

Miospores and chlorococcacean algae from the Los Rastros Formation, Middle to Upper Triassic of central-western Argentina



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Abstract. Lacustrine strata of the Los Rastros Formation (Middle to Upper Triassic) at Río Gualo section (La Rioja province), yield a distinctive palynological assemblage of miospores and chlorococcacean algae. The miospore association is characterized by a relative abundance of corystosperm pollen grains with subordinate inaperturates, diploxylonoid disaccates, spores, monocolpates, monosaccates and striate pollen grains. The phytoplankton are mostly represented by *Botryococcus* but also by *Plaesiodictyon*, a form probably related to the Hydrodictyaceae. Geological data and variations in phytoplankton content indicate that the lacustrine system probably evolved from a stretch of freshwater with eutrophic conditions, into a body with oligotrophic conditions through the middle and upper part of the Río Gualo section. The genus *Variapollenites* is emended in order to amplify its original diagnosis.

Resumen. MIOSPORAS Y ALGAS CHLOROCOCCALES DE LA FORMACIÓN LOS RASTROS, TRIÁSICO MEDIO A SUPERIOR DEL CENTRO-OESTE DE ARGENTINA. El estudio de los niveles lacustres de la Formación Los Rastros (Triásico Medio a Superior) en la sección de Río Gualo (provincia de La Rioja), incluye una interesante palinoflora compuesta por miosporas y algas Chlorococcaceae. Entre las miosporas abundan los granos de polen de Corystospermales, con presencia subordinada de inaperturados, disacados diploxilonoides, esporas, monocolpados, monosacados y polen estriado. En el fitoplancton se destaca *Botryococcus*, pero también se observa *Plaesiodictyon*, que es una forma probablemente relacionada con las Hydrodictyaceae. Datos geológicos y variaciones en el contenido fitoplancológico señalan que el sistema lacustre probablemente evolucionó desde un cuerpo de agua dulce y condiciones eutróficas, a un ambiente de carácter oligotrófico hacia la parte media y superior de la sección de Río Gualo. Así mismo, se enmienda el género *Variapollenites* a fin de ampliar su diagnosis original.

Key words. Argentina. Triassic. Miospores and chlorococcacean algae. Systematics. Lacustrine environment.

Palabras clave. Argentina. Triásico. Miosporas y algas Chlorococcaceales. Sistemática. Ambiente lacustre.

Introduction

In the Triassic of southern South America, one of the best represented lacustrine successions is that of the Los Rastros Formation, which is part of the continental infilling of the Ischigualasto-Villa Unión Basin in central-western Argentina (Stipanicic and Bonaparte, 1979; Stipanicic, 1983; López Gamundí *et al.*, 1989). The unit is characterized by thick deposits of black shales and fine grained sandstones that represent a cyclic lacustrine-deltaic environment. It crops out at different localities in La Rioja and San Juan provinces (figure 1) with slight lateral facies variation (de la Mota, 1946; Bossi, 1971; Milana and Alcober, 1994; Milana, 1998; Rogers *et al.*, 2001).

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The fossil record of the Los Rastros Formation is mainly represented by floral remains. An abundant macrofloral assemblage, belonging to the "Dicroidium-flora", was collected at different levels and localities in the Los Rastros sequence although, the most important records are known from the thick lacustrine black shales, close to the base of the unit (Frenguelli, 1948; Kokogian *et al.*, 1999; Spalletti *et al.*, 1999; Stipanicic and Bonetti, 1969; Stipanicic and Bossi, 2002b; Zamuner *et al.*, 2001). Palynological analysis are known only from selected areas in the basin (Herbst, 1965, 1970, 1972; Yrigoyen and Stover, 1970).

Invertebrate remains exhumed from Los Rastros levels include different groups of conchostracans (clamp-shrimps), insects and bivalves, and they occur throughout the sequence (Gallego, 1997, 1999). Also, a quite rich invertebrate ichnological data has been mentioned from the unit (Melchor *et al.*, 2001; Mancuso, 2003). The vertebrate fauna mainly comprises actinopterigian fishes (Cabrera, 1944; Forster

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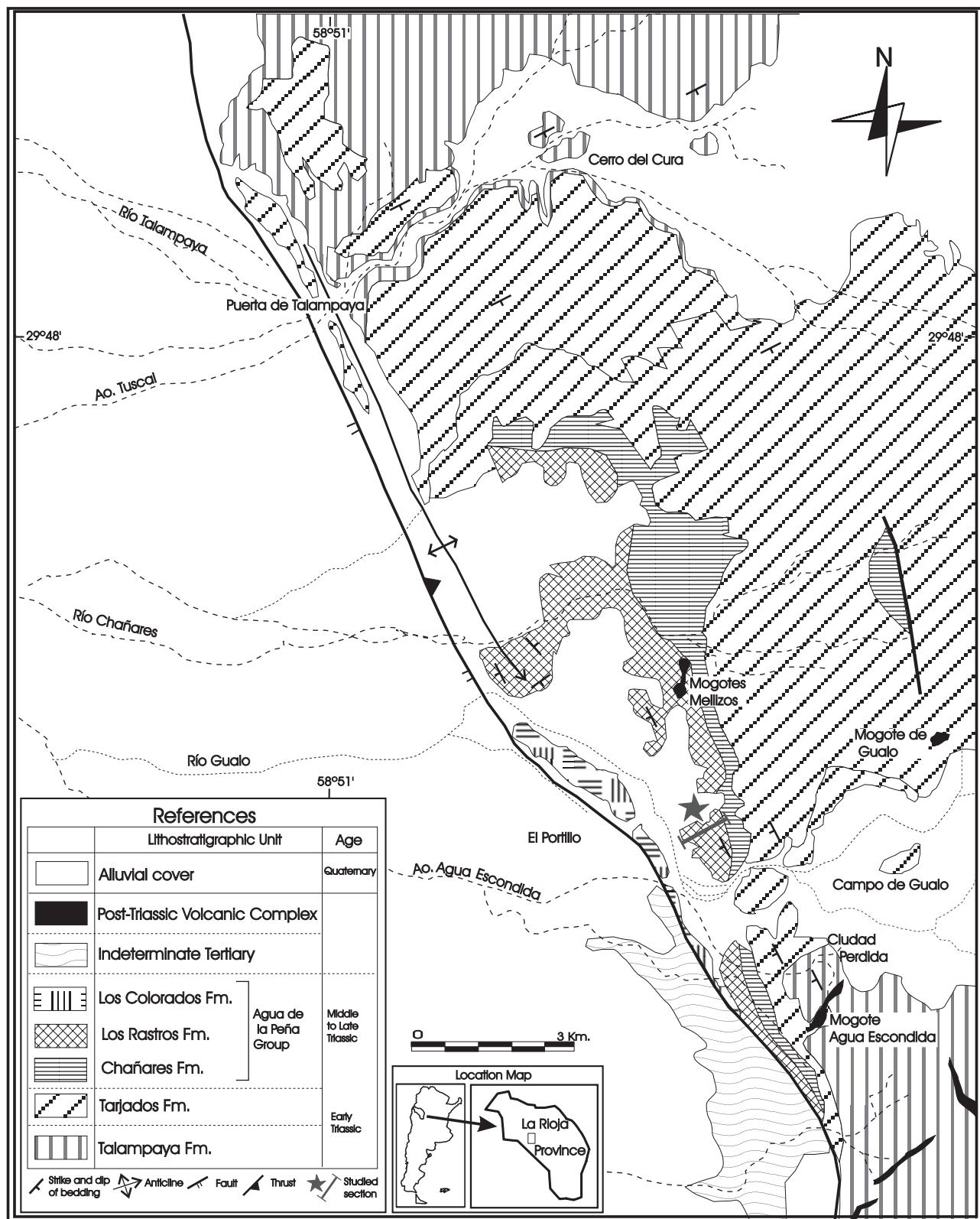


