

FIRST PALYNOLOGIC RECORD OF THE CRETACEOUS LA YESERA FORMATION (SALTA GROUP), NORTHWESTERN ARGENTINA

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ABSTRACT – Thirty-four taxa were documented from six palynologically productive samples of the La Yesera Formation (Brealito and Don Bartolo Members) in the Pucará locality (Salta Province, northwestern Argentina). In the Brealito Member, aquatic species (mainly freshwater algae) dominate the palynoflora, while terrestrial species are represented by trilete spores (mainly Anemiaceae) and gymnosperm pollen grains. In the Don Bartolo Member, *Classopollis* spp. dominate most of the assemblages, trilete Anemiaceae spores constitute half of the total counts in one of the assemblages and a unique angiosperm species (*Tricolpites variabilis*) was found in two assemblages. *Ephedra*-type pollen grains (three genera and six species) appear in both members, although in low abundance. The results support previous sedimentology studies that indicate a perennial lake environment at the time of deposition of the Brealito Member, with evidence for dry seasonality in the Don Bartolo Member. The inferred regional paleoclimate is subtropical with arid conditions. Considering the stratigraphic ranges of selected species and the sedimentology data, an Albian/Cenomanian age is suggested for the unit.

Key words: Palynology, Cretaceous, La Yesera Formation, northwestern Argentina.

RESUMO – Trinta e quatro táxons foram registrados a partir de seis amostras palinológicas provenientes da Formação La Yesera (membros Brealito e Don Bartolo), na localidade Pucará, Província de Salta, noroeste da Argentina. No Membro Brealito, predominam as espécies aquáticas, principalmente de algas de água doce; as espécies terrestres estão representadas por esporos triletes, principalmente de Anemiaceae e por grãos de pólen de gimnospermas. No Membro Don Bartolo, os grãos de pólen *Classopollis* spp. dominam a maioria das assembleias, embora numa das amostras, metade das contagens totais é constituída por esporos triletes de Anemiaceae e, uma única espécie de angiospermas (*Tricolpites variabilis*) foi encontrada em duas assembleias. Grãos de pólen do tipo *Ephedra*, com três gêneros e seis espécies, aparecem em baixa abundância em ambos os membros. Estes resultados corroboram estudos sedimentológicos anteriores e indicam ambiente lacustre perene, no momento da deposição do Membro Brealito, com evidência de sazonalidade seca para a Membro Don Bartolo. O paleoclima regional inferido é subtropical árido. Considerando os intervalos estratigráficos de espécies selecionadas e os dados sedimentológicos, é sugerida idade Albiano/Cenomaniano para a unidade estudada.

Palavras-chave: Palinologia, Cretáceo, Formação La Yesera, noroeste da Argentina.

INTRODUCTION

The tectonic evolution of southern South America has been influenced by a subduction regime in the western margin since the Mesozoic (Uliana & Biddle, 1988). During the Early Cretaceous, extensional ruptures along the mid-Atlantic spreading system propagated northward from southern Argentina to southern Brazil and southwest Africa, giving rise to a narrow, wedge-shaped ocean basin (Rabinowitz & LaBrecque, 1979). As a consequence, numerous rift basins originated in central and northwestern Argentina (Uliana *et al.*, 1989), among them the Salta Group Basin.

The Salta Group includes three subgroups with three formations each: Pirgua (La Yesera, Las Curtiembres, and Los Blanquitos Formations), Balbuena (Lecho, Yacoraite, and

Olmedo/Tunal Formations), and Santa Bárbara (Mealla, Maíz Gordo, and Lumbrera Formations). The deposits range from the Early Cretaceous through the Eocene, and are located in seven sub-basins: Tres Cruces, Lomas de Olmedo, Metán, Alemania, El Rey, Sey, and Brealito (Marquillas *et al.*, 2005) (Figure 1A). Salfity & Marquillas (1994) mention synrift and postrift deposits infilling the basin. The Pirgua Subgroup represents the synrift stage when faults were active, and the Balbuena and Santa Bárbara subgroups represent the postrift stage, when thermal subsidence occurred.

The basal unit of the Pirgua Subgroup, La Yesera Formation, was defined in the Alemania sub-basin (Reyes & Salfity, 1973) where it is mainly comprised of red beds. The deposits have a north-south orientation in the Brealito sub-basin, from the Olacapato ranges in Jujuy Province to the

Brealito lake in southwestern Salta Province (Sabino, 2002). They are connected to the Miraflores Formation in Bolivia, where a Cenomanian marine ingression has been recorded (Sempere, 1995). The depositional environment consists of debris-flow dominated by alluvial fans to braided rivers in the lower section, mud plains to sandy braided rivers in the middle, and debris-flow dominated alluvial fans in the upper section (Marquillas *et al.*, 2005). In the southern part of the basin, the sedimentation of the La Yesera Formation began at the same time as the Alto de Las Salinas Complex volcanic event, from which basalt and rhyolites were dated to 128–112 Ma (K/Ar, total rock; Bossi & Wampler, 1969). Isonza Basalt effusions in the top of the formation were dated from 99±5 to 96±5 Ma (K/Ar total rock; Valencio *et al.*, 1976). Hence, the accumulation of deposits spans the Barremian to the Cenomanian.

Fossil records from the La Yesera Formation are scarce: plant remains, algae, and undifferentiated ostracods were found in the top levels (Brealito sub-basin; Boso *et al.*, 1984). Few palynologic studies have been published from the Pirgua Subgroup. Quattrocchio *et al.* (2005) reported Campanian-Maastrichtian palynoflora from the passage beds between the Los Blanquitos and Lecho Formations in the Vilches locality (in the transition between the Alemania and Metán sub-basins; Figure 1A), with typical Mesozoic taxa, in conjunction with angiosperm pollen grains. These grains have been recorded in younger sediments from lower latitudes of tropical South America and Africa, suggesting a northward migration of the taxa. Narváez & Sabino (2008) provided the first palynologic record of the Morales Member of the Las Curtiembres Formation at El Chorro creek (Alemania sub-basin, Figure 1A), with a prevalence of *Ephedra*-type pollen that suggests semiarid conditions, a warm-dry climate, and an age no older than Campanian, based on the presence of *Peninsulapollis gilli* (Cookson) Dettmann & Jarzen 1988.

Based on the palynoflora, the authors aim to describe the paleoenvironmental context present at the time of deposition of the La Yesera Formation. These data are phytogeographically significant because of their geographical position (northern Argentina), a transition zone between equatorial and austral regions, and because most of the mid-Cretaceous palynologic reports in Argentina are from Patagonia (*e.g.* Archangelsky *et al.*, 1983, 1994, 2008; Baldoni *et al.*, 2001; Archangelsky & Llorens, 2005, 2009; Medina *et al.*, 2008; Perez Loinaze *et al.*, 2012); or to a lesser extent, the central-western part of the country (Prámparo, 1989a,b, 1990, 1994; Prámparo & Milana, 1999; Prámparo *et al.*, 2005). Hence, our main objective is to contribute to the knowledge of mid-Cretaceous subtropical plant communities in South America (~25°S).

Study area

The palynologic samples reported here were collected in the Pucará valley (Figure 1B) within the Brealito sub-basin, south-western Salta Province (Figure 1A). The Pirgua Subgroup in this sub-basin includes the La Yesera and Las Curtiembres Formations, approximately 2280 m and 900 m thick, respectively. The base of the La Yesera Formation

is composed of sandstones and conglomerates (Yacutuy Member, 1000 m thick); the middle portion consists of pelites and scarce sandstones (Las Chacras Member, 660 m) and an overlying pelitic section (Brealito Member, 290 m); the top is composed of sandstones, pelites, and conglomerates (Don Bartolo Member, 330 m) (Figure 2; Sabino, 2004). According to Sabino (2002), the Brealito Member deposits are related to a perennial lake, elongated in north-south direction that did not reach the Alemania sub-basin (located 40 km eastward) (Figure 1A). The scarce distribution of deposits implies that flooding only occurred in areas of greater subsidence. Two stratigraphic sections were analysed in this study, which are from the upper levels of the La Yesera Formation and correspond to the Brealito and Don Bartolo Members (Figure 2).

