F. and BABCOCK, L. E., 2003a. Reevaluation of the timing and extent of late Paleozoic glaciation in Gondwana: Role of Transantarctic Mountains. *Geology*, 31: 977–980.
- ISBELL, J. L., MILLER, M. F., WOLFE, K. L. and LENAHER, P. A., 2003b. Timing of late Paleozoic glaciation in Gondwana: Was glaciation responsible for the development of northern hemisphere cyclothems?. In: Chan, M.A., Archer, A.A., Eds., *Extreme depositional environments: Mega end members in geologic time*, 5–24. Boulder CO: Geological Society of America. Special Paper 370.
- JONES, M. J. and TRUSWELL, E. M., 1992. Late Carboniferous and Early Permian palynostratigraphy of the Joe Joe Group, southern Galilee Basin, Queensland, and implications for Gondwana stratigraphy. *Journal of Australian Geology and Geophysics*, 13: 143–185.
- JONES, A. T., FIELDING, C. R., 2004. Sedimentological record of the late Paleozoic glaciation in Queensland, Australia. *Geology*, 32: 153–156.
- KEMP, E. M., BALME, B. E., HELBY, R. J., KYLE, R. A., PLAYFORD, G. and PRICE, P. L., 1977. Carboniferous and Permian palynostratigraphy in Australia and Antarctica: a review. *Journal of Australian Geology and Geophysics*, 177–208.
- LELE, M., 1964. Studies in the Talchir flora of India: 2. Resolution of the sporegenus *Nuskoisporites* Potonié and Klaus. *The Palaeobotanist*, 12: 147–168.
- LELE, M. and KARIN, R., 1971. Studies in the Talchir Flora of India. 6. Palynology of the Talchir Boulder Beds in Jayanti Coalfield, Bihar. *The Palaeobotanist*, 19: 52–69.
- LESCHIK, G., 1956. Spores aus den Salzten des Zechsteins von Neuhof (Bei Fulda). *Palaeontographica Abteilung B*, 100: 125–141.
- LIMARINO, C. O. and GUTIÉRREZ, P. R., 1990. Diamictites in the Agua Colorada Formation (northwestern Argentina): New evidence of Carboniferous glaciation in South America. *Journal of South American Earth Sciences*, 3: 9–20.
- LIMARINO, C. O. and SPALLETTI, L. A., 2006. Paleogeography of the Upper Paleozoic basins of southern South America: An overview. *Journal of South American Earth Sciences*, 22: 134–155.
- LIMARINO, C. O., CÉSARI, S. N., NET, L. I., MARENSSI, S. A., GUTIERREZ, R. P. and TRIPALDI, A., 2002. The Upper Carboniferous postglacial transgression in the Paganzo and Río Blanco basins (northwestern Argentina): facies and stratigraphic significance. *Journal of South American Earth Sciences*, 15: 445–460.
- LIMARINO, C. O., TRIPALDI, A., MARENSSI, S. and FAUQUÉ, L., 2006. Tectonic, sea-level, and climatic controls on Late Paleozoic sedimentation in the western basins of Argentina. *Journal of South American Earth Sciences*, 22: 205–226.
- LOBOZIAK, S. and CLAYTON, G., 1988. The Carboniferous palynostratigraphy of northeast Libya. In: El-Arnauti, A., Owens, B., Thusu, B., Ed., *Subsurface palynostratigraphy of Northeast Libya*, 129–149. Benghazi: Garyounis University, AGOCO/CIMP.
- LOBOZIAK, S., AVKHIMOVICH, V. I. and STREEL, M., 1997. Miospores from the type locality of the Esneux Formation, Middle Famennian of the Ourthe Valley, eastern Belgium. *Annals de la Société Géologique de Belgique*, 119: 111–118.
- LÓPEZ GAMUNDÍ, O. R., 1997. Glacial–postglacial transition in the Late Paleozoic basins of southern South America. In: Martini, I.P., Ed., *Late Glacial and Postglacial Environmental Changes-Quaternary. Carboniferous–Permian, and Proterozoic*, 47–168. Oxford University Press.
- LÓPEZ GAMUNDÍ, O. R., LIMARINO, C. O. and CÉSARI, S. N., 2002. Late Paleozoic paleoclimatology of central west Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 91: 305–329.
- MAHESHWARI, H. K., 1967. Studies in the *Glossopteris* Flora of India – 29. Miospore assemblage from the Lower Gondwana exposures along Bansloi River in Rajmahal Hills, Bihar. *The Palaeobotanist*, 15: 258–280.
- MAITHY, P. K., 1965. Studies in the *Glossopteris* flora of India – 27. Spores Dispersae from the Karharbari Beds in the Giridih Coalfield, Bihar. *The Palaeobotanist*, 13: 291–307.