Figure 1. Location map of the Río Gualo section, Ischigualasto-Villa Unión Basin, La Rioja province, Argentina / mapa de ubicación de la sección de Río Gualo, Cuenca de Ischigualasto- Villa Unión, provincia de La Rioja, Argentina. Modified from Caselli (1998) / modificado de Caselli (1998).

et al., 1995, Mancuso, 2000, 2003), whereas tetrapods are represented only by a temnospondyl amphibian specimen (Contreras et al., 1997; Mancuso, 2002) and

several tetrapod footprints related to different archosaur groups (von Huene, 1931; Arcucci et al., 1995; Marsicano et al., 2004).

In the present contribution an interesting association of miospores and Chlorococcacean algae recovered from the Los Rastros sequence outcropping at the Río Gualo area, about 10 km to the southeast of the steep-walled, picturesque canyons of the Puerta de Talampaya, La Rioja province (figures 1, 2), are described. The Río Gualo section is near the western margin of the Ischigualasto-Villa Unión Basin (Kokogian *et al.*, 2001). The palynoflora, together with sedimentological data, provide new interpretative insights into the basin evolution.

Material and methods

A stratigraphic section of the Los Rastros Formation have been recognized at Río Gualo. A detailed description of the sedimentology of the section was used to interpret the facies assemblage and to reconstruct the depositional environment. Systematic palynological sampling was conducted; and this paper is based on the study of 15 samples. Laboratory procedures followed conventional practices. Carbonates and silicates were removed by treatment with hydrochloric and hydrofluoric (70%) acids. Residues were sieved on a 25 µm mesh and mounted in unstained glycerine jelly as well as in Cellozise on glass slides. Specimens were examined under a Leitz Orthoplan binocular microscope. Photomicrographs were taken with a Leitz Orthomat camera using AG-FAPAN APX25 and ILFORDPAN NF50 films. Palynological slides are prefixed BAFC-PI. The illustrated specimens are identified with a slide number and England Finder coordinates. The slides are deposited at the Geological Sciences Department, Buenos Aires University. E.G. Ottone prepared the palynological section of the paper. A.C. Mancuso collected the samples and provided geological information. M. Resano collaborated in the study of the Chlorococcales.

Geological setting and age

During the pre-breakup stage of Pangea, during the Late Permian and Early Triassic, several extensional basins were formed along the western margin of Gondwana (Uliana and Biddle, 1988). The Ischigualasto-Villa Unión Basin is situated in central-western Argentina, with a NW-SE orientation, between San Juan and La Rioja provinces (figure 1). The sedimentary infilling of the basin consists of up to 4000 m of alluvial, fluvial and lacustrine deposits of Triassic age. The sedimentary succession has been subdivided lithostratigraphically, in ascending order, into the Talampaya and Tarjados formations

(Romer and Jensen, 1966), and the Agua de la Peña Group, which comprises five units (de la Mota, 1946; Bossi, 1971; Stipanicic, 1983). The lower Chañares Formation (Bossi and Stipanicic, 2002a) is dominated by tuffaceous sandstones and siltstones deposited in a fluvial-lacustrine environment and grades upward into the lacustrine black shales and deltaic sandstones of the Ischichuca and Los Rastros formations (Bossi *et al.*, 2002; Stipanicic and Bossi, 2002a). This sequence passes upward into the sandstones, mudstones and tuffs of the Ischigualasto Formation (Stipanicic and Bossi, 2002b), deposited by a moderate- to high-sinuosity river system. The succession culminates in the red beds of the Los Colorados Formation (Bossi and Stipanicic, 2002b). A regional unconformity separates the Triassic succession from the overlying ?Cretaceous Cerro Rajado Formation (Caselli *et al.*, 2001).

The lacustrine-deltaic Los Rastros Formation is unconformably overlain by the fluvial Ischigualasto Formation and conformably succeeds the fluvial-lacustrine deposits of the Chañares and Ischichuca formations. The Los Rastros Formation deposits are generally interpreted as lacustrine-deltaic cycles with a predominance of lacustrine sedimentation (Stipanicic and Bonaparte, 1979; López Gamundi *et al.*, 1989; Milana and Alcober, 1994; Milana, 1998; Rogers *et al.*, 2001).

The age of the Los Rastros Formation has been referred to the early Late Triassic by some authors, based on its palynological content (Zavattieri and Batten, 1996; Morel *et al.*, 2001). Nevertheless, an older age (Middle Triassic) has been proposed by other authors due to its stratigraphic relationships (Kokogian *et al.*, 2001). Thus, a radioisotopic age data from the base of the overlying Ischigualasto Formation (227.8 ± 0.3 Ma) suggests a minimum late Middle Triassic age for the Los Rastros Formation (Rogers *et al.*, 1993, 2001).

Sedimentology

Fieldwork at the Río Gualo section indicated five lacustrine-deltaic cycles each with two facies assemblages.

Lake facies assemblage

This assemblage is dominated by dark gray to black carbonaceous claystones. Iron mudstones and very fine-grained sandstones are interbedded. The beds are tabular. The clayshales are horizontally laminated, whereas the ironstones may be massive or laminated. Conchostracans, plant debris, insect im-

