

New environmental perspectives on the Jurassic Cuyo and Lotena groups, Neuquén Basin, Argentina, based on a multi-proxy approach

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ABSTRACT. With the main goal of reconstructing the environmental conditions of the Cuyo and Lotena groups during the Middle Jurassic period in the south of the Huincul Arch (central western Argentina), a multi-proxy approach, considering pollen, spores, algae, fungal remains, palynofacies, molluscs, ichnology, X-Ray diffraction, and petrographic and lithological analyses, was carried out. This work suggests a lacustrine environment for the Challacó Formation, shallow marine conditions influenced by strong fluvial discharges for the Lajas, Bosque Petrificado and Lotena formations, and an age no older than latest Early Bajocian for the uppermost part of the Lajas Formation.

Keywords: Palaeoenvironment, Palynology, Sedimentology, Lajas Formation, Challacó Formation, Bosque Petrificado Formation, Lotena Formation.

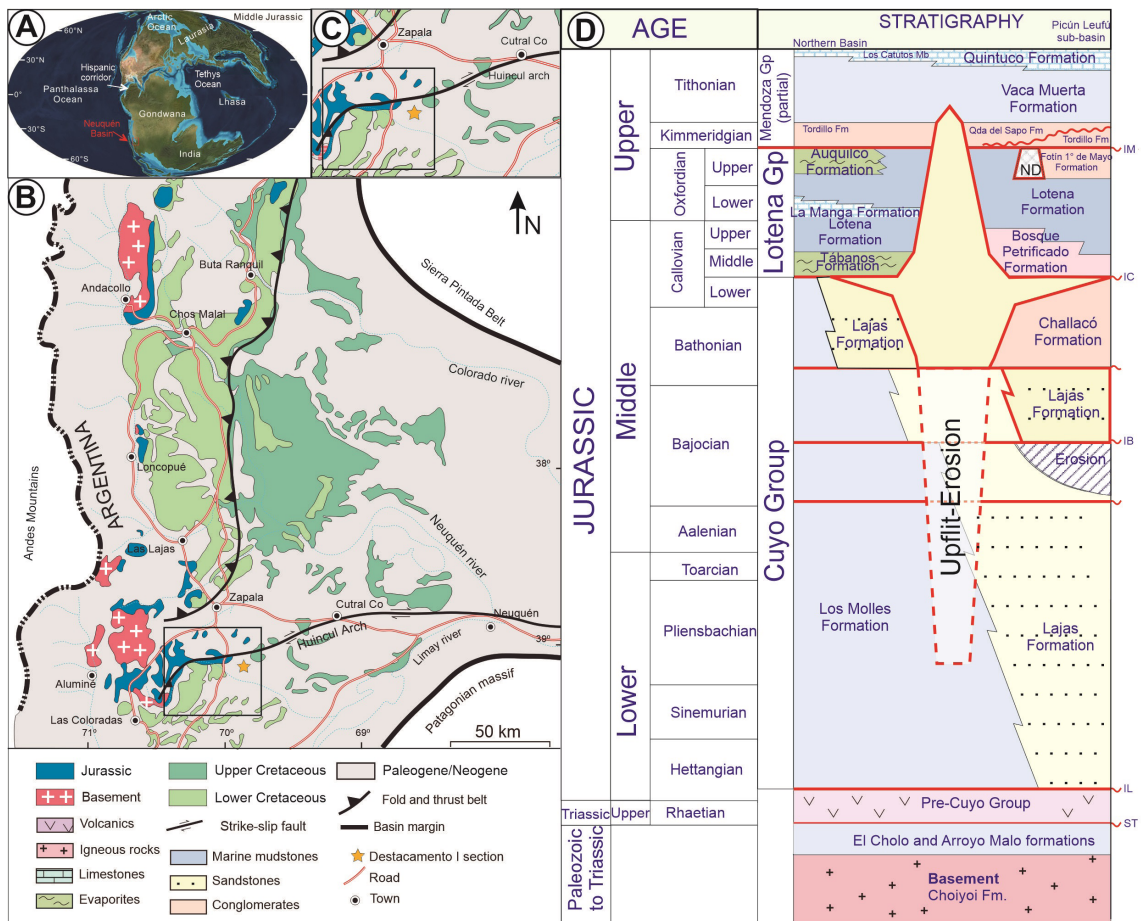
RESUMEN. Nuevas perspectivas paleoambientales de los grupos Cuyo y Lotena (Jurásico), Cuenca Neuquina, Argentina, mediante un análisis *multi-proxy*. Con el objetivo principal de reconstruir las condiciones paleoambientales de los grupos Cuyo y Lotena (Jurásico Medio) al sur de la dorsal de Huincul (centro-oeste argentino), se llevó a cabo un estudio *multi-proxy* mediante polen, esporas, algas, restos fúngicos, palinofacies, moluscos, icnología, difracción de rayos X y análisis petrográficos y litológicos. Se sugiere en este trabajo un ambiente lacustre para la Formación Challacó, condiciones marinas influenciadas por fuertes descargas fluviales para las formaciones Lajas, Bosque Petrificado y Lotena, y una edad máxima del Bajociano temprano tardío para la parte superior de la Formación Lajas.

