



Palynology of the Chigua (Devonian) and Malimán (Carboniferous) formations in the Volcán Range, San Juan Province, Argentina. Part I. Paleomicroplankton and acavate smooth and ornamented spores

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Abstract. Palynological analysis of the Chigua and Malimán formations of Devonian and Early Carboniferous age respectively, cropping out in the Río Blanco Basin, northwestern Argentina, has yielded diverse paleomicroplankton-spore assemblages. In this first part, 35 species of paleomicroplankton and 68 species of acavate spores from both formations are illustrated. Two new species are proposed: *Apiculiretusispora laxa* from the Devonian, and *Pustulatisporites malimanensis* from the Early Carboniferous. Two new combinations are proposed: the spore species *Apiculatisporis castanea* (Butterworth and Williams) nov. comb., and the paleomicroplankton species, *Dictyotidium munificum* (Wicander and Wood) nov. comb., based on the discussion of the main characters of the genera *Dictyotidium*, *Muraticavea*, *Polyedryxium* and *Cymatiosphaera*. The genus *Quadrisporites* Hennelly ex Potonié and Lele is emended. Twelve species are first recorded in the Devonian of South America, such as *Pulvinosphaeridium trifidum* Kiryanov, *Dictyotidium granulosum* Playford in Playford and Dring, *Dictyotidium venulosum* (Playford) Colbath, *Orygmahapsis pachyderma* Colbath, *Polyedryxium leptum* Turner, *Leiotriletes trivialis* Naumova, *Granulatisporites muninensis* Allen, *Dibolisporites varius* Tiwari and Schaarschmidt. Other spore species are first recorded in the Lower Carboniferous of South America, amongst them are cited *Granulatisporites triconvexus* Staplin, *Pustulatisporites papillosus* (Knox) Potonié and Kremp, *Verrucosporites microtuberosus* (Loose) Smith and Butterworth, *Dibolisporites medaensis* (Playford) Playford, *Anapiculatisporites ampullaceus* (Hacquebard) Playford, *Lophotriletes severus* Playford and Satterthwait, *Raistrickia gemmifera* Playford and Satterthwait and *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin and Malloy. Previous worldwide geographic and stratigraphic records of the species studied herein are charted, while those corresponding to South America are cited in the text.

Resumen. PALINOLOGÍA DE LAS FORMACIONES CHIGUA (DEVÓNICO) Y MALIMÁN (CARBONÍFERO) EN LA SIERRA DEL VOLCÁN, PROVINCIA DE SAN JUAN, ARGENTINA. PARTE I. PALEOMICROPLANCTON Y ESPORAS ACAVADAS LISAS Y ORNAMENTADAS. Se presenta el análisis sistemático de las asociaciones palinológicas obtenidas de sedimentitas de las formaciones Chigua y Malimán, del Devónico y Carbonífero Inferior respectivamente, aflorantes en la cuenca Río Blanco. En esta primera parte se ilustran 35 especies de paleomicroplankton y 68 especies de esporas acavadas presentes en ambas formaciones. Se proponen dos nuevas especies de esporas, una del Devónico denominada *Apiculiretusispora laxa* sp. nov. y la otra del Carbonífero Temprano, *Pustulatisporites malimanensis*. Se proponen también dos nuevas combinaciones, la espora *Apiculatisporis castanea* (Butterworth y Williams) nov. comb., y una especie de paleomicroplankton, *Dictyotidium munificum* (Wicander y Wood) nov. comb. basada en la discusión de los caracteres diagnósticos que permiten distinguir los géneros *Dictyotidium*, *Muraticavea*, *Polyedryxium* y *Cymatiosphaera* entre sí. El género *Quadrisporites* Hennelly ex Potonié y Lele es enmendado. Doce especies son registradas por primera vez en el Devónico de América del Sur, entre ellas *Pulvinosphaeridium trifidum* Kiryanov, *Dictyotidium granulosum* Playford en Playford y Dring, *Dictyotidium venulosum* (Playford) Colbath, *Orygmahapsis pachyderma* Colbath, *Polyedryxium leptum* Turner, *Leiotriletes trivialis* Naumova, *Granulatisporites muninensis* Allen, *Dibolisporites varius* Tiwari y Schaarschmidt. En tanto otras son registradas por primera vez en el Carbonífero Inferior de América del Sur, entre ellas *Granulatisporites triconvexus* Staplin, *Pustulatisporites papillosus* (Knox) Potonié y Kremp, *Verrucosporites microtuberosus* (Loose) Smith y Butterworth, *Dibolisporites medaensis* (Playford) Playford, *Anapiculatisporites ampullaceus* (Hacquebard) Playford, *Lophotriletes severus* Playford y Satterthwait, *Raistrickia gemmifera* Playford y Satterthwait y *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin y Malloy. Los registros geográficos y estratigráficos previos mundiales de las especies aquí tratadas son reunidos en un cuadro mientras que sólo los correspondientes a América del Sur figuran en el texto.

Key words. Palynology. Chigua and Malimán formations. Middle Devonian and Early Carboniferous. San Juan Province. Argentina.

Palabras clave. Palinología. Formaciones Chigua y Malimán. Devónico Medio y Carbonífero Temprano. Provincia de San Juan. Argentina.

Introduction

This work is part of the Ph.D. Thesis of one of the authors (C.R.A.) who is carrying out a detailed palynological analysis in Devonian and Carboniferous

sediments of the Río Blanco Basin in the western Argentina. The Río Blanco Basin is one of the Late Palaeozoic basins with the thickest Carboniferous deposits of Argentina, which overlie the Devonian sediments in angular unconformity. The palynomorphs shown in this paper come from samples obtained from the Chigua and Malimán formations, cropping out at the La Cortadera Creek in the western flank of the Volcán Range, Precordillera of San Juan (figure 1).

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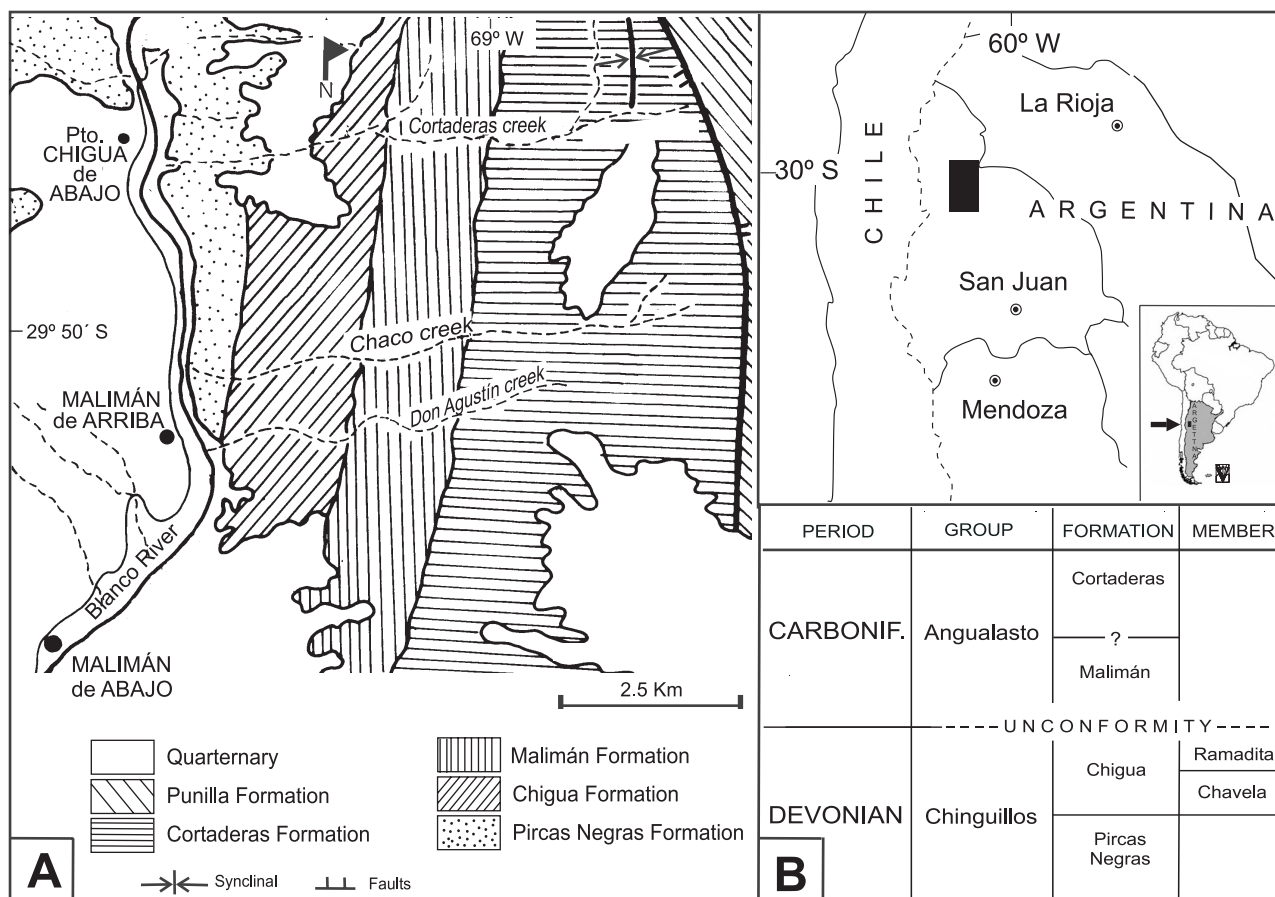


Figure 1. A, Geological map and geographic location of the La Cortadera Creek in San Juan Province, Argentina (modified from Limarino and Césari, 1993) / mapa geológico y ubicación geográfica de la quebrada de La Cortadera (modificado de Limarino y Césari, 1993). B, Chronostratigraphy of the Chinguillos and Angualasto Groups, including the Chigua and Malimán formations, respectively / cronoes-tratigrafía de los Grupos Chinguillos y Angualasto, conteniendo a las formaciones Chigua y Malimán, respectivamente.

The palynological data presented here are the first records for the Chigua Formation. At the moment there are relatively few systematic palynological works on the Devonian of Argentina. Some of them concern to Los Monos Formation in the subsurface of the Tarija Basin (Volkheimer *et al.*, 1986; Barreda, 1986; Ottone, 1996; Grahn and Gutiérrez, 2001; Grahn, 2003), whereas a few purely biostratigraphic works with illustrated lists of species focus on the Precordillera of San Juan have been done (Le Hérissé *et al.*, 1997). Previous palynological studies of the Early Carboniferous Malimán, Cortaderas and El Ratón formations of Argentina are scarce, and correspond partly to studies showing illustrated lists of palynomorphs (Sessarego and Césari, 1989; Césari and Limarino 1992, 1995; Césari and Gutiérrez, 2000), and to works without illustrations (Limarino *et al.*, 1996; Rodríguez Amenábar *et al.*, 2003; Pérez Loinaze and Césari, 2003; Rodríguez Amenábar and di Pasquo, 2004; Amenábar, 2006).

The main objectives of this contribution, which will be presented in three parts, are the following: a) to describe and analyze the palynological assem-

blages identified in the Chigua and Malimán formations, b) to compare and correlate these assemblages mainly with other microfloras from Argentina, Bolivia, Brazil, Perú and Australia, c) to discuss the age of both lithostratigraphic units, especially the basal conglomerates of the Malimán Formation and the marine sediments of the Chigua Formation, and d) to evaluate the hiatus existing between both formations. This first part comprises the palynological study of the microplankton and the acavate smooth and ornamented spores. The second part will present the systematic treatment of all other spore groups (cavate, pseudosaccate and cingulizone). In the third part, the discussion of the proposed objectives will be developed based on qualitative and quantitative information from the whole assemblages studied.

Material and methods

Twelve palynological levels from the Chigua (Chavela Member) and Malimán formations are ana-

lyzed. The Chigua Formation has yielded two palyniferous samples from its upper part, whereas the Malimán Formation has yielded 10 samples along the unit. All sampled levels are shales except the one from the lowest part of the Malimán Formation, which consists of fine-grained sandstones (figure 2). The samples were processed using standard palynological techniques. Palynomorph recognition was made using a Leitz Orthoplan binocular transmitted light microscope N° 871080, with 1000x maximum magnification. The photomicrographs were taken with Pixera and Motic digital cameras. Coordinates of illustrated specimens are denoted by the prefix BAFC-PI, corresponding to the repository of the Palynology Laboratory, Department of Geology, University of Buenos Aires where the slides are stored, followed by the slide number and the England Finder (EF) reference.

Geological setting

Late Carboniferous deposits crop out in the north-western part of the Precordillera Range in San Juan Province, ca. 30°S and 69°W, where marine Devonian and continental Late Carboniferous fossiliferous sediments are recognized. The outcrops form a belt that extends to the east of the Blanco river, in the western slope of the Punilla and Volcán ranges. Devonian and Carboniferous sediments have been studied by Furque (1956, 1958, 1963) who published the first stratigraphic chart of the area, although the Palaeozoic column has been later modified by different authors, see also the review of Baldis and Sarudiansky (1975). Nowadays the following stratigraphy is accepted: the Devonian, Pircas Negras and Chigua formations making up the Chinguillos Group, and the Carboniferous Malimán and Cortaderas formations, included in the Angualasto Group (see figure 1).

The Chigua Formation, with a thickness of 700 m, overlies in tectonic contact the Pircas Negras Formation and underlies in angular unconformity the Malimán Formation. This unit is divided into two Members, the lower Chavela (marine) and the upper Ramadita (mixed-continental). The lithology consists mainly of concretionary shales and calcareous lenses with subordinate sandstone layers. The colours vary from green to brown. The succession is rich in fossiliferous levels, including marine invertebrates such as the trilobites *Punillaspis argentina* Baldis and *Phacops chavelai* Baldis and Longobucco; the cephalopods *Orthoceras* sp.; cnidarians *Conularia* sp., and a paleoflora which is represented by the herbaceous lycophytes "*Haplostigma*" *furquei* Frenguelli and ?*Cyclostigma* sp. (Furque, 1956, 1963; Baldis and Sarudiansky, 1975; Baldis and Longobucco, 1977).

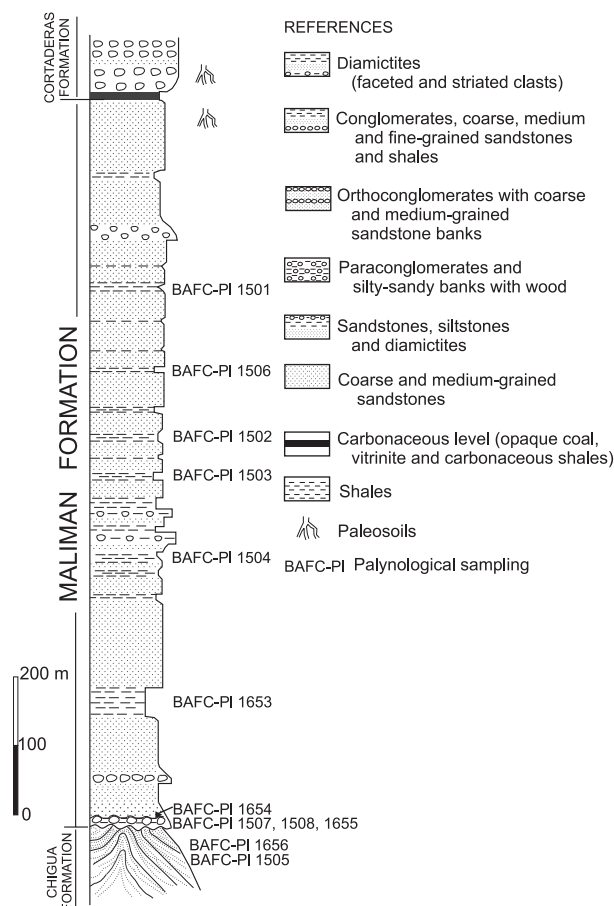


Figure 2. Stratigraphic column of the upper section of the Chigua and Malimán formations at the La Cortadera Creek showing the palynological levels studied here (modified from Limarino and Césari, 1993) / columna estratigráfica de la parte superior de las formaciones Chigua y Malimán en la quebrada de Las Cortaderas indicando los niveles palinológicos estudiados (modificado de Limarino y Césari, 1993).

At the La Cortadera creek, Carboniferous sediments of the Malimán Formation disconformably underlie the Cortaderas Formation. The Malimán Formation, with a thickness of 1300 m, overlies the Chigua Formation (Devonian) by means of an angular unconformity (see figure 2). The contact among these units has been the subject of different interpretations (Azcuay and Caminos, 1988; Caminos and Azcuay, 1996; Carrizo and Azcuay, 1997; Fauqué and Limarino, 1992; Azcuay *et al.*, 2000). The Malimán Formation presents a homoclinal structure; paraconglomerates in basal levels contain a rich association of herbaceous lycophytes and pteridosperms preserved in a sandy and muddy matrix, such as *Frenguella eximia* (Frenguelli) Arrondo, Césari and Gutierrez, *Eusphenopteris devonica* (Frenguelli) Sessarego and Césari and *Diplothmema bodenbenderi* (Kurtz) Césari (Azcuay *et al.*, 2000). Coarse to medium-grained sandstones lie on the conglomerates and also contain a similar paleofloristic association. They

are followed by thick sandstone banks, and thin conglomeratic lenses with intercalations of massive carbonaceous mudstones. The latter contain marine faunas belonging to the *Protocanites scalabrinii*-*Paurorhynchia chavelensis* Zone (Sabattini *et al.*, 2001). The stratigraphic column continues upwards with alternated sandstones and siltstones with subordinate diamictites. This sandy and muddy section also contains the same plant species present in the basal conglomerate, besides some pteridosperms such as "*Rhodea*" sp., "*Hyenia*" sp. and an uncertain affinity taxon named *Paulophyton* sp., which are characteristic of the *Frenguella-Paulophyton* Phytozone (Carrizo and Azcuy, 1997). The upper section is dominated by thick banks of sandstones and orthoconglomerates (see figure 2). According to Limarino and Césari (1993) the Malimán Formation was developed in a littoral palaeoenvironment, with some intercalations of high sea-level deposits in the middle section, grading into more continental facies in its upper part.

Systematic palaeontology

Suprageneric classification of spores follows the scheme introduced by Potonié and Kremp (1954). The latest spanish edition of the ICBN Code (Kiesling, 2002) are here adopted for the treatment of form taxa. Morphological terminology is mainly in accordance with the last glossary provided by Punt *et al.* (1994).