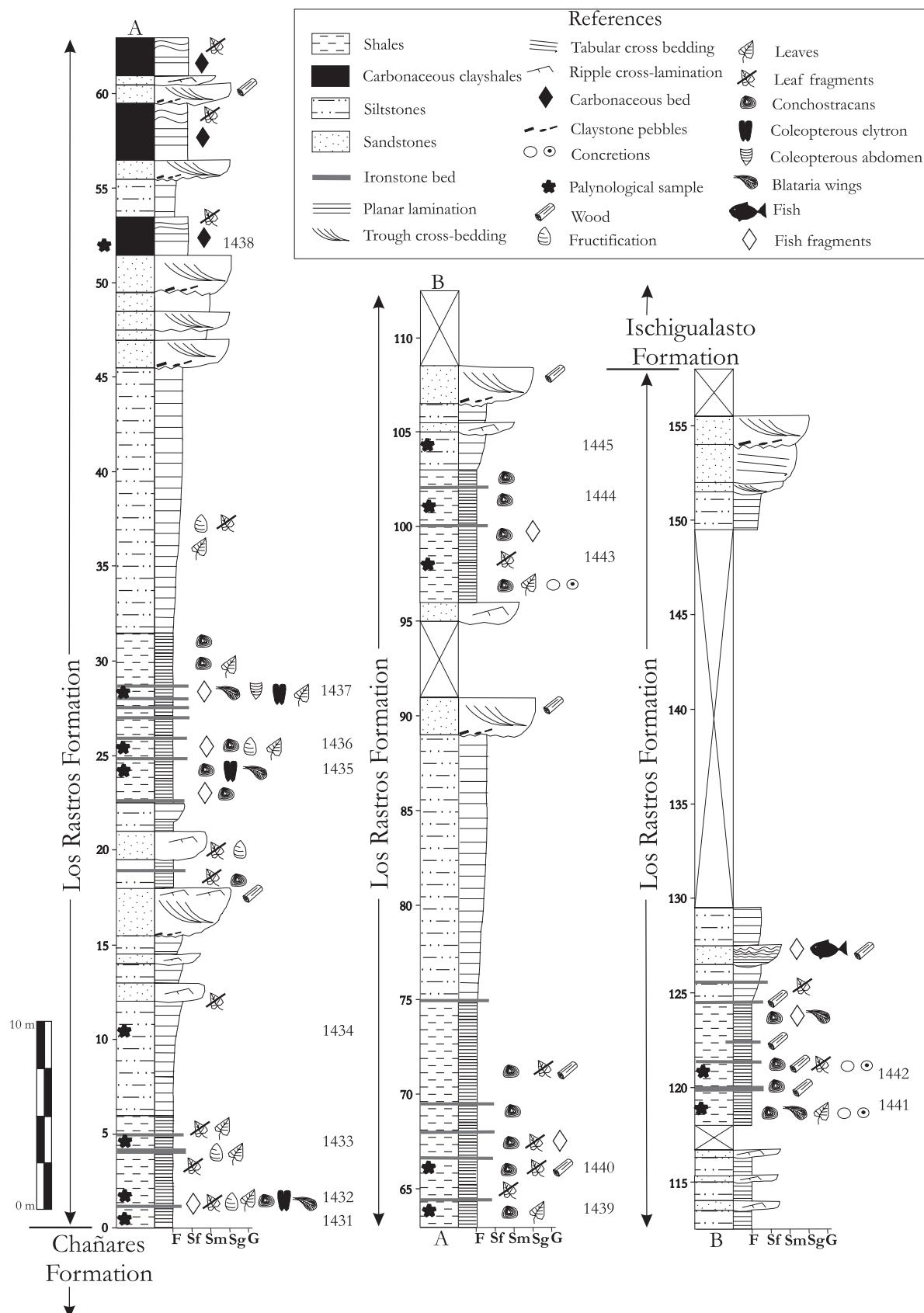


Figure 2. Schematic section of the Los Rastros Formation in Río Gualo indicating palyniferous and other fossiliferous horizons / sección litológica de la Formación Los Rastros en Río Gualo incluyendo horizontes con palinomorfos y otros fósiles. Modified from Mancuso (2003) / modificado de Mancuso (2003).

pressions and rare fish body fossils are found in this assemblage, but with different preservation conditions in the different facies. The clayshales were deposited by suspension in distal-lake conditions whereas the ironstones were deposited by distal turbiditic currents (Mancuso, 2003).

Deltaic facies assemblage

This assemblage includes stream load sediments. The assemblage begins with alternative green siltstones and gray claystones, which form rhythmic packages of massive individual beds containing plant debris. Fine- to medium-grained sandstone beds are intercalated, and are more abundant and thicker upward. Small ripple cross-laminations characterize these sandstones, which also contain plant debris. Medium- to coarse-grained sandstones are dominant upsection. They begin with horizontal lamination, passing to planar cross-bedded and culminate with trough cross-bedded lamination. The sequence coarsens and thickens upwards. Fossil fish bodies and poorly preserved wood fragments occur in the horizontally laminated sandstones while only fossil wood remains were found in the planar and trough cross-bedded sandstones (Mancuso, 2003). In its top, the facies assemblage features dark gray mudstones and very fine-grained sandstones interbedded with planar and trough cross-bedded sandstones. They are internally massive or pass upward from plane to rippled-lamination, and contain a very high percentage of organic matter, mainly carbonized fragments. This facies assemblage represents the progradation of the fluvial system into the lake body (Mancuso, 2003).

Palynological results and discussion

Kerogen is generally abundant and it is composed by a variable amount of wood, cuticle, amorphous organic matter and terrestrial palynomorphs. Fifty-eight species of miospores and three species of Chlorococcacean algae have been recorded at the Río Gualo section (figure 3). Palynomorphs are fairly well preserved, with the exception of those found in samples 1434, 1441 and 1442, which are commonly crushed or corroded.

The palynoflora of the Los Rastros Formation at Río Gualo section is dominated by disaccate pollen grains of corystsperm affinity, especially *Alisporites australis* de Jersey. Also abundant are inaperturate pollen (mainly *Inaperturopollenites reidi* de Jersey, a probable Araucariaceae) and diploxylonoid disaccate pollen grains (*Platysaccus* spp., Podocarpaceae?).

together with spores of pteridophytes (*Cadar gasporites* spp., *Clavatisporites conspicuus* Playford, *Converrucosporites cameronii* (de Jersey) Playford and Dettmann, *Osmundacidites* spp., *Polyiodiisporites ipswiciensis* (de Jersey) Playford and Dettmann, *Rugulatisporites* spp.), lycophytes (mostly *Aratrisporites compositus* Volkheimer and Zavattieri, of pleuromeian affinity) and sphenophytes (*Calamospora impexa* Playford). *Ginkgo biloba*-like monocolpates (*Cycadopites* spp.), monocolpates with alveolar ektextine (*Brachysaccus* sp. A), monosaccates (*Variapollenites* spp., *Coniferales*), striate pollen grains (*Lueckisporites* spp., *Lunatisporites* spp., *Protohaploxylinus* spp., *Striatopodocarpites pantii* (Jansonius) Balme), ephedroid pollen grains (*Equisetosporites cacheutensis* Jain) and *Cedrus*-like pollen grains (*Cedripites* spp.) are also present. Phytoplankton is represented by *Botryococcus* sp., *Plaesiodictyon mosellanicum* spp. *perforatum* Wille and *Plaesiodictyon mosellanicum* spp. *symmetricum* Brenner and Foster.

Comparison of the Río Gualo fossil palynoflora with local fossil macroflora is hindered by the fact that only scarce and generally unidentifiable plant macrofossil remains are present. However, plant macrofossil assemblages from other localities of the basin has strong affinities with the Río Gualo microflora. The commonest elements from the Los Rastros Formation are the Corystspermales (9 species), together with a consistent representation of Sphenophyta (6 species) and, in decreasing importance, Osmundaceae (3 species), Peltaspermales, Cycadales, Voltziaceae and Czekanowskiales (Zamuner *et al.*, 2001).

The palynoflora of the Río Gualo section resembles those Late Triassic assemblages grouped into the cool temperate "Ipswich microflora" (Dolby and Balme, 1976). This microfloral province has been recognized in the south of Australia, New Zealand, Antarctica (Victoria Land), South Africa and Argentina (Zavattieri and Batten, 1996), and is believed to represent plant communities characteristic of high latitudes (40°-70° S lat.).