Palabras clave: Paleoambiente, Palinología, Sedimentología, Formación Lajas, Formación Challacó, Formación Bosque Petrificado, Formación Lotena.

1. Introduction

The Neuquén Basin, located in western central Argentina (Fig. 1), is the most prolific oil-bearing basin in austral South America (Benedetto, 2023). It covers an area of more than 160,000 km² and has a subtriangular shape with boundaries defined by the Sierra Pintada belt to the northeast, the Northeastern Patagonian Massif to the southeast, and the Andes to the west (Olivera *et al.*, 2020). The infill of the Neuquén Basin consists of a >7,000 m-thick siliciclastic succession, accumulated during the Jurassic and Cretaceous periods (Zavala *et al.*, 2020). Marine sedimentation began in the Early

Jurassic with the Cuyo Group and continued, after the first broad oceanic disconnection, with the Lotena Group deposits (Zavala, 2005) (Fig. 1D). During the Middle-Late Jurassic, the Neuquén Basin was separated into two depocentres by the Huincul Arch, an ~E-W oriented deformation belt developed along the Permian suture of the Patagonia terrane with western Gondwana: the southern sector, known as the Picún Leufú sub-basin, and the northern Neuquén Basin (e.g., Zavala *et al.*, 2020; Hernández *et al.*, 2022) (Fig. 1D). Although in recent years fieldwork has focused on the evolutionary history and interrelation between the Cuyo and Lotena groups, there are scarce palynological studies focused on the Picún



Leufú sub-basin (Martínez *et al.*, 2005a; Olivera *et al.*, 2020, 2025; Chalabe *et al.*, 2024).

The Destacamento I area, situated in the Picún Leufú sub-basin (Fig. 1B, C), displays good outcrops of the Cuyo and Lotena groups. This locality is considered in this study as strategic for comprehending the tectono-sedimentary evolution of these groups towards the southern part of the Huincul Arch. The Cuyo and Lotena groups have been extensively studied from a palynological point of view in the north of the Huincul Arch (*e.g.*, Scafati and Morbelli, 1984; García *et al.*, 1994; Martínez, 2000, 2002; Stukins *et al.*, 2013; Chalabe *et al.*, 2022), however, palynological studies of these groups to the south are still very scarce (Martínez *et al.*, 2005a; Olivera *et al.*, 2020, 2025; Chalabe *et al.*, 2024).

The aim of this study is to improve the current understanding of the palaeoenvironmental conditions, the sedimentological setting, and the palaeoecological significance of the recovered palynofloras of the Cuyo and Lotena groups by following a multi-proxy approach. The importance in the evolution of these ecosystems is covered here as well. Finally, the first age of the uppermost part of the Lajas Formation in the south of the Huincul Arch is provided based on a palynostratigraphic analysis.

2. Geological setting

The Neuquén Basin was formed after a long period of rifting during the Late Triassic. In the Jurassic and Cretaceous periods, the basin evolved into a retroarc and finally a foreland basin (*e.g.*, Mosquera *et al.*, 2011; Zavala *et al.*, 2020), storing more than 7,000 m of mainly marine and continental siliciclastic deposits with occasional intercalations of carbonate and evaporite deposits. In the northern part of the basin, marine sedimentation started in the Late Triassic (Norian) with alternating massive and laminated mudstones of the Arroyo Malo Formation (Manceda and Figueroa, 1995; Damborenea *et al.*, 2017; Pérez Panera *et al.*, 2023), followed by interbedded mudstones and sandstones of the El Cholo Formation (Riccardi *et al.*, 1997). In the central and southern parts of the basin, the depositional phase began in the Rhaetian with deposits of the Pre-Cuyo Group (described by Gulisano *et al.*, 1984 as volcanic and volcanoclastic rocks) accumulated mainly in elongated, fault-controlled depocentres.