MATERIAL AND METHODS

Fifteen rock samples were collected and processed for palynology from the upper stratigraphic sections (Figure 2) of the La Yesera Formation in the Pucará valley (Figure 1B). The physical and chemical extraction of palynomorphs was performed in the Paleopalynologic Laboratory at the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA, Mendoza). Samples were treated with hydrochloric and hydrofluoric acids following standard techniques (Volkheimer & Melendi, 1976). Residue was sieved with a 10 µm nylon mesh-sieve.

Only six samples were palynologically productive, two of them from the top of the Brealito Member (laboratory catalogue numbers 8435-8436; Figures 2A-C), and four from the Don Bartolo Member (laboratory catalogue numbers 8446, 8448-8450; Figure 2D). The slides were examined under a light microscope (Olympus BX50 with digital camera) for qualitative and quantitative assessment of palynomorphs. Specimens were located on the slide using an England Finder graticule. Palynologic analysis included systematic study, comparison of palynomorphs with modern families, and counts of 200-250 morphotypes. Palynomorph grains were described following Punt *et al.*'s (2007) terminology, and Dettmann's (1995) for megaspores. The slides are stored at the Paleopalynologic Collection at IANIGLA under the acronym MPLP (Mendoza-Paleopalynoteca-Laboratorio-Paleopalynología).

SYSTEMATIC PALYNOLOGY

A total of 34 palynomorph species were identified (see Appendix for the taxonomic list). In this section are provided descriptions of the taxa with open assignments or with biostratigraphic or paleoenvironmental significance. Described species are included in the following botanical groups: bryophytes and pteridophytes, gymnosperm, angiosperm and algae (see Fensome, 1987 for discussion on methods for organizing fossil species). A complete revision and taxonomic discussion of the cicatricose species found in the La Yesera Formation is included in Narváez *et al.* (2013).

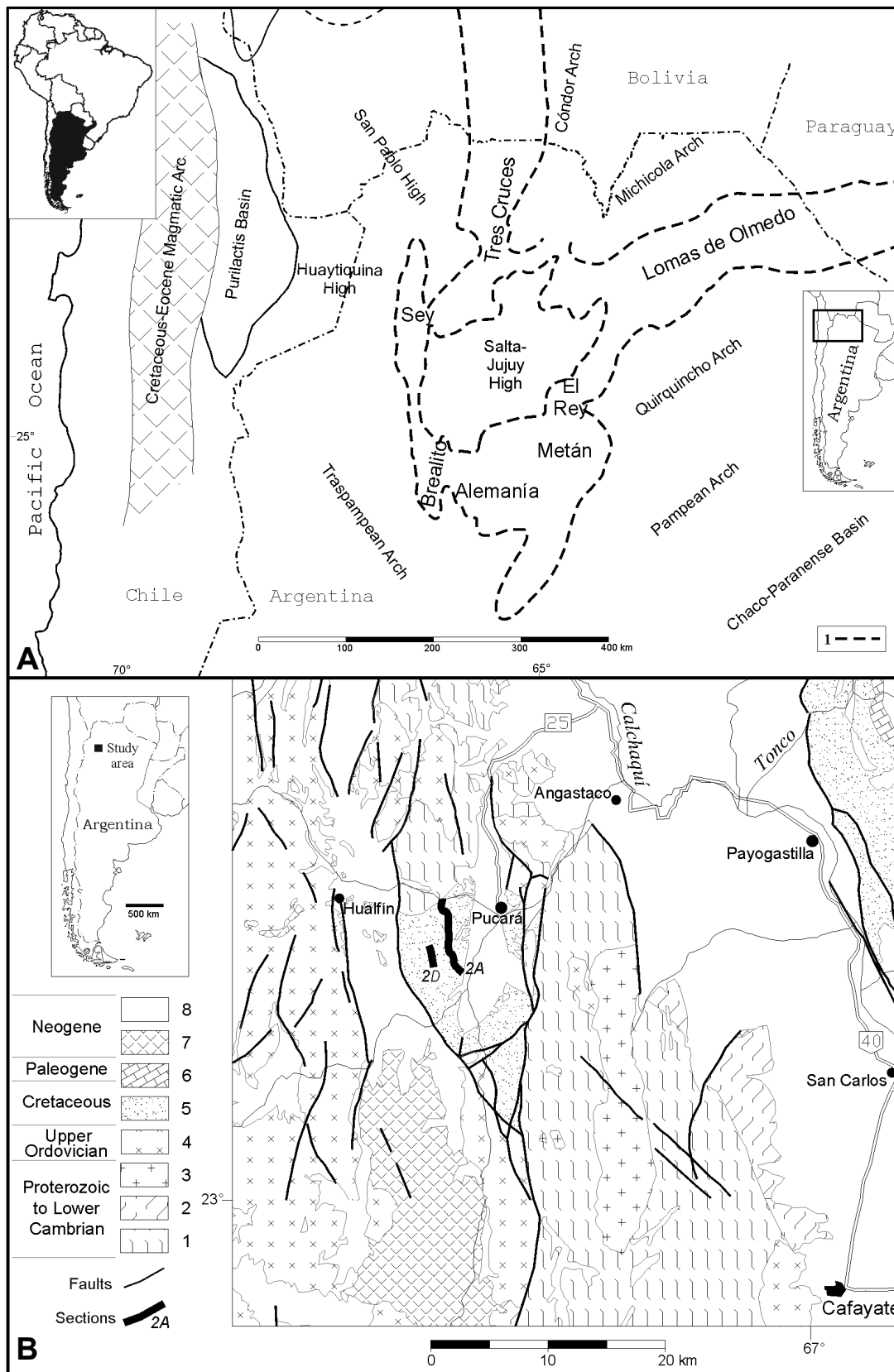


Figure 1. Location maps. **A**, Northwestern Argentina showing main structural highs and sub-basins present during the accumulation of the Pirgua Subgroup (Salta Group), 1. synrift stage basin margin. (from Sabino, 2002); **B**, sample locality: Pucará valley, 1. high-grade metamorphic rocks, 2. low-grade metamorphic rocks, 3. trondhjemite, granite and granodiorite, 4. granite and granodiorite, 5. red beds (Pirgua Subgroup), 6. continental marine deposits (Balbuena and Santa Bárbara subgroups), 7. volcanic rocks, 8. sediments.