- MARENSSI, S. A., TRIPALDI, A., CASELLI, A.T. and LIMARINO, C. O., 2002. Hallazgo de tillitas sobre el flanco occidental del anticlinal de Agua Hedionda (Provincia de San Juan): evidencias de avances y retrocesos del hielo durante la glaciación gondwánica en la Cuenca Paganzo. *Revista de la Asociación Geológica Argentina*, 54: 349–352.
- MARENSSI, S. A., TRIPALDI, A., LIMARINO, C. O. and CASELLI, A. T., 2005. Facies and architecture of a Carboniferous ground-ice system from the Guandacol Formation, Paganzo Basin, Northwestern Argentina. *Gondwana Research*, 8: 187–202.
- MARQUES TOIGO, M. and PICARELLI, T.A., 1984. On the morphology and botanical affinities of *Lundbladispora* Balme 1963 in the Permian of the Paraná Basin, Brazil. *Boletim do Instituto Geociências da Universidade de São Paulo*, 15: 46–52.
- MARTÍNEZ, M., 1993. Hallazgo de fauna marina en la Formación Guandacol (Carbonífero) en la localidad de Agua Hedionda, San Juan, Precordillera Nororiental, Argentina. In: Archangelsky, S., Ed., *2th Congrès International de la Stratigraphie et Géologie du Carbonifère et Permien. Compte Rendus 2*, 291–296.
- MELO J. H. G. and LOBOZIAK S., 2003. Devonian–Early Carboniferous miospore biostratigraphy of the Amazon Basin, Northern Brazil. *Review of Palaeobotany and Palynology*, 124: 131–202.
- MELO J. H. G., LOBOZIAK, S., and STREEL, M., 1999. Latest Devonian to early Late Carboniferous biostratigraphy of northern Brazil: an update. *Bulletin des Centres de Recherches Exploration–Production Elf–Aquitaine*, 22: 13–33.
- MENÉNDEZ, C. A., 1965. Contenido palinológico en sedimentos con *Rhacopteris ovata* (Mc Coy) Walkom de la Sierra de Famatina, La Rioja. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Paleontología*, 1: 45–80.
- MILLAY, M. A. and TAYLOR, T. N., 1974. Morphological studies of Paleozoic saccate pollen. *Palaeontographica Abteilung B*, 147: 75–99.
- OTTONE, E. G., 1989. Palynoflores de la Formación Santa Máxima, Paleozoico Superior, República Argentina. *Palaeontographica Abteilung B*, 213: 89–147.
- , 1991. Palynologie du Carbonifère Supérieur de la coupe de Mina Esperanza, Bassin Paganzo, Argentine. *Revue de Micropaléontologie*, 34: 118–135.
- OTTONE, E. G. and AZCUY, C. L., 1988. *Circumcaticipollis*, nuevo género de polen monosacado del Paleozoico superior de Argentina. *Revista Española de Micropaleontología*, 20: 245–249.

- , 1989. Datos palinológicos de la Formación Guandacol (Carbonífero) en la quebrada de La Delfina, provincia de San Juan, Argentina. *Ameghiniana*, 26: 191–208.
- PEREZ LOINAZE, V. S., 2005. Some trilete spores from Lower Carboniferous strata of the Río Blanco Basin, western Argentina. *Ameghiniana*, 42: 481, 488.
- , 2007. A Mississippian palynological biozone for Southern Gondwana. *Palynology*, 31: 101–118.
- , 2008. Systematic palynological study of the Cortaderas Formation, (Early Carboniferous) Río Blanco Basin, Argentina. Part One. *Ameghiniana*, 45: 33–57.
- , 2009. New palynological data from the Malanzán Formation (Carboniferous), La Rioja Province, Argentina. *Ameghiniana*, 46: 495–512.
- PEREZ LOINAZE, V.S., LIMARINO, C.O., and CÉSARI, S.N., 2011. Palynological study of the Carboniferous sequence at Río Francia Creek, Paganzo Basin, Argentina. *Ameghiniana*, 48: 605–620.
- PHIPPS, D. and PLAYFORD, G., 1984. Laboratory techniques for extraction of palynomorphs from sediments. *Papers of the Department of Geology, University of Queensland*, 11: 1–23.
- PLAYFORD, G., 1962. Lower Carboniferous microfloras of Spitsbergen—Part 1. *Palaeontology*, 5: 550–618.
- , 1971. Lower Carboniferous spores from the Bonaparte Gulf Basin, Western Australia and Northern Territory. Bureau of Mineral Resources, *Journal of Australian Geology and Geophysics*, 115: 1–105.
- PLAYFORD, G. and HELBY, R., 1968. Spores from a Carboniferous section in the Hunter Valley, New South Wales. *Journal of the Geological Society of Australia*, 15: 103–119.
- POORT, R. J. and VELD, H., 1997. Aspects of Permian palaeobotany and palynology XVIII. On the morphology and ultrastructure of *Potoniopsis novicus* (prepollen of Late Carboniferous/Early Permian Walchiaceae). *Acta Botanica Neerlandica*, 46: 161–173.