Thirty five species of paleomicroplankton are presented in alphabetical order and sixty-eight spore species are arranged in a taxonomic scheme. Only new species are described in detail whereas the main diagnostic features and/or remarks are given for previously known species that deserve a taxonomic and/or morphological discussion. Synonymy lists are only provided if not yet published, otherwise reference is made to other papers where they are cited.

Selected systematic works and others providing illustrated lists of palynomorphs are used to recon-

struct the worldwide geographical distribution of selected species recognized in the Chigua and Malimán formations, shown in tables 1.A. and 1.B. South American records are included in the text, using works with systematic descriptions and/or illustrated list of species and avoiding those where only lists of species are mentioned (e.g., abstracts or brief communications). Illustrations of specimens are given in figures 3-11. Quantitative stratigraphic distribution of the complete list of all palynomorphs recognized in the Chigua and Malimán formations, grouped after their botanical affinities and arranged in alphabetical order, are included in the third part of this study (in preparation). Finally, many reworked palynomorphs occur along the Malimán Formation. Their stratigraphic distribution and significance are discussed by Amenábar (2006).

Paleomicroplankton

Group ACRITARCHA Evitt 1963

Genus *Arkonites* Legault 1973

Type species. *Arkonites bilixus* Legault, 1973.

Arkonites bilixus Legault 1973

Figure 3.A

Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996; Rubinstein, 1999); (Listed): Bolivia (Lobo Boneta, 1975; Díaz Martínez *et al.*, 1999).

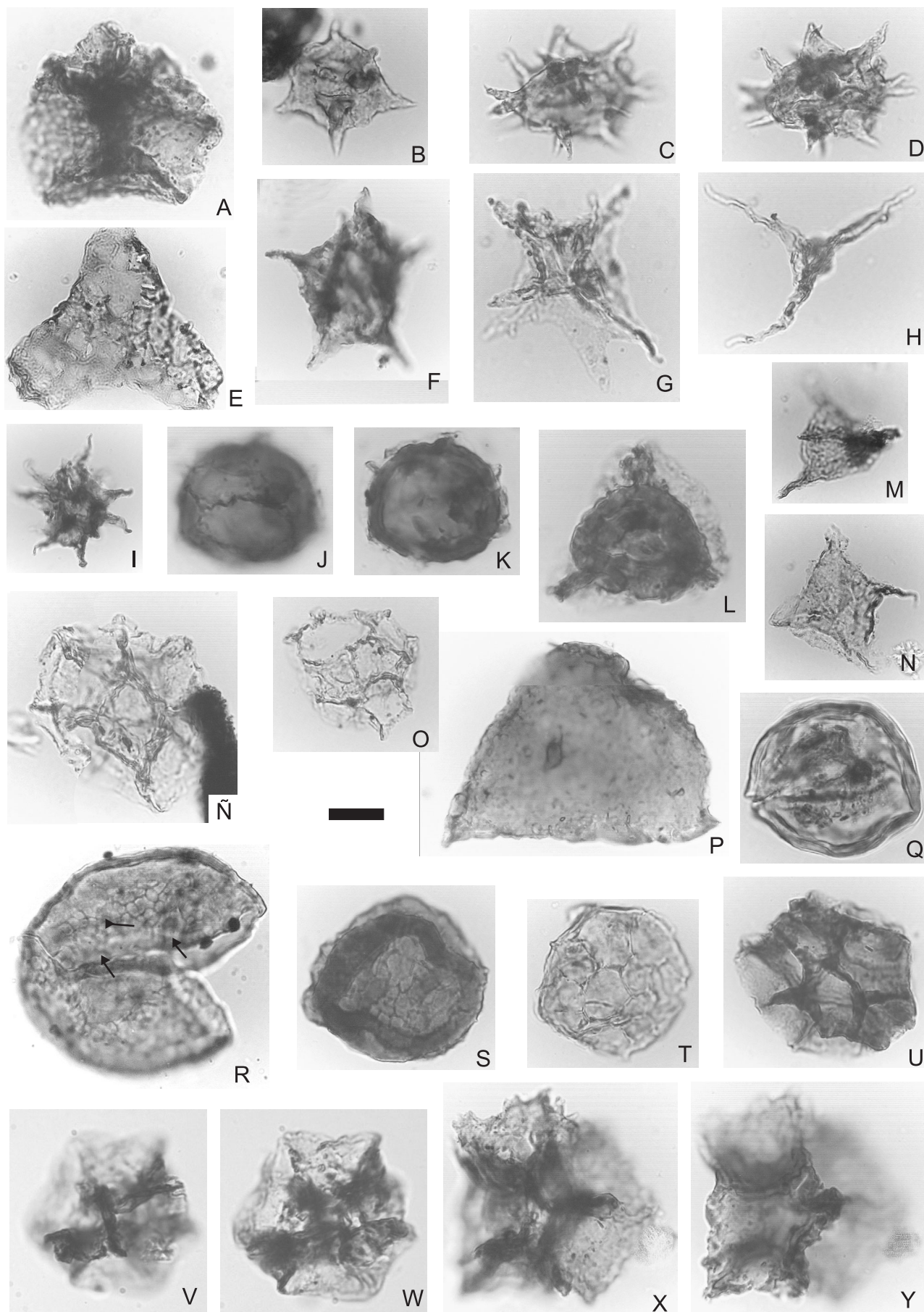
Genus *Crucidia* Ottone 1996

Type species. *Crucidia camirensis* (Lobo Boneta) Ottone, 1996.

Crucidia camirensis (Lobo Boneta) *emend.* Ottone 1996

Figure 4.O

Figure 3. Microplankton from the Chigua Formation. Scale bar: 15 μ m (x 750). Coordinates after EF (England Finder) graticule / microplankton de la Formación Chigua. Escala gráfica: 15 μ m (x 750). Las coordenadas corresponden a la reglilla EF (England Finder). **A**, *Arkonites bilixus* Legault. BAFC-PI 1656 (1): N32/1. **B**, *Micrhystridium* sp. cf. *M. pentagonale* Stockmans and Willière. BAFC-PI 1656 (1): Z22/1. **C-D**, *Micrhystridium* sp. A. BAFC-PI 1656 (1): V51. **E**, *Pulvinosphaeridium trifidum* Kiryanov. BAFC-PI 1505 (1): K46/3. **F**, *Stellinium micropolygonale* (Stockmans and Willière) Playford. BAFC-PI 1505 (3): C36. **G**, *Stellinium octoaster* (Staplin) Jardiné, Combaz, Magloire, Peniguel and Vachey. BAFC-PI 1656(2): T42/2. **H, M**, *Verhachium* spp.; **H**, BAFC-PI 1656 (1): C33; **M**, BAFC-PI 1505(2): B36. **I**, *Polygonium barredae* Ottone. BAFC-PI 1505(5): W36. **J-L**, *Cymatiosphaera* sp. cf. *C. subtrita* Playford in Playford and Dring; **J**, BAFC-PI 1656 (1): S29/3, focus showing the lumina / foco mostrando la lumina; **K**, BAFC-PI 1656 (1): S29/3, focus showing the thick wall / foco mostrando la pared gruesa; **L**, BAFC-PI 1656 (1): W33. **N**, *Duvernaysphaera angelae* Deunff. BAFC-PI 1505 (2): W39/3. **N̄**, *Cymatiosphaera canadensis* Deunff. BAFC-PI 1656 (1): Z32/4. **O**, *Cymatiosphaera perimembrana* Staplin. BAFC-PI 1656 (1): J26/3. **P**, *Onondagaella* sp. cf. *O. asymetrica* (Deunff) Cramer *emend.* Playford. BAFC-PI 1656 (2): X26/3. **Q**, *Hemiruptia legaultii* Ottone. BAFC-PI 1656 (1): D35. **R**, *Orygmahapsis pachyderma* Colbath. BAFC-PI 1656 (1): M49/4. Arrows show fields bearing an internal pore / las flechas indican los campos conteniendo poros internos. **S**, *Dictyotidium venulosum* (Playford) Colbath. BAFC-PI 1505 (3): D22. **T**, *Dictyotidium granulatum* Playford in Playford and Dring. BAFC-PI 1505 (1): R38/1. **U**, *Dictyotidium munificum* (Wicander and Wood) nov. comb. BAFC-PI 1505(5): Z24/2. **V-W**, *Polyedryxium leptum* Turner. BAFC-PI 1505 (3): H48/4. **X-Y**, *Polyedryxium decorum* Deunff. BAFC-PI 1656 (2): D31/3.



Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Ottone, 1996), Bolivia (Lobo Boneta, 1975; Díaz Martínez *et al.*, 1999), Brazil (Quadros, 1999). (Listed): Devonian, Bolivia (Troth, 2004).

Genus *Estiastra* Eisenack 1959

Type species. *Estiastra magna* Eisenack, 1959.

Estiastra rhytidia Wicander and Wood 1981
Figure 4.P

Occurrence. (Illustrated): Middle-Late Devonian, Brazil (Quadros, 1999), Bolivia (Vavrdová *et al.*, 1993), Argentina (Rubinstein, 1999). (Listed): Middle Devonian, Argentina (Rodríguez Amenábar *et al.*, 2003).

Genus *Exochoderma* Wicander 1974

Type species. *Exochoderma irregulare* Wicander, 1974.

Exochoderma arca Wicander and Wood 1981
Figure 4.L

Occurrence. (Illustrated): Late Silurian-Middle Devonian, Bolivia (Kimyai, 1983). Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996). ?Middle Devonian, Brazil (Brito, 1965, 1976). (Listed): Devonian, Bolivia (Vavrdová *et al.*, 1996).

Genus *Micrhystridium* Deflandre 1937

Type species. *Micrhystridium inconspicuum* Deflandre, 1937.

Micrhystridium sp. cf. *M. pentagonale* Stockmans and Willièrè 1963
Figure 3.B

Studied material. BAFC-PI 1656 (1): Z22/1.

Main characters. Vesicle pentagonal in outline with nine processes; each angle is extended to form a simple acuminate process and additionally, other three discrete units of similar form are developed on vesicle faces. Processes and vesicle wall psilate and thin. Interior process hollow and in free communication

with vesicle cavity; tips sharply acute. No excystment structure observed.

Dimension (1 specimen). Overall diameter 37 µm, diameter of vesicle 27 µm, basal breadth of processes 4.6 µm, length of processes 5 µm.

Remarks. The specimen from the Chigua Formation has processes slightly shorter and with a wider base than the original material described by Stockmans and Willièrè (1963). *Micrhystridium* sp. cf. *M. pentagonale* Playford in Playford and Dring 1981 is smaller than the present specimen.

Occurrence. First record for the Middle Devonian of South America.

Micrhystridium sp. A
Figures 3.C-D

Studied material. BAFC-PI 1656 (1): V51.

Description. Vesicle subcircular in outline, wall psilate to scabrate and thin, with thirteen discrete, heteromorphic processes with broad bases that taper to the end with simple apices or bearing a little spine. Interior process hollow and in free communication with vesicle cavity. No excystment structure observed.

Dimension (1 specimen). Overall diameter 46.4 µm, diameter of vesicle 30 µm, basal breadth of processes 3.2 - 11.6 µm, length of processes 8 µm.

Genus *Navifusa* Combaz, Lange and Pansart 1967

Type species. *Navifusa navis* (Eisenack) Combaz, Lange and Pansart, 1967.

Navifusa bacilla (Deunff) Playford 1977
Figure 5.D

1974. *Navifusa eisenacki* Brito and Santos, Pöthe de Baldi, p. 375, pl. 3, figs. 1-2.

Remarks. From the morphotypes considered by Playford (1977) in the synonymy list of this species, *Leiofusa brasiliensis* Brito and Santos 1965, which is larger and narrower than *N. bacilla*, was not registered in the Chigua Formation.

Occurrence. (Illustrated): Early-Late Devonian,

Figure 4. Microplankton from the Chigua Formation. Scale bar: A-K, Ñ, Q 15 µm (x 750), the rest 20 µm (x 500). Coordinates after EF (England Finder) graticule / microplancton de la Formación Chigua. Escala gráfica: A-K, Ñ, Q 15 µm (x 750), el resto 20 µm (x 500). Las coordenadas corresponden a la regilla EF (England Finder). **A**, *Pterospermella* sp. cf. *P. capitata* Wicander. BAFC-PI 1656 (2): Y55/1. **B-C**, *Polyedryxium* sp. **B**, BAFC-PI 1656(2): X28/1-2; **C**, BAFC-PI 1656 (1): Z30. **D, G**, *Botryococcus* sp. **D**, BAFC-PI 1505 (1): W50/1; **G**, BAFC-PI 1505 (3): Y48. **E-F, I**, *Quadrisporites granulatus* (Cramer) Ströther; **E**, BAFC-PI 1505 (3): R43/2; **F**, BAFC-PI 1505 (3): M25; **I**, BAFC-PI 1505 (3): S46/1. **H, J-K, Ñ**, *Quadrisporites variabilis* (Cramer) Ottone and Rosello; **H**, BAFC-PI 1505 (3): M40/3; **J**, BAFC-PI 1505 (5): C38/4; **K**, BAFC-PI 1505 (3): J22. **Ñ**, BAFC-PI 1656 (2): L45. **L**, *Exochoderma arca* Wicander and Wood. BAFC-PI 1656 (1): S24/1-3. **M**, *Polyedryxium pharaonis* Deunff ex Deunff. BAFC-PI 1656 (2): K23/1. **N**, *Verghachium polyaster* Staplin, BAFC-PI 1656 (2): J26/3. **O**, *Crucidia camirensis* (Lobo Boneta) *emend.* Ottone. BAFC-PI 1656 (2): B27. **P**, *Estiastra rhytidia* Wicander and Wood. BAFC-PI 1505 (2): O47/1. **Q**, *Maranhites* sp. BAFC-PI 1505 (2): U43/3. **R-S**, *Tunisphaeridium caudatum* Deunff and Evitt. BAFC-PI 1656 (2): U36.

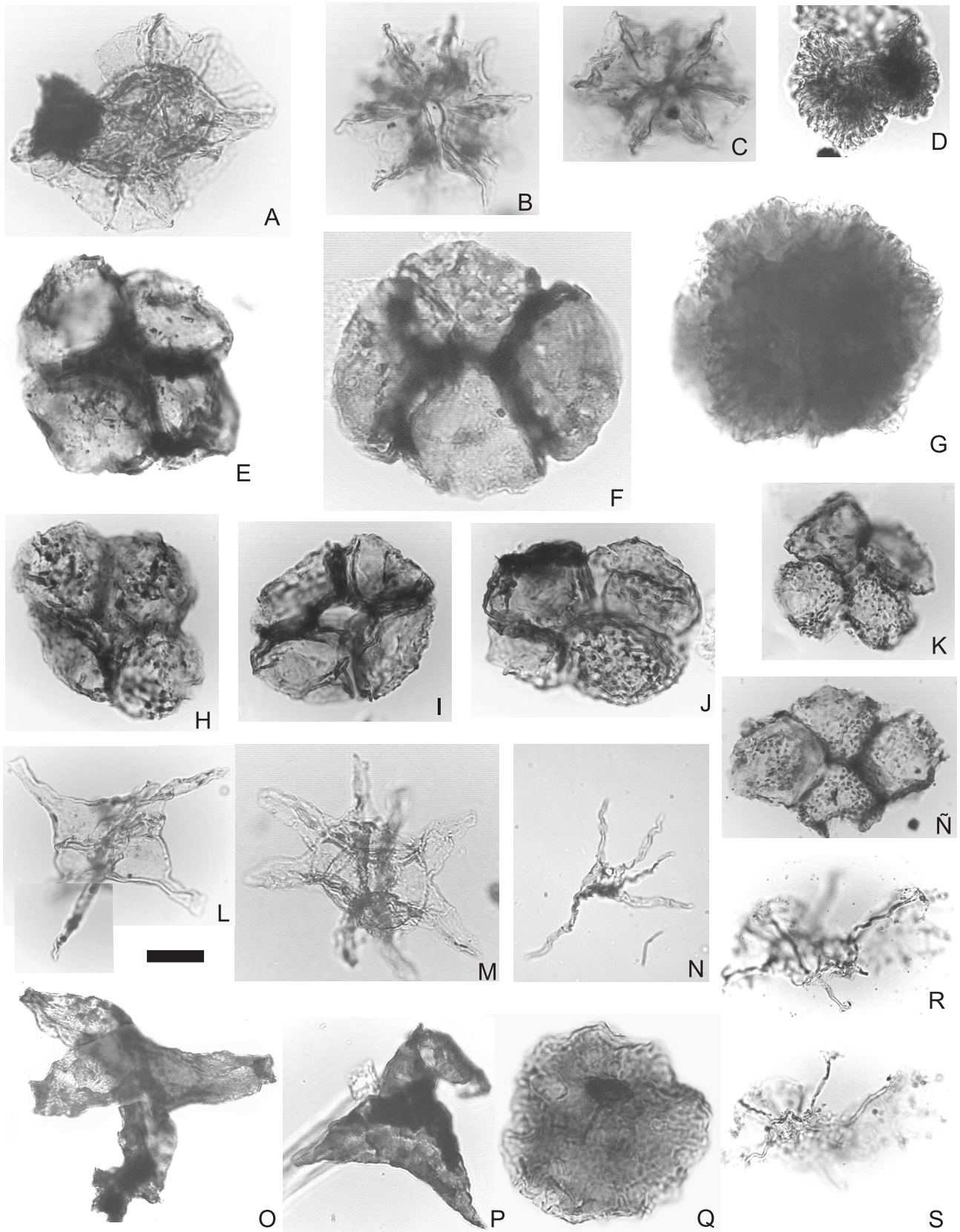


Table 1.A. Worldwide geographical distribution of selected species recognized in the Chigua Formation. Keys to continents: Eurasia (E), South America (SA), North America (NA), Africa (Af), Australia (Au) / *distribución geográfica mundial de las especies seleccionadas reconocidas en la Formación Chigua. Clave de continentes: Eurasia (E), Sud América (SA), Norte América (NA), África (Af), Australia (Au)*. References: for South American records see text. Those for the rest of the world are mainly based on the following selected literature / *referencias: los registros de América del Sur figuran en el texto y aquellos del resto del mundo se basan principalmente en la siguiente literatura seleccionada: McGregor, 1961, 1973; Staplin 1960; Allen, 1965; Tiwari and Schaarschmidt, 1975; Playford, 1977; Playford and Dring, 1981; Wicander and Wood, 1981; Richardson and McGregor, 1986; Le Herisse, 1989; Colbath, 1990; Turner, 1991; Sarjeant and Stancliffe, 1994; Le Hérisse et al., 2000.*