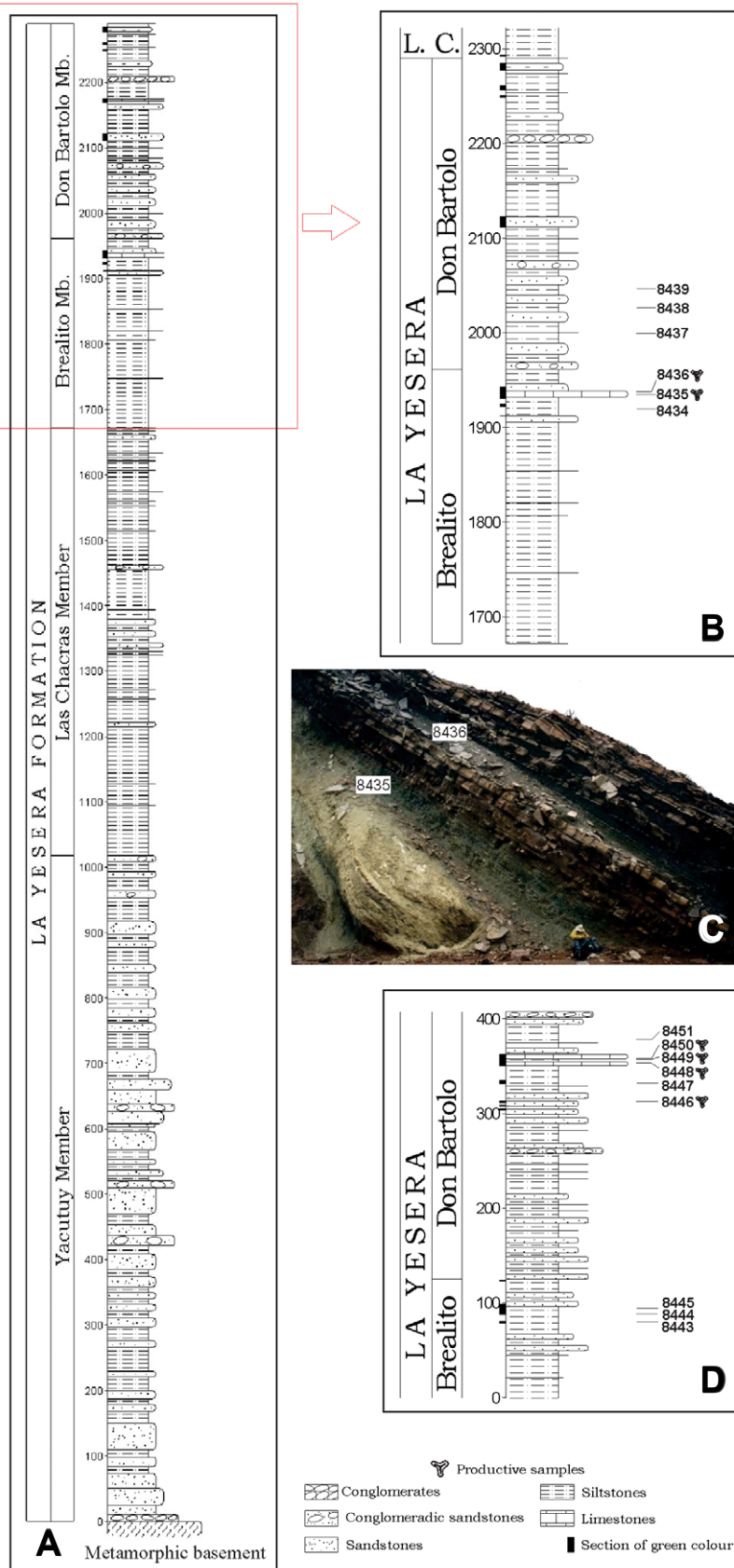


Figure 2. Stratigraphic logs of the La Yesera Formation in the Pucará valley (Brealito sub-basin). **A**, section 1; **B**, detailed upper portion of section 1 showing the location of palynologic samples; **C**, outcrop of the Brealito Member at the Pucará valley composed of yellow calcareous mudstone in the base and two coarsening-upward sequences of green shale and white sandstone. Productive samples (8435-8436) collected from the base of each sequence; **D**, section 2 showing the location of palynologic samples from the Don Bartolo Member.

Bryophytes and pteridophytes

Balmeisporites (Cookson & Dettmann) Dettmann, 1995

Type species. *Balmeisporites holodictyus* Cookson & Dettmann, 1958a.

Balmeisporites sp.1
(Figures 3B-C)

Description. Trilete spores. Circular, oval to irregular equatorial amb. Laesura straight, rays reaching $\frac{3}{4}$ of the spore radius. Spherical exospore encapsulated by an irregular epispore, a pyramidal acrolamella extending 32-40 μm over the exospore in the proximal pole. Episporal surface formed by thin membranous projections (generally torn), closely disposed of 1.5-(3)-5 μm width and 3-(10)-15 μm high; slightly more prominent expansions in each equatorial radial region are observed in some specimens.

Dimensions. Diameter of spore body: 65-(92)-140 μm ; diameter including the epispore: 67-(124)-193 μm (17 specimens).

Comparison. *Balmeisporites holodictyus* has similar spore body size (80-120 μm) and total dimensions including the epispore (equatorial: 120-160 μm ; polar: 170-220 μm), but the acrolamella projection at proximal pole is much higher (80-110 μm) and the episporal surface forms a distinct reticulum with circular to polygonal lumina (Cookson & Dettmann, 1958a; Dettmann, 1995). *B. glenelgensis* Cookson & Dettmann, 1958a is similar to *B. holodictyus* but with a larger spore body (107-135 μm) and shallower and closer mesh. *B. tridictyus* Cookson & Dettmann, 1958a (spore body size 80-115 μm) lacks the reticulate sculpturing and the acrolamella is composed of three leaf-like segments, which are ordered symmetrically around the proximal pole and united at their edge, enclosing the tetrad scar.

Remarks. The genus has botanical affinity to Salviniaceae according to Villar de Seoane & Archangelsky (2008).

Ceratosporites Cookson & Dettmann, 1958b

Type species. *Ceratosporites equalis* Cookson & Dettmann, 1958b.

?*Ceratosporites* sp.
(Figure 3E)

Description. Trilete spore. Subcircular amb. Laesura not visible. Exine 0.5 μm thick. Surface ornamented with bacula 2-4 μm high and 1-1.5 μm diameter at the base, with capitate extremes occasionally bifurcate, distributed along the muri of a reticulum with 2-3 μm lumina or depressions.

Dimensions. Equatorial diameter: 40 μm (1 specimen).

Remarks. The unique specimen is assigned with doubt to *Ceratosporites* as it has an undistinguished laesura and a probable ornamented proximal face.

Comparison. *Ceratosporites equalis* has a prominent and distinct laesura reaching equator and a smooth proximal face (Cookson & Dettmann, 1958b). The ornamentation in the distal face of the extant species *Anthoceros multifidus* Lindb. (Anthocerotophyta, Bryophyte) is very similar to our specimen (see SEM photographs in Warny *et al.*, 2012), indicating a probable botanical affinity.

Cristatitriletes Mädlar, 1964

Type species. *Cristatitriletes baculatus* Mädlar, 1964.

?*Cristatitriletes* sp.
(Figure 3H)

Description. Trilete spore. Oval amb. Laesura straight, rays reaching $\frac{3}{4}$ of the spore radius. Exine 0.5 μm thick. Surface ornamented with bacula and spines, 2-5 μm high and 1-1.5 μm diameter at the base, generally with bifurcated tips, irregularly and densely distributed around surface. Some of the elements fuse at their bases forming irregular crests, more distinct around equator.

Dimensions. Equatorial diameter: 56 μm (1 specimen).

Remarks. Although the genus *Cristatitriletes* includes spores with cristae that consist of fused or coalescing baculae coincident with our specimen, the unique species *C. baculatus* has been recorded in Late Permian and Triassic sediments (Traverse & Ames, 1968; Jansonius & Hills, 1976; Eshet, 1990).

Comparison. *Cristatitriletes baculatus* is larger (*ca.* 75 μm) and the cristae form a reticulate equatorial and distal pattern (Jansonius & Hills, 1976).

Matonisporites Couper, 1958

Type species. *Matonisporites phlebopteroides* Couper, 1958.

?*Matonisporites* sp.
(Figures 3N-O)

Description. Trilete spores. Subtriangular amb with straight to slightly convex sides and rounded angles. Laesura straight, rays reaching $\frac{2}{3}$ to $\frac{3}{4}$ of the spore radius, margo 8-(11)-20 μm width at each side of the laesura. Crassitude around equator in proximal face 7-(13)-20 μm width. Exine 2-3 μm thick, thicker around equator: 5-7 μm , laevigate to scabrate, generally corroded.

Dimensions. Equatorial diameter: 95.5-(118)-155 μm (10 specimens).

Remarks. The large size is the notorious characteristic of these spores. The genus *Matonisporites* was originally created to include large spores with triangular amb, laesura with margo, and laevigate thick exine (Couper, 1958). Dettmann (1963) emended the original diagnosis, restricting the genus to smooth valvate trilete spores (*i.e.* thicker exine in equatorial radial regions). The authors could not differentiate the presence of true valvae in our specimens, so they prefer to assign them with doubt to *Matonisporites*.

Comparison. *Matonisporites equixinus* Couper, 1958 is smaller (40-(58)-68 µm) and has thinner exine (2.5-3,5 µm). *M. sp. A* (see figure 14.T, page 24 in Helby *et al.*, 1987) has an exine of approximately 4 µm thick but there is no description of the illustrated specimen.