This initial deposition stage was followed in the Hettangian by the Cuyo Group rocks (also referred

to as “Cuyano” in early works; Groeber, 1946; Stipanovic, 1969), which comprise >2,500 m-thick marine to continental deposits accumulated after a transgression of the proto-Pacific Ocean during the Early Jurassic. This group reflects a transgressive-regressive cycle extending from the Hettangian up to the Early Callovian (Zavala, 1996; González Estebenet *et al.*, 2021) (Fig. 1D). Several formations are part of the Cuyo Group. The Los Molles Formation (Weaver, 1931), for example, comprises offshore shale deposits up to 1,000 m thick with isolated turbidite (*s.l.*) levels. The Los Molles Formation is transitionally followed by the Lajas Formation (Weaver, 1931), which consists of up to 750 m of sandstones and conglomerates deposited in marine shelf to littoral environments (*e.g.*, Zavala and González, 2001; Gugliotta *et al.*, 2016; Zavala *et al.*, 2020). The regional correlation of the Los Molles and Lajas (Lj1 and Lj2; Zavala *et al.*, 2020) formations is relatively simple between the Hettangian and Early Bajocian ages due to limited and localised tectonic activity. Since Late Bajocian times, however, there was a progressive decrease in subsidence along the Huincul Arch, resulting then in a progressive regional uplift (Zavala *et al.*, 2020). This uplift segmented the Neuquén Basin into two distinct depocentres: the main Neuquén Basin to the north and the Picún Leufú sub-basin to the south (Hogg, 1993) (Fig. 1D). Brackish to lacustrine conditions prevailed in the Picún Leufú sub-basin during the Bathonian-Early Callovian, while open marine sedimentation continued to the north with the accumulation of shelf deposits of the Lajas Formation (Lj3 to Lj6; Zavala *et al.*, 2020; Chalabe *et al.*, 2022) (Fig. 1D). In the Picún Leufú sub-basin, this palaeogeographical change led to the accumulation of fine-grained red beds of the Challacó Formation (De Ferrariis, 1947; Gulisano *et al.*, 1984), the uppermost unit of the Cuyo Group in this depocentre. The Cuyo Group rock record finishes at around the Early-Middle Callovian transition.

The Cuyo Group is overlain by the Lotena Group (Leanza, 1992) (Fig. 1D). The Lotena Group rocks are part of a 700 m-thick clastic-carbonate system accumulated over the regional intra-Callovian Unconformity (Zavala *et al.*, 2020) and represent the second transgressive marine episode identified in the basin. In the Picún Leufú sub-basin, this group begins with the Bosque Petrificado Formation (Zavala and Freije, 2002), accumulated in a fluvial to marine environment. This formation is composed of up to 200 m of red, greenish and dark grey shales

interbedded with sandstones, pebbly sandstones and conglomerate beds, and represents a clastic wedge, with sediments mainly supplied from uplifted areas along the Huincul Arch (Zavala *et al.*, 2020). The Bosque Petrificado Formation is overlain by 500 m of marine shales and sandstones of the Lotena Formation (Gulisano *et al.*, 1984), which represents the period of maximum flooding of the Lotena Group during the Callovian-Oxfordian, and ends with the conglomerates of the Fortín 1° de Mayo Formation (Gulisano *et al.*, 1984). In central and northern basin areas, the Lotena Formation is transitionally followed by shallow water limestones of the La Manga Formation (Stipanovic, 1966; Stipanovic *et al.*, 1975) and evaporites of the Auquilco Formation (Stipanovic, 1969).

The Palaeo-Pacific infill of the Neuquén Basin ends with the >600 m-thick, Late Jurassic to Early Cretaceous Mendoza Group. This group starts with the continental deposits of the Kimmeridgian Tordillo (Groeber, 1946; Stipanovic, 1966) and Quebrada del Sapo (Digregorio, 1972) formations, both of which represent a temporal oceanic isolation of the basin. During the Tithonian, a catastrophic flooding event marked the return to a marine depositional environment with the Vaca Muerta Formation (Leanza and Hugo, 1978; Legarreta *et al.*, 1981; Veiga and Orchueta, 1988; Legarreta and Uliana, 1999). The top of this unit is diachronous and progradational, spanning the mid-Tithonian in the south to the Berriasian-Valanginian transition in the centre of the basin (Doyle *et al.*, 2005). Near the southern boundary of the basin, the Vaca Muerta Formation is laterally replaced by the whitish and greenish calcareous sandstones and the massive whitish limestones of the Quintuco Formation (Digregorio, 1972).