	Selected species	Period					Early Devonian					Middle Devonian					Late Devonian				
		E	SA	NA	Af	Au	E	SA	NA	Af	Au	E	SA	NA	Af	Au	E	SA	NA	Af	Au
CHIGUA FORMATION	MICROPLANKTON	<i>Arkonites bilixus</i>					x	x									x		x		
		<i>Crucidia camirensis</i>						x									x				
		<i>Estiastra rhytidia</i>			x		x	x	x								x		x		
		<i>Exochoderma arca</i>		x	x	x	x	x	x	x	x						x			x	
		<i>Michrhystridium</i> sp. cf. <i>M. pentagonale</i>															x				x
		<i>Navifusa bacilla</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x
		<i>Onondagaella asymmetrica</i>			x	x			x										x		
		<i>Polygonium barredae</i>						x									x				
		<i>Pulvinosphaeridium trifidum</i>	x																		
		<i>Stellinium micropolygonale</i>			x		x	x	x								x	x	x		x
		<i>Stellinium octoaster</i>	x		x	x	x		x	x	x						x		x	x	
		<i>Tunisphaeridium caudatum</i>		x	x			x	x								x				
		<i>Veryhachium polyaster</i>		x			x	x	x								x	x	x		x
		<i>Cymatiosphaera canadensis</i>		x	x			x	x								x				
		<i>Cymatiosphaera perimembrana</i>					x	x									x	x	x	x	x
		<i>Cymatiosphaera</i> sp. cf. <i>C. subtrita</i>																			x
		<i>Dictyotidium munificum</i>		x	x		x		x								x	x	x		
		<i>Dictyotidium granulatum</i>															x				x
		<i>Dictyotidium venulosum</i>									x										x
		<i>Duvernaysphaera angelae</i>			x			x	x								x	x	x	x	x
		<i>Hemiruptia legaultii</i>			x			x	x								x	x			
		<i>Orygmahapsis pachyderma</i>									x										x
		<i>Polyedryxium decorum</i>	x	x				x	x	x									x		
		<i>Polyedryxium pharaonis</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
		<i>Polyedryxium leptum</i>																	x		
		<i>Pterospermella</i> sp. cf. <i>P. capitata</i>						x									x		x		
		<i>Quadrisorites granulatus</i>	x	x		x		x									x				
		<i>Quadrisorites variabilis</i>	x	x		x		x									x				
	ACAVATE SPORES	<i>Apiculatisporis grandis</i>						x													
		<i>Anapiculatisporites microconus</i>			x				x	x	x						x				
		<i>Granulatisporites muninensis</i>				x			x	x											
		<i>Acinosporites lindlarensis</i>		x	x	x			x	x	x						x			x	
		<i>Cyclogranisporites plicatus</i>	x					x	x	x											
		<i>Dibolisporites</i> sp. cf. <i>D. eifeliensis</i>		x		x		x	x	x	x										
		<i>Dibolisporites</i> sp. cf. <i>D. quebecensis</i>		x	x	x			x	x											
		<i>Dibolisporites varius</i>	x					x													
		<i>Dictyotriteles subgranifer</i>	x	x	x	x			x												
		<i>Emphanisporites annulatus</i>	x	x	x	x		x	x	x	x						x			x	x
		<i>Emphanisporites rotatus</i>	x	x	x	x		x	x	x	x	x					x	x		x	x
		<i>Leiotriteles trivialis</i>						x									x				
		<i>Punctatisporites glaber</i>	x					x									x				
		<i>Punctatisporites planus</i>							x										x		
		<i>Verrucosisorites scurrus</i>		x				x	x	x	x						x	x	x	x	x
		<i>Verrucosisorites</i> sp. cf. <i>V. polygonalis</i>			x	x		x		x											

Argentina (Ottone, 1996; Rubinstein, 1999), Bolivia (Pérez Leyton, 1990), Brazil (Daemon, 1974; Brito, 1967a, 1967c, 1976; Quadros, 1982, 1999). Middle-

Late Devonian, Paraguay (Pöthe de Baldi, 1974, 1979). (Listed): Late Devonian, Bolivia (Vavrdová et al., 1996).

Table 1.B. Worldwide geographical distribution of selected species recognized in the Malimán Formation. Keys to continents: Eurasia (E), South America (SA), North America (NA), Africa (Af), Australia (Au) / *distribución geográfica mundial de las especies seleccionadas reconocidas en la Formación Malimán. Clave de continentes: Eurasia (E), Sud América (SA), Norte América (NA), África (Af), Australia (Au).* References: for South American records see in the text and those of the rest of the world are mainly based on the following selected literature / *referencias: los registros de América del Sur figuran en el texto y aquellos del resto del mundo se basan principalmente en la siguiente literatura seleccionada: Hoffmeister et al., 1955; Hughes and Playford, 1961; Playford, 1962, 1964, 1976, 1978; Smith and Butterworth, 1967; Butterworth and Williams, 1958; Clayton, 1971; Smith, 1971; Higgs, 1975; Clayton et al., 1978, 2002; Playford and Powis, 1979; Playford and Satterthwait, 1985, 1986, 1988; Ravn et al., 1986; Higgs et al., 1988; Coquel and Latrèche, 1989; Playford and McGregor, 1993.*

	Selected species	Period					Late Famennian					Early Carboniferous					Late Carb/Early Perm				
		E	SA	NA	Af	Au	E	SA	NA	Af	Au	E	SA	NA	Af	Au	E	SA	NA	Af	Au
MALIMÁN FORMATION	<i>Anapiculatisporites amplus</i>											x									x
	<i>Anapiculatisporites ampullaceus</i>												x		x	x					
	<i>Anapiculatisporites hystricosus</i>											x	x	x		x					
	<i>Apiculatisporis castanea</i>											x					x				
	<i>Apiculiretusispora semisenta</i>												x			x	x				
	<i>Convolutispora insulosa</i>												x	x		x					
	<i>Convolutispora tuberculata</i>											x		x							
	<i>Convolutispora varicosa</i>											x				x	x				
	<i>Convolutispora</i> sp. cf. <i>C. circunvallata</i>											x	x	x							
	<i>Convolutispora</i> sp. cf. <i>C. clavata</i>											x	x	x							
	<i>Convolutispora</i> sp. cf. <i>C. usitata</i>											x		x							
	<i>Cordylosporites marciae</i>	x	x	x	x		x	x	x	x		x	x	x	x						
	<i>Cordylosporites spathulatus</i>	x	x	x	x		x	x	x	x											
	<i>Cyclogranisporites lasius</i>						x			x											
	<i>Dibolisporites medaensis</i>															x					
	<i>Dibolisporites microspicatus</i>												x			x					
	<i>Dibolisporites</i> sp. cf. <i>D. setigerus</i>															x					
	<i>Dictyotriteles trivialis</i>	x		x	x		x		x	x											
	<i>Emphanisporites hibernicus</i>	x			x		x			x											
	<i>Granasporites medius</i>											x					x	x	x		
	<i>Granulatisporites triconvexus</i>													x							
	<i>Leiotriteles ornatus</i>	x			x		x			x		x	x	x	x						
	<i>Lophotriteles severus</i>															x					
	<i>Lophotriteles</i> sp. <i>A</i>															x					
	Playford & Satterthwait 1986																				
	<i>Microreticulatisporites parvirugosus</i>												x	x	x						
	<i>Punctatisporites glaber</i>											x	x	x	x					x	
	<i>Punctatisporites</i> sp. cf. <i>P. aerarius</i>											x	x	x	x			x			
	<i>Pustulatisporites dolbii</i>	x	x	x			x	x	x												
	<i>Pustulatisporites gibberosus</i>						x	x	x	x	x										
	<i>Pustulatisporites papillosus</i>									x							x				
	<i>Raistickia clavata</i>						x	x			x										
	<i>Raistrickia intonsa</i>															x					
	<i>Raistrickia gemmifera</i>															x					
	<i>Raistrickia</i> sp. cf. <i>R. condylosa</i>						x														
	<i>Schopfites claviger</i>						x	x	x	x	x										
	<i>Verrucosisporites baccatus</i>						x			x											
	<i>Verrucosisporites microtuberosus</i>																x				
	<i>Verrucosisporites morulatus</i>						x	x	x	x											
	<i>Verrucosisporites papulosus</i>						x	x	x								x	x	x		
	<i>Waltzispota polita</i>						x	x	x	x	x						x	x			x

Genus *Onondagaella* Cramer emend. Playford 1977

Type species. *Onondagaella asymmetrica* (Deunff) Cramer emend. Playford, 1977.

Onondagaella sp. cf. *O. asymmetrica* (Deunff)
Cramer emend. Playford 1977
Figure 3.P

Studied material. BAFC-PI 1656 (1): D38/1, N42/2, Q26/3; BAFC-PI 1656 (2): M22/3, X26/3.

Dimensions (5 specimens). Overall diameter 68-76.5 µm.

Remarks. *Onondagaella asymmetrica* has two slightly longer processes than the specimens here studied, although they are similar to those illustrated by

Rubinstein (1997, pl. 3, fig. 1) from the Silurian of the Precordillera Argentina.

Occurrence. (Illustrated): Late Silurian, Argentina (Rubinstein, 1997). Late Silurian-Middle Devonian, Bolivia (Kimyai, 1983). (Listed): Devonian, Bolivia (Vavrdová *et al.*, 1996).

Genus *Polygonium* Vavrdová 1966

Type species. *Polygonium gracile* Vavrdová, 1966.

Polygonium barredae Ottone 1996

Figure 3.I

Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996).

Genus *Pulvinosphaeridium* Eisenack 1954 *emend.* Sarjeant and Stancliffe 1994

Type species. *Pulvinosphaeridium pulvinellum* Eisenack, 1954.

Pulvinosphaeridium trifidum Kiryanov 1978

Figure 3.E

1987. *Pulvinosphaeridium* sp. Azcuy and Ottone; p. 249, pl. 3, fig. 6 (as a reworked form from Devonian *s.l.* rocks).

Studied material. BAFC-PI 1505 (1): K46/3.

Description. A star-shaped acritarch, composed of 3 processes situated on a single plane. Processes very broad-based, distally blunt or rounded. Surface psilate. Excystment not observed.

Dimension (1 specimen). Overall diameter 52.2 µm.

Occurrence. First record for the Middle Devonian of South America.

Genus *Stellinium* Jardiné, Combaz, Magloire, Peniguel and Vachey 1972

Type species. *Stellinium micropolygonale* (Stockmans and Willière) Playford, 1977.

Stellinium micropolygonale (Stockmans and Willière) Playford 1977

Figure 3.F

Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996). Late Devonian, Bolivia (Díaz Martínez *et al.*, 1999).

Stellinium octoaster (Staplin) Jardiné, Combaz, Magloire, Peniguel and Vachey 1972

Figure 3.G

Occurrence. (Illustrated): Early Devonian, Argentina (Le Hérissé *et al.*, 1997). Late Devonian, Brazil AMEGHINIANA 43 (2), 2006

(Daemon, 1974). (Listed): Devonian, Bolivia (Vavrdová *et al.*, 1996).

Genus *Tunisphaeridium* Deunff and Evitt 1968

Type species. *Tunisphaeridium tentaculaferum* (Martin) Cramer 1967, originally designated as *T. concentricum* Deunff and Evitt 1968, by Deunff and Evitt (1968, p. 2).

Tunisphaeridium caudatum Deunff and Evitt 1968

Figures 4.R-S

Occurrence. (Illustrated): Silurian, Argentina (Pöthe de Baldi, 1974, 1997). Middle Devonian, Paraguay (Pöthe de Baldi, 1974). Middle-Late Devonian, Argentina (Ottone, 1996), Brazil (Quadros, 1999).

Genus *Veryhachium* Deunff 1954b *ex* Downie 1959

Type species. *Veryhachium trisulcum* (Deunff) Deunff, 1959 (by subsequent designation of Downie, 1959, p. 62).

Veryhachium polyaster Staplin 1961

Figure 4.N

Occurrence. (Illustrated): Late Silurian-Middle Devonian, Bolivia (Kimyai, 1983). Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996; Rubinstein, 1999). (Listed): Devonian, Bolivia (Vavrdová *et al.*, 1996).

Veryhachium spp.
Figures 3.H, M

Remarks. Specimens grouped under this assignment are left in open nomenclature due to their poor preservation.

Green algae

Division PRASINOPHYTA Round 1971

Genus *Cymatiosphaera* Wetzel 1933 *ex* Deflandre 1954

Type species. *Cymatiosphaera radiata* Wetzel, 1933 (by subsequent designation of Deflandre 1954, p. 257).

Cymatiosphaera canadensis Deunff 1954a *ex* Deunff 1961

Figure 3.Ñ

Studied material. BAFC-PI 1505 (2): G39/4; BAFC-PI 1656 (1): J35, Z32/4, Z59/3.

Dimensions (4 specimens). Overall diameter 40.6 -

56 µm, diameter of vesicle 27.8-44 µm, muri 5-12 µm high, wall 1-2 µm thick.

Remarks. The specimens here studied have slightly lower muri (not higher than 6 µm) than *C. canadensis*, a character that it not strong not enough to separate them from this species. According to Playford and Dring (1981), *C. perimembrana* Staplin differs from the present species only because of its smaller overall diameter and lower muri (up to 6 µm high). Nevertheless, a continuum range of these features is observed preventing a clear separation between both species.

Occurrence. (Illustrated): Middle Devonian, Argentina (Rubinstein, 1999). Middle-Late Devonian, Bolivia (Pérez Leyton, 1990). Devonian, Brazil (Brito, 1967c). (Listed): Middle-Late Devonian, Bolivia (Lobo Boneta, 1975; Vavrdová *et al.*, 1996). Late Devonian-Early Carboniferous, Paraguay (Pöthe de Baldi, 2000).

Cymatiosphaera perimembrana Staplin 1961

Figure 3.O

Occurrence. (Illustrated): Middle-Late Devonian, Paraguay (Pöthe de Baldi, 1974, 1979).

Cymatiosphaera sp. cf. *C. subtrita* Playford in Playford and Dring 1981

Figures 3.J-L

Studied material. BAFC-PI 1505 (3): U54/4; BAFC-PI 1656 (1): S29/3, Y34, W33/2.

Main characters. Vesicle spherical; surface divided into about 5 or 6 rectangular, pentagonal or triangular lacunae by very thin, psilate and membranous muri varying from 4-10 µm in height. Lacunae 6 - 10 µm; floor psilate, 1-1.5 µm thick. No excystment structure observed. Wall 2.3-5.8 µm thick.

Dimensions (4 specimens). Overall diameter 35-40 µm, diameter of vesicle 29-35 µm, muri 4-10 µm high, lacunae 6-10 µm, vesicle wall 2.3-5.8 µm thick.

Remarks. The specimens studied here have a larger diameter and a thicker wall than *C. subtrita* Playford in Playford and Dring.

Occurrence. First record for the Middle Devonian of South America.

Genus *Dictyotidium* Eisenack *emend.* Staplin 1961

1974. *Muraticavea* Wicander, p. 14.

For other synonymy see Le Herisse (1989, p. 107).

Type species. *Dictyotidium dictyotum* (Eisenack) Eisenack, 1955.

Generic discussion. According to Wicander (1974),

the separation of *Dictyotidium* Eisenack *emend.* Staplin from *Muraticavea* Wicander, is based on the fact that the latter does not have so many fields on the vesicle and lacks ribs that exceed the edge of the vesicle. Both morphological argumentations are ambiguous and insufficient to separate the two genera. On the other hand, Cramer and Diez Rodríguez (1979) and Colbath (1990) consider *Muraticavea* as a junior synonym of *Polyedryxium* based on the insufficient differentiation between both taxa. Based on this, *Muraticavea* is here placed as a junior synonym of *Dictyotidium* inasmuch as *Polyedryxium* has been separated of *Muraticavea* by Le Hérissé and Deunff (1988), emphasizing the polyhedral character (not subspherical), in addition to the presence of projections in the union of the walls.

Dictyotidium munificum (Wicander and Wood)

nov. comb.

Figure 3.U

Basionym. *Muraticavea munificus* Wicander and Wood, 1981, p. 24, pl. 2, fig. 6.

Studied material. BAFC-PI 1505 (2): C39/2; BAFC-PI 1505 (3): A29/3, Q28/1; BAFC-PI BAFC-PI 1505(4): C24/4; BAFC-PI 1505(5): A34, E25/3, Z24/2; BAFC-PI 1656 (1): C32/2, R41; BAFC-PI 1656 (2): T52.

Description. Vesicle subcircular to polygonal in outline, 72- 03 µm in diameter; vesicle surface faintly granulate-reticulate, divided into concave fields; central polygonal field surrounded by one field on each of the five sides; boundaries of fields delineated by the upturned vesicle wall, forming a ridge; central field 22-37 µm long and 6-11 µm deep. No excystment structure observed.

Dimensions (10 specimens). Overall diameter 35-64 µm, muri up to 6 µm height.

Remarks. The new combination *D. munificum* is based on the presence of simple muri on the vesicle. Even though the Malimán's specimens, as well as the ones from the Los Monos Formation of Argentina (Barreda, 1986, 60 µm; Ottone, 1996, 66-93 µm), show a smaller diameter than those from the coeval palaeoequatorial assemblages (e.g., Wicander and Wood 1981, 72-103 µm), all other features are coincident, suggesting that these specimens are variants of the same species.

Occurrence. (Illustrated): Late Silurian-Late Devonian, Bolivia (Kimyai, 1983; Pérez Leyton, 1990). Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996; Rubinstein, 1999).

Dictyotidium granulatum Playford in Playford and Dring 1981

Figure 3.T

Occurrence. First record for the Middle Devonian of South America.

Dictyotidium venulosum (Playford) Colbath 1990
Figure 3.S

Occurrence. First record for the Middle Devonian of South America.

Genus *Duvernaysphaera* Staplin 1961 *emend.* Deunff 1964

Type species. *Duvernaysphaera tenuicingulata* Staplin, 1961.

Duvernaysphaera angelae Deunff 1964
Figure 3.N

Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996), Brazil (Quadros, 1999). Late Devonian, Bolivia (Vavrdová *et al.*, 1996).

Genus *Hemiruptia* Ottone 1996

Type species. *Hemiruptia legaultii* Ottone, 1996.

Hemiruptia legaultii Ottone 1996
Figure 3.Q

Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Ottone, 1996). (Listed): Late Devonian-Early Carboniferous, Paraguay (Pöthe de Baldis, 2000).