Raistrickia Schopf, Wilson & Bentall, 1944

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

?*Raistrickia* sp.
(Figure 3Q)

Description. Trilete spore. Oval amb. Laesura hardly distinct, straight. Exine 1.5-2 µm thick. Surface ornamented with bacula, 1.5 µm diameter at the base and 5-5.5 µm high, with tips dissected into several papillae, irregularly and densely distributed over the whole surface, 1-4 µm apart.

Dimensions. Equatorial diameter: 63 µm (1 specimen).

Remarks. The specimen is not confidently assigned to *Raistrickia* as this genus has been previously recorded in Upper Paleozoic-Lower Mesozoic sediments of Argentina (e.g. Azcuy, 1975; Zavattieri, 1992; García, 1995).

Comparison. *Raistrickia* sp. A (García, 1995) is similar in size (72 µm), but with larger bacula (3.5-5.8 µm wide and 7-9 µm high).

Gymnosperm

Ephedripites Bolkhovitina ex Potonié, 1958

Type species. *Ephedripites mediolobatus* Bolkhovitina ex Potonié, 1958.

Ephedripites ovatus (Pierce) *comb. nov.*
(Figures 4H-I)

Basionim. *Striainaperturites ovatus* Pierce, 1961. *Minnesota Geological Survey Bulletin*.

42, p. 45, plate 3, fig. 80; holotype 29H-4 33.9/123.7, plate 3, fig. 80.

Synonym. *Equisetosporites ovatus* (Pierce) Singh, 1964.

Description. Polyplicate pollen grains. Oval outline with acute to rounded extremities. Exine 0.5 µm thick, sculptured with 8-12 straight and flat ridges running parallel to the longitudinal axis, each ridge 2-5 µm width in the central part and narrowing towards the longitudinal ends where they fuse in an area of 2-3 µm width. Furrows 0.3-0.5 µm wide.

Dimensions. Length: 29-(32)-36 µm; maximum breadth: 22-(24)-27 µm (5 specimens).

Remarks. The authors make the new combination to the genus *Ephedripites* as they consider it is more indicative of its ephedralean affinity, also taking into account that this genus has been widely used as synonym of *Equisetosporites*.

Angiosperm

Tricolpites (Cookson ex Couper) Jarzen & Dettmann, 1989

Type species. *Tricolpites reticulatus* (Cookson) Jarzen & Dettmann, 1989.

Tricolpites variabilis Burger, 1970
(Figures 4Q-R)

Description. Tricolpate pollen grain, prolate. Colpi medium long, generally indistinct, sometimes costate. Exine 0.7-1 µm thick, semitectate, nexine 0.2-0.3 µm, sexine 0.5-0.7 µm. Reticulum formed by lumina of circular, oblong, or polygonal outline, slightly heterobrochate (0.4-0.7 µm diameter).

Dimensions. Polar length: 21-24 µm; equatorial length: 17-18 µm (3 specimens).

Remarks. The specimens were found only in equatorial view.

Algae

Botryococcus Kützing, 1849

Type species. *Botryococcus braunii* Kützing, 1849

Botryococcus sp.
(Figures 5A-B)

Description. Compound rounded colonies, botryoidal, non branched. Lobules almost spherical, 11-33 µm in diameter, depending on the stage of development. Each lobule contains numerous cups (4-8 µm in diameter), tightly arranged, walls 1-1.5 µm thick. In some colonies, the cups are not clearly distinguished due to poor preservation.

Dimensions. 20-(65)-165 µm (40 colonies).

Remarks. The genus *Botryococcus* belongs to the Family Botryococcaceae within the Order Chlorococcales (Zippi, 1998).

Algae incertae sedis

Leiosphaeridia Eisenack *emend* Downie & Sarjeant, 1963

Type species. *Leiosphaeridia baltica* Eisenack, 1958.

Remarks. The genus *Leiosphaeridia* has a polyphyletic origin and is an *incertae sedis* group that should be included in the acritarch subgroup "Sphaeromorphitae" (see discussion of the genus in Martínez *et al.*, 2005).

Leiosphaeridia-type 1
(Figures 5C-D)

Description. Spheroidal vesicles, usually with folds. Thin wall of approximately 0.2 µm thick, hyaline, laevigate.

Dimensions. Vesicle diameter: 32-(39)-46 µm (5 specimens).

Comparison. The specimens studied have the same

morphologic features as *Leiosphaeridia hyalina* (Deflandre) Downie, 1957.

Leiosphaeridia-type 2
(Figure 5E)

Description. Spheroidal vesicles, sometimes with folds. Thin wall of approximately 0.2 μm thick, hyaline, ornamented with microgranules of less than 1 μm in diameter, less than 1 μm apart, irregularly distributed over the entire surface.

Dimensions. Vesicle diameter: 38-44 μm (2 specimens).

Comparison. The specimens are similar to *Leiosphaeridia* sp. e described in Prámparo (1988, 1989b) for the Late Aptian La Cantera Formation (San Luis Basin).

Echinate vesicle indet.
(Figures 5F-G)

Description. Spheroidal vesicles, usually with folds. Thin wall of approximately 0.2 μm thick, scabrate, densely covered with spines of 1-1.2 μm high, sometimes with bifurcated tip. Some specimens have an internal circular accumulation body of 4-5 μm in diameter.

Dimensions. Vesicle diameter: 24.5-(32)-39 μm (5 specimens).

Comparison. *Comasphaeridium* sp., described from the Late Aptian La Cantera Formation (Prámparo, 1988b, 1989b), is very similar to these vesicles. The freshwater dinoflagellate cyst *Protoellipsoidinium fibratum* (Batten & Lister) Wan Chuanbiao *et al.*, 1997 has similar morphological features (Batten & Lister, 1988; Wan Chuanbiao *et al.*, 1997). Nevertheless, our specimens do not show any kind of apertural structure.

PALEOENVIRONMENTAL AND CLIMATIC CONSIDERATIONS

The palynomorph assemblages of the La Yesera Formation (Pirgua Subgroup) constitute the oldest palynologic record of the Salta Group and one of the few from Cretaceous sediments in northwestern Argentina. Thirty-four species were recovered from the top levels of the Formation, from the Brealito and Don Bartolo Members outcropping in the Pucará locality (Figures 1,2). Counts of the different assemblages are summarized in Figure 6.

Brealito Member

The palynologic assemblages (8435-8436; Figures 2B-C) shows a prevalence of aquatic species (71-76%; Figure 6). The chlorococcal algae *Botryococcus* sp. dominates the assemblage 8435 (71%). These algae have been widely used as paleoenvironmental indicators, based on their colonies' stage of development, preservation, and resistance to variation in saline concentration (*e.g.* Guy-Ohlson, 1992, 1998; Batten & Grenfell, 1996; Rodríguez Amenábar & Ottone, 2003; Ottone *et al.*, 2005; Ottone & Mancuso, 2006; Zavattieri & Prámparo, 2006). They commonly form water blooms in hard water lakes

and ponds (Zippi, 1998). The colonies studied here had a wide size range (20-165 μm) and different stages of development and preservation conditions, which suggest almost uniform environmental conditions.

Leiosphaeridia-type 1 dominates assemblage 8436 (70.8%; Figure 6), while the circular vesicle densely ornamented with spines was scarce (Echinate vesicle indet., 4%; Figures 5F-G). Although aquatic *Leiosphaeridia* forms have been generally associated with brackish or marine environments, Prámparo (1989b) reported their presence in the lacustrine Cretaceous La Cantera Formation (San Luis Basin) with a great variety of forms and high abundances (80%), in association with freshwater algae such as *Botryococcus*, *Scenedesmus*, *Tetrastrum*, *Tetraedron*, and the same echinate vesicle recorded in the La Yesera Formation.

