

# Late Silurian palynomorphs from the Precordillera of San Juan, Argentina: Diversity, palaeoenvironmental and palaeogeographic significance

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The palynological content from the Cerro La Chilca and Quebrada Ancha sections of the Wenlock? to Přídolí Los Espejos Formation, in the Argentinean Precordillera is studied. The marine palynomorphs exhibit higher relative abundance and diversity in almost all the productive samples, except for the uppermost ones from both sections, in coincidence with the shift towards more proximal facies in this part. The Los Espejos Formation yielded a total of 114 species of marine organic walled-phytoplankton, 52 species of miospores and two non-marine phytoplankton species. The lower part of the Los Espejos Formation, dated as Ludfordian, displays the highest phytoplankton diversity and the better-preserved palynomorphs of the studied samples in both sections. Diversity tends to diminish towards the upper part of the Los Espejos Formation, dated as late Ludfordian–Přídolí, in coincidence with the transition to storm-dominated shelf and shoreface environments and subaerial exposures that probably hinder the preservation of palynomorphs. Comparisons with coeval phytoplankton assemblages from Gondwana and other palaeoplates such as Laurentia, Baltica, and Avalonia result in strong similarities, which suggest a cosmopolitan distribution pattern during the Ludlow and the Přídolí. Conversely, the trilete spores display more similarities with those from Gondwana and thus suggest a lesser dispersive potential in comparison to phytoplankton. A new trilete spore species *Emphanisporites? tenuis* is described.

Key words: Organic walled-phytoplankton, miospores, abundance, diversity, palaeoenvironment, palaeobiogeography, Silurian, Argentina.

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## Introduction

The Silurian was considered a relatively stable period, however, in the last decades, several short periods of environmental changes that re-modeled the palaeoceanographic conditions, such as the alternating between humid and arid climates, and oxygen and sulfur cycle variations, were recognized (Munnecke et al. 2003, 2010 and references therein). Accordingly, diversity changes in several marine groups, such as conodonts, graptolites, brachiopods, acritarchs, and chitinozoans were observed (e.g., Jeppsson 1990; Calner 2005, 2008; Lehnert et al. 2007a; Vandenbroucke et al. 2015).

The fossiliferous content of the Los Espejos Formation

(Cuerda 1965), including different groups such as graptolites, conodonts, brachiopods, organic-walled phytoplankton, and miospores, has been studied since the 1960s (e.g., Cuerda 1969; Pöthe de Baldis 1974b; Hünicken and Sarmiento 1988; Sánchez et al. 1991, 1995; Benedetto et al. 1992, 1996; Rubinstein 1992a, b, 1995; Rickards et al. 1996; Rubinstein and Brussa 1999). However, biostratigraphically useful fossils, for instance graptolites and conodonts, are scarce and were recorded from isolated fossiliferous levels. The age of the Los Espejos Formation was interpreted, mainly based on brachiopod faunas, as probably Wenlock, mainly Ludlow, Přídolí and up to early Lochkovian in the northernmost outcrops of the stratigraphic unit (Sánchez et al. 1991; Benedetto et al. 1992). A review and update of

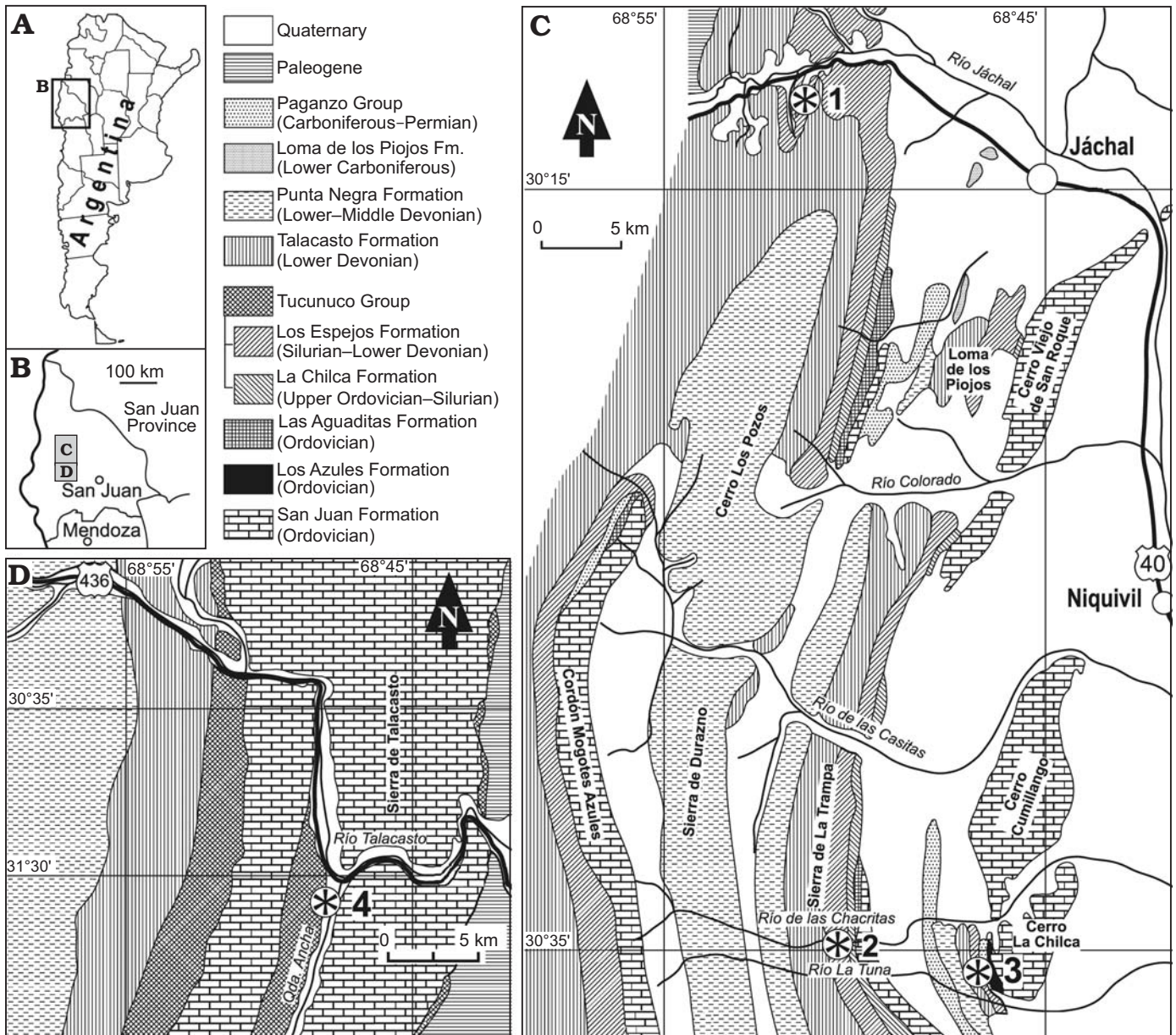


Fig. 1. **A, B.** Geographic location of study areas. **C, D.** Geologic maps showing the fossil localities (asterisks). The northern and middle (**C**) and southern (**D**) part of the Silurian–Devonian Basin. 1, Río Jáchal; 2, Río de las Chacritas; 3, Cerro La Chilca (this paper); 4, Quebrada Ancha (this paper).

the palynological information of the Los Espejos Formation was provided by Rubinstein and García Muro (2013).

Based on new palynological data from several sections throughout the basin, a more accurate biostratigraphic scheme was established for the Late Ordovician to Early Devonian of the Precordillera Basin. This new biostratigraphic proposal contributed to the recognition of the Silurian–Devonian boundary as well as to the series and stage boundaries previously located with uncertainty (García Muro et al. 2014a; García Muro and Rubinstein 2015).

Marine phytoplankton clearly dominates the palynological assemblages from the lower to the middle part of the Los Espejos Formation, which correspond to muddy shelf deposits with no influence of wave action.

Towards the top of the unit, dated as latest Silurian–Early Devonian, the relative abundance of marine palynomorphs tends to decrease while the miospore relative abundance increases until their predominance in the uppermost productive levels in coincidence with the nearshore environment (Rubinstein and García Muro 2011; García Muro et al. 2014a, b).

From a palaeogeographic point of view, the marine phytoplankton from the Los Espejos Formation points to a cosmopolitan distribution pattern (Rubinstein 1993; Rubinstein and García Muro 2013). Based on studies of the La Chilca Formation, in the Precordillera Basin, the cosmopolitanism of the marine palynomorph assemblages was also suggested for the early Silurian (García Muro et al. 2016), when provincialism of marine palynomorphs was assumed to pre-

vail (e.g., Le Herissé and Gourvenec 1995). On the other hand, the terrestrial palynomorph assemblages, especially the trilete spores of the Los Espejos Formation, have more species in common with assemblages from other Gondwana basins located closer to the Precordillera (García Muro et al. 2014b).

The aim of this work is to comprehensively present and analyse the well-preserved organic-walled phytoplankton and miospores from two sections of the Los Espejos Formation, situated at the Cerro La Chilca and the Quebrada Ancha localities; to evaluate the diversity trends in relation to the local palaeoenvironment; and to correlate the studied assemblages with worldwide coeval palynological assemblages enabling palaeobiogeographical inferences. Moreover, many species are herein reported for the first time from Argentina and also from Gondwana, therefore providing new insights regarding palynomorph distribution patterns.

*Institutional abbreviations.*—IANIGLA, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina; CCT, Centro Científico Tecnológico, Mendoza, Argentina; CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas; FNRS, Fonds National de la Recherche Scientifique, Liège, Belgium; MPLP, Mendoza-Paleopalintoteca-Laboratorio de Paleopalintología, IANIGLA, Mendoza, Argentina.

## Geological setting

The active margin of Western Gondwana was affected by the Cuyania terrane accretion during the Mid–Late Ordovician (Benedetto 2010 and references therein). This collision greatly influenced the subsequent Silurian and Devonian deposits of the Central Precordillera of San Juan, resulting in the formation of the Talacasto-Tambolar arch. The stratigraphic units wedged towards this arch and important interruptions of sedimentation took place (Astini et al. 1995).

The Silurian to Lower Devonian rocks of the Central Precordillera crop out with a north-south arrangement. They are represented in the Tucunuco Group, which is composed of the lower La Chilca Formation and the upper Los Espejos Formation (Fig. 1). The thickness of the Los Espejos Formation reaches 500–600 m in the northern Jáchal area and decreases southwards down to 50 m near the Río San Juan (Sánchez et al. 1991; Astini and Maretto 1996; Benedetto et al. 1996). A transgressive to high sea-level stand history was interpreted for the unit based on the presence of a thin iron veneer and phosphate-rich chert conglomerate at the base succeeded by shaly intervals deposited in a low energy open shelf. Upward, the stratigraphic unit gets thicker and coarser, what is consistent with the transition to a storm-dominated inner shelf to shoreface environment (Sánchez et al. 1991; Astini and Maretto 1996; Benedetto et al. 1996).

## Material and methods

The studied areas are located at Cerro La Chilca and Quebrada Ancha, in the middle and southern part of the Silurian–Devonian basin, respectively (Fig. 1). The samples from the Cerro La Chilca section (30°36'3,1" S; 68°47'32,2" W) were collected from the olive-green pelite of the lower 12 m of the Los Espejos Formation (Fig. 2) principally to constrain the age of the contact with the underlying La Chilca Formation (García Muro and Rubinstein 2015).

In the Quebrada Ancha locality (31°2'13" S; 68°45'55.33" W), two sections corresponding to the lower and upper parts of the stratigraphic unit were sampled to accurately date the lower and upper contacts with the La Chilca Formation and the Talacasto Formation, respectively. The lower 27 m of the unit comprise pelitic sediments that represent a low-energy open shelf environment (Fig. 3B, C). The upper 8 m, below the top of the unit (Fig. 3A), consist of pelitic sediments with intercalated sandstone and shell beds related to storm-dominated shelf and shoreface environments (Sánchez et al. 1991; Astini and Maretto 1996).

Seven samples were collected from the Cerro La Chilca section and 18 from the Quebrada Ancha section. Almost all the samples proved to be productive, except for the uppermost four from the upper Quebrada Ancha section (Figs. 2, 3).

The samples were prepared at the Palynology Laboratory of the University of Liège (Belgium). The rock samples were treated with HCl-HF-HCl acid maceration techniques (Traverse 2007). The residues were oxidized with 60% of Schulze solution ( $\text{HNO}_3 + \text{KClO}_3$ ) for two hours and then screened on a 12  $\mu\text{m}$  sieve.