The palynoflora of the Río Gualo section is, in general, comparable with those described from other Middle to Upper Triassic sequences of Argentina (Zavattieri and Batten, 1996), and particularly, from the Ischigualasto-Villa Unión Basin (Herbst, 1965, 1970, 1972; Yrigoyen and Stover, 1970; Zavattieri and Melchor, 1999; Zavattieri and Milana, 2000). *Botryococcus* was previously cited in the Triassic, from the fluvio-lacustrine Las Cabras and Casa de Piedra formations, Cuyo Basin (Zavattieri, 1991b; Barredo *et al.*, 1999; Rodríguez Amenábar and Ottone, 2002, 2003) while *Plaesiodictyon* is known from lacustrine levels of the Ischichuca Formation, Ischigualasto-Villa Unión Basin (Zavattieri and Melchor, 1999). The

FORMATION	SAMPLE	LOS RASTROS														
		1431	1432	1433	1434	1435	1436	1437	1438	1439	1440	1443	1444	1445	1441	1442
SPECIES																
<i>Alisporites australis</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Alisporites lowoodensis</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Alisporites parvus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Alisporites spp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Anapiculatisporites sandrae</i>		■														
<i>Aratrisporites compositus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Aratrisporites sp. cf. A. parvispinosus</i>									■	■						
<i>Araucariacites australis</i>	■							■	■	■	■				■	
<i>Baculatisporites comaumensis</i>	■	■	■	■	■	■	■									
<i>Biretisporites sp.</i>				■							■	■				■
<i>Brachysaccus sp. A</i>	■															
<i>Cadargasporites baculatus</i>		■														
<i>Cadargasporites cuyanensis</i>	■							■		■						
<i>Calamospora impexa</i>	■	■	■													
<i>Cedripites tectus</i>	■	■	■				■			■	■					
<i>Cedripites sp. cf. C. pannellai</i>	■															
<i>Cedripites sp. cf. C. priscus</i>	■	■	■	■	■	■	■	■	■	■	■					
<i>Chordasporites australiensis</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Clavatisporites conspicuus</i>		■										■	■			
<i>Clavatisporites sp.</i>		■														
<i>Converrucosisporites cameronii</i>												■				
<i>Converrucosisporites sp.</i>								■								
<i>Cycadopites sp. cf. C. andrewsii</i>							■									
<i>Cycadopites sp. cf. C. follicularis</i>		■						■	■	■	■	■	■	■	■	■
<i>Cycadopites sp. A</i>		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Deltoidospora sp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Equisetosporites cacheutensis</i>	■															
<i>Inaperturopollenites nebulosus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Inaperturopollenites reidi</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Leptolepidites volkheimeri</i>	■															
<i>Leptolepidites sp. cf. L. crassibalteus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Leptolepidites sp.</i>		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Lueckisporites spp.</i>	■															
<i>Lunatisporites sp. cf. L. noviaulensis</i>		■														
<i>Lunatisporites spp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Lundbladispora spp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Neoraistrickia sp.</i>											■					
<i>Osmundacidites senectus</i>	■						■	■	■	■	■	■	■	■	■	■
<i>Osmundacidites wellmanii</i>											■	■	■	■	■	■
<i>Platysaccus papilionis</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Platysaccus queenslandi</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Playfordiaspora cancellosa</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Polyiodisporites ipsviciencis</i>	■															
<i>Protodiploxylinus sp.</i>							■	■	■	■	■	■	■	■	■	■
<i>Protohaploxylinus sp. cf. P. limpidus</i>	■						■					■				
<i>Protohaploxylinus sp. cf. P. microcorpus</i>	■						■					■				
<i>Protohaploxylinus sp. cf. P. varius</i>	■						■	■	■	■	■	■	■	■	■	■
<i>Protohaploxylinus spp.</i>							■	■	■	■	■	■	■	■	■	■
<i>Pteruchipollenites spp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Punctatisporites sp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Rugulatisporites nelsonensis</i>							■									
<i>Rugulatisporites sp.</i>	■						■									
<i>Striatopodocarpites pantii</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Uvaesporites verrucosus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Variapollenites curvifolius</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Variapollenites rhombicus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Variapollenites trisulcus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Vitreisporites pallidus</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Botryococcus sp.</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
<i>Plaesiodyction mosellanum ssp. perforatum</i>	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■

Figure 3. Stratigraphic distribution of palynomorphs in samples studied / distribución estratigráfica de los palinomorfos en los niveles estudiados.

presence of planktonic forms, mainly *Botryococcus* which has extant representatives of known ecological preferences, facilitate palaeoenvironmental interpretations about the lacustrine system at the Río Gualo area (Batten and Grenfell, 1996; Guy-Ohlson, 1992).

Botryococcus Kützing 1849, is an euryhaline, freshwater chlorococcacean that grows preferentially in shallow, oligotrophic lakes or ponds (Tyson, 1995; Rodríguez Amenábar and Ottone, 2003). It is relatively abundant (about 5-10% of total palynomorphs content) in levels BAFC-PI 1433, 1437, 1444. In samples 1431, 1432, 1435, 1436, 1438, 1439, 1440, 1443 and 1445, *Botryococcus* occurs in moderate quantities (less than 5% of total palynomorphs content). In levels 1441 and 1442, no *Botryococcus* has been recorded (figure 2). Structureless mass was found in the whole section (figure 5.K) suggesting that the colonies growth either in a stressed environment or with restricted access to oxygen during deposition (Guy-Ohlson, 1992, 1998; Guy-Ohlson and Lindström, 1994; Rodríguez Amenábar and Ottone, 2003). Level 1433 contains simple, globular colonies (40-70 µm in diameter), together with compound colonies showing branching processes and compound colonies with botryoidal form. In level 1437, there are large, compound colonies, with or without branches, with size range of 80-145 µm; and young simple colonies of about 60 µm in diameter (figures 5.G-H). The variable forms found in samples 1433 and 1437 suggest varying seasonal conditions of environment and/or climate (Guy-Ohlson, 1992, 1998; Guy-Ohlson and Lindström, 1994; Rodríguez Amenábar and Ottone, 2003). In level 1444, numerous large, botryoidal compound colonies are present, suggesting a uniform seasonal growth. *Botryococcus* is unusually abundant in this sample, making up about 99% of the palynoflora. In general, the occurrences of phytoplankton blooms follow occasional freshening stages in the water body, due to heavy rains or changes in water inflow that increased the availability of dissolved phosphorous in the basin (Warren, 1986).

Plaesiodictyon Wille 1970 is a freshwater form probably related to the Hydrodictyaceae (Wood and Benson, 2000). It is relatively abundant in sample 1431 (about 5% of total palynomorphs content), where is the most consistently represented planktonic form, and is also present, as a minor constituent in samples 1432, 1433 and 1435 (less than 5% of total palynomorphs content) (figure 2, figures 5.E-F, I). The Río Gualo coenobia of *Plaesiodictyon* lack any dehiscent slit in its cells. This feature, in extant planar coenobia of Hydrodictyaceae, currently reflects a decrease in ability of cell division due to changes in the environment, rising salinity, stressed conditions or competition for nutrients (Brenner and Foster, 1994). *Plaesiodictyon* is strikingly similar to *Pediastrum*

Meyen 1829, both genera display planar coenobia commonly with holes, and marginal cells usually with lobes and processi. The main difference between this two genera lies in the cell arrangement, which determine the shape of the coenobia. While *Pediastrum* is circular in outline and has a circular arrangement of cells, *Plaesiodictyon* displays rectangular coenobia with cells in perpendicular rows (Brenner and Foster, 1994; Komárek and Jankovská, 2001). However, an extant species of *Pediastrum*, (*P. orbitale* Komárek 1983) includes circular and oval coenobia. It is difficult to know, simply by analogy with living *Pediastrum*, the precise ecological needs of *Plaesiodictyon*, mostly considering that extant *Pediastrum* includes many species and subspecies which display different ecological preferences (Komárek and Jankovská, 2001).