Pteridophyte species in both palynofloras were mostly represented by cicatricose spores of the Anemiaceae family (8.1 and 16.4%, in assemblages 8435 and 8436 respectively) and only about 1% belonged to other taxa (*e.g.* *Deltoidospora minor*) (Figure 6). Gymnosperm pollen grains were more abundant and diverse in assemblage 8435 (12.5%), including *Balmeiopsis limbatus*, *Alisporites* sp., *Classopollis* sp., *Ephedra*-type pollen, *Cycadopites* sp., and inaperturate grains; whereas in assemblage 8436, only *B. limbatus* and *Ephedra*-type pollen (4%) were present.

Considering the palynological assemblages described here and the sedimentologic data provided by Sabino (2004), the inferred depositional environment for the sediments yielding assemblage 8435 is a shallow, perennial lake, represented mainly by marls and yellow limestones. For the sediments containing assemblage 8436, lacustrine conditions associated with deltaic facies are inferred. Pteridophyte species would have grown surrounding bodies of water where the aquatic forms developed, while gymnosperms would have grown in more elevated areas farther from the depositional site.

Don Bartolo Member

Unlike the Brealito Member, aquatic forms were scarce in the Don Bartolo Member assemblages (Figures 2D and 6). *Classopollis* pollen grains dominate the assemblages; making up almost three-quarters of the total from samples 8446, 8448 and 8450 (Figure 6). *Classopollis simplex* was the most common, followed by *C. classoides*. These rimulated grains belong to the extinct Cheirolepidiaceae family of conifers, which may have been present in tropical to subtropical coastal environments (Vakrameev, 1981), although they have also been associated with fluvial and lake deposits, growing in well-drained soils. This family is associated with hot, arid, and seasonally dry climatic conditions (Herngreen & Chlonova, 1982; Lima, 1983; Batten & MacLennan, 1984).

Other gymnosperm include *Cycadopites* sp. (2.5-6.3%) and *Ephedra*-type pollen (4.9-8.8%) (Figure 6), with three genera and six species, present in all samples. Gnetales have been widely used as indicators of semiarid to arid environments based on comparison to their extant representatives (Srivastava, 1968). However, these interpretations have been questioned by Frederiksen (1985) and Archangelsky

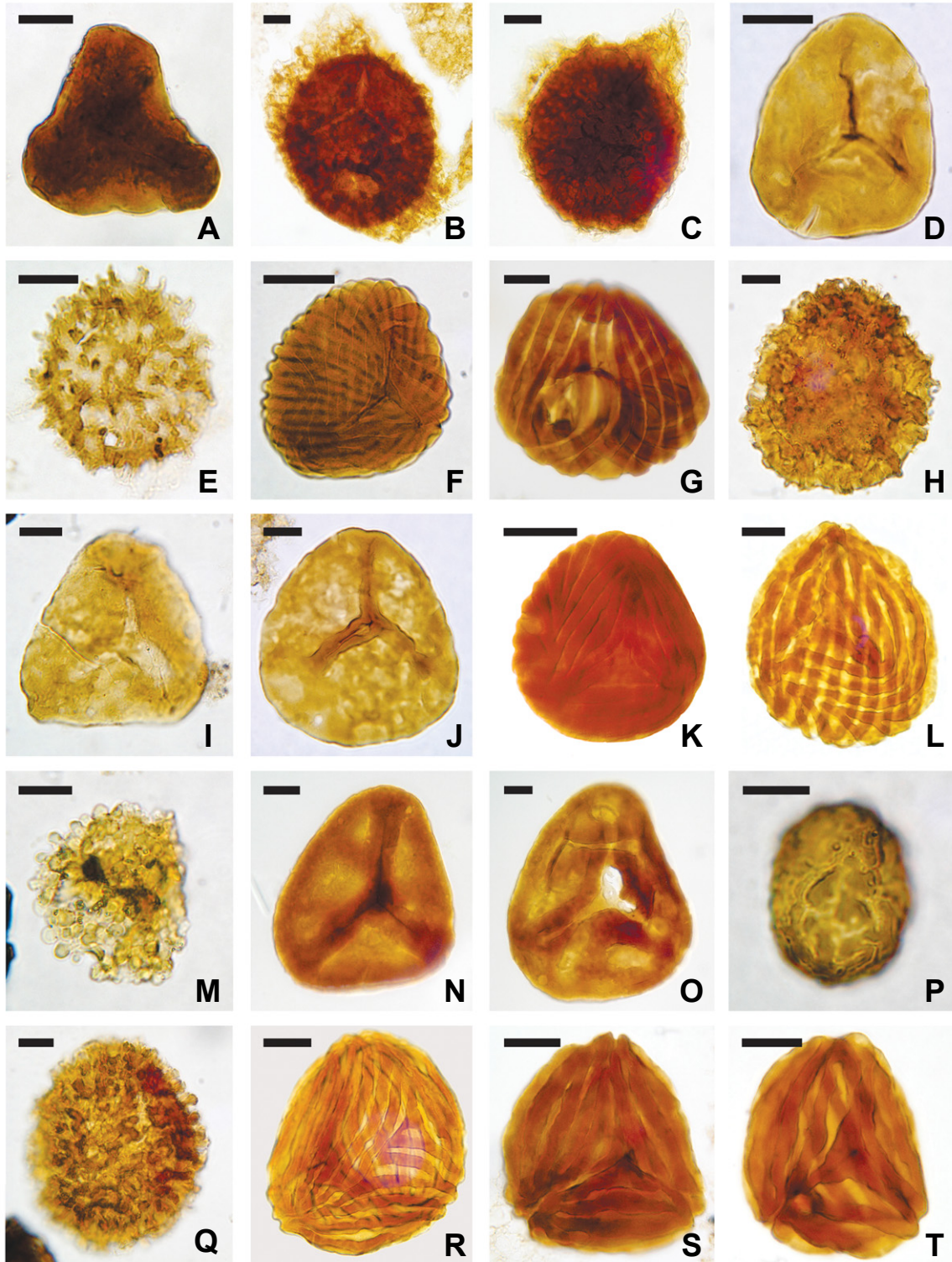


Figure 3. Trilete and monolete spores. Sample/slide numbers, England Finder coordinates and collection acronym are indicated for all specimens. **A**, *Auritulinasporites* sp., 8449A: Z22/2 MPLP; **B-C**, *Balmesporites* sp. 1, B. 8449G: R41 MPLP, C. 8449F: M29/4 MPLP; **D**, *Biretisporites* sp., 8449F: N33/3 MPLP; **E**, *?Ceratospores* sp., 8449C: E29/4 MPLP; **F**, *Cicatricosporites cuneiformis* Pocock, 1964, 8449B: X34 MPLP; **G**, *Cicatricosporites* sp. 1 (in Narváez et al., 2013), 8435B: T21/1 MPLP, distal view; **H**, *?Cristatitriletes* sp., 8449U: P39 MPLP; **I**, *Deltoidospora minor* (Couper) Pocock, 1970, 8435P: G33/2 MPLP; **J**, *Dictyophyllidites* sp., 8449F: T35/1 MPLP; **K**, *Fisciniasporites* sp. cf. *F. brevilaesuratus* (Couper) Dettmann & Clifford, 1992, 8436C: U41/2 MPLP, proximal view; **L**, *Fisciniasporites* sp. (in Narváez et al., 2013), 8449I: Y33/1 MPLP; **M**, *Leptolepidites* sp., 8449U: F23 MPLP; **N-O**, *?Matonisporites* sp., H. 8449F: D29/1 MPLP, I. 8449I: H35 MPLP; **P**, *Polypodiisporites* sp., 8435N: R37/1 MPLP, distal view; **Q**, *?Raistrickia* sp., 8449X: L28/4 MPLP; **R**, *Ruffordiaspora ludbrookiae* (Dettmann) Dettmann & Clifford, 1992, 8449H: G41/1 MPLP; **S**, *Ruffordiaspora* cf. *R. ticoensis* (Archangelsky & Gamero) Archangelsky A.; Archangelsky S.; Poiré & Canessa, 2008, 8449F: D42/4 MPLP, proximal view; **T**, *Ruffordiaspora* sp. 1 (in Narváez et al., 2013), 8449K: Q49/3 MPLP, proximal view. Scales bars: A-D, F-I, M, N, R-T = 20 µm; E, J-L, O-Q = 10 µm.