3. Materials and methods

3.1. Sampling and laboratory treatments

3.1.1. Sedimentology and palynology

At the Destacamento I section, a detailed 237 m-thick section including the Lajas, Challacó, Bosque Petrificado and Lotena formations, was measured with a Jacob's staff and georeferenced from base to top using global positioning system (GPS 39°12'17.62" S - 70°02'44.87" W) by C.Z. (Zavala *et al.*, 2020). The study focused on characterising lithology, sedimentary structures, stratigraphic contacts, geometry, palaeocurrent directions, ichnology, and

fossil remains. Thirty-five outcrop samples of siltstone, mudstone, and fine-grained sandstone were collected for palynological studies (Fig. 2). The samples were prepared using techniques that include treatment with hydrochloric (33%) and hydrofluoric (70%) acids to remove carbonates and silicates (see Volkheimer and Melendi, 1976). No oxidation was performed so as not to affect the colour and preservation of the organic particles. After digestion of the mineral matrix, a first unsieved slide was mounted (slide a). The residues were then sieved through a 10 µm mesh and a second slide was mounted (slide b). Slides were examined by using transmitted white light (TWL) microscopes (Olympus BX40 and Nikon Eclipse50i) and a reflected fluorescence light (RFL) microscope (Olympus BH2) equipped with an Olympus CAMEDIA C-5060 digital camera. The slides are housed at the Instituto Geológico del Sur, Universidad Nacional del Sur, Bahía Blanca, Argentina. Catalogue numbers are preceded by the abbreviation UNSP (Universidad Nacional del Sur, Palynology), followed by the denomination of the section studied: DI (Destacamento I). England FINDER coordinates (EF) are used to locate specimens.

3.1.2. Petrography

Thin sections were made on 10 samples from the Lotena Formation for petrographic studies. At the Destacamento I section, this unit is ~50 m thick so the samples were taken at ~3 m intervals. The samples were prepared at the Petrology Laboratory of the Department of Geology-INGEOSUR, of the Universidad Nacional del Sur and CONICET. The thin sections were analysed by using a Leica DM750P microscope. Mineral abbreviations were taken from Vernon (2018).

3.1.3. X-Ray diffraction analysis

The crystalline structure of the minerals in the Lotena Formation samples were studied through X-Ray diffraction (XRD). Eleven samples were analysed and the semiquantitative mineral compositions determined. For the treatment, the samples were ground with an agate mortar and mounted in a glass sample holder. Sample preparation was carried out at the X-Ray Laboratory of the Universidad Nacional del Sur by using a Rigaku D-Max III diffractometer, with Cu-Kα radiation and a graphite monochromator at 35 Kv and 15 mA. For the identification of the mineral phases, the Jade 7 software was used.