Changes in relative abundances of *Botryococcus* and *Pediastrum* (Tyson, 1995), or by roughly analogy, *Botryococcus* and *Plaesiodictyon*, are considered a consequence of ecological changes. Therefore, the variable percentages of these coccal forms throughout the Río Gualo section could indicate that depositional conditions varied through time. The low *Botryococcus*/ *Plaesiodictyon* ratio at the base of the sequence and its increase towards upsection would presumably reflect changing environmental conditions. Initially, a stretch of freshwater of probably eutrophic conditions would develop, mainly at the level represented by sample 1431, where the eutrophic character appears reinforced by the presence of abundant microscopic, ill preserved filaments of probable algal affinity (A. Godeas, personal communication). This situation would change, through the middle and upper part of the Río Gualo section, to a milieu of oligotrophic conditions.

From a sedimentological viewpoint, each cycle was inferred in the Río Gualo section (figure 2), according to the parasequence criterion (Vail *et al.*, 1991), as shallowing-upward. Gore (1988) noted that the lakes gradually infilled by sediment from deltaic input and shoreline progradation, produce regressive, coarsening-upward, lacustrine sequences overlain by a fluvial system. This is apparently the case with the Ischigualasto-Villa Unión Basin, wherein each cycle starts with fine sediments deposited in a lacustrine environment and finishes with sandstones of fluvial origin. The palynological analyses indicates that the richest assemblages are those associated with the lacustrine (pelitic) facies. Moreover, the most abundant phytoplankton occur in the upper distal-lake facies of each cycle. This facies is characterized by black shales which suggest an anoxic bottom; furthermore, the local absence of grazing trails reinforce this hypothesis. The anoxic conditions might result from stratification of the water column, since the cir-

culation of the oxygen water would be blocked by the stratification, thus preventing the oxygenation of the bottom (Wetzel, 1981). Bottom anoxic conditions are typically produced by a significant lake deepening, however, if there are high organic productivity in saline and shallow waters, the black shales may be accumulated (Gore, 1988).

The scarce records of phytoplankton blooms through the section appear to indicate that the lake was probably deficient in dissolved phosphorous (Warren, 1986). The chemical composition of the lake could explain the lack of fish bones in the distal-lake facies.

The conspicuous record of conchostracans through the section indicate the presence of temporary freshwater bodies with development of alternating dry and wet bottom conditions (Vannier *et al.*, 2003). Adaptations to environmental stress conditions of growth are also reflected in the morphology of the phytoplanktonic forms (structureless mass in *Botryococcus*, lack of dehiscent slits in *Plaesiadictyon*).

Systematic palynology

A complete list of palynomorphs recovered at Río Gualo section is given. Spore and pollen grains genera are listed alphabetically. Taxa are only described systematically, in the case of the emendation of the genus *Variapollenites* Ottone, or when an additional comment was deemed requisite.

Spores

- Anapiculatisporites sandrae* Ottone in Ottone *et al.* 1992
- Aratrisporites compositus* Volkheimer and Zavattieri 1991
- Aratrisporites* sp. cf. *A. parvispinosus* Leschik 1955
- Baculatisporites comauimensis* (Cookson) Potonié 1956
- Biretisporites* sp.
- Cadargasporites baculatus* de Jersey and Paten 1964 *emend.* Reiser and Williams 1969
- Cadargasporites cuyanensis* Azcuy and Longobucco 1983
- Calamospora impexa* Playford 1965
- Clavatisporites conspicuus* Playford in Playford *et al.* 1982
- Clavatisporites* sp.
- Converrucosporites cameronii* (de Jersey) Playford and Dettmann 1965
- Converrucosporites* sp.
- Deltoidospora* sp.
- Leptolepidites volkheimeri* Zavattieri 1986
- Leptolepidites* sp. cf. *L. crassibalteus* Filatoff 1975
- Leptolepidites* sp.
- Lundbladispora* spp.
- Osmundacidites senectus* Balme 1963
- Osmundacidites wellmanii* Couper 1958
- Neoraistrickia* sp.
- Playfordiaspora cancellosa* (Playford and Dettmann) Maheshwari and Banerji 1975
- Polypodiisporites ipsviciensis* (de Jersey) Playford and Dettmann 1965
- Punctatisporites* sp.

- Rugulatisporites nelsonensis* Raine in de Jersey and Raine 1990
- Rugulatisporites* sp.
- Uvaesporites verrucosus* (de Jersey) Helby in de Jersey 1971

Pollen grains

- Alisporites australis* de Jersey 1962
- Alisporites lowoodensis* de Jersey 1963
- Alisporites parvus* de Jersey 1962
- Alisporites* spp.
- Araucariacites australis* Cookson 1947
- Brachysaccus* sp. A
- Cedripites tectus* Ottone and Rodríguez Amenábar 2001
- Cedripites* sp. cf. *C. pannellai* Jain 1968
- Cedripites* sp. cf. *C. priscus* Balme 1970
- Chordasporites australiensis* de Jersey 1962
- Cycadopites* sp. cf. *C. andrewsii* Cornet and Traverse 1975
- Cycadopites* sp. cf. *C. follicularis* Wilson and Webster 1946
- Cycadopites* sp. A
- Equisetosporites cacheutensis* Jain 1968
- Inaperturopollenites nebulosus* Balme 1970
- Inaperturopollenites reidi* de Jersey 1959
- Lueckisporites* spp.
- Lunatisporites* sp. cf. *L. noviaulensis* (Leschik) Foster 1979
- Lunatisporites* spp.
- Platysaccus papilionis* Potonié and Klaus 1954
- Platysaccus queenslandi* de Jersey 1962
- Protodiploxylinus* sp.
- Protohaploxylinus* sp. cf. *P. limpidus* (Balme and Hennelly) Balme and Playford 1967
- Protohaploxylinus* sp. cf. *P. microcorpus* (Schaarschmidt) Clarke 1965
- Protohaploxylinus* sp. cf. *P. varius* (Bharadwaj) Balme 1970
- Protohaploxylinus* spp.
- Pteruchipollenites* spp.
- Striatopodocarpites partii* (Jansonius) Balme 1970
- Variapollenites curviplacatus* Ottone in Ottone *et al.* 1992
- Variapollenites rhombicus* Ottone in Ottone *et al.* 1992
- Variapollenites trisulcus* Ottone in Ottone *et al.* 1992
- Vitreisporites pallidus* (Reissinger) Nilsson 1958

Phytoplankton

- Botryococcus* sp.
- Plaesiadictyon mosellatum* ssp. *perforatum* Wille 1970
- Plaesiadictyon mosellatum* ssp. *symmetricum* Brenner and Foster 1994

Genus *Brachysaccus* Mädler 1964

Type species. *Brachysaccus ovalis* Mädler 1964.