A minimum of 250 specimens per sample was counted in order to obtain the relative abundance of the different palyno-

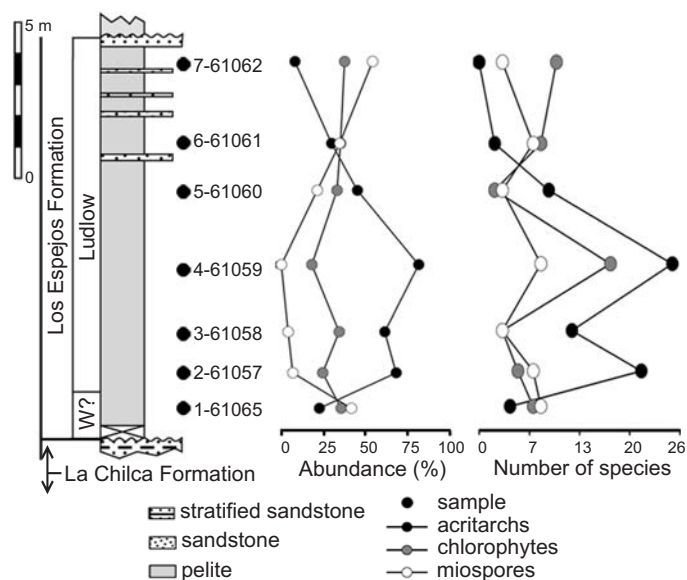
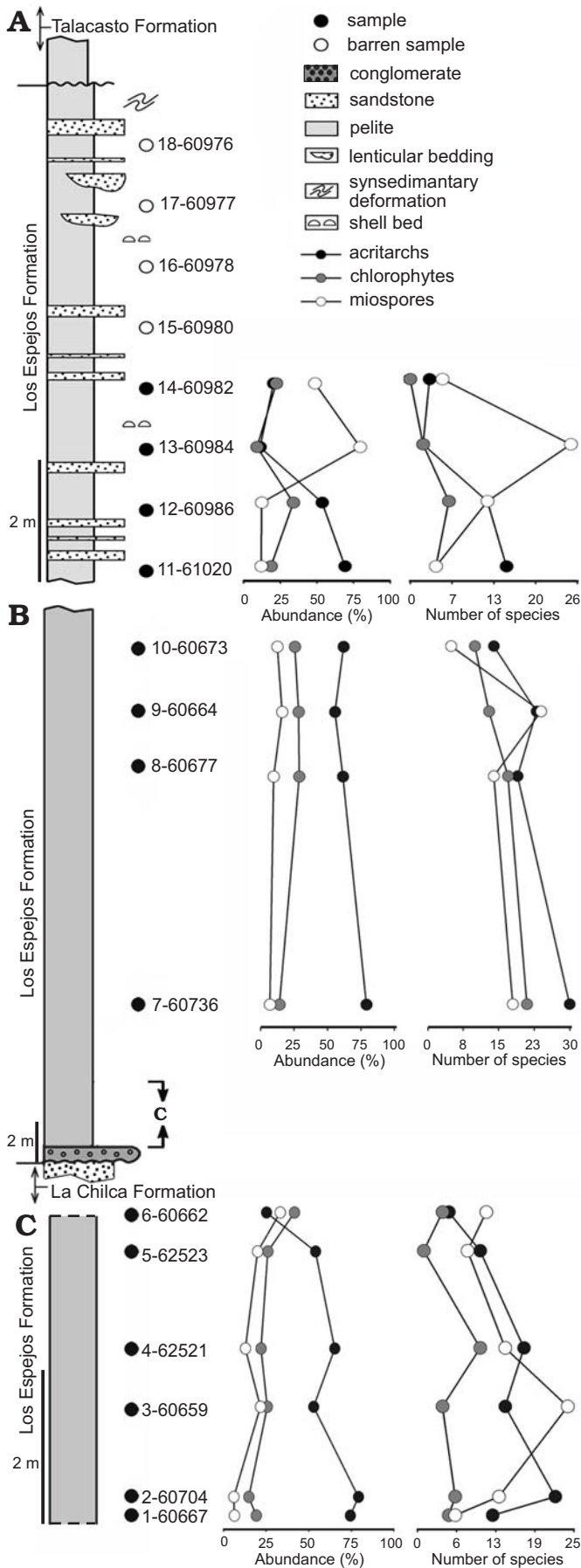


Fig. 2. Stratigraphic section of the Los Espejos Formation in Cerro La Chilca, showing relative abundance (%) and diversity (number of species) of acritarchs, chlorophytes, and miospores per sample. W?: Wenlock?



morph groups throughout the section and compare fluctuations in palynomorph distribution with changes in the depositional environment (De Vernal et al. 1987; Vecoli et al. 2009).

The comparison of the Quebrada Ancha and the Cerro La Chilca palynomorph assemblages with coeval assemblages from Gondwana and other palaeoplates, such as Armorica, Avalonia, Baltica, and Laurentia enabled the identification of species in common and the consequent recognition of palaeobiogeographic trends. Selected phytoplankton and miospore assemblages were plotted on a palaeogeographical reconstruction using BugPlates software (Torsvik 2009) at 424 My and subsequently improved in graphic software.

The terrestrial palynomorphs of the Los Espejos Formation from the Quebrada Ancha locality were published in detail in García Muro et al. (2014b). In the present contribution, special emphasis is therefore placed on the marine palynomorphs.

The organic-walled phytoplankton and the miospore taxa from both sections of the Los Espejos Formation are alphabetically listed and ordered in the Appendix 1 according to Le Hérissé et al. (2009) and Wellman et al. (2015). Some remarks are provided in case of doubtful assignments or differences with the original diagnosis of the species. The stratigraphic distribution of the recorded species is provided by section and level in the SOM (Supplementary Online Material available at [http://app.pan.pl/SOM/app63-Garcia-Muro\\_etal\\_SOM.pdf](http://app.pan.pl/SOM/app63-Garcia-Muro_etal_SOM.pdf)). All the species are illustrated in Figs. 5–11, except those taxa already illustrated for the Quebrada Ancha and Cerro La Chilca sections (García Muro et al. 2014b; García Muro and Rubinstein 2015) and some taxa left in open nomenclature.

The palynological slides are housed in the palaeopalynological collection MPLP (Mendoza-Paleopalintoteca-Laboratorio de Paleopalintología) at IANIGLA, CCT CONICET Mendoza, Argentina. Specimen locations are referred to by using England Finder coordinates between brackets.

## Results

The marine phytoplankton is more diverse than the miospores in most of the samples from the studied sections at Cerro La Chilca and Quebrada Ancha. In samples MPLP 4-61059 from the Cerro La Chilca section and MPLP 7-60736 from the Quebrada Ancha section, the highly diverse and exceptionally well-preserved assemblages compared to the general preservation of the Silurian and Devonian palynomorphs from the Argentinean Precordillera, are of special interest. The samples from the Cerro La Chilca section contained a total of 44 species of acritarchs, 24 of chlorophytes, 19 of miospores and two non-marine phytoplankton species (Fig. 2). The lower part of the Quebrada Ancha section

Fig. 3. Stratigraphic section of the Los Espejos Formation in the Quebrada Ancha area upper (A) and lower (B, C) parts, showing relative abundance (in %) and diversity (number of species) of acritarchs, chlorophytes, and miospores per sample.

yielded the most diversified assemblages, with 71 species of acritarchs, 39 of chlorophytes, 49 of miospores, and one of non-marine phytoplankton (Fig. 3B, C). With 19 species of acritarchs and 9 of chlorophytes as well as 28 of miospores denoting an important increase of terrestrial influence, the upper part of the Quebrada Ancha section yielded relatively poorly preserved palynomorphs compared to the lower part of the section (Fig. 3A).

The organic-walled phytoplankton exhibits higher abundance than the terrestrial palynomorphs in most samples from both localities. Miospores become dominant towards the top of the sections, what is consistent with previous sedimentological and palaeoenvironmental studies that indicate a shallowing trend upward the sequence.

Some levels reveal higher relative abundance of terrestrial palynomorphs even though there are no evident changes in the sedimentary record, for instance an increase of terrestrial input, which could explain this variation between marine and terrestrial palynomorph abundances. Such is the case of sample MPLP 1-61065 in the Cerro La Chilca section and sample MPLP 6-60662 in the Quebrada Ancha section (Figs. 2, 3B, C).

The comparison of the marine phytoplankton from both sections of the Los Espejos Formation with coeval assemblages (Table 1, Fig. 4) indicates that more than half of the species are shared with Avalonia (e.g., Mullins 2001 and references therein; Richards and Mullins 2003) and Baltica (e.g., Porębska et al. 2004; Stricanne et al. 2006). Around 20% of the species are common to Armorica (e.g., Cramer 1964a) and Laurentia (e.g., Cramer 1970; Mullins 2001 and references therein), and almost 30%, to other Gondwanan regions (e.g., Le Hérisse et al. 1997; Cardoso 2005). On the other hand, the miospore assemblages of the Precordillera share more species with coeval assemblages from other Gondwanan and peri-Gondwanan areas such as North Africa, Brazil, and Spain (e.g., Richardson et al. 2001; Rubinstein and Steemans 2002; Steemans et al. 2008). Besides, the Cerro La Chilca and Quebrada Ancha studied sections yielded 12 species of phytoplankton which were recognized for the first time for Gondwana. *Ammonidium marvillosum*, *Cymatiosphaera acuminata*, *Cymatiosphaera lawsonii*, *Dilatisphaera cf. williereae*, and *Helosphaeridium malvernense* were previously recorded only from Avalonia and Baltica (Cramer 1970; Lister 1970; Dorning 1981; Mullins 2001).

Table 1. Marine and terrestrial taxa (in %) from the Los Espejos Formation (Precordillera Argentina) also present in coeval palaeoplates worldwide and in other Gondwanan localities.

	Marine palynomorphs	Terrestrial palynomorphs
Armorica	19.81	38.46
Avalonia	53.77	38.46
Baltica	59.43	33.33
Gondwana	27.35	56.41
Laurentia	20.75	17.94

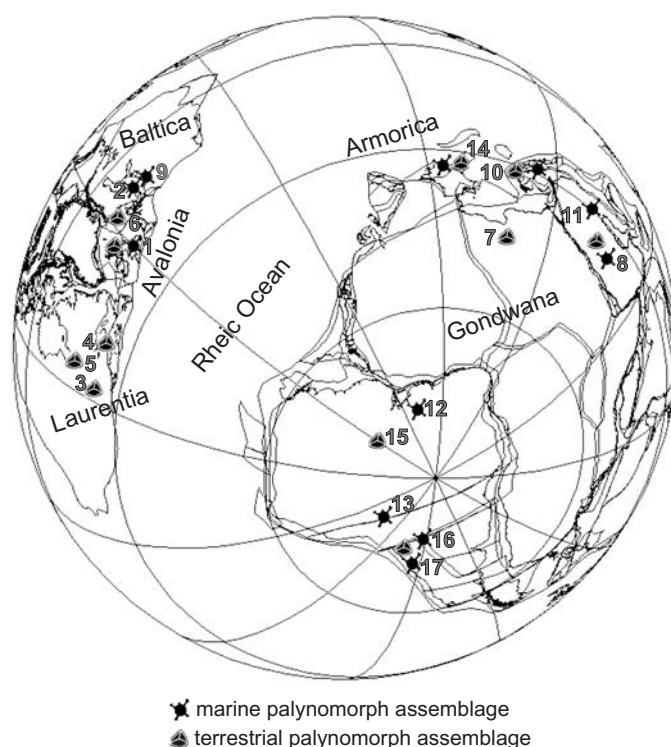


Fig. 4. Ludlow–Přidolí (424 My) phytoplankton and miospore assemblages plotted on a palaeogeographic reconstruction using BugPlate software (Torsvik 2009). 1, UK (Richardson and Lister 1969; Lister 1970; Richardson et al. 1981; Burgess and Richardson 1995; Wellman and Richardson 1996; Richards and Mullins 2003; Mullins 2001, 2004); 2, Gotland, Sweden (Stricanne et al. 2004; Stricanne et al. 2006); 3, Allenport, USA (Beck and Strother 2008); 4, Nova Scotia, Canada (Beck and Strother 2001); 5, Ontario, Canada (McGregor and Camfield 1976); 6, Sweden (Mehlqvist et al. 2012; Mehlqvist et al. 2014); 7, Libya (Richardson and Ioannides 1973; Rubinstein and Steemans 2002; Le Hérisse 2002); 8, Saudi Arabia (Le Hérisse et al. 1995; Wellman et al. 2000; Breuer et al. 2017); 9, Poland (Porębska et al. 2004); 10, Turkey (Stemans et al. 1996; Lakova and Göncüoğlu 2005); 11, Iraq (Al-Almeri 1984; 2010); 12, Maranhão Basin, Brazil (Brito 1967); 13, Bolivia (Cramer et al. 1974; Kimyai 1983; Racheboeuf et al. 2012); 14, Spain and West France (Rodríguez González 1978; 1983; Steemans 1989; Cramer 1964a; Richardson et al. 2001); 15, Amazon Basin, Brazil (Cardoso 2005; Steemans et al. 2008); 16, Santiago del Estero, Argentina (Pöthe de Baldis 1974a); 17, Precordillera Argentina (Rubinstein 1992a, b, 1995; García Muro et al. 2014b; this contribution). References discussed in the papers are also included.

## Systematic palaeontology

### Marine Chlorophytes

#### Prasinophytes

#### Genus *Melikeriopalla* Tappan and Loeblich, 1971

*Type species: Melikeriopalla amydra* Tappan and Loeblich, 1971; Waldron Formation, Indiana, USA; Wenlock.

#### *cf. Melikeriopalla* sp.

Fig. 9A–F.