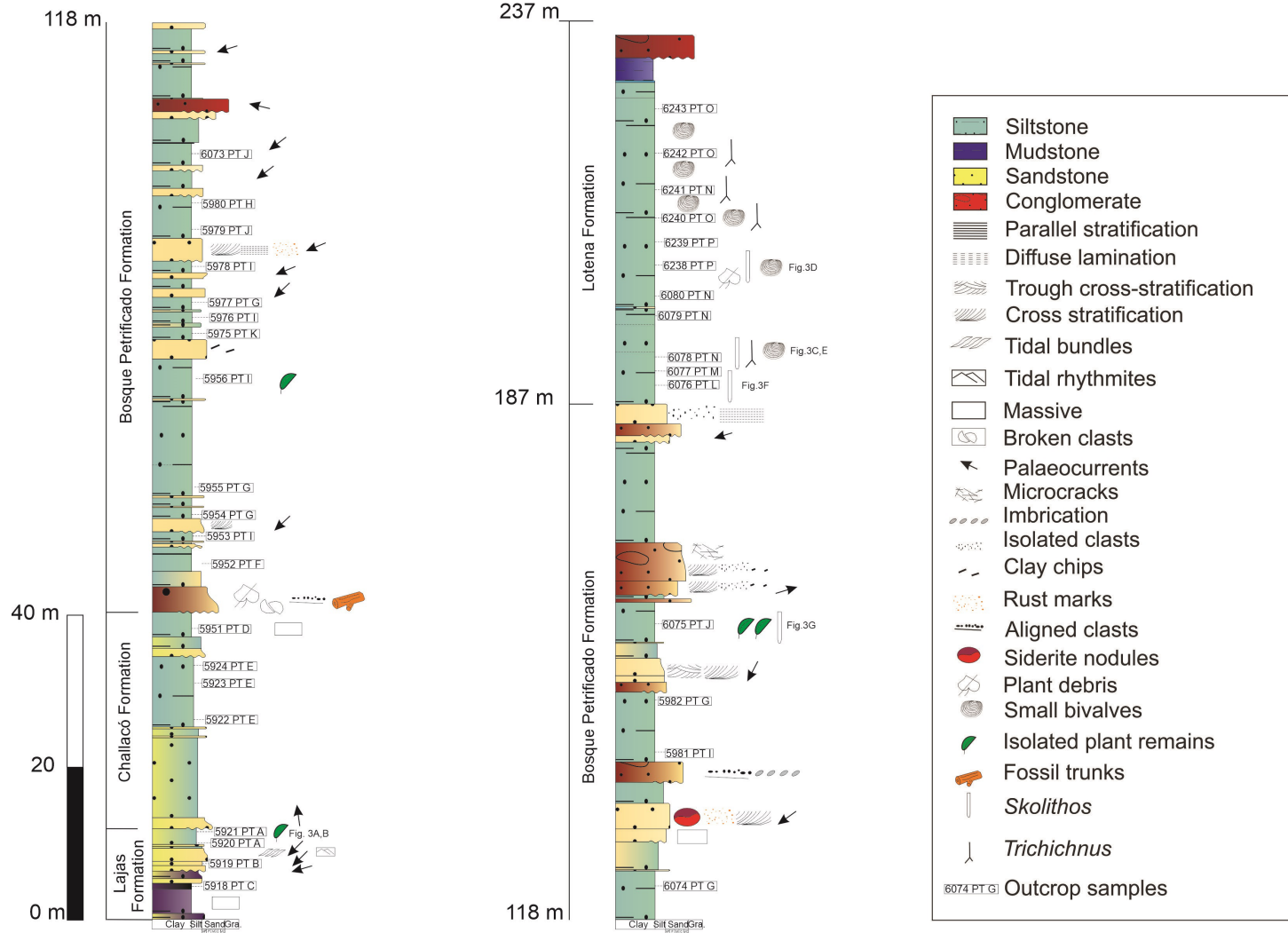


FIG. 2. Stratigraphical section at the Destacamento I site through the Lajas, Challacó, Bosque Petrificado and Lotena formations. The sedimentological and fossiliferous characteristics of the units and the location of the palynological samples and palynofacies types (PT) are indicated. VF: Very fine. F: Fine. M: Medium. C: Coarse. VC: Very coarse.

3.2. Palynological analysis

The palynological analysis included both palynostratigraphic and palynofacies analyses. Quantitative palynofacies analysis was carried out in slide b. To quantify the relative amount of particulate organic matter, at least 500 particles were counted per sample (see Tyson, 1995). The palynological matter was grouped into two main categories: structured (*i.e.*, palynomorphs, translucent phytoclasts, and opaque phytoclasts) and structureless (commonly referred to as amorphous) organic matter. These major groups were subsequently subdivided into minor categories according to Batten (1983), Tyson (1995), and Oboh-Ikuenobe and de Villiers (2003) (see Table 1).

The diagrams of the relative frequencies of palynological matter were made using the TGView 2.0.2 software (Grimm, 2004). Cluster analysis (Q-mode) was performed with the Palaeontological Statistics (PAST) software (Hammer *et al.*, 2009), based on the composition and abundance (number of components) of the different types of organic matter present in each sample. Samples with similar assemblages of palynological matter were grouped into palynofacies types, identified by using the Euclidean distance and the unweighted pair group method (UPGM) of Sneath and Sokal (1973). The relative abundance of different plant families is important in these datasets because some plant communities tend to be dominant and characteristic of certain habitats (*e.g.*, Kovach, 1989; Olivera *et al.*, 2015). Cluster analysis plots show the cophenetic correlation coefficient, which can be used to check the cluster quality (*e.g.*, Carvalho *et al.*, 2019). This coefficient compares the original distances between samples and the distances resulting from the clustering method to assess the degree of similarity between the original distances and the transformed distances represented in the dendrogram (*e.g.*, Anderberg, 1973; Kovach, 1989). The magnitude of this value should be close to 1 for a high-quality solution. As palynofacies types reflect specific features that allow more accurate palaeoenvironmental interpretations, different parameters were considered, such as opaque:translucent phytoclasts (op:tp) and equidimensional:blade-shaped opaque particles (eo:bo) ratios.