Remarks. Following Potonié (1970) and de Jersey (1972), it is considered that *Brachysaccus* includes monosulcate pollen grains having an endoreticulate exine. The monosulcate character of the genus is clearly evident in Mädler's (1964) illustration of the type. Amb and sulcus shape are extremely variable in monosulcate pollen grains displaying a homogeneous or granular ektextine. This is extensively discussed below under the genus *Cycadopites* Wodehouse *ex* Wilson and Webster 1946. In *Brachysaccus*, a monosulcate pollen grain with an alveolar ektextine, amb and sulcus shape are relatively uniform, and its structured ektextine probably controls, in different

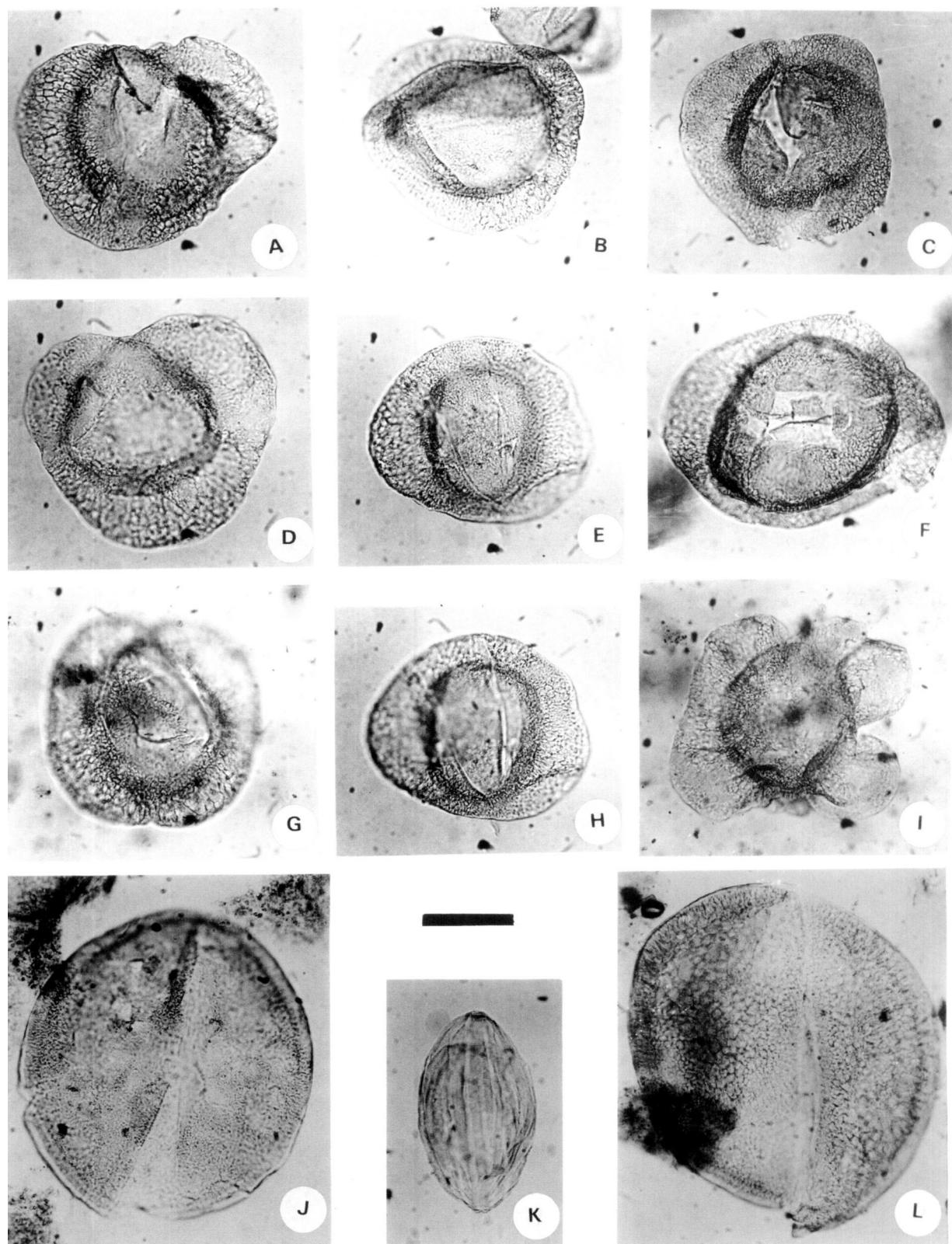


Figure 4. A-D, *Variapollenites trisulcus* Ottone; A, BAFC-Pl 1431(14) W42/2; B, BAFC-Pl 1431(10) R37/3; C, BAFC-Pl 1431(12) Z39/1; D, BAFC-Pl 1431(11) Y42/0. E-F, H, *Variapollenites curviplicatus* Ottone; E, BAFC-Pl 1431(11) C22/2, proximal view/ *vista proximal*; F, BAFC-Pl 1431(13) T26/1; H, BAFC-Pl 1431(11) C22/2, distal view/ *vista distal*. G, I, *Variapollenites rhombicus* Ottone; G, BAFC-Pl 1431(8) Q30/4; I, BAFC-Pl 1431(3) Q36/4. J, L, *Brachysaccus* sp. A; J, BAFC-Pl 1431(11) T30/2; L, BAFC-Pl 1431(11) G41/4. K, *Equisetosporites cacheutensis* Jain BAFC-Pl 1431(11) Z26/2. Scale bar/ *escala gráfica* = 30 µm.

states of pollen hydration, the contraction or stretching of the wall to a significant extent.

Brachysaccus sp. A
Figures 4.J, L

Material estudiado. BAFC-PI 1431 (11) T30/2; BAFC-PI 1431 (11) G41/4.

Description. Monosulcate pollen grain. Amb almost circular. Wall endoreticulate (alveolar ektexine). Exine thickness 3.5-5.5 μm . Ektexine infratectal bacula-like elements forming brochi, 1-2.5 μm in diameter, which are perpendicularly disposed all around the grain. Prothallic pole without apertures, lacking folds or splits. Germinal pole defined by a narrow sulcus, ca. about one tenth of the grain diameter. Sulcus margins occasionally accompanied by folds.

Measurements (25 specimens). Equatorial diameter 55(85)106 μm .

Comparison. Judging from its illustration, *Brachysaccus triassicus* Tripathi *et al.* 1990 seems to be comparable to *B.* sp. A, however, the Indian form was originally described as disaccate. *B.* sp. A differs from *B. ovalis* Mädler 1964 and *B. eskensis* de Jersey 1972 by its almost circular amb. *B. indicus* Kumaran and Maheshwari 1980, originally also described as disaccate, displays an elliptical to oval amb. The specimen figured by Zavattieri (1991a) as *Brachysaccus* cf. *neomundanus* (Leschick) Mädler 1964, from the Triassic Las Cabras Formation, Cuyo Basin, Argentina, is disaccate.

Genus *Cycadopites* Wodehouse ex Wilson and Webster 1946

Type species. *Cycadopites follicularis* Wilson and Webster 1946.