*Material.*—14 specimens measured. Samples MPLP 1-61065 (U47/2, W30/3); MPLP 3-61058 (L33); MPLP

6-61061 (M31/3); MPLP 7-61062 (D39, D45/3, P43/3, P50/3); MPLP 2-60704 (L26/4); MPLP 3-60659 (F38/3, R38/1); MPLP 4-62521 (T40/4, T40/4); MPLP 6-60662 (J25/2). Vesicle divided into fields by muri. Homerian–Ludfordian of Argentina. Cerro La Chilca and Quebrada Ancha localities, Los Espejos Formation.

*Description.*—Vesicle square to sub-spherical, divided into 6–13 polygonal fields by thick muri. Each field is ornamented by a ring and/or a granum; when both are present the granum is located in the center of the ring.

*Dimensions.*—Vesicle 16–(23)–30  $\mu\text{m}$ , fields 6–(9)–12  $\mu\text{m}$ , muri high 0.3–1  $\mu\text{m}$ , grana high 0.5–(1)–3  $\mu\text{m}$ , grana diameter 1–(3)–5  $\mu\text{m}$ , rings high 0.3–(0.5)–1  $\mu\text{m}$ , rings thick 0.5–(1.5)–3  $\mu\text{m}$  (14 specimens measured; number in brackets is the mean value).

*Discussion.*—According to the emended diagnosis of Mullins (2001), in the centre of each field a circular node beneath which a pore may or may not be present. Because of the poor preservation, the pore cannot be observed in the specimens from the Los Espejos Formation. The genus was assigned with doubts because no ring was described for *Melikeriopalla*.

## Non-marine palynomorphs

### Zygnemataceae

#### Genus *Clypeolus* Miller, Playford, and Le Hérisse, 1997

*Type species:* *Clypeolus tortugaides* (Cramer, 1966a) Miller, Playford, and Le Hérisse, 1997; León, Spain; Llandovery.

#### *Clypeolus tortugaides* (Cramer, 1966a) Miller, Playford, and Le Hérisse, 1997

Fig. 50.

*Material.*—One specimen recorded. Sample 4-62521 (V42/2). Subcircular vesicle, divided in fields by the concavo-convex wall. Ludfordian of Argentina. Quebrada Ancha locality, Los Espejos Formation.

*Remarks.*—It is considered as a fresh water palynomorph, from transitional marine-freshwater environment (Le Hérisse et al. 2013). The specimen from the Los Espejos Formation constitutes the first record of South America.

*Stratigraphic and geographic range.*—It was only recognized in the Upper Ordovician of Chad (Le Hérisse et al. 2013) and Canada (Delabroye et al. 2011), in the middle Llandovery of Saudi Arabia and in the Silurian of Spain (Miller et al. 1997 and references therein).

## Trilete spores

### Genus *Emphanisporites* McGregor, 1961

*Type species:* *Emphanisporites rotatus* (McGregor, 1961) emend. McGregor, 1973; Quebec, Canada; Lower Devonian.

#### *Emphanisporites? tenuis* sp. nov.

Fig. 11K–N.

1981 *Emphanisporites* sp. D; Richardson et al. 1981: 215, pl. 1.3.

2008 *Emphanisporites* sp. D Richardson, Rasul, and Al-Ameri, 1981; Steemans et al. 2008: 274, figs. 8–10.

2014 *Emphanisporites* sp. D Richardson et al. 1981; García Muro et al. 2014b: 485, fig. 8f.

2015 *Emphanisporites* sp. D Richardson et al. 1981; García Muro and Rubinstein 2015: 272, fig. 3.7.

*Etymology:* From Latin *tenuis*, tenuous; in references to the characteristic thin ribs.

*Type material:* Holotype: MPLP 13-60984 (N30/2) (Fig. 11K). Paratype: MPLP 2-61065 (Q42) (Fig. 11L) from Cerro La Chilca section.

*Type locality:* Quebrada Ancha upper section, Los Espejos Formation, San Juan, Argentina (Fig. 1D, 4).

*Type horizon:* Storm-dominated inner shelf environment of the Los Espejos Formation, Pírdolí.

*Material.*—Seven specimens measured. Samples MPLP 1-61065 (O28/3); MPLP 2-61057 (O47/1; Q42/1, U27); MPLP 2-60704 (K38/4), MPLP 9-60664 (S28), MPLP 10-60673 (J23/1). Wenlock?–Pírdolí of Argentina, Cerro La Chilca and Quebrada Ancha localities, Los Espejos Formation.

*Diagnosis.*—Trilete patinate spore with numerous tenuous ribs on the proximal face.

*Description.*—Trilete patinate spore with subtriangular to subcircular amb. The thickness of the patina is variable. Laesure straight, extends to the equator, accompanied by labra about 2–4  $\mu\text{m}$  in overall width. Equatorially thickened, 2–4  $\mu\text{m}$  wide. Proximally, 18–26 ribs of less than 1  $\mu\text{m}$  of width per interradial area, extending to the patina.

*Dimensions.*—42–(50)–55  $\mu\text{m}$  (7 specimens measured).

*Remarks.*—Other species of *Emphanisporites* differ in presenting broader radial ridges and having no patina. *Artemopyra inconspicua* Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans, and Wellman, 2007 is ornamented by similar thin radial ribs in the hilum but lacks the trilete mark and the patina. According to the original diagnosis of McGregor (1961), the genus *Emphanisporites* does not comprise patinate forms. Possibly, a new genus should be considered for the specimens included in *Emphanisporites? tenuis* although the specimens are not enough to create it in the present contribution.

*Stratigraphic and geographic range.*—Richardson et al. (1981) recorded *Emphanisporites* sp. D from the late Ludlow of Libya and the early Pírdolí of England and Wales but did not describe the species and the latter was not even illustrated. Lochkovian of the Amazon Basin, Brazil (Steemans et al. 2008). Wenlock? to Pírdolí of the Precordillera, Argentina (García Muro et al. 2014b; García Muro and Rubinstein 2015).

## Indeterminate organic-walled phytoplankton

Fig. 11I.

*Material.*—One specimen recorded. Sample 4-61059 (G35/4). Ludfordian of Argentina. Cerro La Chilca locality, Los Espejos Formation.

*Description.*—Spherical vesicle with granulated wall, en-

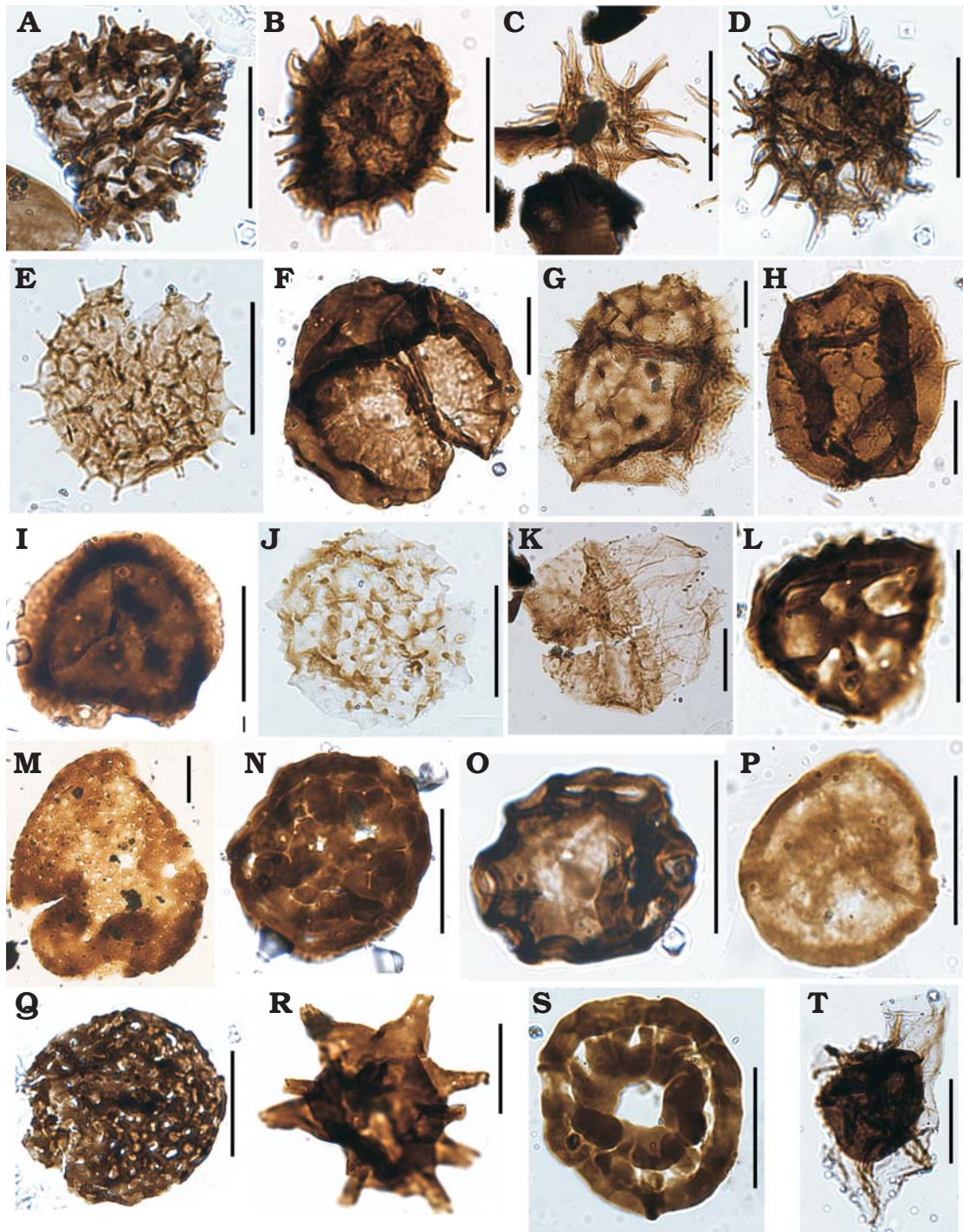


Fig. 5. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, Quebrada Ancha, Gorstian?–Ludfordian? (A, T), Quebrada Ancha, Ludfordian (B–F, H–K, N, O, Q, R), Cerro La Chilca, Ludfordian (G, L, M, P, S). **A.** *Ammonidium cornuatum* Loeblich and Wicander, 1976; MPLP 8-60677 (H27/3). **B.** *Ammonidium ludoviense* (Dorning, 1981) Mullins, 2001; MPLP 2-60704 (T22/2). **C.** *Ammonidium maravillosum* (Cramer, 1969) Thusu, 1973a; MPLP 7-60736 (S29/1). **D.** *Ammonidium waldronense* (Tappan and Loeblich, 1971) Dorning, 1981; MPLP 8-60677 (T50/2). **E.** *Ammonidium* sp. A in Mullins 2001; MPLP 7-60736 (N27/1). **F.** Indetermined miospore, MPLP 8-60677 (O44/2). **G.** *Baculatireticulatus baculatus* Al-Ameri, 1984; MPLP 4-61059 (J45/4). **H.** *Baculatireticulatus* sp.; MPLP 7-60736 (N43/2). **I.** *Breconisporites* sp.; MPLP 8-60677 (U33). **J.** *Buedingiisphaeridium lunatum* Le Hérisse, 1989; MPLP 4-61059 (D47). **K.** *Carminella maplewoodensis* Cramer, 1968; slide MPLP 7-60736 (R26/2). **L.** *Chelinospora* cf. *cantabrica* Richardson, Rodríguez, and Sutherland 2001; MPLP 5-61060 (U38). **M.** *Chelinospora sanpetrensis* (Rodríguez, 1978) Richardson, Rodríguez, and Sutherland 2001; MPLP 7-61062 (C35). **N.** *Chelinospora verrucata* var. *verrucata* Morphon in García Muro et al., 2014b; slide MPLP 8-60677 (K43/1). **O.** *Clypeolus tortugoides* (Cramer, 1966a) Miller, Playford, and Le Hérisse, 1997; MPLP 4-62521 (V42/2). **P.** cf. *Concentricosisporites agradabilis* (Rodríguez, 1978) Rodríguez, 1983; MPLP 6-61061 (H45/1). **Q.** *Confossospora* sp.; MPLP 2-60704 (O42/1). **R.** *Cordobesia uruguayensis* (Martinez-Macchiavello, 1968) Pöthé de Baldis, 1977; MPLP 3-60659 (E46/4). **S.** *Coronaspora cromatica* (Rodríguez, 1978) Richardson, Rodríguez, and Sutherland, 2001; MPLP 4-61059 (Q28). **T.** *Cymatiosphaera acuminata* Mullins, 2001; MPLP 8-60677 (G48/3). Scale bars 20  $\mu$ m.