Genus *Leiosphaeridia* Eisenack 1958 *emend.* Downie and Sarjeant 1963

Type species. *Leiosphaeridia baltica* Eisenack, 1958.

Leiosphaeridia spp.
Figures 5.A-B

Remarks. This group includes vesicles with several diameters, and with both thin and coarse walls.

Dimensions (20 specimens). Overall diameter 50 - 136 μm .

Genus *Maranhites* Brito 1965

Type species. *Maranhites brasiliensis* Brito, 1965.

Maranhites sp.
Figure 4.Q

Studied material. BAFC-PI 1505 (2): U43/3.

Description. Vesicle circular, scalloped margin with AMEGHINIANA 43 (2), 2006

12-20 thickened peripheric pads poorly defined that are projected distally in a thin membrane.

Dimension (1 specimen). Overall diameter 52.2 μm .

Remarks. The bad preservation of the only one specimen recovered precludes a more precise assignment. *Maranhites* sp. B in Playford (1981, pl. 4, fig. 1), with 12-14 pads, described from the Late Devonian of Australia, is somewhat similar.

Genus *Orygmahapsis* Colbath 1987

Type species. *Orygmahapsis fistulosa* (Colbath) Colbath, 1987.

Orygmahapsis pachyderma Colbath 1990
Figure 3.R

Occurrence. First record for the Middle Devonian of South America.

Genus *Polyedryxium* Deunff 1954a *ex* Deunff 1961 *emend.* Deunff 1971

Type species. *Polyedryxium deflandrei* Deunff *ex* Deunff, 1961.

Generic remarks. In this work, *Polyedryxium* Deunff *ex* Deunff 1961 *emend.* Deunff 1971 embraces polyhedral vesicle forms whose angles extend in digitations or fleurons that communicate freely with the vesicle. As indicated by Deunff (1971), *Staplinium* Jansonius 1962 differs from *Polyedryxium* by the absence of fleurons at the angles of the muri and these are also smooth, not crenulate. *Cymatiosphaera* Wetzel *ex* Deflandre 1954 is separated owing to the presence of a more or less spheroidal central vesicle with diaphanous (membranous) walls without projections in its angles. In agreement with Le Hérisse (1989), *Dictyotidium* Eisenack 1955 *emend.* Staplin 1961 is distinguished from the latter genus by the absence of membranous walls. The authors do not agree with the proposal of Colbath (1990), who considers *Muraticavea* Wicander as a junior synonym of *Polyedryxium* (see also discussion in *Dictyotidium*).

Polyedryxium decorum Deunff 1955
Figures 3.X-Y

Occurrence. (Illustrated): Middle Devonian, Argentina (Rubinstein, 1999). Middle-Late Devonian, Brazil (Quadros, 1999).

Polyedryxium leptum Turner 1991
Figures 3.V-W

Occurrence. First record for the Middle Devonian of South America.

Polyedryxium pharaonis Deunff 1954a ex Deunff 1961

Figure 4.M

Comparison. *P. ambitum* Wicander and Wood 1981 has six (rarely five or seven) processes, which are all more or less in the same plane displaying an starry amb.

Occurrence. (Illustrated): Early-Late Devonian, Brazil (Quadros, 1999). Middle-Late Devonian, Argentina (Barreda, 1986; Ottone, 1996).

Polyedryxium sp.

Figures 4.B-C

Studied material. BAFC-PI 1656 (1): A23/3, Z30; BAFC-PI 1656(2): J35/1, X28/1-2.

Description. Vesicle surface divided into concave membranaceous polygonal faces, four on one side and six on the opposite. The planes have smooth and thick boundaries (ridges) but some surmounting baculate elements may be present. The ridges taper to the margin of the faces with pointed ends. Voids in ridges indistinct.

Dimensions (4 specimens). Overall diameter 40- 52.2 µm.

Comparisons. *Polyedryxium skalensis* Turnau and Racki, 1999 is very similar but the ridges are slightly thicker and their endings are bifurcate. *Polyedryxium membranaceum* Deunff 1955 differs in having a small central vesicle from which polygonal faces are extended.

Genus *Pterospermella* Eisenack 1972

Type species. *Pterospermella aureolata* (Cookson and Eisenack) Eisenack, 1972.

Pterospermella sp. cf. *P. capitana* Wicander 1974

Figure 4.A

Studied material. BAFC-PI 1505 (3): F45; BAFC-PI 1656 (1), S30; BAFC-PI 1656 (2): Y55/1.

Main characters. Vesicle subspherical to oval, surrounded by an equatorial flange; vesicle wall 1.2 µm thick, scabrate; flange laevigate, 11.6-17.4 µm wide, continuous, characterized by some folds that extend from the vesicle to the flange's, giving the appearance of supporting rods. Excystment by splitting of vesicle wall.

Dimensions (3 specimens). Overall diameter 58-65 µm, diameter of vesicle 25.5-39.4 µm, flange 11.6-17.4 µm wide, vesicle wall 1.2 µm thick.

Comparisons. *Pterospermella capitana* Wicander 1974 has a circular vesicle and more folds in the flange. *P.*

pernambucensis Brito 1967b has a circular vesicle, smaller than the total diameter (central body is 3 times smaller than the total diameter), and more numerous and thinner radial folds.

Occurrence. (Illustrated): Middle-Late Devonian, Argentina (Ottone, 1996).

Division CHLOROPHYTA Pascher 1914

Class CHLOROPHICEAE Kützing 1843

Order CHLOROCOCCALES (Marchand) Pascher 1915

Family BOTRYOCOCCACEAE Wille, 1909

Genus *Botryococcus* Kützing 1849

Type species. *Botryococcus braunii* Kützing, 1849.

Botryococcus sp.

Figures 4.D, G

Studied material. BAFC-PI 1505 (1): W50/1; BAFC-PI 1505 (2): L40; BAFC-PI 1505 (3): Y48.

Description. Colonies with coccoid amb; several units grouped with their margins generally fibrous, probably due to the voids left by the missing cells, others with more amorphous aspect.

Dimensions (3 specimens). Overall diameter 35-62.6 µm.

Remarks. The first accurate records of *Botryococcus* are from the Early Carboniferous (e.g. Hemer and Nygreen, 1967; Utting, 1987; Fasolo *et al.*, 2004) whereas a broad stratigraphic range (Ordovician to Recent) is given by some other authors such as Cookson (1953, apud Batten and Grenfell, 1996). Nevertheless, Pre-Carboniferous records are scarce, and correspond mostly to the Strunian sediments as illustrated by Pérez Leyton (1990) and mentioned by Pöthe de Baldi (2000), from Bolivia and Paraguay, respectively. Coquel and Latrèche (1989) illustrated similar forms from the Strunian of North Africa (Sahara), in a transgressive marine palaeoenvironment with great abundance of acritarchs. The oldest records probably are due to Sanders (1967), who illustrated botrioidal bodies (pl. 1, fig. 1) with probable algal affinity in a Middle Devonian marine assemblage from USA, that are very similar to the present specimens.

The palaeoecology of *Botryococcus* indicates shallow and fresh water bodies, low proportion of rains and oligotrophic water condition. Although they also tolerate certain amount of salinity (mixed palaeoenvironments), their presence in marine sediments, such it is the case of the Chigua Formation, generally indicates transportation by rivers into marine settings (Batten and Grenfell, 1996).

Occurrence. First record for the Middle Devonian of South America.

Family SCENEDESMACEAE Oltmanns 1904

Genus *Quadrisporites* Hennelly 1958 ex Potonié and Lele 1961 *emend.*

1966. *Tetraletes* Cramer, p. 77-78.

1967. *Disectispora* Tiwari and Navale, p. 598.

Type species. *Quadrisporites horridus* Hennelly 1958 (by subsequent designation by Potonié and Lele 1961, p. 25, pl. 5, fig. 7).

Botanical affinity and systematic discussion. According to Brenner and Foster (1994) the genus is included in the Division Chlorophyta Pascher 1914, and after Batten (1996) it is part of the Family Scenedesmaceae Oltmanns 1904 due to its similarity with the living crucigenioid species *Tetrastrum punctatum* (Schmidle) Ahlstrom and Tiphany 1934 (apud Brenner and Foster, 1994), except for the larger size of the fossil colony. Other authors such as Hennelly (1958) have proposed a vascular plant origin based on the persistent tetrad with monolete condition unless the dehiscence mechanism was alete or not clearly defined. This concept was refuted by Tiwari and Meena (1989) on the bases of the appearance of an entity by itself and not like a real tetrad derived from vascular plants, relating the genus to the group Acritarcha.

The history of the validation of this genus by Potonié and Lele (1961) has been cited by several authors, such as Jansonius and Hills (1976, card 2312), but none had noticed that, for example, colonies without ornamentation could not be included in it. Therefore, other two genera, *Tetraletes* Cramer 1966 and *Disectispora* Tiwari and Navale 1967, were created with exactly the same morphological features, only differing from the type species *Q. horridus* based on their ornamentation. Therefore, in this contribution a new emendation of *Quadrisporites* is proposed in replacement to the emendation of Potonié and Lele (1961), who maintained a strict ornamentation of grana, pilae and baculae and the lack of germinal aperture, as described originally by Hennelly (1958) for the type material. The other two genera mentioned above are considered as junior synonyms of *Quadrisporites*.

The genus *Deflandrastrum* Combaz 1962 differs from *Quadrisporites* in having strongly enlarged triangular units frequently ending with a long, filiform or spinose process. The units are fused by two extremes leaving a central circular or quadrangular void.

Emended diagnosis. This genus includes colonies composed of 4 units in a tetragonal tetrad. The contact zone of the exine connecting the individual

members is variable, creating a cross generally laevigate and sometimes thickened or with semilunar shape, leaving or not a small free space in the centre. Members laevigate to ornamented, ovoid, rounded, slightly triangular to trapezoidal in shape. Overall size variable, generally less than 100 µm. Excystment by splitting of the distal portion of the units is sometimes observed. The species are distinguished due to their different ornamentation patterns.

Remarks. The emendation aims mainly to assign the colonies of *Quadrisporites* a more diverse ornamentation, including e.g. smooth and verrucose forms, with greater morphologic variation of the members due to the presence (or not) of a excystment structure in their distal portion.

Quadrisporites granulatus (Cramer) Ströther 1991
Figures 4.E-F, I

1967. *Disectispora lobata* Tiwari and Navale, p. 598, pl. 4, figs. 68-72.

1975. *Quadrisporites lobatus* (Tiwari and Navale) Ybert, p. 203, pl. 8, figs. 132-133.

1977. *Tetraletes* spp. Pöthe de Baldi, p. 249, pl. 2, fig. 3, pl. 4, figs. 2, 6.

1982. *Tetraletes* sp. Miller and Eames, p. 250, pl. 4, fig. 7.

1983. *Tetraletes granulatus* Cramer; Le Hérisse, p. 55, pl. 10, figs. 3-4.

1995. *Tetraletes granulatus* Cramer; Dino and Rodrigues, p. 109, pl. 2, fig. 39.

1996. *Quadrisporites* sp. cf. *Q. granulatus* (Cramer) Ströther; Ottone, p. 116, pl. 3, fig. 5.

1996. *Quadrisporites* sp. Oliveira and Burjack; p. 50, pl. 2, fig. 5.

1996. *Quadrisporites* sp. cf. *Q. lobatus* (Tiwari and Navale) Ybert; García, p. 20, pl. 5, fig. 2.

1999. Algal coenobium Díaz Martínez, Vavrdová, Bek and Isaacson, pl. 1, fig. 8; pl. 4, fig. 3.

For additional synonymy see Le Hérisse (1983) and Ottone (1996).

Studied material. BAFC-PI 1505 (1): A42, E56/2, G25/1, J30, L43; BAFC-PI 1505 (2): M47; BAFC-PI 1505 (3): M25, S46/1, R43/2; BAFC-PI 1505 (4): W58/2.

Amplification of diagnosis. Colony with 4 members limited by straight ridges up to 2-3 µm wide. Wall surface laevigate, scabrate to finely granulate.

Dimensions (10 specimens). Overall diameter 44-70.7 µm, individual diameter of members 17.4-34.8 µm.

Comparisons. The only difference between the colonies originally described by Cramer (1966) from the Silurian of Spain, and younger forms found in Devonian and Permian microfloras, is the size which shows a marked variability in the latter. Nevertheless, this characteristic along with the smooth or scabrate condition, are of low taxonomic value to separate either species or genera. In this way, *Q. lobatus*, from the Permian of Brazil, displays the same characteristics as *Q. granulatus*, and is therefore considered here a junior synonym of the latter.

Occurrence. (Illustrated): Late Silurian-Early Permian, Brazil (Tiwari and Navale, 1967; Ybert, 1975; Dino and Rodrigues, 1995; Oliveira and Burjack, 1996). Middle-Late Devonian-Late Carboniferous, Argentina (Barreda, 1986; García, 1996; Ottone, 1996). Late Devonian, Paraguay (Pöthe de Baldis, 1979). Late Devonian, Bolivia (Díaz Martínez *et al.*, 1999).

***Quadrisporites variabilis* (Cramer) Ottone and Rossello 1996**
Figures 4.H, J-K, Ñ

1983. *Tetraletes variabilis* Cramer; Le Hérisse, p. 54, pl. 10, fig. 1.
1984. *Tetraletes variabilis* Cramer; McGregor, pl. 2, figs. 9-10.
1995. *Tetraletes variabilis* Cramer; Dino and Rodrigues, p. 109, pl. 2, fig. 35.
1995. *Tetraletes* sp., Dino and Rodrigues, p. 109, pl. 2, fig. 36.

For additional synonymy see Le Hérisse (1983) and Steemans *et al.* (1996).

Studied material. BAFC-PL 1505 (1): X22/3, L34/3, S36/4, F39/3, L43/0-1; BAFC-PL 1505 (2): C21/2, V28, B27/2, M34, X45/4; BAFC-PL 1505 (3): J22, M40/3; BAFC-PL 1505 (4): D34, V34/2; BAFC-PL 1505 (5): C38/4; BAFC-PL 1656 (1): W30/0-1; BAFC-PL 1656 (2): L45.

Amplification of diagnosis. Colony with 4 cells limited by straight ridges up to 4 µm wide. Cells sculptured mainly with dense verrucose ornamentation, somewhat fused and subordinated coni and biform elements; 0.5-2 µm high, 0.5-3 µm wide, 0.5 µm apart.

Dimensions (17 specimens). Overall diameter 37-67.2 µm, individual diameter of members 18.5-29 µm.

Remarks. The diagnosis proposed by Cramer (1966) is extended to include formally subordinate coni and biform elements. The description proposed by Steemans *et al.* (1996) for *Q. variabilis* does not reflect the morphology of the species according to either its original description or the amplified diagnosis herein. The reason could be that the single specimen illustrated by those authors (Pl. 4, fig 4) would represent the final condition of the total range of variability in the ornamentation of *Q. variabilis*, displaying a predominance of apiculate elements over verrucose ones.

Comparisons. *Q. variabilis* (Cramer) Ottone and Rossello differs from *Q. horridus* (Hennelly) Potonié and Lele 1961, widely reported from Permian basins of Gondwana (e.g., Foster, 1975), in having an essentially apiculate ornamentation that consists of spinae, baculae and pilae, 2-4 µm in height and up to 2 µm wide, with grains and cones subordinated. The size of the colonies in both species is equally ample, between 20-80 µm in diameter. *Q. acanthifer* Cramer and Díez Rodríguez 1976, from the Emsian of Spain, has smaller size range (20-30

µm) and an ornamentation composed exclusively of taped coni up to 2.5 µm in height and width, arranged preferentially in the distal zone of the units. The specimen identified as ? *Quadrisporites* sp. by Oliveira and Burjack (1996, pl. 2, fig. 6) differs from all other species of this genus because of its strongly spinose ornamentation, 3-5 µm in height and 1-2 µm in width. The specimen figured as *Q. horridus* by Rubinstein *et al.* (2005, pl. 4, fig. 11) from the Early Devonian of Brazil, could be better assigned to ? *Quadrisporites* sp. Oliveira and Burjack based on its apiculate ornamentation without smaller elements interspersed.

Occurrence. (Illustrated): Late Silurian-Early Devonian, Brazil (Dino and Rodrigues, 1995). Early-Late Devonian, Bolivia (McGregor, 1984; Ottone and Rosello, 1996).

Group CHITINOZOA Eisenack 1931

Genus *Belonechitina* Jansonius 1964

Type species. *Conochitina micracantha robusta* Eisenack, 1959.

***Belonechitina* sp.**
Figure 5.C

Studied material. BAFC-PL 1656 (1): Z39/2.

Description. Vesicle with a conocylindrical form, lacking a clear differentiation between neck and chamber. The cylindrical neck is broken, but the vesicle length/width ratio is not less than 1.2. Chamber conical, shoulder absent, flexure inconspicuous. Aboral end slightly straight. Neck cylindrical, incomplete. Vesicle surface sculptured with poorly defined apiculate elements.

Dimension (1 specimen). Vesicle 102 µm long, 81.2 µm wide, preserved portion of neck 34.8 µm long, 40.6 µm wide.

Comparisons. *Belonechitina holfeltzii* Ottone 1996 has bi- or tri- furcate spinose projections.

Spores

Anteturma PROXIMEGERMINANTES Potonié 1970
Turma TRILETES Reinsch *emend.* Dettmann 1963
Suprasubturma ACAVATITRILETES Dettmann 1963
Subturma AZONOTRILETES Lubner *emend.* Dettmann 1963
Infraturma LAEVIGATI Bennie and Kidston *emend.* Potonié 1956

Genus *Leiotriletes* Naumova *emend.* Potonié and Kremp 1954

Type species. *Leiotriletes sphaerotriangulus* (Loose) Potonié and Kremp, 1955.

***Leiotriletes ornatus* Ishchenko 1956**

Figure 8.F

Occurrence. (Illustrated): Early Carboniferous, Bolivia (Lobo Boneta, 1975). Viséan, Perú (Azcuy and di Pasquo, 2005). (Listed): Viséan, Bolivia (Fasolo *et al.*, 2004).

***Leiotriletes trivialis* Naumova 1953**

Figures 6.A-B

Occurrence. First record for the Middle Devonian of South America.

***Leiotriletes* sp. A**

Figures 5.E-J

Studied material. BAFC-PI 1505 (1): D33, W37/4, W38/3; BAFC-PI 1505 (2): B37; BAFC-PI 1505 (2): B35, B37, W37/3; BAFC-PI 1505 (3): D24/3, W51/2; BAFC-PI 1505 (5): N25, T37, P28/0-2, B41, W41; BAFC-PI 1656 (1): N31, X32, Z59.