Discussion. Following Ottone and García (1991), *Cycadopites* includes monosulcate pollen grains having a fusiform, oval, subpolygonal to subcircular amb, with a homogeneous wall (homogeneous or granulate ektexine), prothallic pole without apertures; germinal pole defined by a sulcus extending over the full grain length, and absent or minute surficial sculpture. Extant pollen grains of Ginkgophytes, Cycadophytes and some Magnoliaceae, together with fossil pollen grains of Bennettitales, Caytoniales, ?Corytospermales and Pentoxyiales are entirely comparable to those here observed (Ottone and García, 1991). Figures 6.A-F are different specimens of extant *Ginkgo biloba* Linnaeus collected *in situ* from a microsporangiate organ in Buenos Aires, and mounted, as well as the fossil material, in unstained glycerin jelly. See also the different specimens of *G. biloba* illustrated by Audran and Masure (1978, plate I). In *G.*

biloba, pollen grain shape (and sulcus shape) reflect differences in orientation within the slide or, most probably, variable states of pollen grain hydration. Furthermore, generic and specific distinctions of fossil pollen grains similar to *G. biloba* are impossible only using transmitted light microscopy (Ottone and García, 1991). In the Triassic of Argentina, Jain (1968), Herbst (1970), Zavattieri (1987, 1991b, 1992) and Zavattieri and Batten (1996) used different genera for monosulcate pollen grains; *e.g.*, *Bharadwijapollenites* Jain 1968, *Cycadopites* Wodehouse ex Wilson and Webster 1946, *Monosulcites* Cookson ex Couper 1953, *Megamonoporites* Jain 1968, *Pilasporites* Balme and Hennelly emend. Jain 1968, *Punctamonocolpites* Pierce 1961, and *Sulcatopites* Jain 1968. These forms should be *Cycadopites* in view of the above discussion.

Cycadopites sp. cf. *C. follicularis* Wilson and Webster 1946
Figures 5.B-C

Material estudiado. BAFC-PI 1432 (2) T41/4; BAFC-PI 1432 (2) K53/4.

Description. Monosulcate pollen grain, wall smooth, ca. 0.8-1 μm thick.

Measurements (3 specimens). Equatorial diameter 45(46)48 μm .

Comparison. The Argentine specimens are comparable, except for their thinner exine, with the miospores described by Wilson and Webster (1946). Balme (1970) also included in the species *Cycadopites follicularis* specimens with an exine about 1 μm thick.

Cycadopites sp. A
Figures 5.A, D

Material estudiado. BAFC-PI 1432 (2) Q50/0; BAFC-PI 1433 (1) J39/3.

Description. Monosulcate pollen grain, wall smooth to chagrinate, ca. 1.2 μm thick. In fusiform specimens, sulcus margin occasionally folded.

Measurements (8 specimens). Equatorial diameter 62(77)101 μm .

Comparison. Specific differences within the genus are often subtle and hard to observe; hence, *Cycadopites* sp. A superficially resembles many species referred to *Cycadopites* or related genera. *Cycadopites* sp. A essentially differs from the type of *Cycadopites* by its larger size. It resembles specimens referred by Jain (1968) to *Pilasporites calculus* Balme and Hennelly 1956 and *P. crateriformis* Jain 1968. *Cycadopites linae* Herbst 1965 and *C. magnus* Herbst 1965, cited later by Herbst (1970), Jain (1968) and Zavattieri (1987, 1991b), are also similar to *Cycadopites* sp. A.

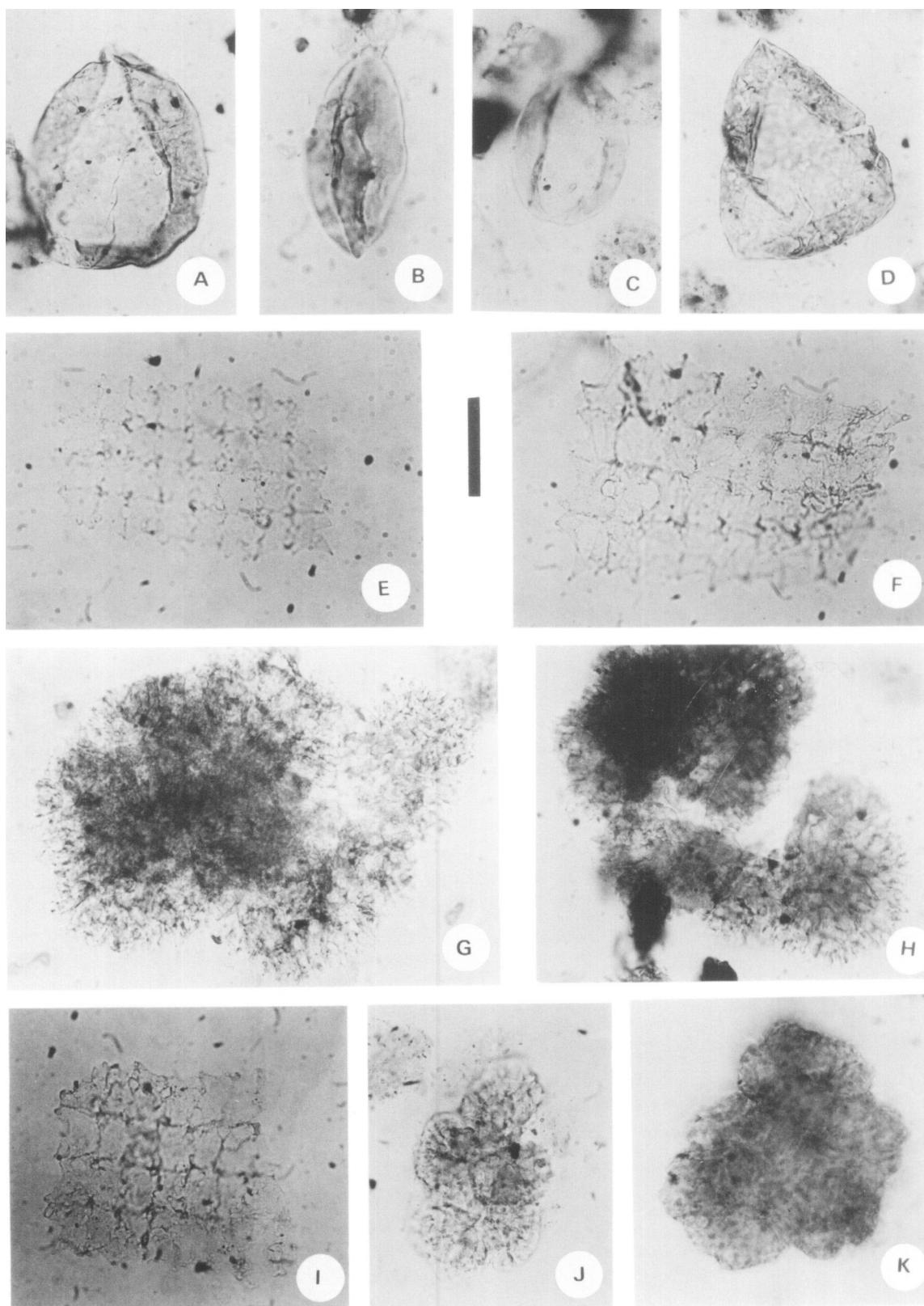


Figure 5. A, D, *Cycadopites* sp. A; A, BAFC-PI 1432(2) Q50/0; D, BAFC-PI 1433(1) J39/3. B-C, *Cycadopites* sp. cf. *C. follicularis* Wilson and Webster; B, BAFC-PI 1432(2) T41/4; C, BAFC-PI 1432(2) K53/4. E-F, *Plaesiodictyon mosellianum* ssp. *symmetricum* Brenner and Foster; E, 1431(11) N35/2; F, 1431(11) Q24/0. G-H, J-K, *Botryococcus* sp.; G, BAFC-PI 1437(1) U55/0, botryoidal colony/ *colonia botroidal*; H, BAFC-PI 1437(1) Y52/0, compound colony showing branches/ *colonia compuesta con ramas*; J, BAFC-PI 1443(1) L51/3, botryoidal colony/ *colonia botroidal*; K, BAFC-PI 1444(1) O41/3, structureless mass/ *masa amorfa*. I, *Plaesiodictyon mosellianum* ssp. *perforatum* Wille 1970 BAFC-PI 1431(12) S43/0. Scale bar/ escala gráfica = 30 µm.