- POTONIÉ, R. and SAH, S. C. D., 1960. *Sporae dispersae* of the lignites from Cannanore Beach on the Malabar Coast of India. *The Palaeobotanist*, 7: 121–135.
- POTONIÉ, R. and LELE, K. M., 1961. Studies in the Talchir Flora of India – 1. *Sporae dispersae* from the Talchir Beds of South Rewa Gondwana Basin. *The Palaeobotanist*, 8: 22–37.
- RAVN, R. L., 1991. Miospores of the Kekikuk Formation (Lower Carboniferous), Endicott field area, Alaska North Slope. *American Association of Stratigraphic Palynologists Foundation, Contribution Series*, 27: 1–173.
- RENAULT, B., 1879. Structure comparée de quelques tiges de la flore carbonifère. *Muséum National d'Histoire Naturelle, Nouvelles Archives*, 2: 213–326.
- SARJEANT, W. A. S. and STANCLIFFE, R. P. W., 1994. The *Micrhystridium* and *Veryhachium* complexes (Acritarcha: Acanthomorphae and Polygonomorphae): a taxonomic reconsideration. *Micropaleontology*, 40: 1–77.
- SAXENA, R. K., 1993. New names for some palynofossil later homonyms from India. *Geophytology*, 23: 195–196.
- SEGROVES, K. L., 1969. Saccate plant microfossils from the Permian of Western Australia. *Grana Palynologica*, 9: 174–227.
- ŠIMŮNEK, Z., OPLUŠTIL, S. and DRÁBKOVÁ, J., 2009. *Cordaites borassifolius* (Sternberg) Unger (Cordaitales) from the Radnice Basin (Bolshevik, Czech Republic). *Bulletin of Geosciences*, 84: 301–336.
- SOUZA, P. A., 2006. Late Carboniferous palynostratigraphy of the Itararé Subgroup, northeastern Paraná Basin, Brazil. *Review of Palaeobotany and Palynology*, 138: 1–29.
- SOUZA, P. A., PETRI, S. and DINO, R., 2003. Late Carboniferous Palynology from the Itararé Subgroup (Paraná Basin), at Araçoiaba da Serra, São Paulo State, Brazil. *Palynology*, 27: 39–74.
- STANCLIFFE, R. P. W. and SARJEANT, W. A. S., 1994. The acritarch genus *Veryhachium* Deunff 1954, emend. Sarjeant and Stancliffe 1994: A taxonomic restudy and a reassessment of its constituent species. *Micropaleontology*, 40: 223–241.
- STEPHENSON, M. H., 2004. Early Permian spores from Oman and Saudi Arabia. In: Al-Husseini, M.I., Ed., *Carboniferous, Permian and Early Triassic Arabian Stratigraphy*, 185–215. Bahrain: Gulf PetroLink. GeoArabia Special Publication 3.
- SULLIVAN, H. J., 1964. Miospores from the Drybrook Sandstone and associated measures in the Forest of Dean Basin, Gloucestershire. *Palaeontology*, 7: 57–61.
- SUN KEQIN and DENG SHENGHUI, 2004. The center of origin of the Cathaysia Flora. *Geological Review*, 50: 337–342.
- TARASOV, P. E., VOLKOVA, V. S., WEBB III, T., et al., 2000. Last glacial maximum biomes reconstructed from pollen and plant macrofossil data from Northern Eurasia. *Journal of Biogeography*, 27: 609–620.
- TIWARI, R. S., 1965. Miospores assemblage in some coals of Barakar stage (Lower Gondwana) of India. *The Palaeobotanist*, 13: 168–214.
- URBAN, J. B., 1971. Palynology and the Independence Shale of Iowa. *Bulletin of American Paleontology*, 60: 103–189.
- VEEVERS, J. J. and POWELL, C., 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive–regressive depositional sequences in Euramerica. *Geological Society of America Bulletin*, 98: 475–487.
- WANG, N. Z., JIN, F. and WANG, W. 2004. Early Carboniferous fishes (Acanthodian, Actinopterygians and Chondrichthyes) from the east sector of north Qilian Mountain China. *Vertebrata Palasiatica*, 4: 89–110.
- YBERT, J. P., 1975. Etude des miospores du bassin Houiller de Candiota–Hulha Negra, Rio Grande do Sul, Brésil. *Pesquisas*, 5: 181–226.
- ZAVIOLOVA, N. E. and STEPHENSON, M. H., 2006. The exine ultrastructure of *Plicatipollenites malabarensis* (Potonié et Sah) Foster, 1975. *Review of Palaeobotany and Palynology*, 139: 241–252.
- ZHU, H., 1993. A revised palynological sub-division of the Namurian of Jingyuan, northwest China. *Review of Palaeobotany and Palynology*, 77: 273–300.
- , 1995. Namurian miospores from China and their correlation with Europe and North America. *Review of Palaeobotany and Palynology*, 89: 335–357.

Received December 1, 2010

Accepted January 10, 2012

Published November 2012