Description. Spore radial trilete, amb subtriangular, with slightly convex sides. Laesurae accompanied by elevated and slightly sinuous labra, 3.5-5.8 µm high, extending almost to the equator. Exine smooth to scabrate, thin, 0.6-0.8 µm thick.

Remarks. The specimens frequently display an incomplete margin due to the thinness of the exine, but is always present the labiate laesurae.

Dimensions (17 specimens). Equatorial diameter 81-128 µm.

Comparisons. *Leiotriletes pyramidalis* (Luber) Allen 1965 (illustrated by Tiwari and Schaarschmidt, 1975, pl. 1, figs. 5-6), is similar but has a better defined outline and a thicker exine.

***Leiotriletes* sp. B**

Figures 6.C-D

Studied material. BAFC-PI 1505 (1): B53/1, X30; BAFC-PI 1505 (2): X24/4; BAFC-PI 1505 (3): M30/3.

Description. Spore radial trilete, amb triangular, with straight to slightly concave sides and rounded radial apices. Laesurae straight, extending to the equator, accompanied by elevated labra up to 6 µm wide. Exine smooth and thin, 1 µm thick.

Dimensions (4 specimens). Equatorial diameter 48.7-52.2 µm.

Comparisons. *Leiotriletes* sp. A in de Jersey (1966) differs from *Leiotriletes* sp. B in its smaller size and more convex interradian sides.

AMEGHINIANA 43 (2), 2006

Genus *Waltzispora* Staplin 1960

Type species. *Waltzispora lobophora* (Waltz) Staplin, 1960.

***Waltzispora polita* (Hoffmeister, Staplin and Malloy) Smith and Butterworth 1967**

Figure 8.E

Occurrence. (Illustrated): Late Viséan, Brazil (Loboziak *et al.*, 1991, 1998; Melo and Loboziak, 2000, 2003). Viséan, Perú (Azcuy and di Pasquo, 2005). It is also recognized in Upper Carboniferous rocks of South America.

Genus *Punctatisporites* Ibrahim *emend.* Potonié and Kremp 1954

Type species. *Punctatisporites punctatus* (Ibrahim) Ibrahim, 1933.

***Punctatisporites glaber* (Naumova) Playford 1962**

Figure 6.H

Remarks. Despite the absence of previous records of the Devonian of South America, it is possible that they could have passed under the nomination *Punctatisporites* spp.

Occurrence. First record for the Middle Devonian of South America. (Listed): Viséan, Bolivia (Fasolo *et al.*, 2004). For previous records from the Devonian to the Bashkirian of Europe and Russia see Playford (1962).

***Punctatisporites planus* Hacquebard 1957**

Figure 6.F

Occurrence. First record for the Middle Devonian of South America.

***Punctatisporites* sp. cf. *P. aerarius* Butterworth and Williams 1958**

Figure 8.D

Dimension (1 specimen). Equatorial diameter 68.4 µm.

Remarks. *Punctatisporites aerarius* has a shorter laesurae with lips.

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005).

***Punctatisporites* sp. in de Jersey 1966**

Figure 6.G

Studied material. BAFC-PI 1505 (2): C48/1, F33/2, H23, N27, S24/2, S45/2; BAFC-PI 1505 (3): J47; BAFC-PI 1505 (4): W34/2.

Description. Spore radial trilete, circular to subcircular amb. Laesurae distinct, simple, straight, length 2/3 or up to the equatorial edge. Exine 2.3-3.5 µm thick, laevigate, rarely folded.

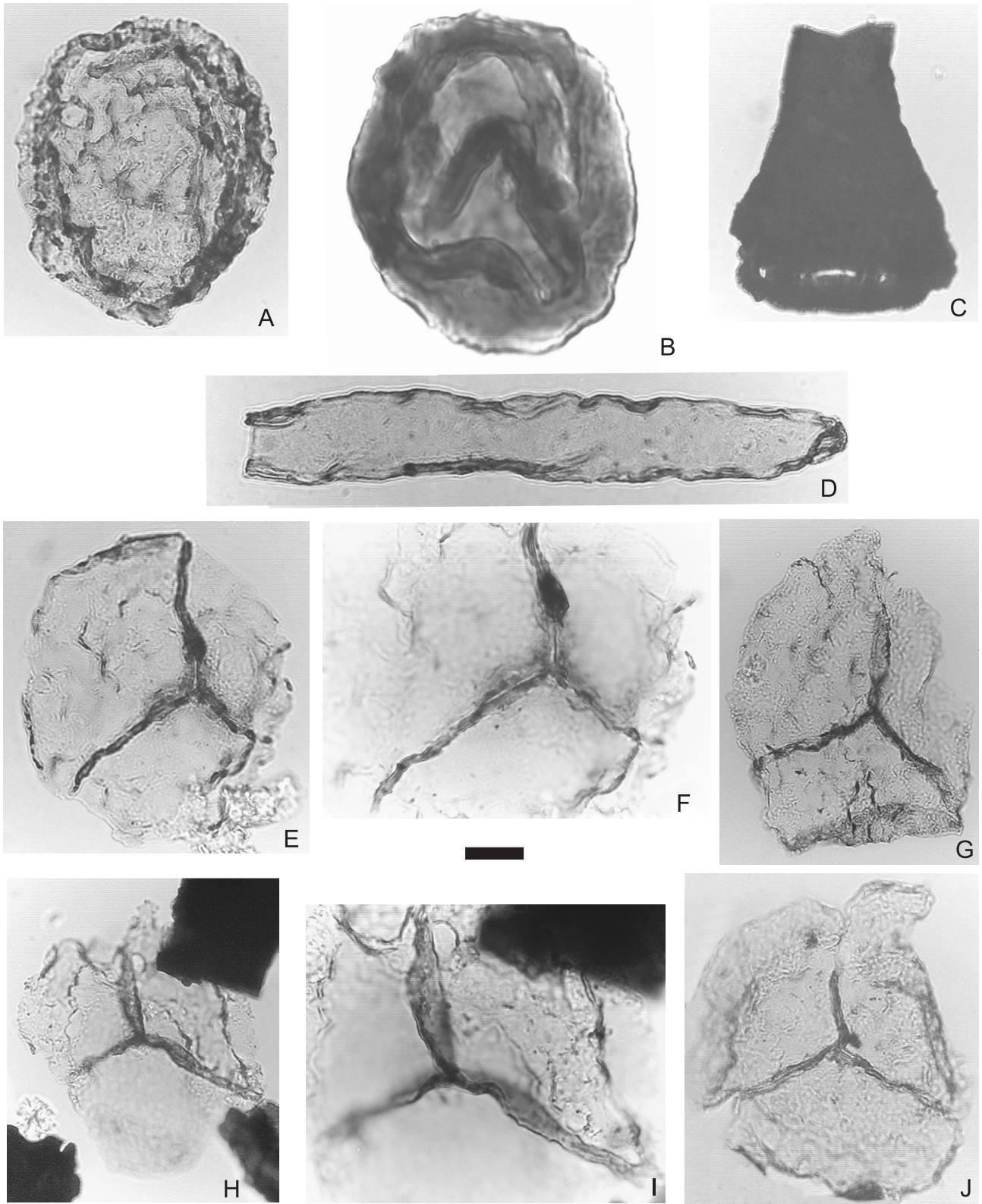


Figure 5. Microplankton and acavate spores from the Chigua Formation. Scale bar: all 20 μm ($\times 500$), except B, F and I 10 μm ($\times 1000$). Coordinates after EF (England Finder) graticule / microplankton y esporas acavadas de la Formación Chigua. Escala gráfica: todas 20 μm ($\times 500$), excepto B, F e I 10 μm ($\times 1000$). Las coordenadas corresponden a la reglilla EF (England Finder). **A-B**, *Leiosphaeridia* spp.; **A**, BAFC-PI 1656 (2): K22; **B**, BAFC-PI 1505 (5): R24/2. **C**, *Belonechitina* sp. BAFC-PI 1656 (1): Z39/2. **D**, *Navifusa bacilla* (Deunff) Playford, BAFC-PI 1656 (1): B28/1. **E-J**, *Leiotriletes* sp. **A**; **E-F**, BAFC-PI 1505 (2): B37; **G**, BAFC-PI 1505 (5): N25; **H-I**, BAFC-PI 1505 (5): T37; **J**, BAFC-PI 1656 (1): Z59.

Dimensions (8 specimens). Equatorial diameter 50-64 μm .

Remarks. *Punctatisporites* sp. differs from other species of the genus because it has a thick exine and simple laesurae that reach the amb. De Jersey (1966) grouped under this designation Devonian specimens from Australia, with simple characteristics (smooth exine, long laesurae, circular to subcircular amb), which preclude any specific classification.

Punctatisporites sp.

Figure 8.H

Studied material. BAFC-PI 1501 (1): Z24/2.

Description. Spore radial trilete, subcircular amb. Lesurae distinct, almost extending to the equator, accompanied by slightly sinuous raised lips, 1.2 - 2.3 μm high, that become widen toward the equatorial margin. Exine 2 - 3 μm thick, infragranulose.

Dimension (1 specimen). Equatorial diameter 61.4 μm .

Comparisons. This species resembles *P. solidus* Hacquebard 1957, but differs in having a trilete mark with rays of same length and lips that almost extend to the equator.

Infraturma RETUSOTRILETI Streele ex Becker, Bless, Streele and Thorez 1974

Genus *Apiculiretusispora* Streele 1964 emend. Streele 1967

Type species. *Apiculiretusispora brandtii* Streele, 1964.

Apiculiretusispora laxa sp. nov.

Figures 6.J-N

1974. *Dibolisporites quebecensis* McGregor 1973; McGregor, p. 77, pl. 2, figs. 41-43.

Holotype. BAFC-PI 1505 (2): V32 (figures 6.J-K).

Paratypes. BAFC-PI 1505 (2): B30/4 (figure 6.L); BAFC-PI 1505 (3): D43/3 (figures 6.M-N).

Diagnosis. Spore radial trilete, circular amb and margin slightly irregular. Lesurae distinct, simple and straight, length two thirds of spore radius. Proximal surface with broad smooth contact areas. Distal and

subequatorial areas bear coni and subordinate discrete grana, 0.6-1.2 μm high and wide, regularly distributed on the surface, one to four times the basal diameter of elements apart. Exine 0.6-1 μm thick.

Derivatio nominis. Lat., *laxus*, loose.

Dimensions (7 specimens). Equatorial diameter 47.5-56 μm .

Comparisons. *Dibolisporites quebecensis* McGregor 1973 (p. 32, pl. 3, figs. 11, 14-16) differs from *Apiculiretusispora laxa* sp. nov. in having a more varied and larger ornamentation.

Apiculiretusispora semisenta (Playford) Massa, Coquel, Loboziak and Taugordeau-Lantz 1980
Figures 8.N-O

Occurrence. (Illustrated): Early Carboniferous, Argentina (Césari and Limarino, 1995), Bolivia (Azcuy and Ottone, 1987), Brazil (Melo and Loboziak, 2000). Viséan, Perú (Azcuy and di Pasquo, 2005). (Listed): Early Carboniferous, Argentina (Rodríguez Amenábar *et al.*, 2003). Viséan, Bolivia (Fasolo *et al.*, 2004).

Genus *Retusotriletes* Naumova 1953 emend. Streele 1964

Type species. *Retusotriletes simplex* Naumova, 1953.

Retusotriletes sp.

Figure 6.E

Studied material. BAFC-PI 1505 (1): P53; BAFC-PI 1505 (2): H44/4; BAFC-PI 1505 (3): O33; BAFC-PI 1505 (5): Z37.

Description. This nomination includes spores radial trilete, amb oval to subcircular, with smooth margin and curvaturae imperfectae, lips absent or very thin (1 μm). Exine 1.5-2 μm thick, laevigate.

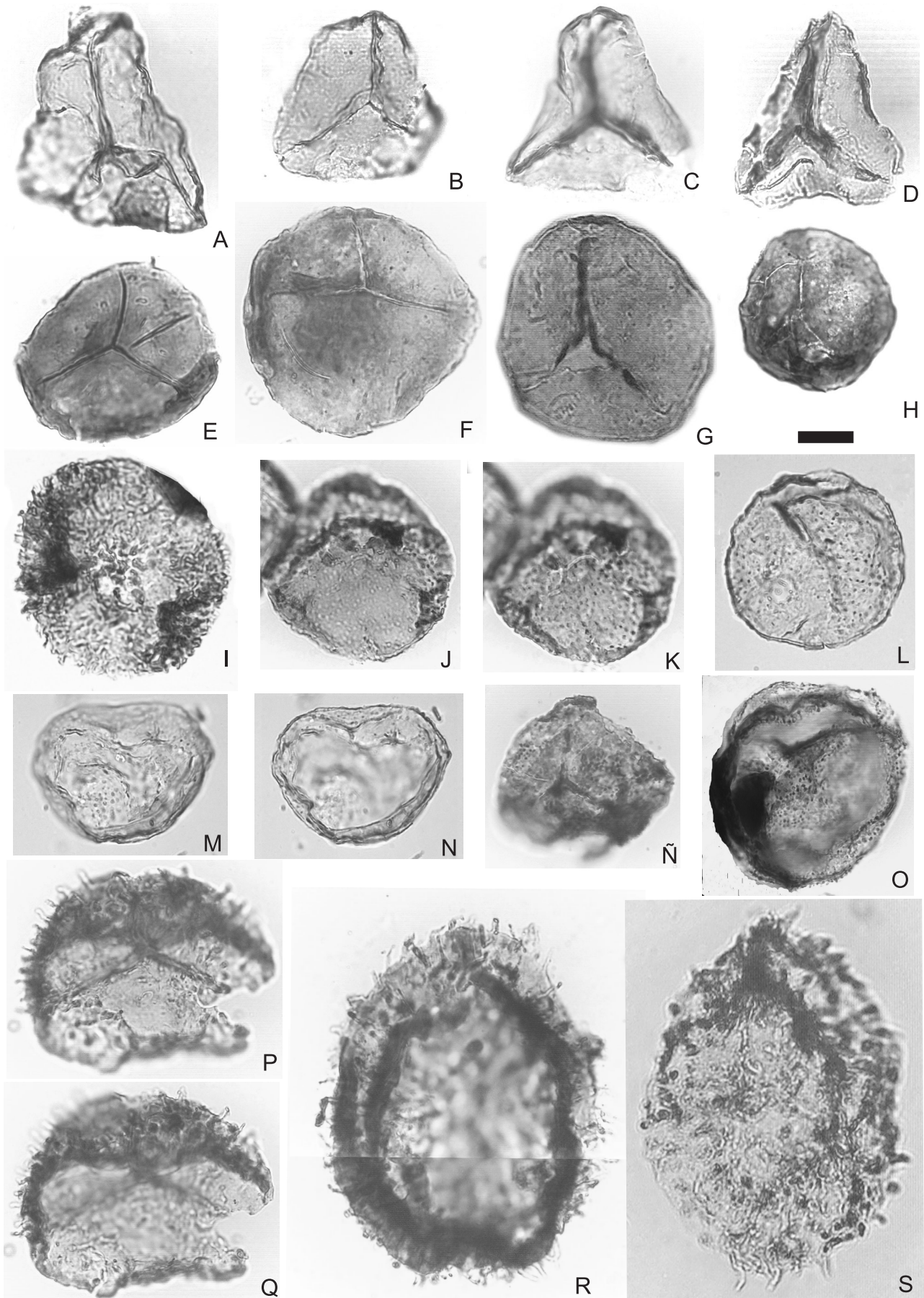
Dimensions (4 specimens). Equatorial diameter 52 - 56 μm .

Remarks. The poor preservation of the specimens prevents an accurate taxonomic assignment.

Genus *Verruciretusispora* Owens 1971

Type species. *Verruciretusispora robusta* Owens, 1971.

Figure 6. Acavate spores from the Chigua Formation. Scale bar: 15 μm (x 750). Coordinates after EF (England Finder) graticule / *Esporas acavadas de la Formación Chigua*. Escala gráfica: 15 μm (x 750). Las coordenadas corresponden a la reglilla EF (England Finder). **A-B**, *Leiotriletes trivialis* Naumova; **A**, BAFC-PI 1505 (2): M45/4; **B**, BAFC-PI 1505 (5): C42/4. **C-D**, *Leiotriletes* sp. **B**; **C**, BAFC-PI 1505 (1): X30; **D**, BAFC-PI 1505 (2): X24/4. **E**, *Retusotriletes* sp. BAFC-PI 1505 (5): Z37. **F**, *Punctatisporites planus* Hacquebard. BAFC-PI 1505 (1): H39. **G**, *Punctatisporites* sp. in de Jersey. BAFC-PI 1505 (3): J47. **H**, *Punctatisporites glaber* (Naumova) Playford. BAFC-PI 1505 (3): J47. **I**, *Verruciretusispora* sp. BAFC-PI 1656 (1): D24/3. **J-N**, *Apiculiretusispora laxa* sp. nov.; **J-K**, BAFC-PI 1505 (2): V32, holotype / holotipo; **L**, BAFC-PI 1505 (2): B30/4, paratype / paratipo; **M-N**, BAFC-PI 1505 (3): D43/3, paratype / paratipo; **N**, *Granulatisporites muninensis* Allen. BAFC-PI 1656 (2): J34. **O**, *Cyclogranisporites plicatus* Allen. BAFC-PI 1505 (3): G30. **P-S**, *Dibolisporites* sp. cf. *D. eifeliensis* (Lanning) McGregor. **P-Q**, BAFC-PI 1656 (2): N57; **R**, BAFC-PI 1656 (1): R44/3; **S**, BAFC-PI 1656 (2): H23/1.



Verruciretusispora sp.

Figure 6.I

Studied material. BAFC-PI 1656 (1): D24/3.

Description. Spore radial trilete, retusoid, with circular amb and irregular margin modified by the projection of the ornaments. Laesurae indistinct. Proximal face laevigate. Distal and equatorial areas densely ornamented with coni, baculae and truncated baculae up to 4.6 μm high and 2.3 μm wide. Exine 2 μm thick.

Dimension (1 specimen). Equatorial diameter 43 μm .

Comparisons. The species here studied resembles *Verruciretusispora* sp. in Balme (1988), but differs in having slightly larger elements.