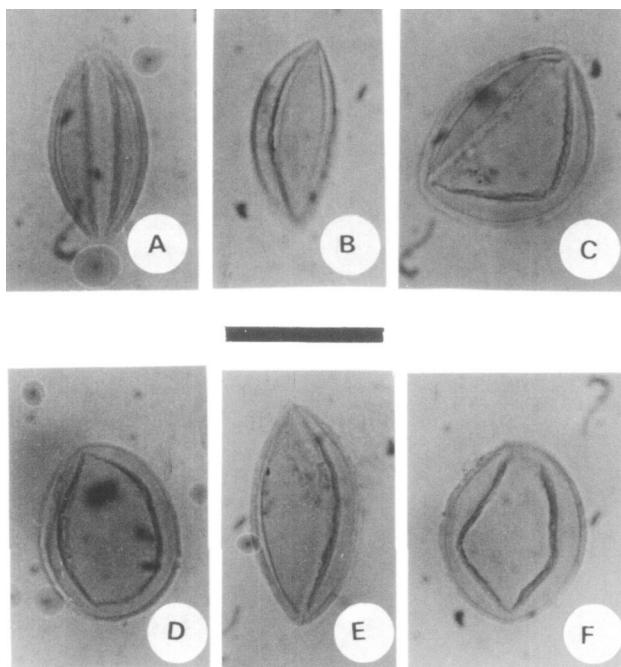


Figure 6. A-F, Pollen grains of extant *Ginkgo biloba* Linnaeus collected *in situ* from a microsporangiate organ in Buenos Aires. Specimens show variations in the shape of pollen grain and sculus / granos de polen de *Ginkgo biloba* actual colectados *in situ* de un microsporangio en Buenos Aires. Los especímenes muestran variaciones en la forma del grano y del sulco. Scale bar/ escala gráfica = 30 µm.

Genus *Equisetosporites* Daugherty emend. Pocock and Jansonius in Pocock, 1964

Type species. *Equisetosporites chinleana* (Daugherty) Pocock and Jansonius in Pocock, 1964.

Equisetosporites cacheutensis Jain 1968
Figure 4.K

Material estudiado. BAFC-PI 1431 (11) Z26/2.

Discussion. Following Jain (1968), this species is retained in *Equisetosporites*. Generic re-attribution is not justified for *E. cacheutensis* because, in acceptance of its probable ephedroid affinity, pollen grains that display a clear separation between the nexine (endexine?) and the sexine (ektexine?) also characterize extant *Ephedra americana* Humboldt and Bonpland ex Willdenow (Steeves and Barghoorn, 1959), and the Triassic *Masculostrobus clathratus* Ash 1972 (a probable gnetalean). The type species of *Equisetosporites*, *E. chinleana* Daugherty 1941, also displays a central endexinal core detached from its banded outer wall. However, attribution of *E. cacheutensis* to *Equisetosporites*, implies a slightly expansion of Pocock and Jansonius' (in Pocock, 1964) circumscription of the genus.

Genus *Variapollenites* Ottone in Ottone *et al.*, 1992, emend. Ottone

Type species. *Variapollenites curviplicatus* Ottone in Ottone *et al.*, 1992.

Discussion. *Variapollenites* was first described from the Triassic Rancho de Lata Formation, Main Cordillera, Argentina (Ottone *et al.*, 1992). The genus encompasses monosaccate pollen grains that display a reticulate pattern on the exine of both the saccus and corpus. Several well-preserved specimens of *Variapollenites* have been found at Río Gualo section, and also in equivalent horizons at the Hoyada de Ischigualasto. The Los Rastros specimens are better preserved than the ones of the type material, thus providing the basis for an emended generic diagnosis. The Los Rastros specimens show differences in ektextine endoreticulum of opposite faces of the corpus not clearly distinguishable in the (lesser preserved) type material due to preservation.

Emended diagnosis. Radial to bilaterally symmetrical monosaccate pollen grains. Tetrad mark absent. Ektextine endoreticulate, detached from endexine toward the equator. The endoreticulum shows a tendency to radial elongation with larger brochi towards the saccus margin (alveolar ektextine). Endexine forms an almost circular or roundly polygonal, mainly triangular or rhombic, corpus (polar view). Corpus margin exhibits a circumpolar fold system. On one face, the ektextine of the corpus is finely structured (ektextine incipiently alveolar?). On the opposite face, corpus ektextine is finely structured towards the equator, becoming smooth and thinner towards the center. Saccus of almost uniform width, not lobed, or constricted; tri- or quadrilobated.

Comparison. Aberrant extant monosaccate grains of Pinaceae (Vishnu-Mitre, 1957, pl. XX, 10) and Podocarpaceae (Pocknall, 1981, fig. 9, I) are comparable to the type species of *Variapollenites*, as are specimens figured as cf. *Walchia* by Reissinger (1950, pl. XVII, fig. 22) from the Lias of Germany, and Monosaccate, undet. by Dybkjaer (1988, pl. 6, fig. 7) from the Liias of Denmark. *Walchites gradatus* Bolkhovitina 1956, from the Jurassic of Russia, seems to be structurally similar to *V. curviplicatus* Ottone, but its corpus lacks a circumpolar fold system. *Picea* sp. from the Miocene of Oregon (Gray, 1964, pl. I, fig. 1) exhibits a morphology closely akin to that of *V. rhombicus* (for further comparison see Ottone *et al.*, 1992).

Variapollenites curviplicatus
Ottone in Ottone *et al.* 1992
Figures 4.E-F, H

Material estudiado. BAFC-PI 1431 (11) C22/2; BAFC-PI 1431 (13) T26/1; BAFC-PI 1431 (11) C22/2.

Discussion. The species, as viewed in polar orientation, includes suboval monosaccates displaying a subcircular corpus. The saccus is not lobed. The specimens from Los Rastros often show, conversely to the ones of the type material, a saccus of variable width.

***Variapollenites rhombicus* Ottone in Ottone et al. 1992**
Figures 4.G, I

Material estudiado. BAFC-PI 1431 (8) Q30/4; BAFC-PI 1431 (3) Q36/4.

Discussion. As viewed in polar orientation, the species includes suboval to subrectangular monosaccates with a roundly rhomboidal corpus. The saccus is quadrilobed and constricted at the apices of the corpus. The Los Rastros material include subrectangular forms with a slightly constricted saccus (figure 13), as well as specimens having a highly incised saccus.

***Variapollenites trisulcus* Ottone in Ottone et al. 1992**
Figures 4.A-D

Material estudiado. BAFC-PI 1431 (14) W42/2; BAFC-PI 1431 (10) R37/3; BAFC-PI 1431 (12) Z39/1; BAFC-PI 1431 (11) Y42/0.

Discussion. The species, as viewed in polar orientation, includes subtriangular monosaccates with a roundly triangular corpus. The saccus is trilobate and often constricted at the corpus apices. The saccus of specimens from Los Rastros is, in some cases, less constricted than those of the type specimens.

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