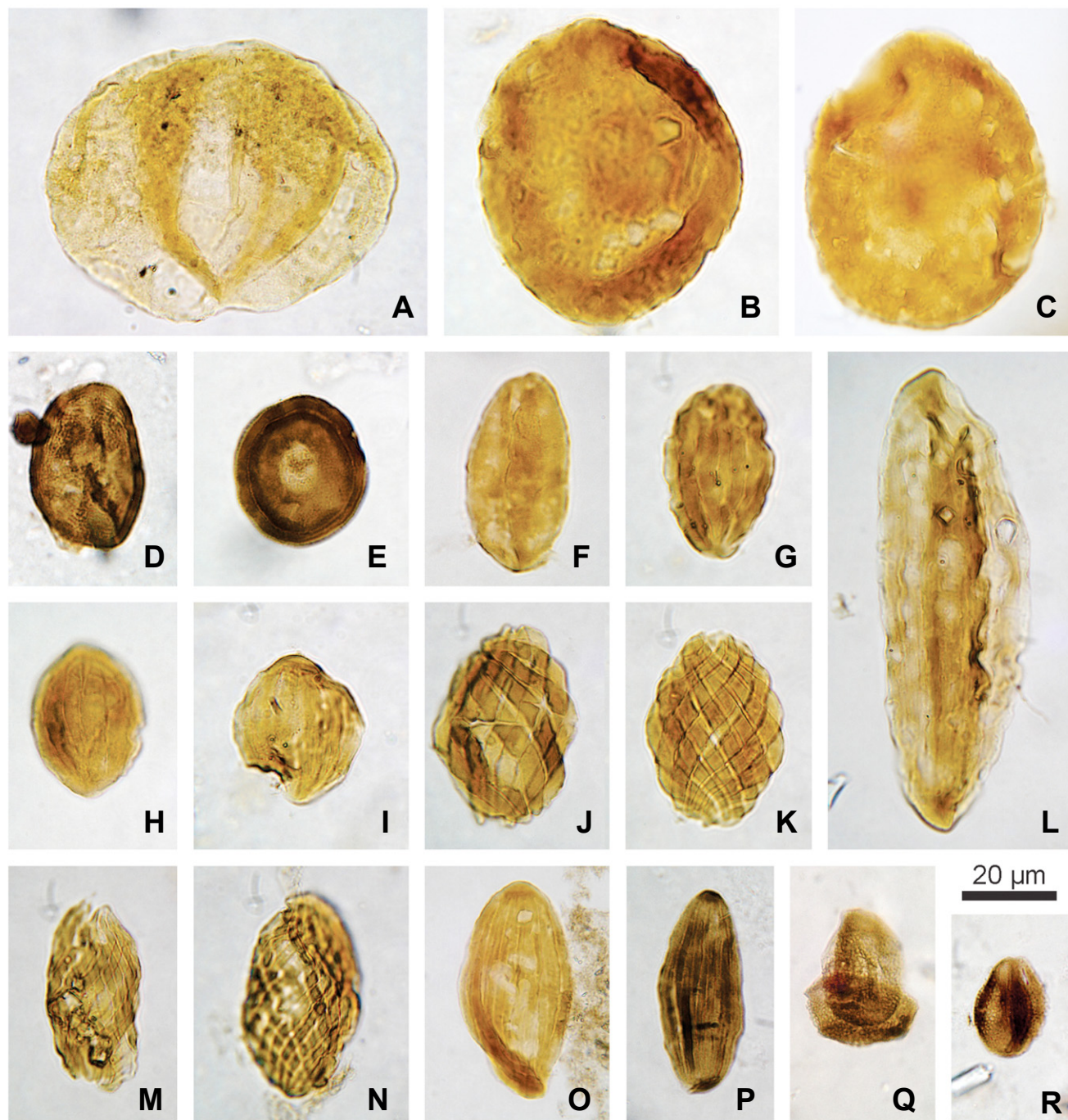


Figure 4. Pollen grains. Sample/slide numbers, England Finder coordinates and collection acronym are indicated for all specimens. **A**, *Alisporites* sp., 8435D: E34 MPLP; **B-C**, *Balmeiopsis limbatus* (Balme) Archangelsky, 1977, B. 8436F: W22 MPLP, C. 8436I: X25/2 MPLP; **D**, *Classopollis classoides* (Pflug) Pocock & Jansonius, 1961, 8446F: R43 MPLP; **E**, *Classopollis simplex* (Danzé; Corsin & Laveine) Reiser & Williams, 1969, 8446M: U23/3 MPLP; **F**, *Cycadopites* sp., 8449A: H38/2 MPLP; **G**, *Ephedripites caichiguensis* (Volkheimer & Quattrocchio) Narváez & Sabino, 2008, 8449X: U30/1 MPLP; **H-I**, *Ephedripites ovatus* (Pierce) comb. nov., H. 8449E: T38/3 MPLP, I. 8436R: G40/1 MPLP; **J-K**, *Gnetaceapollenites barghoornii* (Pocock) Lima, 1980, J. 8435D: S28/2 MPLP, K. 8436O: H24 MPLP; **L**, *Ephedripites montanaensis* Brenner, 1968, 8449W: Y34 MPLP; **M-N**, *Gnetaceapollenites jansonii* (Pocock) Lima, 1980, M. 8435N: L29/4 MPLP, N. 8436R: P47/3 MPLP; **O-P**, *Steevesipollenites binodosus* Stover, 1964, O. 8435K: G21/4 MPLP, P. 8446C: P36 MPLP; **Q-R**, *Tricolpites variabilis* Burger, 1970, Q. 8448C: X39 MPLP, R. 8446D: N48/2 MPLP. Scale bar = 20 μ m.