The distribution of each palynomorph species was based on counts of at least 250 palynomorphs per palynologically productive sample (*i.e.*, statistical count). When palynomorphs were present in a number

of less than 250 specimens they were recorded as “presence”.

The thermal alteration index was determined for some of the studied samples depending on their abundance of psilate spores. This technique is based on the spore colour changes in response to an increase in the thermal maturation of the organic matter in the rock. Thermal alteration index values were determined by comparing the spore colours following Staplin (1969) by using the colour chart of Pearson (1990).

4. Results

4.1. Sedimentology and ichnology

The Destacamento I section starts with mudstones, carbonaceous sandstones and siltstones, assigned to the uppermost part of the Lajas Formation. Evidence of tidal action and fossil remains of indeterminate plants are present in some levels (Figs. 2, 3A, B). The Challacó Formation, which sharply overlies the marine deposits of the Lajas Formation, consists of massive grey siltstones, while the Bosque Petrificado Formation, which makes up more than 50% of the stratigraphic column, is composed by siltstones with minor conglomerates and fine-grained, cross-bedded sandstone beds with plant debris, broken clasts, plant remains, clay chips, rust spots, siderite concretions, and imbricated clasts (Fig. 2). The ichnogenus *Skolithos* isp. occurs at ~148 m from the base of the section (sample UNSP-DI6075; Fig. 3F, G). The Bosque Petrificado Formation is overlain by siltstones, mudstones and conglomerates of the Lotena Formation which is also characterised by fine-grained marine sediments and laminated shales with diagenetic gypsum (beef). This unit shows abundant plant debris, small bivalves (*Bositra*), and trace fossils assigned to *Trichichnus* isp. and *Skolithos* isp. (Figs. 2 and 3).

4.2. Palynofacies analysis

Five palynofacies types were defined in the Cuyo Group (Figs. 4A, B, 5A-E): three for the Lajas Formation and two for the Challacó Formation (Table 2). In the Lotena Group, eleven palynofacies types were defined (Figs. 4C, D, 5F-Q): six for the Bosque Petrificado Formation and five for the Lotena Formation (Table 2). In all these formations the most abundant organic material is terrestrial in origin

TABLE 1. CLASSIFICATION SCHEME OF THE PALYNOLOGICAL MATTER SPECIFYING THE DIFFERENT CATEGORIES AND SOURCE AFFINITIES SUGGESTED (AFTER BATTEN, 1983; TYSON, 1995; AND OBOH-IKUENOBÉ AND DE VILLERS, 2003).

Group	Categories			Source
Structured organic matter	Palynomorphs	Sporomorphs	Pollen and spores	Reproductive structures of vascular land plants
		Organic-walled microplankton Fungal remains Cyanobacteria remains	Dinoflagellate cysts Acritarchs	Organic-walled marine microplankton
			Freshwater algae	Chlorophyta and Charophyta algae
			Fungal spores and mycelia	Reproductive structures of fungi
			Sheath and filaments	Microbial mats
	Phytoclasts	Translucent	Tracheids	Macrophyte plant debris
			Other woody remains Cuticles	
			Membranes Tubes and filaments	
			Other tissues	
			Dark brown to black fragments	
			Yellow to light brown fragments	
			Degraded	
		Opaque	Blade-shaped	
			Charcoal	
			Equidimensional	
Structureless organic matter	Amorphous organic matter	Spongy		Mainly derived from degradation of continental algae
		Fibrous		Mainly derived from degradation of macrophyte tissues
		Membranous		Microplankton derived
		Granular Pelicular		Microplankton or bacterially derived Phytoplankton or bacterially derived
		Jelly		Terrestrially derived
		Resins		Natural secretions or exudations of taller plants
		Amber coloured amorphous		Uncertain
		Amorphous indet.		Uncertain