Infraturma APICULATI Bennie and Kidston *emend.*
Potonié 1956

Subinfraturma GRANULATI Dybová and Jachowicz
1957

Genus *Granasporites* Alpern *emend.* Ravn,
Butterworth, Phillips and Peppers 1986

Type species. *Granasporites medius* (Dybová and Jachowicz) Ravn,
Butterworth, Phillips and Peppers, 1986.

Granasporites medius (Dybová and Jachowicz)
Ravn, Butterworth, Phillips and Peppers 1986
Figure 8.L

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005). Late Carboniferous, Argentina (di Pasquo, 2002), Brazil (di Pasquo *et al.*, 2003). (Listed): Viséan, Bolivia (Fasolo *et al.*, 2004).

Genus *Cyclogranisporites* Potonié and Kremp 1954

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

Cyclogranisporites lasius (Waltz) Playford 1962
Figure 8.M

Occurrence. First record for the Early Carboniferous of South America.

Cyclogranisporites plicatus Allen 1965
Figure 6.O

Occurrence. (Listed): Middle Devonian, Bolivia (Vavrdová *et al.*, 1996).

Cyclogranisporites sp.
Figure 8.A

Studied material. BAFC-PI 1508 (4): D21.

AMEGHINIANA 43 (2), 2006

Description. Spore radial trilete, amb circular and almost smooth margin. Laesurae distinct, simple and straight, extending one half to two thirds of distance to equator. Surface densely ornamented with small grana less than 0.5 μm high and wide. Exine 2.3 μm thick.

Dimension (1 specimen). Equatorial diameter 92.8 μm .

Comparisons. *Cyclogranisporites* sp. is distinguished from *C. naevulus* Hacquebard 1957 by the absence of a "limbus-like" margin. *Cyclogranisporites* sp. A in Hacquebard (1957) has laesurae with lips.

Genus *Granulatisporites* Ibrahim 1933 *emend.*
Potonié and Kremp 1954

Type species. *Granulatisporites granulatus* Ibrahim, 1933.

Granulatisporites muninensis Allen 1965
Figure 6.Ñ

Occurrence. First record for the Middle Devonian of South America.

Granulatisporites triconvexus Staplin 1960
Figure 8.J

1955. *Punctatisporites* sp. Hoffmeister, Staplin and Malloy, pl. 3,
fig. 1.

Occurrence. First record for the Early Carboniferous of South America.

Genus *Dibolisporites* Richardson 1965 *emend.*
Playford 1976

Type species. *Dibolisporites echinaceus* (Eisenack) Richardson, 1965.

Dibolisporites medaensis (Playford) Playford 1976
Figure 8.K

Occurrence. First record for the Early Carboniferous of South America.

Dibolisporites microspicatus Playford 1978
Figures 8.B-C, G

Occurrence. (Illustrated): Early Carboniferous, Argentina (Césari and Limarino, 1992). Viséan, Perú (Azcuy and di Pasquo, 2005).

Dibolisporites varius Tiwari and
Schaarschmidt 1975
Figure 7.C

Occurrence. First record for the Middle Devonian of South America.

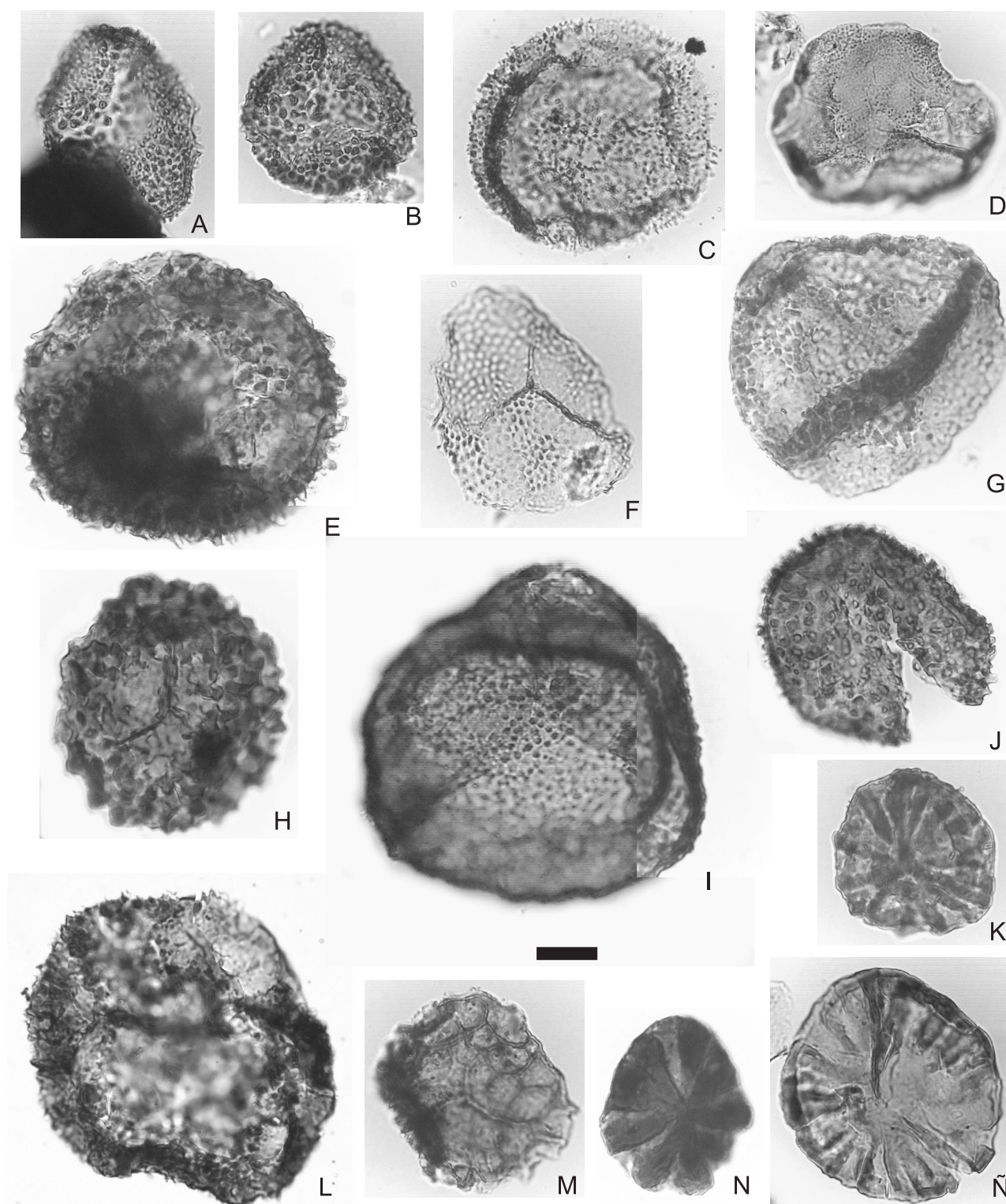


Figure 7. Acavate spores from the Chigua Formation. Scale bar: 15 μ m (x 750). Coordinates after EF (England Finder) graticule / esporas acavadas de la Formación Chigua. Escala gráfica: 15 μ m (x 750). Las coordenadas corresponden a la reglilla EF (England Finder). **A-B**, *Dibolisporites* sp. cf. *D. quebecensis* McGregor; A, BAFC-PI 1505 (2): A23; B, BAFC-PI 1505 (1): K40/1. **C**, *Dibolisporites varius* Tiwari and Schaarschmidt. BAFC-PI 1656 (1): J29/3. **D**, *Apiculatasporites microconus* (Richardson) McGregor and Camfield. BAFC-PI 1505 (3): H29/3. **E**, *Apiculatisporis grandis* Menéndez and Pöthe de Baldi. BAFC-PI 1505 (1): R52/1. **F**, *Apiculatisporis* sp. A. BAFC-PI 1505 (2): D25/3. **G**, *Verrucosisporites* sp. cf. *V. polygonalis* Lanninger. BAFC-PI 1656 (2): D25/3. **H**, *Verrucosisporites scurrus* (Naumova) McGregor and Camfield. BAFC-PI 1505 (5): 47/1. **I**, *Anapiculatisporites* sp. A. BAFC-PI 1505 (3): G44/2. **J**, *Verrucosisporites* sp. BAFC-PI 1505 (5): Y42. **K**, *Emphanisporites annulatus* McGregor. BAFC-PI 1656 (1): Z24. **L**, *Acinosporites lindlarensis* Riegel. BAFC-PI 1656 (2): K34. **M**, *Dictyotriletes subgranifer* McGregor. BAFC-PI 1656 (1): W28/2. **N-N̄**, *Emphanisporites rotatus* McGregor emend. McGregor; N, BAFC-PI 1656 (1): V27; N̄, BAFC-PI 1505(5): Y31/3.

Dibolisporites sp. cf. *D. eifeliensis* (Lanninger)
McGregor 1973
Figures 6.P-S

1984. *Anapiculatisporites* sp. McGregor, pl. 4, fig. 5.

Studied material. BAFC-PI 1505 (3): Y36/4; BAFC-PI 1656 (1): D23/2, E40/4, F48, H25, K25, R44/3, W23; BAFC-PI 1656 (2): A45/2, B30/4, C27/3, E24/2, H23/1, K25, N57, T26, V24/3.

Dimensions (17 specimens). Equatorial diameter 58-104 μm , biform elements and baculae 2.3 μm wide and 3.5-11.6 μm high.

Remarks. *Dibolisporites eifeliensis* (Lanninger) McGregor 1973 presents slightly smaller ornamentation.

Occurrence. (Illustrated): Early Devonian, Brazil (Rubinstein *et al.*, 2005). Middle Devonian, Bolivia (McGregor, 1984). (Listed): Early Devonian, Brazil (Dino, 1999).

Dibolisporites sp. cf. *D. quebecensis* McGregor 1973
Figures 7.A-B

Studied material. BAFC-PI 1505 (1): K40/1; BAFC-PI 1505 (2): A23; BAFC-PI 1505 (5), G24/2; BAFC-PI 1656 (1), L27/2; BAFC-PI 1656 (2), N30/3, U34/2; X43/4, Z43/2, Z45/4.

Dimensions (9 specimens). Equatorial diameter 40-61.5 μm .

Remarks. *D. quebecensis* McGregor 1973 has more varied and discrete ornamentation.

Occurrence. (Illustrated): Early-Middle Devonian, Bolivia (McGregor, 1984).

Dibolisporites sp. cf. *D. setigerus* Playford and
Satterthwait 1986
Figures 8.N, P

Studied material. BAFC-PI 1508 (1): T39; BAFC-PI 1508 (5): W31.

Dimensions (2 specimens). Equatorial diameter 50-65 μm .

Remarks. The specimens from the Malimán Formation display somewhat more reduced ornamentation on the proximal face.

Occurrence. First record for the Early Carboniferous of South America.

Subinfraturma NODATI Dybová and Jachowicz 1957

Genus *Anapiculatisporites* Potonié and Kremp 1954
emend. Smith and Butterworth 1967

Type species. *Anapiculatisporites isselburgensis* Potonié and Kremp, 1954.

AMEGHINIANA 43 (2), 2006

Anapiculatisporites amplus Playford and
Powis 1979
Figures 9.A-B

Dimensions (4 specimens). Equatorial diameter 48.7-75.4 μm , elements 2-3.5 μm high and 1.2-2 μm wide, exine 2-2.3 μm thick.

Remarks. The specimens from the Malimán Formation present more irregular distribution of the ornaments, which may project interradially and are somewhat smaller.

Occurrence. (Illustrated): Viséan, Argentina (Sessarego and Césari, 1989).

Anapiculatisporites ampullaceus (Hacquebard)
Playford 1964
Figure 9.G

Remarks. The specimen here illustrated presents a subtriangular amb, probably as a result of folding.

Occurrence. First record for the Early Carboniferous of South America.

Anapiculatisporites hystricosus Playford 1964
Figures 9.D-F

Occurrence. (Listed): Early Carboniferous, Argentina (Rodríguez Amenábar and di Pasquo, 2004).

Anapiculatisporites sp. A
Figure 7.I

Studied material. BAFC-PI 1505 (3): G44/2.

Description. Spore radial trilete, subcircular amb and margin slightly irregular due to the ornamentation. Laesurae distinct, simple and straight, length three fourths of spore radius. Proximal surface concave, with smooth contact areas. Distal and subequatorial areas bear discrete coni with circular bases, 1.2-2.3 μm wide and 2.3 μm high, regularly distributed on the surface, one time the basal diameter of elements apart. Exine 2 μm thick.

Dimension (1 specimen): Equatorial diameter 83.5 μm .

Genus *Apiculatasporites* Potonié and Kremp 1956

Type species. *Apiculatasporites spinulistratus* (Loose) Ibrahim, 1933.

Apiculatasporites microconus (Richardson)
McGregor and Camfield 1982
Figure 7.D

Occurrence. (Illustrated): Early-Late Devonian, Bolivia (McGregor, 1984). (Listed): Early-Late Devonian, Bolivia (Vavrdová *et al.*, 1996).

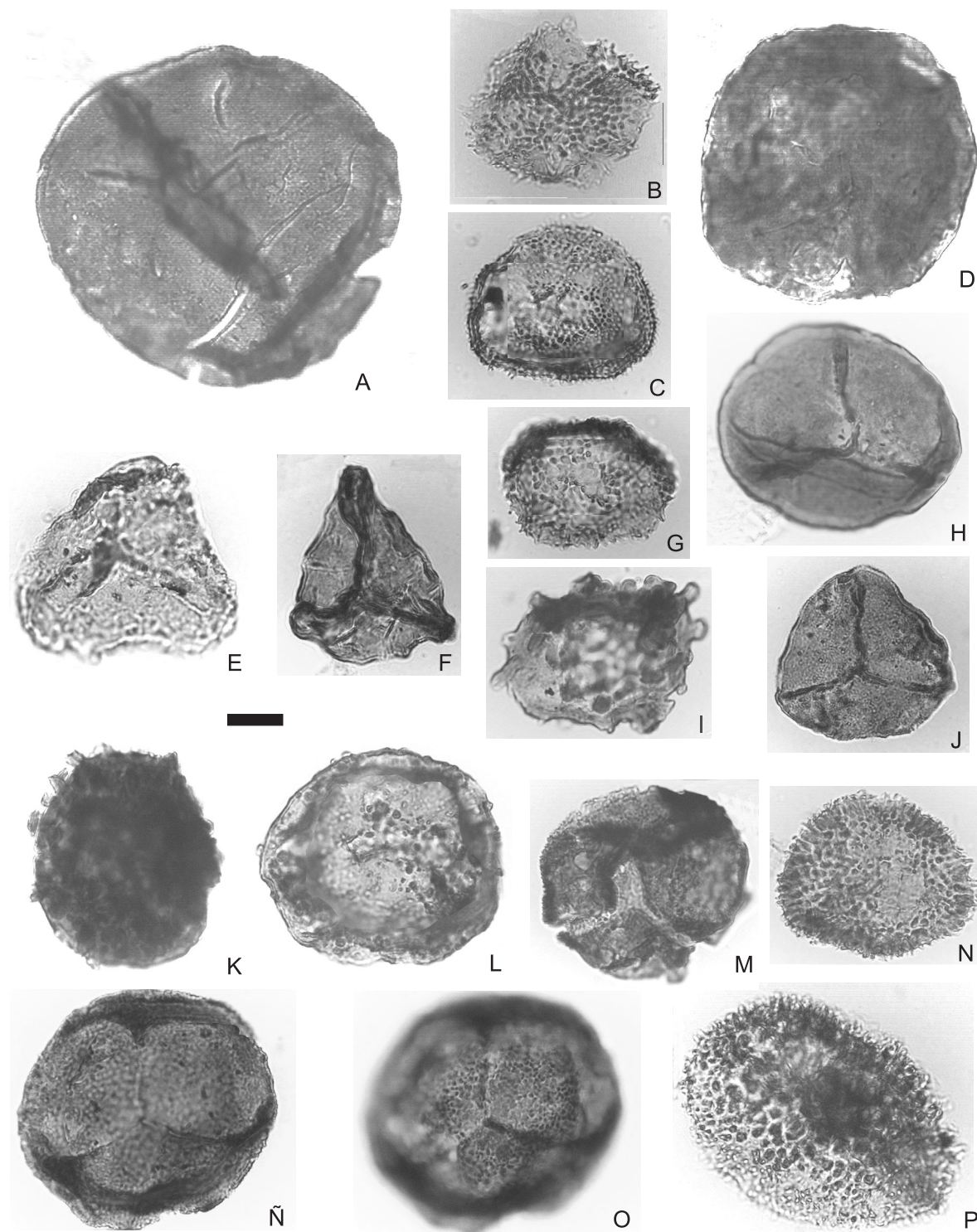


Figure 8. Acavate spores from the Malimán Formation. Scale bar: 15 μm ($\times 750$). Coordinates after EF (England Finder) graticule / esporas acavadas de la Formación Malimán. Escala gráfica: 15 μm ($\times 750$). Las coordenadas corresponden a la regilla EF (England Finder). **A**, *Cyclogranisporites* sp. BAFC-PI 1508 (4): D21. **B-C, G**, *Dibolisporites microspicatus* Playford; B, BAFC-PI 1655 (2): O25; C, BAFC-PI 1655 (2): R31/2; G, BAFC-PI 1655 (2): M26/3. **D**, *Punctatisporites* sp. cf. *P. aerarius* Butterworth and Williams. BAFC-PI 1503 (1): X31/2. **E**, *Waltzispora polita* (Hoffmeister, Staplin and Malloy) Smith and Butterworth. BAFC-PI 1508 (4): A45. **F**, *Leiotriletes ornatus* Ishchenko. BAFC-PI 1655 (2): S23. **H**, *Punctatisporites* sp. BAFC-PI 1501 (1): Z24/2. **I**, *Raistickia clavata* Hacquebard emend. Playford. BAFC-PI 1501 (1): P27. **J**, *Granulatisporites triconvexus* Staplin. BAFC-PI 1655 (2): X35/3. **K**, *Dibolisporites medaensis* (Playford) Playford. BAFC-PI 1506 (1): R25/2. **L**, *Granaspores medius* (Dybová and Jachowicz) Ravn, Butterworth, Phillips and Peppers. BAFC-PI 1508 (4): T42. **M**, *Cyclogranisporites lasius* (Waltz) Playford. BAFC-PI 1504 (1): B29/4. **N, P**, *Dibolisporites* sp. cf. *D. setigerus* Playford and Satterthwait; N, BAFC-PI 1508 (1): T39; P, BAFC-PI 1508 (5): W31. **N-O**, *Apiculiretusispora semisenta* (Playford) Massa, Coquel, Loboziak and Taugordeau-Lantz. BAFC-PI 1508(3): X44.