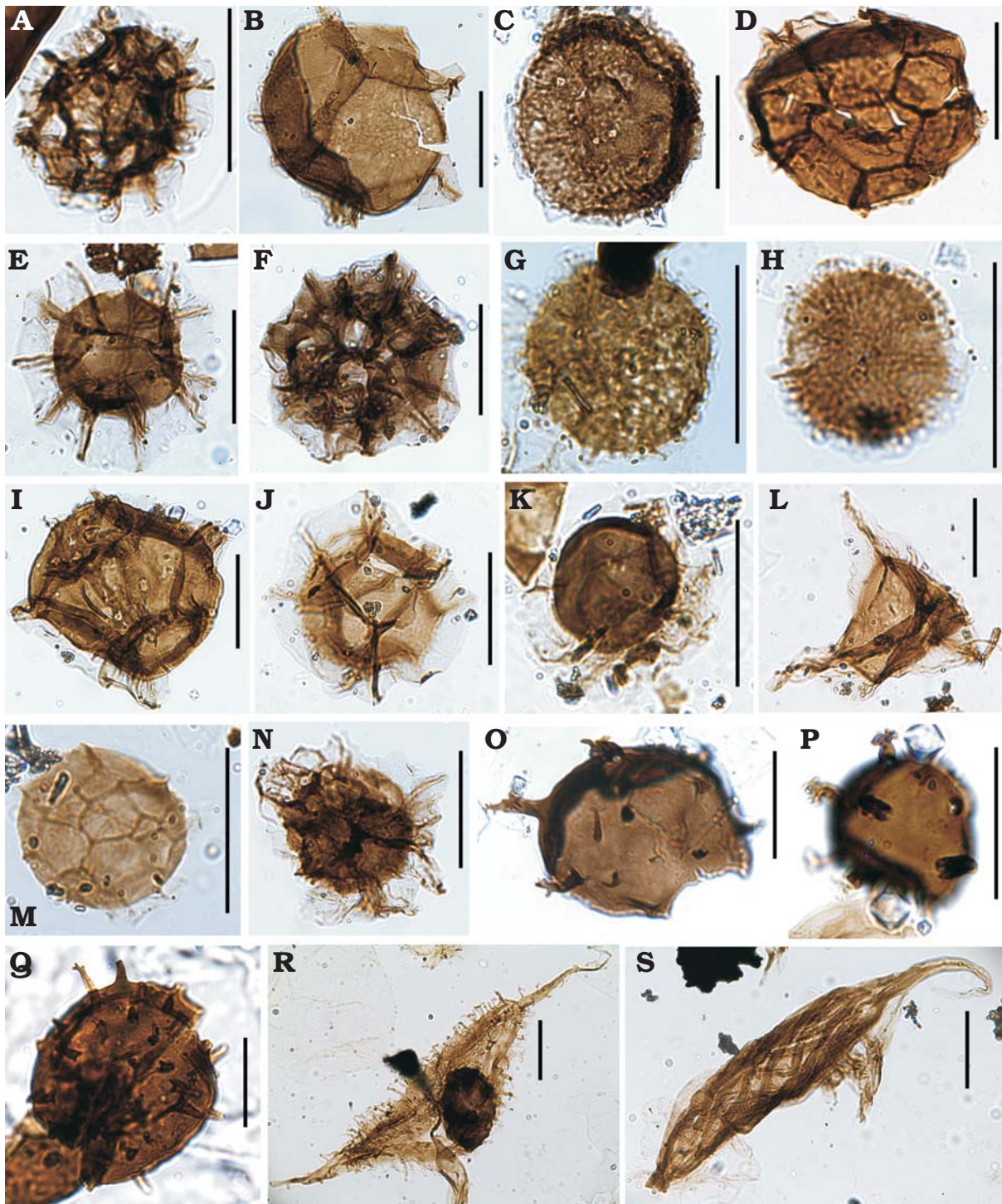


Fig. 6. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, Quebrada Ancha, Pírdoli (A, B, D, H, N), Quebrada Ancha, Ludfordian (C, E, F, I, J, L, O–Q), Cerro La Chilca, Ludfordian (G, K, M, R, S). A. *Cymatiosphaera* cf. *densisepta* Le Hérisse, 2000; MPLP 10-60673 (J43/1). B. *Cymatiosphaera heloderma* Cramer and Diez, 1972; MPLP 9-60664 (X27/2). C. *Cymatiosphaera jardinei* Cramer and Diez, 1976; MPLP 8-60677 (U51/3). D. *Cymatiosphaera lawsonii* Mullins, 2001; MPLP 9-60664 (O28/3). E. *Cymatiosphaera* aff. *ledburica* Mullins, 2001; MPLP 7-60736 (L41/2). F. *Cymatiosphaera* cf. *mirabilis* Deunff, 1959; MPLP 8-60677 (U50/1). G. *Cymatiosphaera multicristata* Mullins, 2001; MPLP 4-61059 (G28/2). H. *Cymatiosphaera* aff. *multisepta* Deunff, 1955, Mullins, 2001; MPLP 10-60673 (K46/3). I. *Cymatiosphaera nimia* Le Hérisse, 2002; MPLP 8-60677 (T50/1). J. *Cymatiosphaera octoplana* (Downie, 1959) Mullins, 2001; MPLP 7-60736 (Q32/2). K. *Cymatiosphaera paucimembranae* Mullins, 2001; MPLP 6-61061 (P36/2). L. *Cymatiosphaera prismatica* (Deunff, 1954) Deunff, 1961; MPLP 7-60736 (G47/2). M. *Cymatiosphaera salopensis* Mullins, 2001; MPLP 7-61062 (J38/3). N. *Cymatiosphaera* sp.; MPLP 10-60673 (E41/1). O. *Cymbosphaeridium carinosum* (Cramer, 1964a) Jardine, Combaz, Magloire, Peniguel, and Vachey, 1972; MPLP 2-60704 (T43). P. *Cymbosphaeridium pilar* (Cramer, 1964a) Lister, 1970; MPLP 4-62521 (D42/1). Q. *Cymbosphaeridium* sp. A Mullins, 2001; MPLP 8-60677 (T51/4). R. *Dactylofusa maranhensis* Brito and Santos, 1965; MPLP 4-61059 (G33/3). S. *Dactylofusa* cf. *striatogranulata* Jardiné, Combaz, Magloire, Peniguel, and Vachey, 1974; MPLP 4-61059 (L44). Scale bars 20  $\mu$ m.



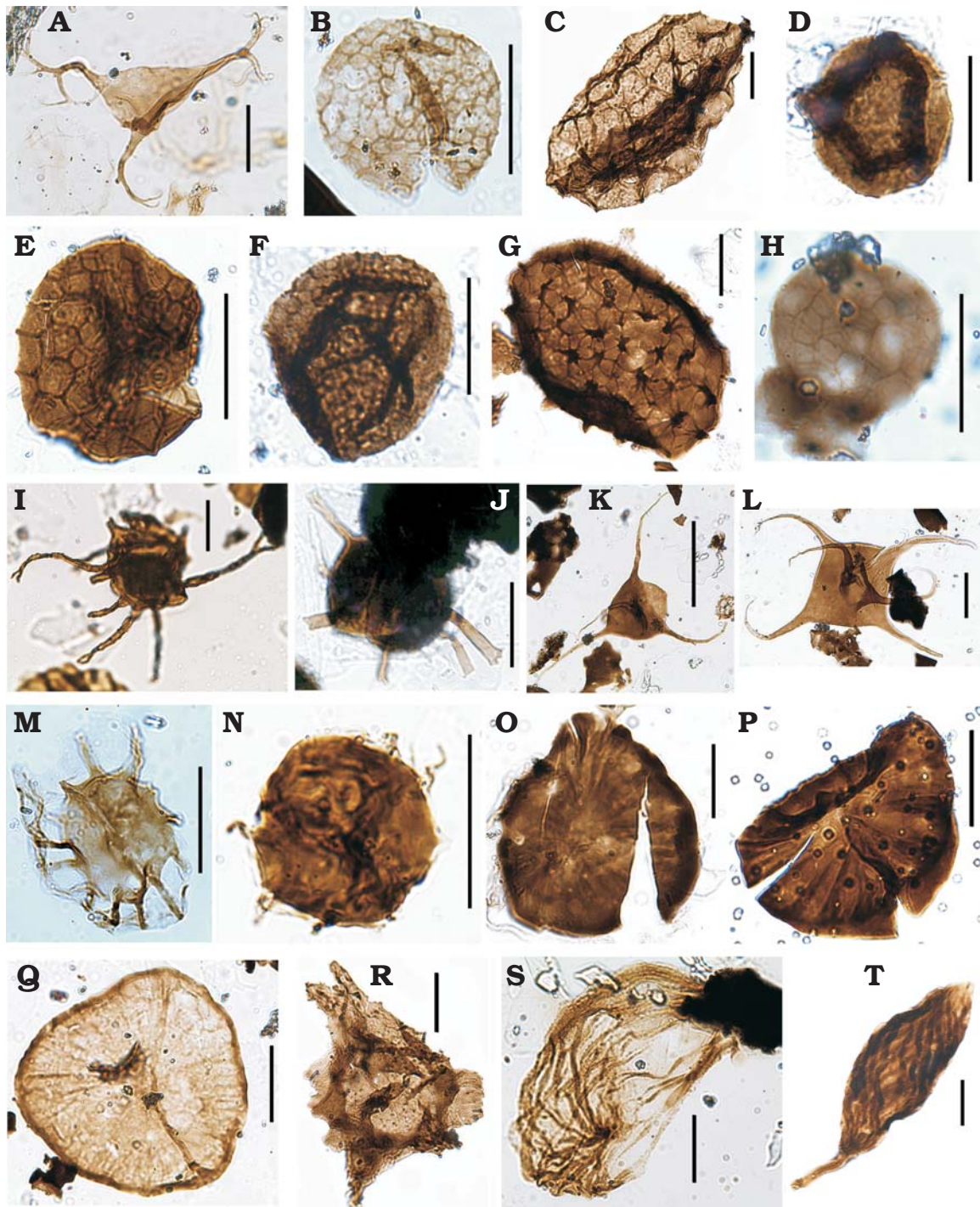


Fig. 7. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, from Cerro La Chilca, Ludfordian (A, M, O), Cerro La Chilca, Gorstian?–Ludfordian? (B, N, P, S), Quebrada Ancha, Ludfordian (C, D, F, H, J, K, L, Q, R), Quebrada Ancha, Přídolí (E, G, I), Quebrada Ancha, Gorstian?–Ludfordian? (T). **A.** *Dateriocradus lindus* (Cramer and Diez, 1976) Sarjeant and Vavrdová, 1997; MPLP 4-61059 (Q42/3). **B.** *Dictyotidium alveolatum* (Kiryanov, 1978) Le Hérisse, 1989; MPLP 2-61057 (O41). **C.** *Dictyotidium biscutulatum* Kiryanov, 1978; MPLP 7-60736 (Q27). **D.** *Dictyotidium callum* Al-Ruwaili, 2000; MPLP 3-60659 (P45/1). **E.** *Dictyotidium dictyotidium* (Eisenack, 1938) Eisenack, 1955; MPLP 12-60986 (J28/4). **F.** *Dictyotidium faviforme* Schultz, 1967; MPLP 2-60704 (H38/3). **G.** *Dictyotidium stellatum* Le Hérisse, 1989; MPLP 10-60673 (D39/3). **H.** *Dictyotidium tenuior-natum* Eisenack, 1955; MPLP 6-60662 (G25/1). **I.** *Diexallophasis remota* Group Mullins, 2001; MPLP 10-60673 (H34). **J.** *Dilatysphaera williereae* (Martin, 1966) Lister, 1970; MPLP 2-60704 (Q39/2). **K.** *Dorsennidium europaeum* (Stockmans and Willière, 1960) Mullins, 2001; MPLP 7-60736 (L34/4). **L.** *Dorsennidium pertonense* (Dorning, 1981) Sarjeant and Stancliffe, 1996; MPLP 7-60736 (U41). **M.** *Duvernaysphaera aranaides* (Cramer, 1964a) emend. Cramer and Diez, 1972; MPLP 4-61059 (C47/3). **N.** cf. *Eisenackidium argentinum* Pöthe de Baldis, 1997; MPLP 2-61057 (Q42). **O.** *Emphanisporites rotatus* (McGregor, 1961) McGregor, 1973; MPLP 4-61059 (W47/2). **P, Q.** *Emphanisporites* sp.; MPLP 2-61057 (Q42), MPLP 7-60736 (K43), respectively. **R.** *Estiastra barbata* (Downie, 1963) Sarjeant and Stancliffe, 1994; MPLP 8-60677 (X37/3). **S.** *Dactylofusa* sp.; MPLP 3-61058 (T35/3). **T.** *Eupoikilofusa* cf. *stratifera* (Cramer, 1964b) Cramer, 1970; MPLP 1-60667 (R48). Scale bars 20  $\mu$ m.