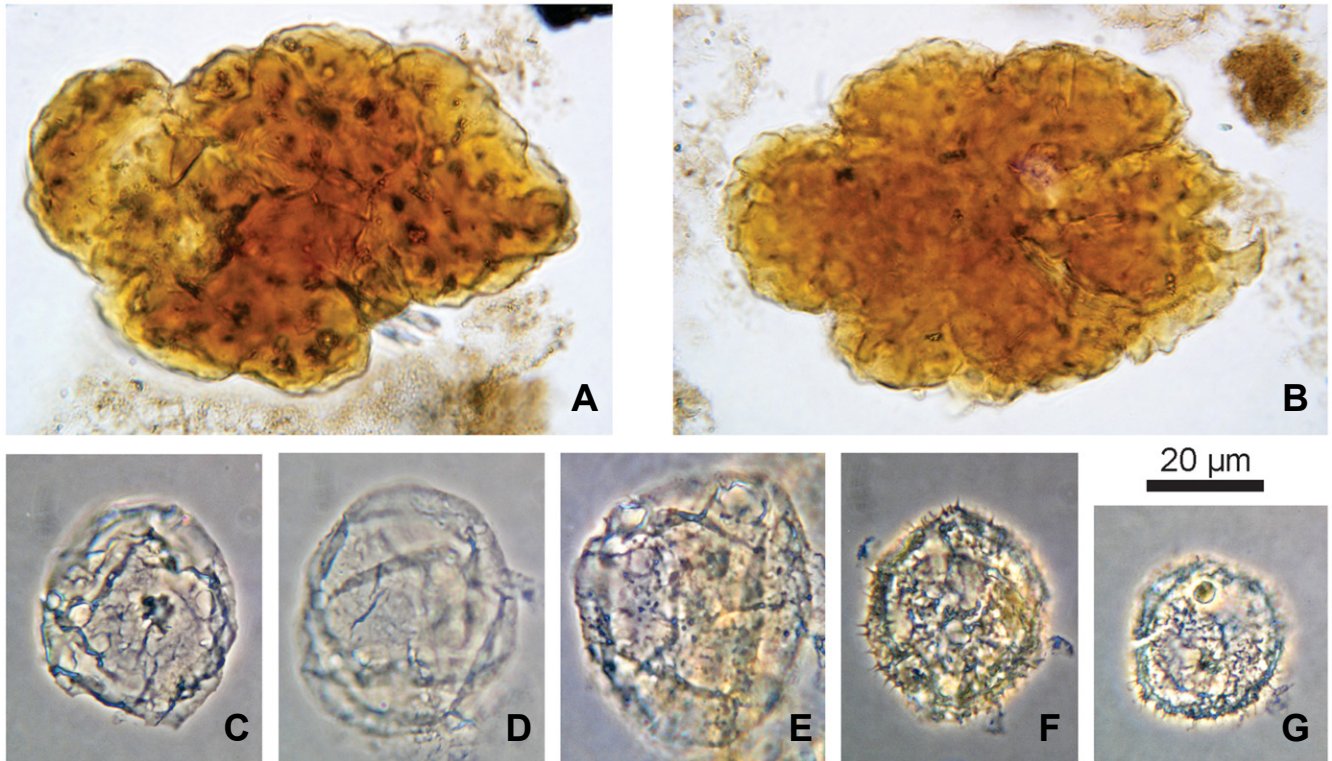


Figure 5. Aquatic species. Sample/slide numbers, England Finder coordinates and collection acronym are indicated for all specimens. **A-B**, *Botryococcus* sp., A. 8435O: D40/1 MPLP, B. 8435L: M41 MPLP; **C-D**, *Leiosphaeridia*-type 1, C. 8436B: X26/4 MPLP, D. 8436B: V23/1 MPLP; **E**, *Leiosphaeridia*-type 2, 8436B: F35 MPLP; **F-G**, Echinata vesicle indet., F. 8436D: K26/1 MPLP, G. 8436D: P25/3 MPLP. Scale bar = 20 µm.

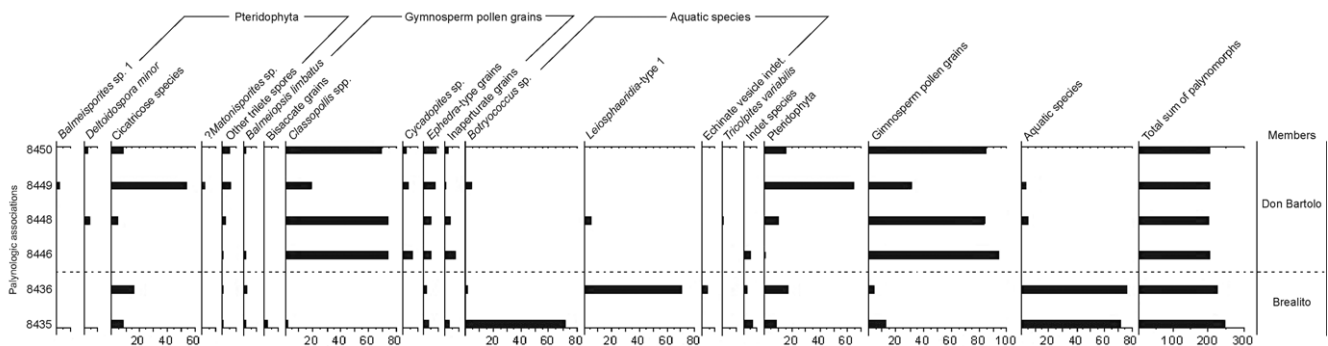


Figure 6. Percentages and total sum of species and suprageneric groups from the palynologic assemblages of the La Yesera Formation.

& Zamaloa (2003), who mention that ephedroid pollen may indicate more diverse environments than today, such as brackish to coastal marine areas, areas associated with lakes or water courses, or even in tropical and subtropical forests. The authors agree with the assumption that *Ephedra*-type pollen suggests aridity, considering their present-day distribution in arid regions of Europe, Asia, and North and South America, including ten modern species present in Argentina, five of which are present in the northwest of the country (Hunziker & Novara, 1998).

Among the spores, the Anemiaceae (three genera and seven species; Narváez *et al.*, 2013) are dominant in the Don Bartolo Member assemblages, with the highest percentage in assemblage 8449 (54.2%) (Figure 6). Schizaeales are currently

distributed in tropical and subtropical areas. In Argentina, the order's three families have one genus each: Anemiaceae (*Anemia*), Lygodiaceae (*Lygodium*), and Schizaeaceae (*Schizaea*). In northwestern Argentina, *Anemia* has four species, including *A. tomentosa*, which is found in the dry soils of the Lerma valley, Salta Province (Martínez *et al.*, 2003).

At the time of accumulation of the Don Bartolo Member, there were alluvial fans throughout the whole basin, and desiccation cracks indicate periodic drying of the bodies of water (Sabino, 2004). The palynologic assemblages described here agree with these seasonal climatic conditions, with dry periods and well-drained soils indicated by the high representation of thermophilous, and drought adapted *Classopollis* associated with ephedroid pollen.

The notable scarcity of angiosperms in the assemblages from both members may be attributed to post-depositional taphonomic processes, or to the probable low abundance of angiosperm plants near the site. In the overlying Las Curtiembres Formation (Campanian-Maastrichtian?), Narváez & Sabino (2008) indicate the presence of seven angiosperm species in poorly preserved palynoflora.

The regional climate inferred for the time of accumulation of the top levels of the La Yesera Formation is subtropical to semiarid, a conclusion based on the present-day distribution of palynomorph families found in this study (*i.e.* Anemiaceae, Ephedraceae, Lycopodiaceae/Selaginellaceae), and the absence of indicators of temperate conditions.

PALYNOSTRATIGRAPHIC ANALYSIS

Within Argentina, the palynoflora of the La Yesera Formation has similarities to the La Cantera Formation (Late Aptian, San Luis Basin, central-western Argentina; Prámparo, 1989b). Common morphotypes are *Balmeiopsis limbatus*, *Classopollis simplex*, and *Gnetaceaepollenites barghoornii*, the occurrence of abundant aquatic forms such as *Leiosphaeridia*, and the Echinate vesicle indet. (aff. *Comasphaeridium?*). In both, Anemiaceae, Cheirolepidaceae, and Ephedraceae families are diverse and abundant.

The authors can only make limited comparisons with other assemblages from mid-Cretaceous formations of southern Argentina (*i.e.* Austral, San Jorge, and Neuquén basins). For example, the La Yesera Formation palynoflora is similar to that of the Late Albian-Cenomanian Kachaika Formation (Austral Basin; Archangelsky & Llorens, 2003, 2005, 2009; Barreda & Archangelsky, 2006; Archangelsky & Archangelsky, 2010); both show a predominance of *Classopollis* and the presence of bisaccate grains and cicatricose spores (*Cicatricosisporites cuneiformis*, *Ruffordiaspora ludbrookiae*, and *R. cf. R. ticoensis*; Narváez *et al.*, 2013). There are only three genera (*Alisporites*, *Cicatricosisporites*, and *Classopollis*) in common with the Late Albian-Cenomanian Caleta Olivia Member of the Cañadón Seco Formation (San Jorge Basin; Archangelsky *et al.*, 1994). Finally, there are three species (*Deltoidospora minor*, *Classopollis classoides*, and *C. simplex*) also found in the Huitrín Formation in the Neuquén Basin (Valanginian-Albian; Volkheimer & Salas, 1976; Volkheimer, 1980); *Ephedripites ovatus*, *Cicatricosisporites* sp. and the genus *Cycadopites* are found in the La Yesera and Huincul Formations (Albian?-Cenomanian; Vallati, 2001).

The genus *Balmeisporites* originated in the Tethyan region during the Barremian or Early Aptian and then migrated to austral areas in the Late Aptian (Dettmann, 1995). This genus has been found in Albian-Campanian sediments from the Northern Hemisphere and Australia (Kovach & Batten, 1989; Dettmann, 1995). In Argentina, *B. holodictyus* has been recorded in Albian strata of the Kachaika Formation, Patagonia (Baldoni & Batten, 1991; Villar de Seoane & Archangelsky, 2008).