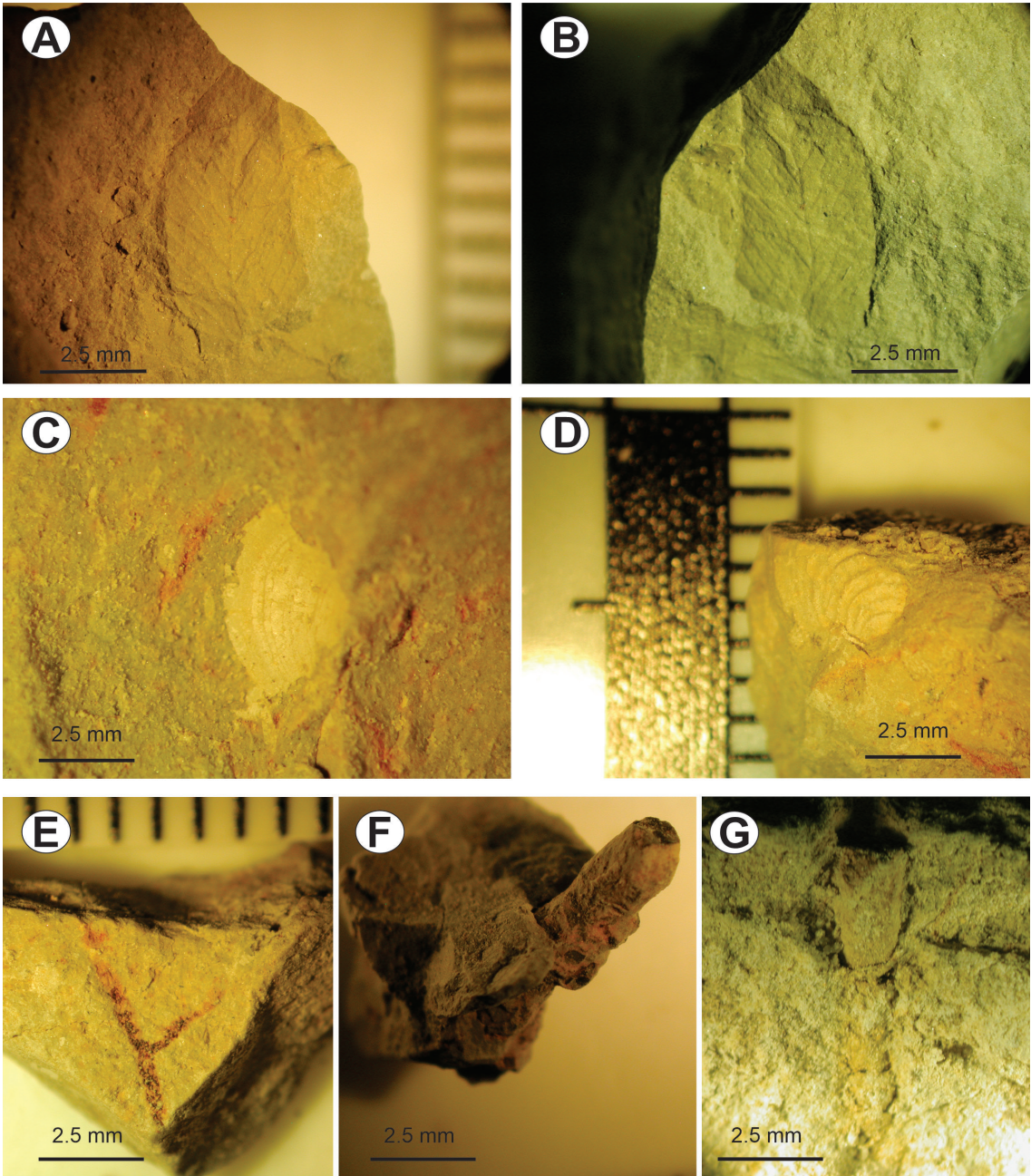


FIG. 3. Photographs of the outcrop samples with fossil plants remains (Lajas Formation, UNSP-DI5921: **A-B**), molluscs (Lotena Formation, UNSP-DI6078: **C**, UNSP-DI6238: **D**), and traces (Lotena Formation, UNSP-DI6078: **E**, UNSP-DI6076: **F**; Bosque Petrificado Formation, UNSP-DI6075: **G**).