Genus *Apiculatisporis* Potonié and Kremp 1956

Type species. *Apiculatisporis aculeatus* Ibrahim, 1933.

Apiculatisporis castanea (Butterworth and Williams) nov. comb.
Figure 9.H

Basionym. *Acanthotriletes castanea* Butterworth and Williams, 1958, p. 365, pl. 1, fig. 35.

Dimensions (2 specimens). Equatorial diameter 42–43 µm, spinae 3.5 µm high and 1.2 µm wide.

Occurrence. First record for the Early Carboniferous of South America.

Apiculatisporis grandis Menéndez and Pöthe de Baldi 1967
Figure 7.E

Studied material. BAFC-PI 1505 (1): R52/1, Q51/2.

Dimensions (2 specimens). Equatorial diameter 74–77 µm, coni 2.3–4.6 µm high and 2–3.5 µm wide. Exine 3.5 µm thick.

Occurrence. (Illustrated): Devonian, Paraguay (Menéndez and Pöthe de Baldi, 1967).

Apiculatisporis sp. A
Figure 7.F

Studied material. BAFC-PI 1505 (1): P32; BAFC-PI 1505 (2): D25/3, L40/3, Q52/1.

Description. Spore radial trilete, amb subtriangular, smooth margin. Laesurae straight with thin lips (1.5 µm) that reach the equatorial margin of the spore. Exine bears tapering coni, 2–2.3 µm high and wide, which do not overpass the spore margin. Elements spaced one or two basal diameters apart. Exine 0.8 µm thick.

Dimensions (4 specimens). Equatorial diameter 42–53 µm.

Genus *Lophotriletes* Naumova ex Ishchenko 1952

Type species. *Lophotriletes gibbosus* (Ibrahim) Potonié and Kremp, 1955 (see Jansonius and Hills, 1976, card 1514).

Lophotriletes severus Playford and Satterthwait 1986
Figure 9.C

Occurrence. First record for the Early Carboniferous of South America.

Lophotriletes sp. A in Playford and Satterthwait 1986
Figures 9.I–J

AMEGHINIANA 43 (2), 2006

Studied material. BAFC-PI 1506 (4): J34.

Description. Spore radial trilete, amb subtriangular with rounded apices. Laesurae distinct, simple, straight, length three-fifths of spore radius. Exine sculptured with discrete coni, 0.6–1.5 µm wide and high, which are regularly distributed, but in the polar region scarce elements can be fused. The ornamentation is reduced within the contact areas. Exine 1 µm thick.

Dimension (1 specimen). Equatorial diameter 53.3 µm.

Occurrence. First record for the Early Carboniferous of South America.

Genus *Pustulatisporites* Potonié and Kremp 1954
emend. Imgrund 1960

Type species. *Pustulatisporites pustulatus* Potonié and Kremp, 1954.

Pustulatisporites dolbii Higgs, Clayton and Keegan 1988
Figures 9.L–M

Occurrence. (Illustrated): Late Devonian–Early Carboniferous, Bolivia (Díaz Martínez *et al.*, 1999).

Pustulatisporites gibberosus (Hacquebard) *emend.* Playford 1964
Figures 9.P–R

Occurrence. (Illustrated): Early Carboniferous, Bolivia (Azcuy and Ottone, 1987). Early Carboniferous, Argentina (Césari and Limarino, 1995). (Listed): Late Devonian–Early Carboniferous, Bolivia (Vavrdová *et al.*, 1996).

Pustulatisporites malimanensis sp. nov.
Figures 10.G–L

Holotype. BAFC-PI 1655 (2): Z47/3 (figure 10.G)

Paratypes. BAFC-PI 1655 (2): V39 (figure 10.H); BAFC-PI 1655 (2): V36/1 (figure 10.I); BAFC-PI 1655 (2): R38 (figure 10.J); BAFC-PI 1655 (2): O54 (figures 10.K–L).

Diagnosis. Spore radial trilete, amb subtriangular with somewhat rounded apices and straight to slightly convex sides. Laesurae poorly distinct, accompanied by sharp folds mainly placed along one of the rays of the laesurae. Exine sculptured with coni with broad bases and pointed or truncated apices; subordinate verrucae and pustulae may be present. Elements discrete and very loosely disposed. Frequent exinal folds.

Derivatio nominis. Referred to the homonymous locality.

Description. Spore radial trilete, amb subtriangular with somewhat rounded apices and straight to

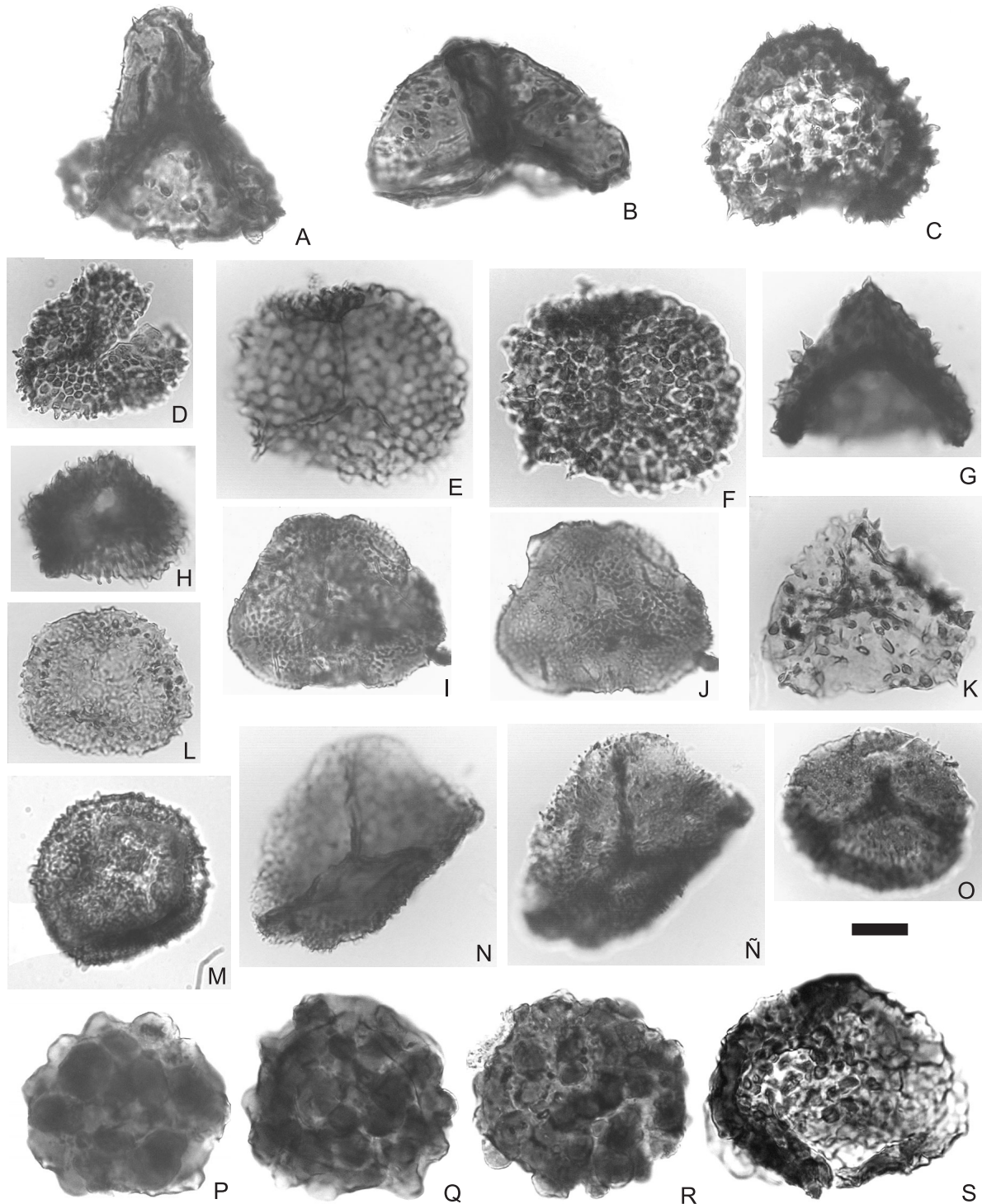


Figure 9. Acavate spores from the Malimán Formation. Scale bar: 15 μm (x 750). Coordinates after EF (England Finder) graticule / esporas acavadas de la Formación Malimán. Escala gráfica: 15 μm (x 750). Las coordenadas corresponden a la reglilla EF (England Finder). A-B, *Anapiculatisporites amplus* Playford and Powis; A, BAFC-PI 1655 (2): Y50; B, BAFC-PI 1655 (2): D35/4. C, *Lophotriletes severus* Playford and Satterthwait. BAFC-PI 1504 (3): A53/1. D-E, *Anapiculatisporites hystricosus* Playford; D, BAFC-PI 1654 (2): A28/3; E-F, BAFC-PI 1503 (1): R31/4; E, proximal focus / foco proximal; F, distal focus / foco distal. G, *Anapiculatisporites ampullaceus* (Hacquebard) Playford. BAFC-PI 1655 (2): S32/2. H, *Apiculatisporis castanea* (Butterworth and Williams) nov. comb. BAFC-PI 1503 (2): J27/1. I-J, *Lophotriletes* sp. A Playford and Satterthwait. BAFC-PI 1506 (4): J34. K, *Pustulatisporites papillosus* (Knox) Potonié and Kremp. BAFC-PI 1655 (2): W29. L-M, *Pustulatisporites dolbii* Higgs, Clayton and Keegan; L, BAFC-PI 1503 (2): F30/4; M, BAFC-PI 1508 (1): B50. N-O, *Raistrickia intonsa* (Playford) Playford and Satterthwait; N-Ñ, BAFC-PI 1501 (1): F41; O, BAFC-PI 1508 (4): D22/2. P-R, *Pustulatisporites gibberosus* (Hacquebard) emend. Playford; P, BAFC-PI 1503 (1): V25/2; Q, BAFC-PI 1503 (2): E56/2; R, BAFC-PI 1503 (1): N43/3. S, *Verrucosisporites morulatus* (Knox) Smith and Butterworth. BAFC-PI 1503 (2): C24.

slightly convex sides, smooth margin. Laesurae poorly distinct, accompanied by sharp folds mainly placed in one of the rays of the laesurae. Exine ornamented with discrete coni with broad bases and pointed or truncated apices, 1.2-2.3 μm wide and 1.2-2.3 μm high, together with subordinate verrucae and pustulae, up to 2.5 μm wide and 2 μm high. Elements irregularly and loosely distributed. Exine up to 2.5 μm thick with frequent exinal folds.

Dimensions (16 specimens). Equatorial diameter 47.5-73 μm .

Comparisons. It is separated from *Neoraistrickia loganii* (Winslow) Coleman and Clayton 1987 by having not biform apiculate and pustulate elements, randomly distributed on the spore exine (not specially at the the radial extremes as it happens in *N. loganii*). Sharp folds placed in one of the rays of the laesurae are typical of this species. *Anapiculatisporites amplus* Playford and Powis 1979 has an anisopolar apiculate, and larger size sculpture.

Pustulatisporites papillosus (Knox) Potonié
and Kremp 1955
Figure 9.K

Occurrence. First record for the Early Carboniferous of South America. (Illustrated): Namurian-Westphalian, Argentina (Azcuy, 1975).

Subinfraturma VERRUCATI Dybová and Jachowicz
1957

Genus *Verrucosisporites* Ibrahim *emend.* Smith and
Butterworth 1967

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

Verrucosisporites baccatus Staplin 1960
Figures 10.E-F

Occurrence. First record for the Early Carboniferous of South America.

Verrucosisporites microtuberosus (Loose) Smith
and Butterworth 1967
Figure 10.B

Occurrence. First record for the Early Carboniferous of South America.

Verrucosisporites morulatus (Knox) Potonié and
Kremp *emend.* Smith and Butterworth 1967
Figures 9.S, 10.A

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005). (Listed): Viséan, Bolivia (Fasolo *et al.*, 2004).

Verrucosisporites papulosus Hacquebard 1957
Figures 10.C-D

1995. *Verrucosisporites* sp. cf. *V. papulosus* Hacquebard; Césari and Limarino, p. 80, pl. 1, fig. 13.

Studied material. BAFC-PI 1503 (1): V25/2; BAFC-PI 1501 (1): M25.

Dimensions (2 specimens). Equatorial diameter 49-70 μm .

Occurrence. (Illustrated): Early Carboniferous (Césari and Limarino, 1995). This species has been also registered in the Late Carboniferous and Early Permian of Argentina, Uruguay and Brazil.

Verrucosisporites scurrus (Naumova) McGregor
and Camfield 1982
Figure 7.H

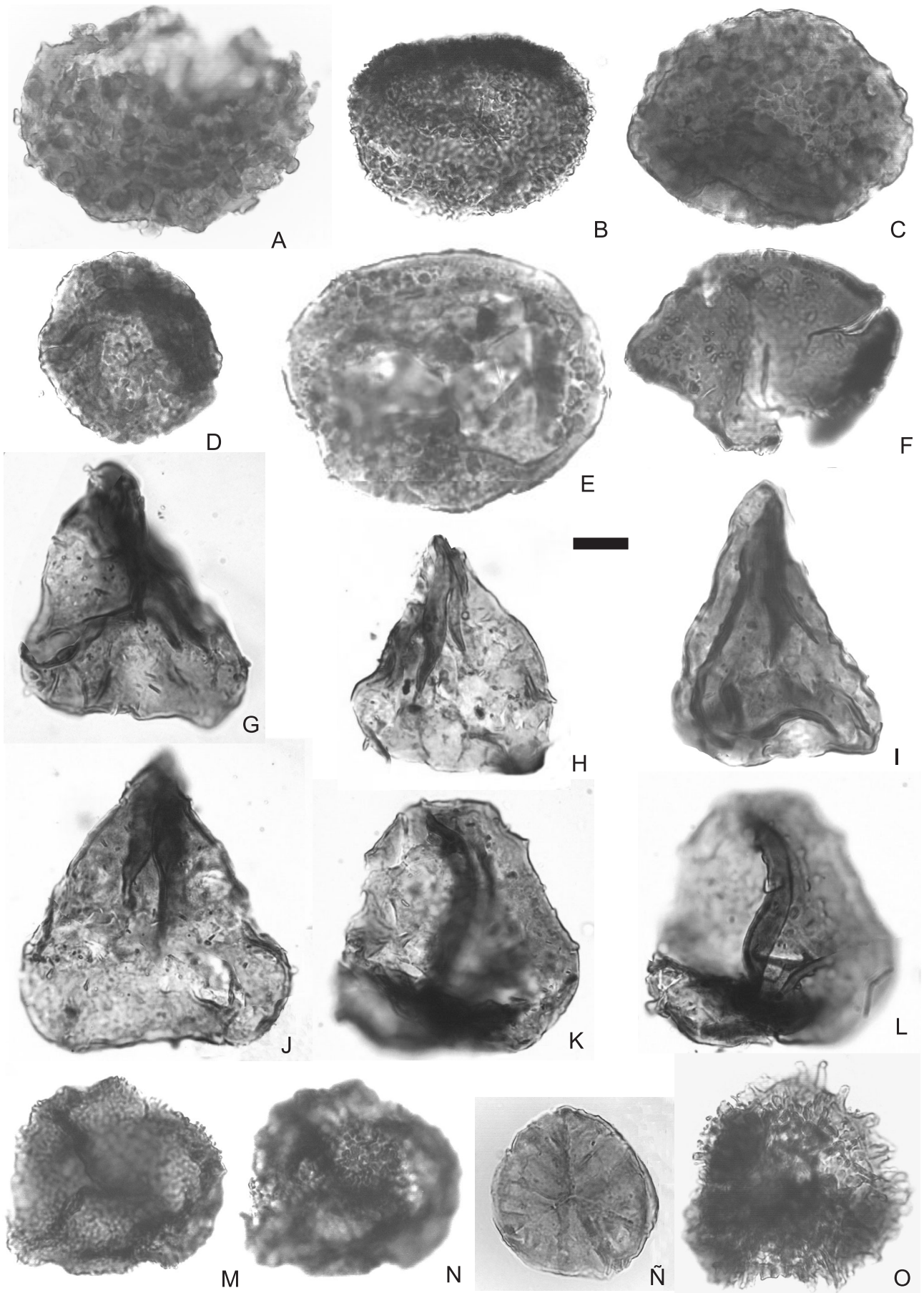
1953. *Lophozonotriletes scurrus* Naumova; p. 38, pl. 3, figs. 22-23.
1965. *Verrucosisporites* cf. *proscurrens* (Kedo) Richardson; p. 573, pl. 90, figs. 10-11.
1965. *Raistrickia aratra* Allen; p. 701, pl. 96, figs. 3-4.
1977. *Pustulatisporites* cf. *gibberosus* (Hacquebard) Playford; Keegan, pl. 1, fig. 8.

Dimensions (10 specimens). Equatorial diameter 35 - 80 μm .

Remarks. In the synonymy lists presented by McGregor and Camfield (1982) and Higgs *et al.* (1988), *Lophozonotriletes bellus* Kedo and *L. excisus* Naumova display smooth contact areas. According to Van der Zwan (1980) and Playford (1991), species with smooth contact areas must be excluded from the genus *Verrucosisporites*.

Occurrence. (Illustrated): Early-Late Devonian, Bolivia (Pérez Leyton, 1990), Middle-Late

Figure 10. Acavate spores from the Malimán Formation. Scale bar: 15 μm (x 750). Coordinates after EF (England Finder) graticule / *esporas acavadas de la Formación Malimán. Escala gráfica: 15 μm (x 750). Las coordenadas corresponden a la reglilla EF (England Finder). A, *Verrucosisporites morulatus* (Knox) Smith and Butterworth. BAFC-PI 1502 (2): P42. B, *Verrucosisporites microtuberosus* (Loose) Smith and Butterworth, BAFC-PI 1508 (1): U30/1. C-D, *Verrucosisporites papulosus* Hacquebard; C, BAFC-PI 1503 (1): V25/2; D, BAFC-PI 1501 (1): M25. E-F, *Verrucosisporites baccatus* Staplin; E, BAFC-PI 1501(1): X23/4; F, BAFC-PI 1506 (5): Z24/4. G-L, *Pustulatisporites malimansis* sp. nov.; G, BAFC-PI 1655 (2): Z47/3, holotype / *holotipo*; H, BAFC-PI 1655(2): V39, paratype / *paratipo*; I, BAFC-PI 1655(2): V36/1, paratype / *paratipo*; J, BAFC-PI 1655 (2): R38, paratype / *paratipo*; K-L, BAFC-PI 1655 (2): O54, paratype / *paratipo*; M-N, *Convolutispora* sp. cf. *C. clavata* (Ischenko) Hughes and Playford. BAFC-PI 1506 (1): Q35. Ñ, *Emphanisporites hibernicus* Clayton, Higgs and Keegan. BAFC-PI 1508 (4): X28/4. O, *Raistrickia* sp. cf. *R. condylosa* Higgs. BAFC-PI 1506 (4): U36/4.*



Devonian, Argentina (Ottone, 1996; Rubinstein, 1999), Brazil (Loboziak *et al.*, 1988, 1992; Dino, 1999; Melo and Loboziak, 2003). (Listed): Early-Late Devonian, Bolivia (Vavrdová *et al.*, 1996). Middle Devonian, Argentina (Rodríguez Amenábar *et al.*, 2003).