Among gymnosperms, *Ephedripites ovatus* (Pierce) *comb. nov.* has been recorded in Albian-Cenomanian sediments

from Argentina (Vallati, 2001), Brazil (Lima, 1980), Canada (Singh, 1964), Egypt (Schrank & Ibrahim, 1995), and the USA (Pierce, 1961; Paden Phillips & Felix, 1971). *Balmeiopsis limbatus* is usually found in Early Cretaceous sediments, particularly in southwestern Gondwana (Archangelsky & Del Fueyo, 2010).

Hochuli *et al.* (2006) indicated the consistently occurrence of poly (tri) aperturate pollen grains in the early and mid-Albian assemblages for the North Atlantic and Tethyan realm. In tropical areas, Heimhofer & Hochuli (2010) mentioned the presence of tricolpate pollen since the Late Aptian (Rio da Batateira Formation, Araripe Basin) in northern Brazil. Regarding early angiosperms from Argentina, Prámparo *et al.* (2007) reviewed their evolutionary history based on existing palynologic and paleobotanic records. The oldest findings correspond to palynomorph genera *Asteropollis* and *Clavatipollenites* from Patagonian sediments of Barremian to Aptian age (see citations in Prámparo *et al.*, 2007), but always subordinate in number to both gymnosperms and pteridophytes until the Campanian. Archangelsky *et al.* (2009) analysed angiosperm diversification in Argentina and concluded that tricolpate morphotypes evolved during the Albian (Stage III). In the Don Bartolo Member of the La Yesera Formation, the only three angiosperm grains found were assigned to *Tricolpites variabilis* (Figures 4 Q-R). This species was previously recorded in Australia and included in the middle Albian and early Cenomanian, *Phimopollenites pannosus* Zone (Burger, 1993). In Argentina, Vallati (2001) mentioned *T. cf. variabilis* in Albian?-Cenomanian sediments from the Huincul Formation in the Neuquén Basin.

Hence, the current resolution of the pollen assemblages recovered from the top of the La Yesera Formation allows us to suggest an Albian/Cenomanian age for these records (Table 1), based mainly on tricolpate pollen grains, which have appeared in Argentina since the Albian (Archangelsky *et al.*, 2009), and corroborated by the age range of *Tricolpites variabilis*. An Albian/Cenomanian age agrees with the sedimentologic data (Sabino, 2004), which suggest that the sedimentation of the Brealito Member levels occurred between the Late Albian and Cenomanian; the age also agrees with radiometric dating of the Isonza Basalt (96±5 to 99±5 Ma; Valencio *et al.*, 1976), indicating a Cenomanian age for sediments coeval with the Don Bartolo Member.

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Table 1. Stratigraphic ranges of selected species reported in southern Gondwana. 1. Prámparo (1994), Atta-Peters & Salami (2006), Olivera *et al.* (2010), Eisawi *et al.* (2012); 2. Dettmann & Clifford (1992), Cranwell & Srivastava (2009), Narváez *et al.* (2013); 3. Lima (1978), Lima *et al.* (1980), Narváez *et al.* (2013); 4. Herrngreen (1973), Lima (1980), Sinanoglu (1984), Prámparo (1989b), Vajda-Santivanez (1999); 5. Herrngreen (1973), Kotova (1978), Lima (1980), Schrank & Ibrahim (1995), Vajda-Santivanez (1999), Limarino *et al.* (2000); 6. Lima (1980), Schrank & Ibrahim (1995), Vallati (2001); 7. Archangelsky *et al.* (2009), Heimhofer & Hochuli (2010); 8. Kovach & Batten (1989), Baldoni & Batten (1991), Dettmann (1995), Villar de Seoane & Archangelsky (2008); 9. Stover (1964), Herrngreen (1973), Regali *et al.* (1974), Kotova (1978), Morgan (1978), Lima (1978, 1980), Lawal & Moullade (1986), Schrank (1990), Jaillard (1997), Masure *et al.* (1998), Bettar & Meon (2006), Boboye (2012), Ola-Buraimo & Olúwájánà (2012); 10. Burger (1993), Vallati (2001).

| Taxa | Period/ Epoch/Age | Jurassic | Cretaceous | | | | | | | | | | | |
|--|----------------------|----------|------------|-----|-----|------|-----|-------|-----|-----|-----|-----|-----|------|
| | | | Lower | | | | | Upper | | | | | | |
| | | | Berr | Val | Hau | Barr | Apt | Alb | Cen | Tur | Con | San | Cam | Maas |
| <i>Balmeiopsis limbatus</i> ¹ | | | | | | | | | | | | | | |
| <i>Ruffordiaspora ludbrookiae</i> ² | | | | | | | | | | | | | | |
| <i>Fisciniasporites</i> spp. ³ | | | | | | | | | | | | | | |
| <i>Gnetaceapollenites barghoornii</i> ⁴ | | | | | | | | | | | | | | |
| <i>Gnetaceapollenites jansonii</i> ⁵ | | | | | | | | | | | | | | |
| <i>Ephedripites ovatus</i> ⁶ | | | | | | | | | | | | | | |
| Tricolpate pollen grains ⁷ | | | | | | | | | | | | | | |
| <i>Balmeisporites</i> spp. ⁸ | | | | | | | | | | | | | | |
| <i>Steevesipollenites binodosus</i> ⁹ | | | | | | | | | | | | | | |
| <i>Tricolpites variabilis</i> ¹⁰ | | | | | | | | | | | | | | |

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Appendix. List of identified species in alphabetic order.

Terrestrial palynomorphs

- Alisporites* sp. (Figure 4A)
Auritulinasporites sp. (Figure 3A)
Balmeiopsis limbatus (Balme) Archangelsky, 1977 (Figures 4B-C)
Balmeisporites sp. 1 (Figures 3B-C)
Biretisporites sp. (Figure 3D)?
?Ceratosporites sp. (Figure 3E)
Cicatricosisporites cuneiformis Pocock, 1964 (Figure 3F)
Cicatricosisporites sp. 1 (in Narváez *et al.*, 2013) (Figure 3G)?
?Cristatitriteles sp. (Figure 3H)
Classopollis classoides (Pflug) Pocock & Jansonius, 1961 (Figure 4D)
Classopollis simplex (Danzé, Corsin & Laveine) Reiser & Williams, 1969 (Figure 4E)
Cycadopites sp. (Figure 4F)
Deltoidospora minor (Couper) Pocock, 1970 (Figure 3I)
Dictyophyllidites sp. (Figure 3J)
Ephedripites caichiguensis (Volkheimer & Quattrocchio) Narváez & Sabino, 2008 (Figure 4G)
Ephedripites montanaensis Brenner, 1968 (Figure 4L)
Ephedripites ovatus (Pierce) *comb. nov.* (Figures 4H-I)
Fisciniasporites sp. cf. *F. brevilaesuratus* (Couper) Dettmann & Clifford, 1992 (Figure 3K)
Fisciniasporites sp. (in Narváez *et al.*, 2013) (Figure 3L)
Gnetaceaepollenites barghoornii (Pocock) Lima, 1980 (Figures 4J-K)
Gnetaceaepollenites jansonii (Pocock) Lima, 1980 (Figures 4M-N)
Leptolepidites sp. (Figure 3M)
?Matonisporites sp. (Figures 3N-O)
Polypodiisporites sp. (Figure 3P)
?Raistrickia sp. (Figure 3Q)
Ruffordiaspora ludbrookiae (Dettmann) Dettmann & Clifford, 1992 (Figure 3R)
Ruffordiaspora cf. *R. ticoensis* (Archangelsky & Gamero) Archangelsky A.; Archangelsky S.; Poiré & Canessa, 2008 (Figure 3S)
Ruffordiaspora sp. 1 in Narváez *et al.*, 2013 (Figure 3T)
Steevesipollenites binodosus Stover, 1964 (Figures 4O-P)
Tricolpites variabilis Burger, 1970 (Figures 4Q-R)

Aquatic palynomorphs

- Botryococcus* sp. (Figures 5A-B)
Leiosphaeridia-type 1 (Figures 5C-D)
Leiosphaeridia-type 2 (Figure 5E)
 Echinate vesicle indet. (Figures 5F-G)