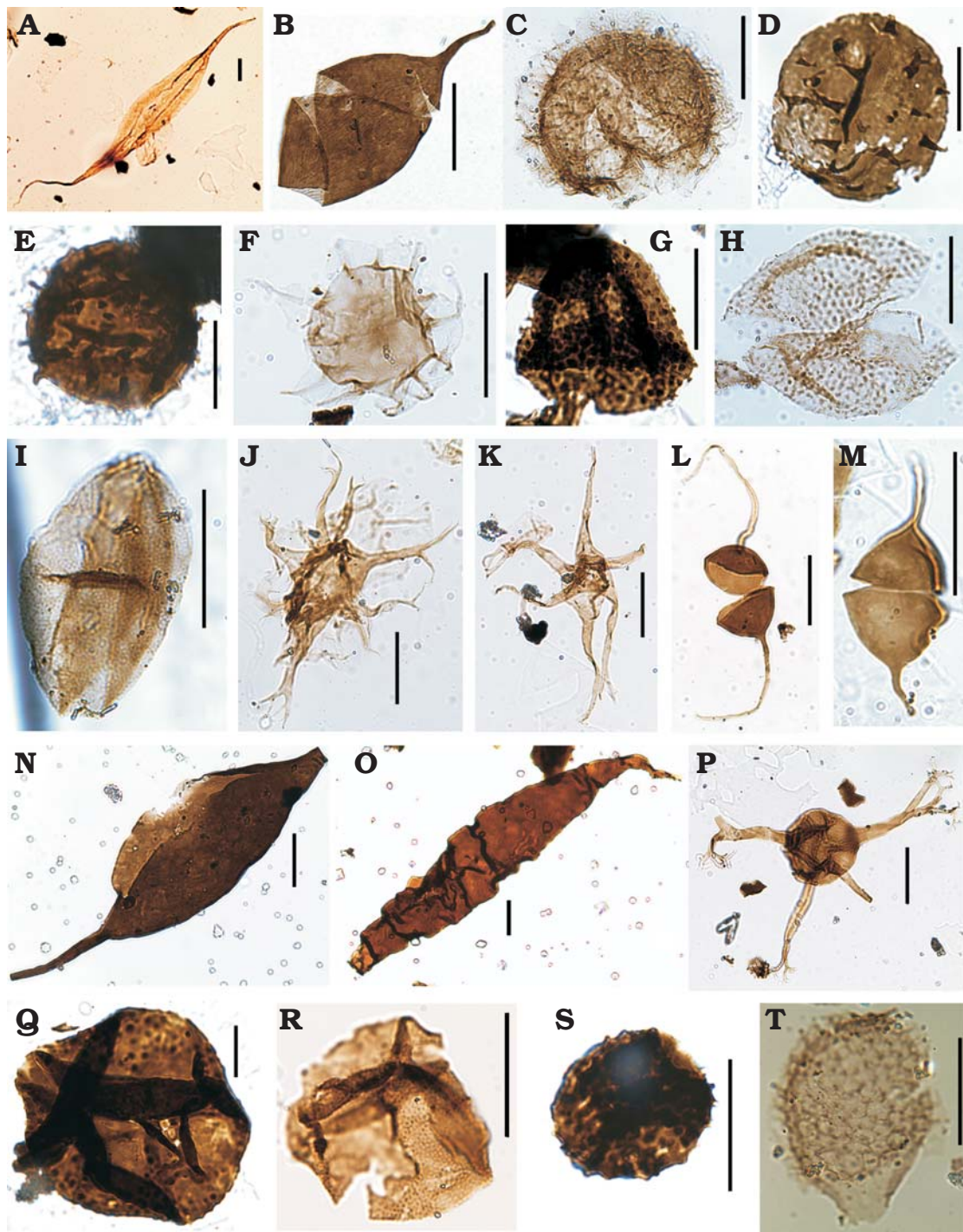


Fig. 8. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, Cerro La Chilca, Ludfordian (A), Quebrada Ancha, Pridoli (B, G, R, T), Quebrada Ancha, Ludfordian (C, E, F, H–L, N–P, S), Quebrada Ancha, Gorstian?–Ludfordian? (D), Cerro La Chilca, Gorstian?–Ludfordian? (M, Q). **A.** *Eupoikilofusa striatifera* (Cramer, 1964b) Cramer, 1970; MPLP 4-61059 (H25). **B.** *Eupoikilofusa cantabrica* (Cramer, 1964b) Cramer, 1970; MPLP 9-60664 (U41/1). **C.** *Fimbiaglomerella divisa* Loeblich and Drugg, 1968; MPLP 7-60736 (U29/1). **D.** *Gorgonisphaeridium saharicum* (Lister, 1964b) Sarjeant and Vavrdová, 1997; MPLP 1-60667 (M47). **E.** *Gorgonisphaeridium* sp. A Le Hérisse, 1989; MPLP 2-60704 (O39/1). **F.** *Helios aranaides* Cramer, 1964a; MPLP 7-60736 (F28/4). **G.** *Helosphaeridium malvernense* Dorning, 1981; MPLP 9-60664 (F27/3). **H.** *Helosphaeridium pseudo-dictyum* Lister, 1970; MPLP 7-60736 (P24). **I.** *Helosphaeridium* sp.; MPLP 8-60677 (L51). **J.** *Hoegklintia gogginensis* Mullins, 2001; MPLP 4-61059 (G49/3). **K.** *Hoegklintia longispina* Pöthe de Baldi, 1998; MPLP 7-60736 (D26/1). **L.** *Leiofusa banderillae* Cramer, 1964b; MPLP 7-60736 (G50). **M.** *Leiofusa bernesgae* Cramer, 1964b; MPLP 2-61057 (N37/1). **N.** *Leiofusa estrecha* Cramer, 1964b; MPLP 8-60677 (N50/2). **O.** *Leiofusa fusiformis* (Eisenack, 1934) Eisenack, 1938; MPLP 8-60677 (E40/1). **P.** *Leptobrachion arbusculiferum* (Downie, 1963) Dorning, 1981; MPLP 7-60736 (B31/3). **Q.** *Lophosphaeridium magnum* Pöthe de Baldi, 1971; MPLP 2-61057 (N31/3). **R.** *Lophosphaeridium* cf. *microgranulosum* Thusu, 1973b; MPLP 10-60673 (V46/3). **S.** *Lophosphaeridium parvarum* Stockmans and Willière, 1963; MPLP 3-60659 (W47/3). **T.** *Melikeriopalla polygonia* (Staplin, 1961) Mullins, 2001; MPLP 7-60736 (W37/2). Scale bars 20  $\mu$ m.

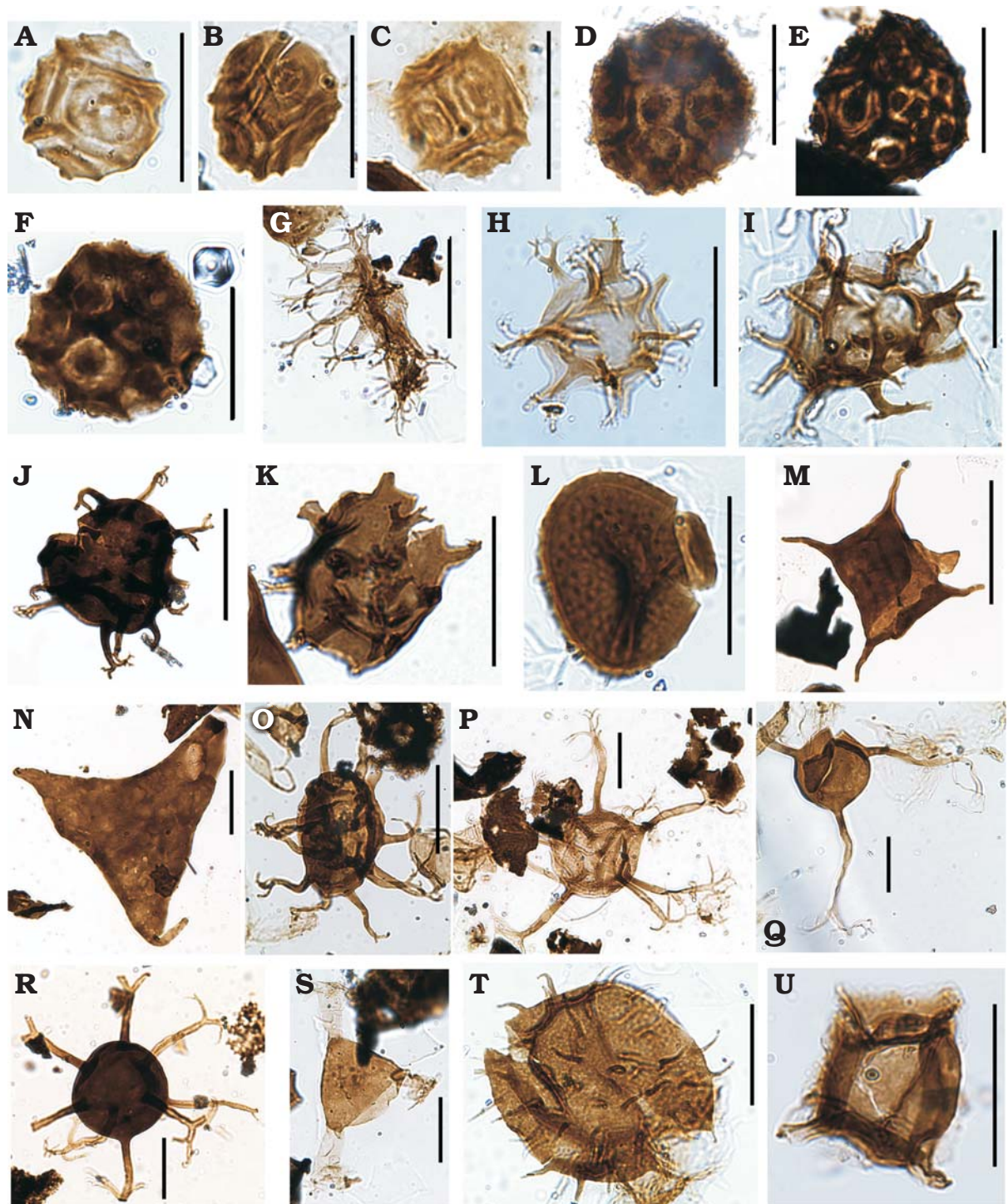


Fig. 9. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, Cerro La Chilca, Homerian? (A, L), Cerro La Chilca, Gorstian?–Ludfordian? (B, I), Cerro La Chilca, Ludfordian (C, H, O, Q, T), Quebrada Ancha, Ludfordian (D–G, J, N, P, R, S), Quebrada Ancha, Pfidoli (K, U), Quebrada Ancha, Gorstian?–Ludfordian? (M). **A–F.** cf. *Melikeriopalla* sp. **A.** MPLP 1-61065 (W30/3). **B.** MPLP 3-61058 (L33). **C.** MPLP 7-61062 (P43/3). **D.** MPLP 2-60704 (L26). **E.** MPLP 3-60659 (F38). **F.** MPLP 4-62521 (T40/4). **G.** *Multiplicisphaeridium arbusculum* forma A of Mullins (2001); MPLP 7-60736 (D30/1). **H.** *Multiplicisphaeridium cladum* (Downie, 1963) Eisenack, 1969; MPLP 4-61059 (E50/1). **I.** *Multiplicisphaeridium mingusi* Le Hérisse, 1989; MPLP 2-61057 (M31/1). **J.** *Multiplicisphaeridium monki* Le Hérisse, 1989; MPLP 3-60659 (O45/2). **K.** *Multiplicisphaeridium rochesterensis* Cramer and Diez, 1972; MPLP 9-60664 (U27). **L.** *Nanocycloptia* sp.; MPLP 1-61065 (U38/1). **M.** *Neoveryhachium carminae* (Cramer, 1964a) Cramer, 1970; MPLP 1-60667 (P45/2). **N.** *Onondagella asymmetrica* (Deunff, 1961) Playford, 1977; MPLP 7-60736 (X44). **O.** cf. *Oppilatala frondis* (Cramer and Diez, 1972) Dorning, 1981; MPLP 4-61059 (F45). **P.** *Oppilatala grahni* Le Hérisse, 1989; MPLP 7-60736 (E38/1). **Q.** *Oppilatala insolita* (Cramer and Diez, 1972) Dorning, 1981; MPLP 4-61059 (Q50). **R.** *Oppilatala ramusculosa* (Deflandre, 1945) Dorning, 1981; MPLP 7-60736 (N37/4). **S.** *Ozotobranchion palidodigitatus* (Cramer, 1966b) Playford, 1977; MPLP 7-60736 (P48/4). **T.** *Percultisphaera incompta* Richards and Mullins, 2003; MPLP 4-61059 (W47/4). **U.** *Polyedrixium?* cf. *embudum* Cramer, 1964a; MPLP 9-60664 (D39/1). Scale bars 20  $\mu$ m.