Verrucosisporites sp. cf. *V. polygonalis*

Lanninger 1968

Figure 7.G

Studied material. BAFC-PI 1505 (3): D38, X26/4; BAFC-PI 1656 (2): D25/3.

Dimensions (3 specimens). Equatorial diameter 57–65 µm, 0.6–2.3 µm wide and 1–2 µm high, exine 1.2 µm thick.

Remarks. The features of the trilete mark are little defined in the scarce specimens found.

Occurrence. (Illustrated): Early Devonian, Brazil (Melo and Loboziak, 2003).

Verrucosisporites sp.

Figure 7.J

Studied material. BAFC-PI 1505 (5): Y42.

Description. Spore radial trilete, amb subcircular, irregular margin modified by the ornamentation. Laesurae not distinct. Exine ornamented with verrucae, sometimes surmounted by a sharply pointed spine, and truncated coni, 2–3.5 µm wide and 1.2–2.3 µm high, together with subordinate pointed coni and baculae, 1.2 µm wide and 2.3 µm high. Elements irregularly distributed two or three basal diameters apart. Occasionally some elements are fused. Exine 1.8–2.3 µm thick.

Dimension (1 specimen). Equatorial diameter 56 µm.

Comparison. *Verrucosisporites* sp. differs from *V. scurrus* (Naumova) McGregor and Camfield 1982 in having smaller and less commonly fused elements. *V. bulliferus* Richardson and McGregor 1986 bears a sculpture consisting only of flat-topped tabulae which are larger and more densely distributed than in *Verrucosisporites* sp., often with smooth contact areas. The specimen illustrated by Rubinstein (1999, fig. 3 J) as *V. bulliferus*, from the Devonian of Argentina, has a similar ornamentation, although it is slightly denser than in the specimen studied here.

Genus *Schopfites* Kosanke 1950

Type species. *Schopfites dimorphus* Kosanke, 1950.

Schopfites claviger (Sullivan) emend. Higgs,

Clayton and Keegan, 1988

Figures 11.A–B

AMEGHINIANA 43 (2), 2006

Occurrence. (Illustrated): Viséan, Brazil (Loboziak *et al.*, 1991; Melo and Loboziak, 2003); Perú (Azcuy and di Pasquo, 2005). (Listed): Viséan, Brazil (Loboziak *et al.*, 1998).

Subinfraturma BACULATI Dybová and

Jachowicz 1957

Genus *Raistrickia* Schopf, Wilson and Bental

emend. Potonié and Kremp 1954

Type species. *Raistrickia grovensis* Schopf in Schopf, Wilson and Bental, 1944.

Raistrickia clavata Hacquebard 1957 emend.

Playford 1964

Figure 8.I

Occurrence. (Illustrated): Late Tournaisian, Brazil (Melo and Loboziak, 2003). Early Carboniferous, Bolivia (Azcuy and Ottone, 1987). (Listed): Middle-Late Tournaisian-Viséan, Brazil (Loboziak *et al.*, 1992, 1998). Viséan, Bolivia (Fasolo *et al.*, 2004).

Raistrickia gemmifera Playford and

Satterthwait 1986

Figures 11.E–F

Occurrence. First record for the Early Carboniferous of South America.

Raistrickia intonsa (Playford) Playford and

Satterthwait 1986

Figures 9.N–O

Occurrence. First record for the Early Carboniferous of South America.

Raistrickia sp. cf. *R. condylosa* Higgs 1975

Figure 10.O

Studied material. BAFC-PI 1506 (4): U36/4.

Dimension (1 specimen). Equatorial diameter 58 µm, baculae 1.2–2.3 µm wide and 3–5.8 µm high.

Remarks. The specimen studied here has a slightly denser ornamentation than *R. condylosa*.

Occurrence. First record for the Early Carboniferous of South America.

Infraturma MURONATI Potonié and Kremp 1954

Genus *Acinosporites* Richardson 1965

Type species. *Acinosporites acanthomammillatus* Richardson, 1965.

Acinosporites lindlarensis Riegel 1968

Figure 7.L

Occurrence. (Illustrated): Early Devonian, Argentina (Le Hérissé *et al.*, 1997). Early-Late Devonian, Brazil (Loboziak *et al.*, 1988; Dino, 1999; Loboziak and Melo, 2002; Melo and Loboziak, 2003), Bolivia (Pérez Leyton, 1990; McGregor, 1984).

Genus *Convolutispora* Hoffmeister, Staplin and Malloy 1955

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

Convolutispora insulosa Playford 1978
Figure 11.C

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005). (Listed): Early Carboniferous, Argentina (Rodríguez Amenábar *et al.*, 2003).

Convolutispora tuberculata (Waltz) Hoffmeister,
Staplin and Malloy 1955
Figure 11.O

Occurrence. First record for the Early Carboniferous of South America.

Convolutispora varicosa Butterworth and
Williams 1958
Figure 11.G

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005).

Convolutispora sp. cf. *C. circumvallata*
Clayton 1971
Figures 11.I-J

Studied material. BAFC-PI 1501 (1): Z33.

Dimension (1 specimen). Equatorial diameter 88 µm, muri projections 4.6-9.3 µm wide and 8 µm high.

Remarks. The lack of additional specimens prevents a more precise assignment.

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005).

Convolutispora sp. cf. *C. clavata* (Ischenko) Hughes
and Playford 1961
Figures 10.M-N

Studied material. BAFC-PI 1503 (2): R26; BAFC-PI 1506 (1): J22, Q35.

Dimensions (3 specimens). Equatorial diameter 53.3-68.4 µm, rugulae 2.3-4.6 µm wide and up to 2 µm high, exine 3.5 µm thick.

Remarks. The specimens studied here are compara-

ble to *C. clavata*, but the original material is a bit larger and has a relative thicker exine (4.5-6 µm).

Occurrence. (Illustrated): Middle-Late Tournaisian, Brazil (Loboziak *et al.*, 1992).

Convolutispora sp. cf. *C. usitata* Playford 1962
Figure 11.H

Studied material. BAFC-PI 1508 (3): G28/1.

Dimension (1 specimen). Equatorial diameter 62.6 µm, muri 2.3-5.8 µm wide, exine 5.8 µm thick.

Remarks. *C. usitata* is a bit larger than the specimen here studied.

Occurrence. First record for the Early Carboniferous of South America.

Genus *Cordylosporites* Playford and
Satterthwait 1985

Type species. *Cordylosporites sepositus* Playford and Satterthwait, 1985.

Cordylosporites marciae Playford and
Satterthwait 1985
Figure 11.K

Occurrence. (Illustrated): Late Devonian-Early Carboniferous, Bolivia (Lobo Boneta, 1975; Pérez Leyton, 1990; Vavrdová *et al.*, 1993), Brazil (Loboziak and Melo, 2002; Melo and Loboziak, 2003). Early Carboniferous, Argentina (Césari and Limarino, 1995; Césari and Gutiérrez, 2000). (Listed): Late Devonian-Early Carboniferous, Bolivia (Pérez Leyton, 1991; Díaz Martínez *et al.*, 1999).

Cordylosporites spathulatus (Winslow) Playford
and Satterthwait 1985
Figure 11.L

1990. *Raistrickia spathulata* (Winslow) Playford and Satterthwait; Pérez Leyton, p. 36, pl. 9, figs. 18-20.

Occurrence. (Illustrated): Late Devonian, Bolivia (Pérez Leyton, 1990). Late Devonian-Early Carboniferous, Brazil (Loboziak and Melo, 2002; Melo and Loboziak, 2003). (Listed): Late Devonian, Bolivia (Vavrdová *et al.*, 1996).

Genus *Dictyotriletes* Naumova ex Ischenko *emend.*
Smith and Butterworth 1967

Type species. *Dictyotriletes bireticulatus* (Ibrahim) Potonié and Kremp, 1955 (by subsequent designation of Potonié and Kremp, 1955, p. 108; see Jansonius and Hills, 1976, card 790).

Dictyotriletes subgranifer McGregor 1973
Figure 7.M

1984. *Dictyotriletes* sp. McGregor, pl. 4, fig. 1.

Occurrence. (Illustrated): Early Devonian, Brazil (Dino and Rodrigues, 1995; Melo and Loboziak, 2003; Rubinstein *et al.*, 2005). Early-Middle Devonian, Bolivia (McGregor, 1984).

Dictyotriletes trivialis Naumova in litt.
in Kedo 1963
Figure 11.M

Occurrence. First record for the Early Carboniferous of South America.

Genus *Emphanisporites* McGregor 1961

Type species. *Emphanisporites rotatus* McGregor, 1961.

Emphanisporites annulatus McGregor 1961
Figure 7.K

Occurrence. (Illustrated): Early-Middle Devonian, Brazil (Loboziak *et al.*, 1992; Dino, 1999; Loboziak and Melo, 2002; Melo and Loboziak, 2003), Bolivia (McGregor, 1984). Middle Devonian, Argentina (Rubinstein, 1999).

Emphanisporites rotatus McGregor 1961 *emend.*
McGregor 1973
Figures 7.N-Ñ

Remarks. A few specimens of *E. rotatus* seem to be transitional to *E. mcgregorii* Cramer 1967 by showing some ridges arranged in a chevron pattern along one of the arms of the laesurae. *E. hibernicus* Clayton, Higgs and Keegan has thin ridges that mainly arise from the arms of the suturae, forming a chevron structure and only scarce ridges can merge from the pole.

Occurrence. (Illustrated): Late Silurian-Late Devonian, Bolivia (McGregor, 1984; Vavrdová *et al.*, 1996). Early-Late Devonian, Argentina (Ottone, 1996; Le Hérissé *et al.*, 1997), Paraguay (Menéndez and Pöthe de Baldi, 1967), Brazil (Loboziak *et al.*, 1988; Dino

and Rodrigues, 1995; Dino, 1999; Melo and Loboziak, 2003; Rubinstein *et al.*, 2005).

Emphanisporites hibernicus Clayton, Higgs
and Keegan 1977
Figure 10.Ñ

1987. *Emphanisporites* sp. Azcuy and Ottone, p. 248, pl. 2, fig. 10.

Occurrence. (Illustrated): Early Carboniferous, Bolivia (Azcuy and Ottone, 1987, as a reworked form).

Genus *Microreticulatisporites* (Knox) Potonié
and Kremp 1954

Type species. *Microreticulatisporites lacunosus* (Ibrahim) Knox, 1950
(by subsequent designation of Potonié and Kremp, 1954).

Microreticulatisporites parvirugosus Staplin 1960
Figure 11.D

Occurrence. (Illustrated): Viséan, Perú (Azcuy and di Pasquo, 2005).

Gen. et sp. indet.
Figures 11.N-Ñ

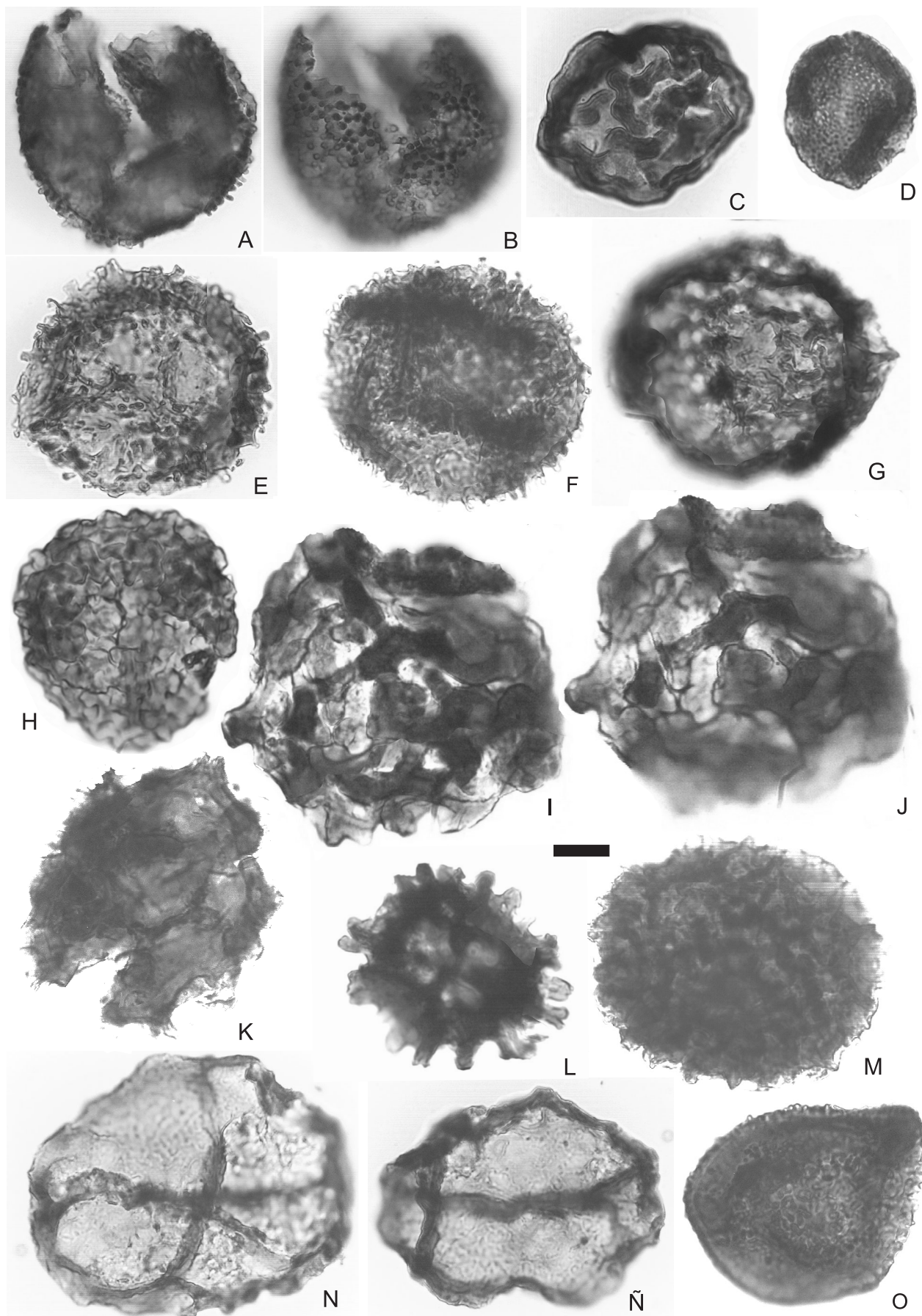
Studied material. BAFC-PI 1506 (1): L22/4, T21/2, T27, W30/2, X20/4, U21/2; BAFC-PI 1506 (2): Q57/1; BAFC-PI 1506 (3): Q37; BAFC-PI 1506 (4): H30/2, F36; E37/3, S41; BAFC-PI 1506 (5): E48/4, F28, P49, Y28/2; BAFC-PI 1501 (1): D23/0-3; BAFC-PI 1502 (3): D23.

Description. Spore acamerate, with subcircular to oval amb. Laesurae indistinct (alete?). Proximal and distal face with few straight folds, 4.6-8.2 µm wide and extended to the full length of the spore. The margin is thickened, around 2-6 µm in width. The folds on both faces run more or less perpendicular to each other, and join at the marginal limbus. At these points the fold ends originate curvaturae-like features. Exine relatively thin and chagrinata.

Dimensions (18 specimens). Equatorial diameter 64-106.7 µm.

Remarks. This species differs from others because

Figure 11. Acavate spores from the Malimán Formation. Scale bar: 15 µm (x 750). Coordinates after EF (England Finder) graticule / esporas acavadas de la Formación Malimán. Escala gráfica: 15 µm (x 750). Las coordenadas corresponden a la reglilla EF (England Finder). **A-B**, *Schopfites claviger* (Sullivan) *emend.* Higgs, Clayton and Keegan. BAFC-PI 1504 (2): D33/2. **C**, *Convolutispora insulosa* Playford. BAFC-PI 1508 (1): V22. **D**, *Microreticulatisporites parvirugosus* Staplin. BAFC-PI 1502 (4): X34. **E-F**, *Raistrickia gemmifera* Playford and Satterthwait; **E**, BAFC-PI 1508 (4): Y42/4; **F**, BAFC-PI 1508 (5): Z33. **G**, *Convolutispora varicosa* Butterworth and Williams. BAFC-PI 1655 (2): R31/2. **H**, *Convolutispora* sp. cf. *C. usitata* Playford, BAFC-PI 1508 (3): G28/1. **I-J**, *Convolutispora* sp. cf. *C. circumvallata* Clayton. BAFC-PI 1501 (1): Z33. **K**, *Cordylosporites marciae* Playford and Satterthwait. BAFC-PI 1503 (1): Z53/2. **L**, *Cordylosporites spathulatus* (Winslow) Playford and Satterthwait. BAFC-PI 1506 (1): J26/2. **M**, *Dictyotriletes trivialis* Naumova in litt. in Kedo. BAFC-PI 1506 (1): S23. **N-Ñ**, Gen. et sp. indet; **N**, BAFC-PI 1506 (2): Q57/1; **Ñ**, BAFC-PI 1506 (1): T27. **O**, *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin and Malloy. BAFC-PI 1504 (2): Q39/2.



they have a marginal fold with two sets of one to three folds each, that are present on both faces generally perpendicularly distributed. Germinal aperture not visible.

Comparisons. *Plicatispora* Higgs, Clayton and Keegan 1988 has distinct laesurae, simple or with labra, and folds, wrinkles, rugulae and fine muri only on the distal face.

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