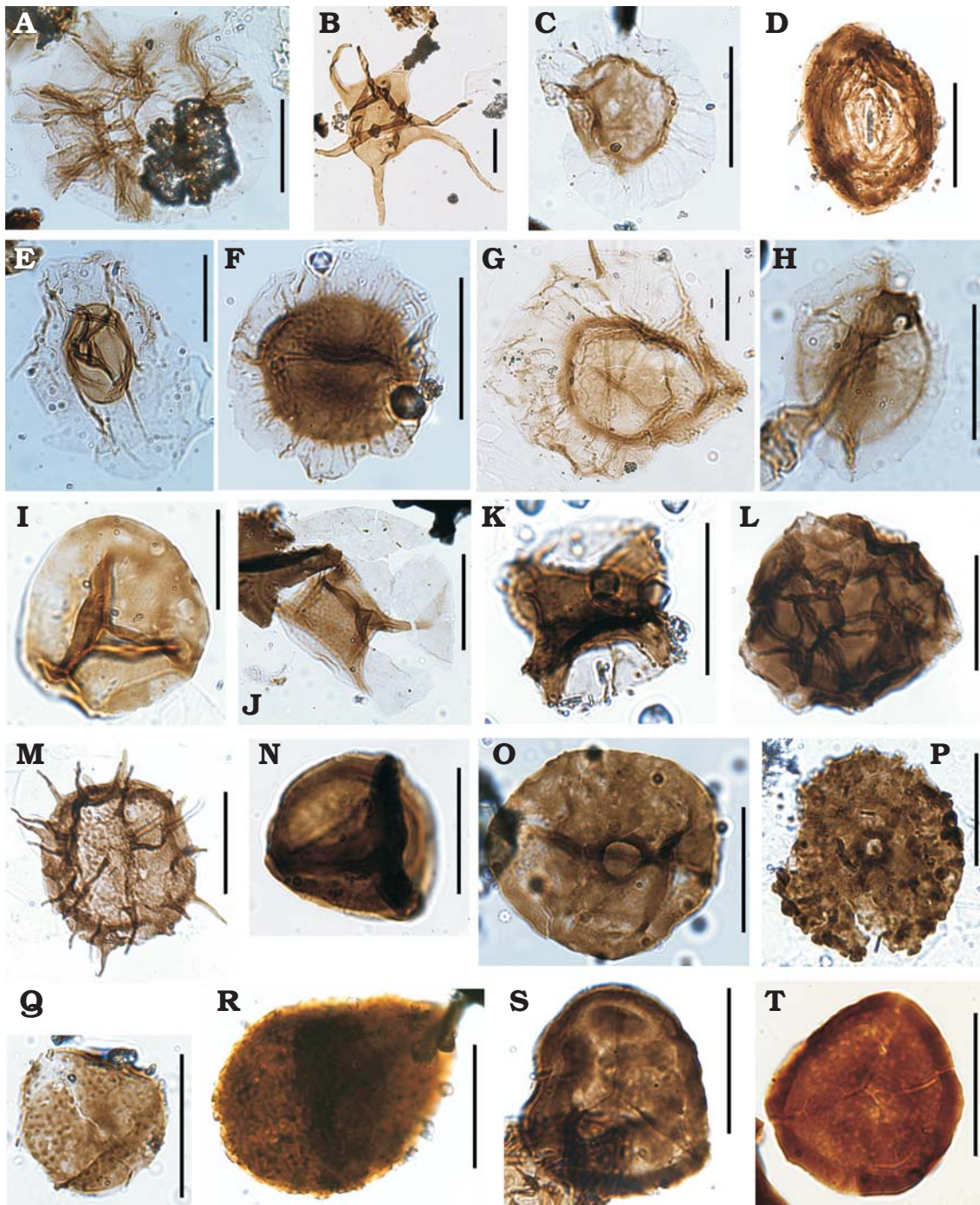


Fig. 10. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, Cerro La Chilca, Ludfordian (A, E, G, N), Quebrada Ancha, Ludfordian (B, C, F, H, J, K, M, P, R), Quebrada Ancha, Prídolí (D, O, Q, S), Cerro La Chilca, Homerian? (I), Quebrada Ancha, Gorstian?–Ludfordian? (L), Cerro La Chilca, Gorstian?–Ludfordian? (T). **A.** *Polydrixyium wenlockium* (Dorning, 1981) Le Hérisse, 1989; MPLP 4-61059 (G33). **B.** *Polygonium* sp.; MPLP 7-60736 (E30/1). **C.** *Pterospermella bernardinae* (Cramer, 1964a) Eisenack, Cramer, and Diez, 1973; MPLP 7-60736 (F28/4). **D.** cf. *Pterospermella circumstriata* (Jardiné, Combaz, Magloire, Penguel, and Vachey, 1972) Eisenack, Cramer, and Diez, 1973; MPLP 9-60664 (U47). **E.** *Pterospermella elliptica* Pöthe de Baldis, 1981; MPLP 4-61059 (D46/2). **F.** *Pterospermella* (*Pterospermopsis*) *marysae* Le Hérisse, 1989; MPLP 8-60677 (V50/4). **G.** *Pterospermella martinii* (Cramer, 1966b) Eisenack, Cramer, and Diez, 1973; MPLP 4-61059 (S41/4). **H.** *Pterospermella* cf. *pertonensis* (Dorning, 1981) Mullins, 2001; MPLP 7-60736 (O36/1). **I.** *Punctatisporites* sp.; MPLP 1-61065 (F44/1). **J.** *Quadraditum fantasticum* Cramer, 1964a; MPLP 7-60736 (F29/3). **K.** *Quadraditum incisum* Cramer, 1964a; MPLP 4-62521 (F42/1). **L.** cf. *Rugosphaera tuscarorensis* Strother and Traverse, 1979; MPLP 1-60667 (U47/2). **M.** *Salopidium granuliferum* (Downie, 1959) Mullins, 2001; MPLP 2-60704 (G44/3). **N.** *Tetraedraletes medinensis* (Strother and Traverse, 1979) Wellman and Richardson, 1993; MPLP 6-61061 (G48/1). **O.** *Schismatosphaeridium longhopense* Dorning, 1981; MPLP 9-60664 (N39). **P.** *Schismatosphaeridium* cf. *rugulosum* (Dorning, 1981) Mullins, 2001; MPLP 2-60704 (O30/1). **Q.** *Schismatosphaeridium* sp. B Le Hérisse, 1989; MPLP 11-61020 (J35/2). **R.** cf. *Segestrespora membranifera* (Johnson, 1985) Burgess, 1991; MPLP 6-60662 (V40). **S.** *Synorisporites verrucatus* Richardson and Lister, 1969; MPLP 9-60664 (R33). **T.** *Vermiverruspora rumneyi* (Burgess and Richardson, 1995) Beck and Strother, 2001; MPLP 2-61057 (V34). Scale bars 20  $\mu$ m.

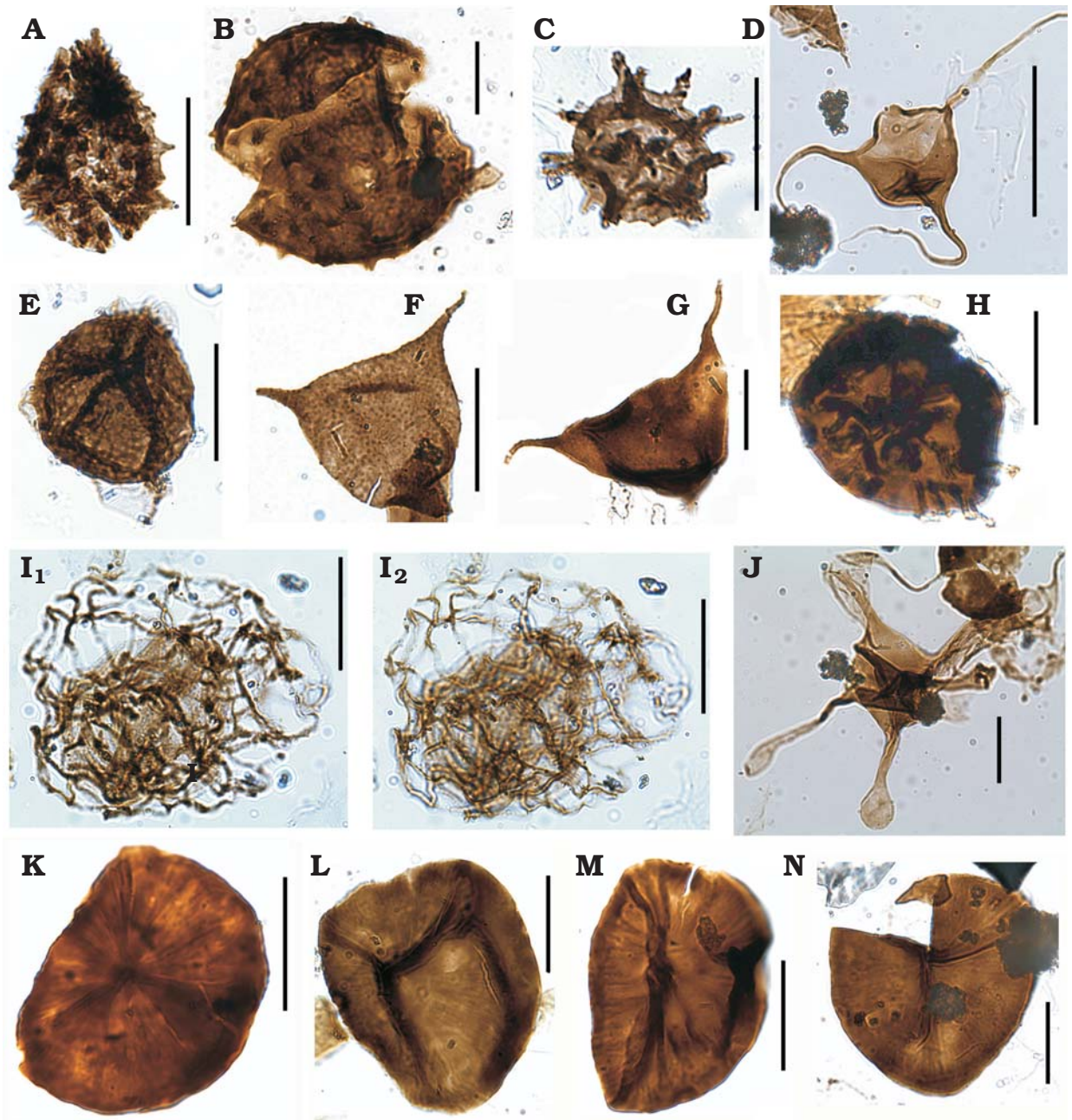


Fig. 11. Palynomorphs from the studied sections of the Los Espejos Formation of Argentina, Quebrada Ancha, Pírdoli (A, F, K, M, N), Cerro La Chilca, Gorstian?–Ludfordian? (B, L), Quebrada Ancha, Ludfordian (C, E, H), Cerro La Chilca, Ludfordian (D, G, I, J). **A.** *Tylotopalla caelamenicutis* Loeblich, 1970; MPLP 14-60982 (E32/3). **B.** *Tylotopalla deerlijkianum* (Martin, 1973) Martin, 1978; MPLP 2-61057 (K42/2). **C.** *Tylotopalla robustispinosa* (Downie, 1959) Mullins, 2001; MPLP 2-60704 (L42/2). **D.** *Veryhachium trispinosum* Group Servais, Vecoli, Li, Molyneux, Raevskaya, and Rubinstein, 2007; MPLP 4-61059 (E33). **E.** *Vestitusdyadus* sp.; MPLP 8-60677 (G31/1). **F.** *Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich and Tappan, 1976; MPLP 9-60664 (Q30). **G.** *Villosacapsula* sp.; MPLP 5-61060 (U32/2). **H.** *Visbysphaera* cf. *pirifera* (Eisenack, 1954) Kiryanov, 1978; MPLP 8-60677 (T33). **I.** Indeterminate palynomorphs; MPLP 4-61059 (G35/4) (I<sub>1</sub>, I<sub>2</sub> are different focus). **J.** cf. *Veryhachium* sp., with abnormal processes, distally expanded; MPLP 4-61059 (P25/3). **K–N.** *Emphanisporites? tenuis* sp. nov. **K.** MPLP 13-60984 (N30/2). **L.** MPLP 2-61057 (Q42). **M.** MPLP 10-60673 (J23). **N.** MPLP 12-60986 (R34). Scale bars 20  $\mu$ m.

closed in a reticulate envelope, without connection to the vesicle.

**Remarks.**—Even though it is well preserved, only one specimen was recovered and there are not palynomorphs with similar morphology in the literature; thus, hindering its classifications.

## Discussion

Phytoplankton is sensitive to external factors such as light, salinity, temperature and terrestrial nutrient inputs. Therefore, variations in its diversity and abundance are supposed to reflect changes in the depositional environment (e.g., Al-

Ameri 1983; Richardson and Rasul 1990; Le Hérissé 2002; Rubinstein and García Muro 2011; García Muro et al. 2016). The abundance of miospores in marine deposits reflects environmental conditions favourable for the development of plant producers as well as the proximity to the shoreline (e.g., Al-Ameri 1983; Traverse 2007).

**Diversity.**—The lower part of the Quebrada Ancha section (Fig. 3B, C) displays a high diversity of marine and terrestrial palynomorphs and yields almost twice the number of species than the Cerro La Chilca section (Fig. 2) despite the fact that both sections would be coeval (García Muro and Rubinstein 2015). Such variations could be related to their different positions within the basin since Quebrada Ancha is located at its southern part. From palaeocurrent analyses, a general deepening trend towards the south of the basin was observed (Astini and Maretto 1996). Therefore, the more distal environment towards the south could have created conditions under which the phytoplankton diversity was higher (e.g., Dorning 1981; Li et al. 2004). Furthermore, the preservation of the palynomorphs and the organic matter, in general, is better in distal environments than in nearshore environments due to less destructive taphonomic processes (Versteegh and Riboulleau 2010 and references therein). On the other hand, the base of the Los Espejos Formation, in the Cerro La Chilca section, is unexposed. Also, as evidenced by the intercalation of sandstone beds, the studied part of Cerro La Chilca represents more proximal facies than those of the lower part in the Quebrada Ancha section, therefore possibly preventing the preservation of the palynomorphs.

A total of 105 species of phytoplankton and 43 species of miospores were recorded from the Los Espejos Formation, considering the palynomorphs from Río de Las Chacritas (Rubinstein and García Muro 2011) and Río Jáchal (García Muro et al. 2014a) as well as from the Quebrada Ancha (García Muro et al. 2014b and this contribution) and the Cerro La Chilca (this contribution) sections (Fig. 1). Even though it cannot be ensured that both levels are equivalent, the palynomorph assemblages from sample MPLP 4-61059 of the Cerro La Chilca section and sample MPLP 7-60736 of the Quebrada Ancha section, both of which were dated as Ludfordian based on palynomorphs (García Muro and Rubinstein 2015), are highly diversified as regards phytoplankton and present a better preservation than other assemblages of the unit. A high diversity during the Ludfordian in the Central Precordillera of San Juan was also noticed in a previous study (Rubinstein and García Muro 2013) and local palaeoenvironmental conditions that would have favoured phytoplankton development during this age was thus suggested. According to Le Hérissé (2002), an increase in the diversity of marine palynomorphs could be interpreted as a consequence of more favourable water mass conditions for algal cysts development. Hagström (1997) and Stricanne et al. (2006) recorded abundant, diverse, and exceptionally well-preserved marine and terrestrial palynomorphs from the Ludfordian of Gotland. This was attributed by Stricanne et al. (2006) to humid climatic conditions that

trigger an increase in nutrient input to the sea, indicated by low stable isotopic values and named as the late Ludfordian A-period. Further studies need to be carried out in order to understand the global and local environmental conditions and their effects on the phytoplankton and miospore distribution in this part of western Gondwana.

Upwards in the sections, miospore diversity is higher than phytoplankton diversity, thus suggesting a close proximity to land in coincidence with a more proximal environment, which had been previously interpreted based on sedimentological studies (Astini and Maretto 1996). As evidenced in the Quebrada Ancha section, as well as in previous contributions (Rubinstein and García Muro 2013 and references therein; García Muro and Rubinstein 2015 and references therein), palynomorphs completely disappear in the uppermost part of the Los Espejos Formation, probably as a result of coarser sediment deposition in more proximal environment, which is unsuitable for the palynomorph preservation. This part of the section probably span the Silurian/Devonian boundary at the northernmost outcrops of the Los Espejos Formation, as it was palynologically identified for the first time in Precordillera in the northern Río Jáchal section (García Muro et al. 2014a).

**Abundance.**—The lowest sample from the Cerro La Chilca section yielded a similar abundance of acritarchs, chlorophytes, and miospores, even though this part of the section corresponds to a low-energy open shelf. There is no sedimentological evidence in the bearing level that suggests deposits of shallowing-up sequence. Upwards, in the following four samples, acritarchs, followed by chlorophytes and miospores, display the higher relative abundance. In sample MPLP 6-61061 of Cerro La Chilca, the relative abundance of miospores and chlorophytes increases and is accompanied by a decline in acritarchs (Fig. 2). Acritarch relative abundance continues to decrease toward the uppermost sample, MPLP 7-61062, and reaches its minimum at this level, while miospores reach their maximum relative abundance of this section. The dominance of terrestrial palynomorphs occurs during the late Ludfordian in the Cerro La Chilca section and the Přídolí in the Quebrada Ancha section. Such changes coincide with the recurrence of sandstone beds associated with more proximal facies and terrestrial input. Terrestrial influence normally produces a decrease in salinity, therefore providing a suitable environment for chlorophytes and resulting in their increase in abundance (e.g., Le Hérissé 2002; Rubinstein and García Muro 2011).

Marine palynomorphs exhibit higher relative abundance in almost all the samples of the Quebrada Ancha section except for sample MPLP 6-60662, which displays a higher relative abundance of chlorophytes and miospores. As with sample MPLP 1-61065 from the Cerro La Chilca section, there is no evidence of terrestrial influence in the sedimentary record, which was interpreted to have been deposited in a low energy open shelf (Astini and Maretto 1996). Generally, miospores tend to be more abundant in proximity to the shoreline (e.g.,

Al-Ameri 1983; Tyson 1993; Batten 1996; Filipiak and Zatoń 2011). The presence of hinterland miospores in distal marine facies could be related to climatic conditions. Specifically, their small size together with the early Palaeozoic atmospheric-environmental conditions would have contributed to their transport into the basin by wind and water (Al Ameri 1983; Stricanne et al. 2006; Wellman et al. 2013; Hagström 1997 and references therein; Traverse 2007; García Muro et al. 2014; Mehlqvist et al. 2014). According to Ferrero's (2006) geochemical analyses, there are small shallowing-up cycles, of 4<sup>th</sup> and 5<sup>th</sup> order, in the lower and middle part of the Los Espejos Formation, in the Quebrada Ancha locality. These subtle environmental changes, not reflected in the lithology, would have possibly influenced palynomorph relative abundances and therefore resulted in a similar abundance of marine and terrestrial palynomorphs in the same level.

**Palaeoenvironmental and palaeogeographic interpretations.**—The comparison of the marine phytoplankton taxa from the Los Espejos Formation with coeval assemblages worldwide suggests that marine phytoplankton presents a wide distribution, even across the Rheic Ocean, as already suggested by Rubinstein (1993). In more recent years, different contributions point to a narrow to almost closed Rheic Ocean since the late Silurian that did not constitute an impassable barrier for marine phytoplankton and chitinozoans (e.g., Jaglin and Paris 2002; Le Hérissé 2002; Rubinstein et al. 2008; Breuer et al. 2017) and thus enabled the exchange of species.

As regards trilete spores, the highest percentages of species in common with the Precordillera assemblages correspond to localities from the same Gondwana palaeocontinent, such as North Africa and Brazil (Rubinstein and Steemans 2002; Steemans et al. 2008; Spina and Vecoli 2009), and from peri-Gondwana, such as Spain (e.g., Richardson et al. 2001). Breuer et al. (2017) observed close similarities between Saudi Arabia miospore assemblages of the Přídolí and those from Spain. Even though the geographical position of Armorica is still under discussion (e.g., Torsvik and Cocks 2004), the similarities observed between the assemblages from Armorica (Spain), Saudi Arabia and Argentina would indicate that Armorica (Spain) was possibly located at an intermediate position between the remaining two regions. The similarities between miospore assemblages from different palaeolatitudes in the same continent, such as Tunisia (North Africa), Urubu (Brazil) and Precordillera, denote that the distribution of spores could have been influenced by palaeolatitudes as well as by local environments (Steemans et al. 2007; García Muro et al. 2014b). It should be taken into account that, nowadays, miospore assemblages are still scarce and geographically restricted, which inhibits reliable correlations. On the other hand, plant cryptospore-producers were widely distributed, hence revealing their plasticity in adapting to different climates and environmental conditions and/or their higher dispersal potential (Steemans et al. 2007; García Muro et al. 2016 and references therein).

Sample MPLP 4-61059 of the Cerro La Chilca section contains a remarkable specimen of a possible *Veryhachium* that presents abnormal processes, distally expanded (Fig. 11J). The presence of teratological specimens with, for instance, deformed or inflated processes could have resulted from perturbations in the environmental conditions such as variations in intensity of light, temperature, and chemistry, as well as volcanic events (Le Hérissé 1989) and sea level fluctuations. The latter would be the case for the Llandovery/Wenlock boundary (Rodrigues and Cardoso 2005). Vandenbroucke et al. (2015) interpreted the malformations of plankton, even if it represents a very small proportion of the assemblage, as induced by the presence of metals (Fe, Mo, Pb, Mn, and As) in the early Palaeozoic and as possible indicators of subsequent mass extinction events. In contrast to what was observed for other palaeoplates such as Baltica and Laurentia (Calner 2005), there is hitherto no evidence of environmental crises and mass extinctions during the late Silurian in neither Precordillera nor Western Gondwana. However, there would be some evidence of Ludfordian Lau Event effects in the peri-Gondwanan Bohemia terrane (Lehnert et al. 2007b) in northern Gondwana, Tunisia (Vecoli et al. 2009), and in East Gondwana, Australia (Talent et al. 1993; Jeppsson et al. 2007). Nevertheless, further studies are needed before confirming the occurrence of such event in the Precordillera Basin.

In the last few years, the knowledge of palynomorphs from Precordillera has much advanced (Rubinstein and García Muro 2011, 2013; García Muro et al. 2014a, b, 2016; García Muro and Rubinstein 2015). Notably, in such contributions, 58 species of phytoplankton and 28 of miospores were recognized for the first time in the Palaeozoic of Argentina. Moreover, 34 species of phytoplankton and one of a trilete spore were recorded for the first time for Gondwana. These findings of marine phytoplankton, previously known from other paleoplates (Avalonia, Baltica, Laurentia), would support their cosmopolitan distribution pattern. In view of the present state of knowledge, further palynological studies on the Silurian of Precordillera are required in order to establish more reliable correlations with other assemblages from Gondwana and other palaeocontinents.

## Conclusions

Marine palynomorphs are predominant in almost all of the studied samples from the Los Espejos Formation. Terrestrial palynomorphs tend to be more abundant in the upper part of the sections, which is consistent with the transition, from base to top, of an open shelf to a nearshore environment.

A relatively high diversity of organic-walled phytoplankton and miospores was recorded. The highest diversified and better preserved marine phytoplankton, probably related to more favourable environmental conditions, comes from levels dated as Ludfordian in both studied sections. However, more studies are needed to evaluate the influence of the local environment on the diversity and abundance of phytoplankton.

Based on regional and inter-continental correlations, the phytoplankton evidences a wide palaeogeographic distribution during the late Silurian. The trilete spore assemblages show stronger similarities with those from other Gondwanan and peri-Gondwanan localities, such as Brazil, Tunisia, and Spain, therefore suggesting their more restricted dispersal ability. Moreover, the correlation between trilete spore assemblages from Gondwana, peri-Gondwana, and Armorica may contribute to constrain the palaeogeographical position of Armorica.

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## Appendix 1

Complete list of recorded phytoplankton and miospore species from Cerro La Chilca and Quebrada Ancha sections, at Los Espejos Formation.

### Chlorophytes

- Baculatireticulatus baculatus* Al-Ameri, 1984 (Fig. 5G)  
*Baculatireticulatus* sp. (Fig. 5H)  
*Cymatiosphaera acuminata* Mullins, 2001 (Fig. 5T)  
*Cymatiosphaera* cf. *densisepta* Le Hérisse, 2000 (Fig. 6A)  
*Cymatiosphaera heloderma* Cramer and Díez, 1972 (Fig. 6B)  
*Cymatiosphaera jardinei* Cramer and Díez, 1976 (Fig. 6C)  
*Cymatiosphaera lawsonii* Mullins, 2001 (Fig. 6D)  
*Cymatiosphaera* aff. *ledburica* Dorning, 1981 of Mullins (2001) (Fig. 6E)  
*Cymatiosphaera* cf. *mirabilis* Deunff, 1959 (Fig. 6F)  
*Cymatiosphaera multicristata* Mullins, 2001 (Fig. 6G)  
*Cymatiosphaera* aff. *multisepta* Mullins, 2001 (Fig. 6H)  
*Cymatiosphaera nimia* Le Hérisse, 2002 (Fig. 6I)  
*Cymatiosphaera octoplana* (Downie, 1959) Mullins, 2001 (Fig. 6J)  
*Cymatiosphaera paucimembranae* Mullins, 2001 (Fig. 6K)  
*Cymatiosphaera prismatica* (Deunff, 1954) Deunff, 1961 (Fig. 6L)  
*Cymatiosphaera salopensis* Mullins, 2001 (Fig. 6M)  
*Cymatiosphaera* spp. (Fig. 6N)  
*Dictyotidium alveolatum* (Kiryanov, 1978) Le Hérisse, 1989 (Fig. 7B)  
*Dictyotidium biscutulatum* Kiryanov, 1978 (Fig. 7C)  
*Dictyotidium callum* Al-Ruwaili, 2000 (Fig. 7D)  
*Dictyotidium dictyotidium* (Eisenack, 1938) Eisenack, 1955 (Fig. 7E)  
*Dictyotidium faviforme* Schultz, 1967 (Fig. 7F)  
*Dictyotidium stellatum* Le Hérisse, 1989 (Fig. 7G)  
*Dictyotidium tenuiornatum* Eisenack, 1955 (Fig. 7H)  
*Dictyotidium* spp.  
*Duvernaysphaera aranaides* (Cramer, 1964a) Cramer and Díez, 1972 (Fig. 7M)  
*Helios aranaides* Cramer, 1964 (Fig. 8F)  
*Leiosphaeridia* spp.  
*Melikeriopalla polygonia* (Staplin, 1961) Mullins, 2001 (Fig. 8T)  
 cf. *Melikeriopalla* sp. (Fig. 9A–F)  
*Polyedrixium* cf. *embudum* Cramer, 1964 (Fig. 9U)  
*Polyedrixium* spp.  
*Polyedrixium wenlockium* (Dorning, 1981) Le Hérisse, 1989 (Fig. 10A)  
*Pterospermella bernardinae* (Cramer, 1964a) Eisenack, Cramer, and Díez, 1973 (Fig. 10C)  
 cf. *Pterospermella circumstriata* (Jardiné, Combaz, Magloire, Penguel, and Vachey, 1972) Eisenack, Cramer, and Díez, 1973 (Fig. 10D)  
*Pterospermella elliptica* Pöthe de Baldis, 1981 (Fig. 10E)  
*Pterospermella (Pterospermopsis) marysae* Le Hérisse, 1989 (Fig. 10F)  
*Pterospermella martinii* (Cramer, 1966b) Eisenack, Cramer, and Díez, 1973 (Fig. 10G)  
*Pterospermella* cf. *pertonensis* Dorning, 1981 of Mullins (2001) (Fig. 10H)  
*Pterospermella* spp.  
*Quadratum fantasticum* Cramer, 1964a (Fig. 10J)  
*Quadratum incisum* Cramer, 1964a (Fig. 10K)
- ### Acritarchs
- Ammonidium cornuatum* Loeblich and Wicander, 1976 (Fig. 5A)  
*Ammonidium ludloviense* (Dorning, 1981) Mullins, 2001 (Fig. 5B)  
*Ammonidium maravillosum* (Cramer, 1969) Thusu, 1973a (Fig. 5C)  
*Ammonidium waldronense* (Tappan and Loeblich, 1971) Dorning, 1981 (Fig. 5D)  
*Ammonidium* sp. A Mullins, 2001 (Fig. 5E)  
*Ammonidium* spp.  
*Buedingiisphaeridium lunatum* Le Hérisse, 1989 (Fig. 5J)  
*Buedingiisphaeridium pyramidale* Lister, 1970  
*Carminella maplewoodensis* Cramer, 1968 (Fig. 5K)  
*Comasphaeridium brevispinosum* (Lister, 1970) Mullins, 2001  
*Cordobesia uruguayensis* (Martinez-Macchiavello, 1968) Pöthe de Baldis, 1977 (Fig. 5R)  
*Cymbosphaeridium carinosum* (Cramer, 1964a) Jardine, Combaz, Magloire, Peniguel, and Vachey, 1972 (Fig. 6O)  
*Cymbosphaeridium pilar* (Cramer, 1964a) Lister, 1970 (Fig. 6P)  
*Cymbosphaeridium* sp. A Mullins, 2001 (Fig. 6Q)  
*Cymbosphaeridium* spp.  
*Dactylofusa maranhensis* Brito and Santos, 1965 (Fig. 6R)  
*Dactylofusa* cf. *striatogranulata* Jardiné, Combaz, Magloire, Peniguel, and Vachey, 1974 (Fig. 6S)  
*Dactylofusa* sp. (Fig. 7S)  
*Dateriocradus lindus* (Cramer and Díez, 1976) Sarjeant and Vavrdová, 1997 (Fig. 7A)  
*Dateriocradus* sp.  
*Diexallophasis remota* Group Mullins, 2001 (Fig. 7I)  
*Dilatisphaera williereae* (Martin, 1966) Lister, 1970 (Fig. 7J)  
*Dorsennidium europaeum* (Stockmans and Willièrè, 1960) Mullins, 2001 (Fig. 7K)  
*Dorsennidium pertonense* (Dorning) Sarjeant and Stancliffe, 1996 (Fig. 7L)  
*Dorsennidium* sp.  
 cf. *Eisenackidium argentinum* Pöthe de Baldis, 1997 (Fig. 7N)  
*Eisenackidium* sp.  
*Estiastra barbata* (Downie) Sarjeant and Stancliffe, 1994 (Fig. 7R)  
*Estiastra* sp.  
*Eupoikilofusa striatifera* (Cramer, 1964b) Cramer, 1970 (Fig. 8A)  
*Eupoikilofusa* cf. *stratifera* (Cramer, 1964b) Cramer, 1970 (Fig. 7T)  
*Eupoikilofusa cantabrica* (Cramer, 1964b) Cramer, 1970 (Fig. 8B)  
*Fimbrigliomerella divisa* Loeblich and Drugg, 1968 (Fig. 8C)  
*Gorgonisphaeridium saharicum* (Lister, 1970) Sarjeant and Vavrdová, 1997 (Fig. 8D)  
*Gorgonisphaeridium* sp. A Le Hérisse, 1989 (Fig. 8E)  
*Gorgonisphaeridium* spp.  
*Helosphaeridium malvernense* Dorning, 1981 (Fig. 8G)  
*Helosphaeridium pseudodictyum* Lister, 1970 (Fig. 8H)  
*Helosphaeridium* sp. (Fig. 8I)  
*Hoegkintia gogginensis* Mullins, 2001 (Fig. 8J)  
*Hoegkintia longispina* Pöthe de Baldis, 1998 (Fig. 8K)  
*Leiofusa banderillae* Cramer, 1964b (Fig. 8L)  
*Leiofusa berneseae* Cramer, 1964b (Fig. 8M)  
*Leiofusa estrecha* Cramer, 1964b (Fig. 8N)  
*Leiofusa fusiformis* (Eisenack, 1934) Eisenack, 1938 (Fig. 8O)  
*Leptobrachion arbusculiferum* (Downie, 1963) Dorning, 1981 (Fig. 8P)  
*Leptobrachion* sp.  
*Lophosphaeridium magnum* Pöthe de Baldis, 1971 (Fig. 8Q)  
*Lophosphaeridium* cf. *microgranulosum* Thusu, 1973b (Fig. 8R)  
*Lophosphaeridium parverarum* Stockmans and Willièrè, 1963 (Fig. 8S)  
*Lophosphaeridium* sp.  
*Micrhystridium* spp.  
*Multiplicisphaeridium arbusculum* forma A of Mullins (2001) (Fig. 9G)  
*Multiplicisphaeridium cladum* (Downie, 1963) Eisenack, 1969 (Fig. 9H)

- Multiplicisphaeridium mingusi* Le Hérisse, 1989 (Fig. 9I)  
*Multiplicisphaeridium monki* Le Hérisse, 1989 (Fig. 9J)  
*Multiplicisphaeridium rochesterensis* Cramer and Diez, 1972 (Fig. 9K)  
*Multiplicisphaeridium* spp.  
*Nanocyclopa* sp. (Fig. 9L)  
*Neoveryhachium carminae* (Cramer, 1964a) Cramer, 1970 (Fig. 9M)  
*Onondagella asymmetrica* (Deunff, 1961) Playford, 1977 (Fig. 9N)  
 cf. *Oppilatala frondis* (Cramer and Diez, 1972) Dorning, 1981 (Fig. 9O)  
*Oppilatala grahni* Le Hérisse, 1989 (Fig. 9P)  
*Oppilatala insolita* (Cramer and Diez, 1972) Dorning, 1981 (Fig. 9Q)  
*Oppilatala ramusculosa* (Deflandre, 1945) Dorning, 1981 (Fig. 9R)  
*Oppilatala* sp.  
*Ozotobranchion palidodigitatus* (Cramer, 1966b) Playford, 1977 (Fig. 9S)  
*Ozotobranchion* sp.  
*Percultisphaera incompta* Richards and Mullins, 2003 (Fig. 9T)  
*Polygonium* spp. (Fig. 10B)  
*Salopidium granuliferum* (Downie, 1959) Mullins, 2001 (Fig. 10M)  
*Salopidium* sp.  
*Schismatosphaeridium algerense* Cramer and Diez, 1976  
*Schismatosphaeridium longhopense* Dorning, 1981 (Fig. 10O)  
*Schismatosphaeridium* cf. *rugulosum* (Dorning, 1981) Mullins, 2001 (Fig. 10P)  
*Schismatosphaeridium* sp. B Le Hérisse, 1989 (Fig. 10Q)  
*Tylotopalla caelamenicutis* Loeblich, 1970 (Fig. 11A)  
*Tylotopalla deerlijkianum* (Martin, 1973) Martin, 1978 (Fig. 11B)  
*Tylotopalla robustispinosa* (Downie, Eisenack, Cramer, and Diez, 1973) Mullins, 2001 (Fig. 11C)  
*Tylotopalla* sp.  
*Veryachium lairdii* Group Servais, Vecoli, Li, Molyneux, Raevskaya, and Rubinstein, 2007  
*Veryhachium trispinosum* Group Servais, Vecoli, Li, Molyneux, Raevskaya, and Rubinstein, 2007 (Fig. 11D)  
*Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich and Tappan, 1976 (Fig. 11F)  
*Villosacapsula* spp. (Fig. 11G)  
*Visbysphaera* cf. *pirifera* (Eisenack, 1954) Kiryanov, 1978 (Fig. 11H)
- Non marine palynomorphs**  
*Quadrisporites* sp.
- Zygnemataceae**  
*Clypeolus tortugaides* (Cramer, 1966a) Miller, Playford, and Le Hérisse, 1997 (Fig. 5O)
- Trilete spores**  
*Ambitisporites avitus-dilutus* Morphon in Steemans, Le Hérisse, and Bozdogan, 1996  
*Ambitisporites* sp.  
*Amicosporites streelii* Steemans, 1989  
*Amisporites* spp.  
*Apiculiretusispora* sp.  
*Archaeozonotriletes chulus* Morphon in Steemans, Le Hérisse, and Bozdogan, 1996  
*Breconisporites* sp. B Richardson, Rodríguez, and Sutherland, 2001  
*Breconisporites* sp. (Fig. 5I)  
*Brochotriletes foveolatus* Naumova, 1953  
*Chelinospora* cf. *cantabrica* Richardson, Rodríguez, and Sutherland, 2001 (Fig. 5L)  
*Chelinospora* cf. *hemisferica* Richardson, Rodríguez, and Sutherland, 2001  
*Chelinospora obscura* Burgess and Richardson 1995  
*Chelinospora sanpetrensis* (Rodríguez, 1978) Richardson, Rodríguez, and Sutherland, 2001 (Fig. 5M)  
*Chelinospora verrucata* var. *verrucata* Morphon in Garcia-Muro, Rubinstein, and Steemans, 2014b (Fig. 5N)  
*Concentricosporites agradabilis* (Rodríguez, 1978) Rodríguez, 1983 cf. *Concentricosporites agradabilis* (Rodríguez, 1978) Rodríguez, 1983 (Fig. 5P)  
 cf. *Concentricosporites sagittarius* (Rodríguez, 1978) Rodríguez, 1983  
*Coronaspora cromatica* (Rodríguez, 1978) Richardson, Rodríguez, and Sutherland, 2001 (Fig. 5S)  
*Cymbosporites* cf. *catillus* Richardson and Lister, 1969  
*Coronaspora* sp.  
*Emphanisporites* cf. *splendens* Richardson and Ioannides, 1979  
*Emphanisporites neglectus* Vigran, 1964  
*Emphanisporites protophanus* Richardson and Ioannides, 1973  
*Emphanisporites rotatus* (McGregor, 1961) McGregor, 1973 (Fig. 7O)  
*Emphanisporites* spp. (Fig. 7P, Q)  
*Leonispora argovejae* Cramer and Diez, 1975  
*Punctatisporites* sp. (Fig. 10I)  
*Retusotriletes* cf. *maccullochii* Wellman and Richardson, 1996  
*Retusotriletes* cf. *warringtoni* Richardson and Lister, 1969  
*Retusotriletes* spp.  
*Scylaspora* cf. *scripta* Richardson, Rodríguez, and Sutherland, 2001  
*Scylaspora vetusta* (Rodríguez, 1978) Richardson, Rodríguez, and Sutherland, 2001  
*Stellatispora inframurinata* var. *inframurinata* (Richardson and Lister, 1969) Burgess and Richardson, 1995  
*Synorisporites* spp.  
*Synorisporites tripapillatus* Richardson and Lister, 1969  
*Synorisporites verrucatus* Richardson and Lister, 1969 (Fig. 10S)  
*Vermiverruspora rumneyi* (Burgess and Richardson, 1995) Beck and Strother, 2001 (Fig. 10T)
- Cryptospore monad**  
*Rugosphaera* cf. *tuscarorensis* Strother and Traverse, 1979 (Fig. 10L)  
*Rugosphaera* sp.
- Cryptospore dyad**  
*Dyadospora murusattenuata/murudensa* Morphon in Steemans, Le Hérisse, and Bozdogan, 1996  
*Pseudodyadospora petasus* Wellman and Richardson, 1993  
*Segestrespora* cf. *membranifera* (Johnson, 1985) Burgess, 1991 (Fig. 10R)
- Cryptospore tetrads**  
*Rimosotetras problematica* Burgess, 1991  
*Sphaerassacus glabellus* Steemans, Higgs, and Wellman, 2000  
*Tetraedraletes medinensis* (Strother and Traverse, 1979) Wellman and Richardson, 1993 (Fig. 10N)
- Spores physically separated from cryptospore tetrads**  
*Imperfectotriletes patinatus* Steemans, Higgs, and Wellman, 2000
- Hilate spores**  
*Chelinohilates lornensis* Wellman and Richardson, 1996  
*Hispanaediscus lamontii* Wellman, 1993  
*Hispanaediscus verrucatus* (Cramer, 1966b) Burgess and Richardson, 1991  
*Hispanaediscus wenlockensis* Burgess and Richardson, 1991  
*Hispanaediscus* sp.  
*Gneudnaspora divellomedia* (*Gneudnaspora divellomedia* Tchibrikova, 1959) Balme, 1988 var. *minor* Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans, and Wellman, 2007  
*Artemopyra urubuense* Steemans, Rubinstein, and Melo, 2008  
*Confossuspora* sp. (Fig. 5Q)  
*Vestitusdyadus* sp. (Fig. 11E)  
 Indeterminate miospore (Fig. 5F)  
 Indeterminate organic-walled phytoplankton (Fig. 11I)