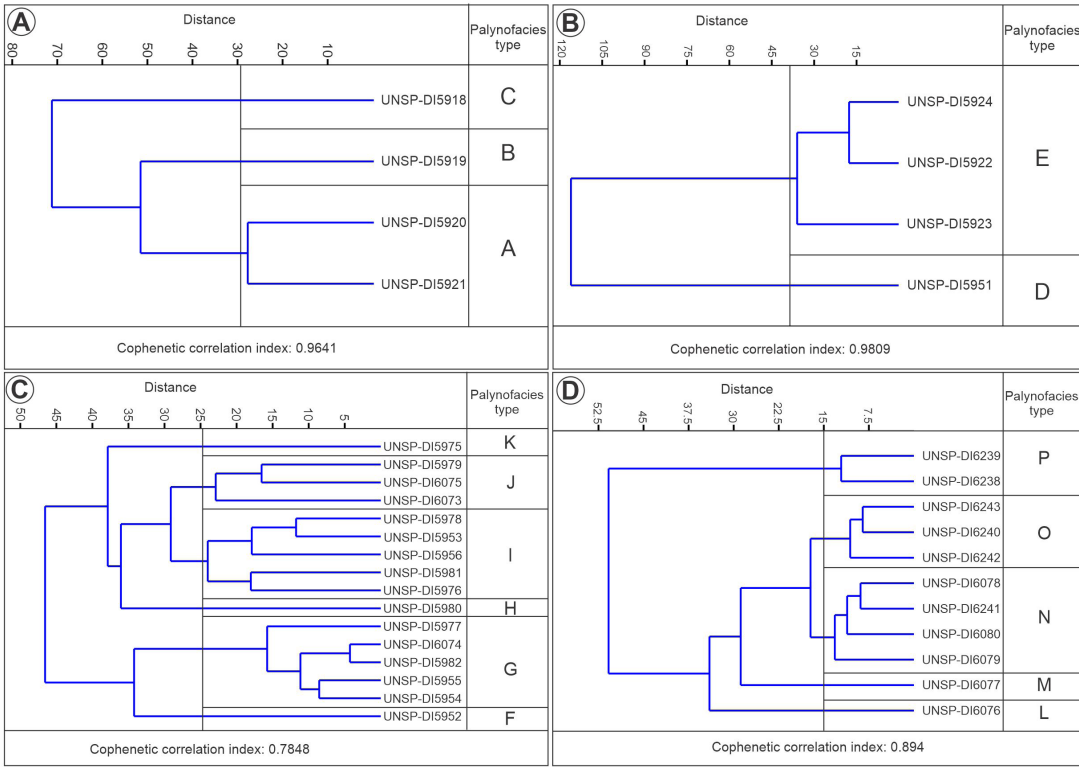


FIG. 4. Cluster analysis, using the Euclidean distance and the unweighted pair group method of Sneath and Sokal (1973). The grouping of the identified palynofacies types for: **A.** the Lajas Formation, **B.** The Challacó Formation, **C.** The Bosque Petrificado Formation, and **D.** The Lotena Formation, are shown. Palynofacies types further described in table 2.

(up to 99.7% of the total organic spectra) (Figs. 5, 6 and 7). The main organic matter components identified, as well as their palaeoenvironmental interpretations, are shown in table 1.

4.3. Composition of the palynoflora at the Destacamento I section

The studied samples from the Cuyo and Lotena groups contain taxonomically diverse assemblages of spores, pollen grains, freshwater and marine organic-walled microplankton, fungal spores and zoomorphs; comprising 66 species (Figs. 8-12; Supplementary Table S1). A total of 20 species of trilete spores belonging to 16 genera, and one species of monolet spore were recorded. Pollen grains are represented by 22 species belonging to 12 genera. Organic-walled microplankton is characterised by low diversity species, represented by Zygnemataceae (5), Oedogoniaceae (1), Botryococcaceae (1), dinoflagellate cysts (1), Prasinophyceae (1), and acritarchs (3). Fungal spores were classified

according to the artificial morphological system (Saccardo System) proposed by Pirozynski and Weresub (1979) and accounted 6 artificial supra-generic taxa. Zoomorphs are only represented by copepod eggs.

4.3.1. Cuyo Group Lajas Formation

This unit is characterised by a high diversity of palynomorphs. The most striking feature of this palynoflora is the dominance of Marattiaceae spores, mainly monolet spores (*Marattisporites scabratus*), which reach up to 51.4% (Figs. 8 and 10). This family is associated with several trilete spores (up to 26%) and Caytoniaceae pollen grains (up to 19%), which constitute the second most important sporomorph group. The dominant fungal spore form is Amerosporae with up to 4%. Although Podocarpaceae pollen grains only reach up to 4%, a noteworthy feature within this family is the presence of *Microcachryidites antarticus* which is an important palynobiomarker in Argentina.

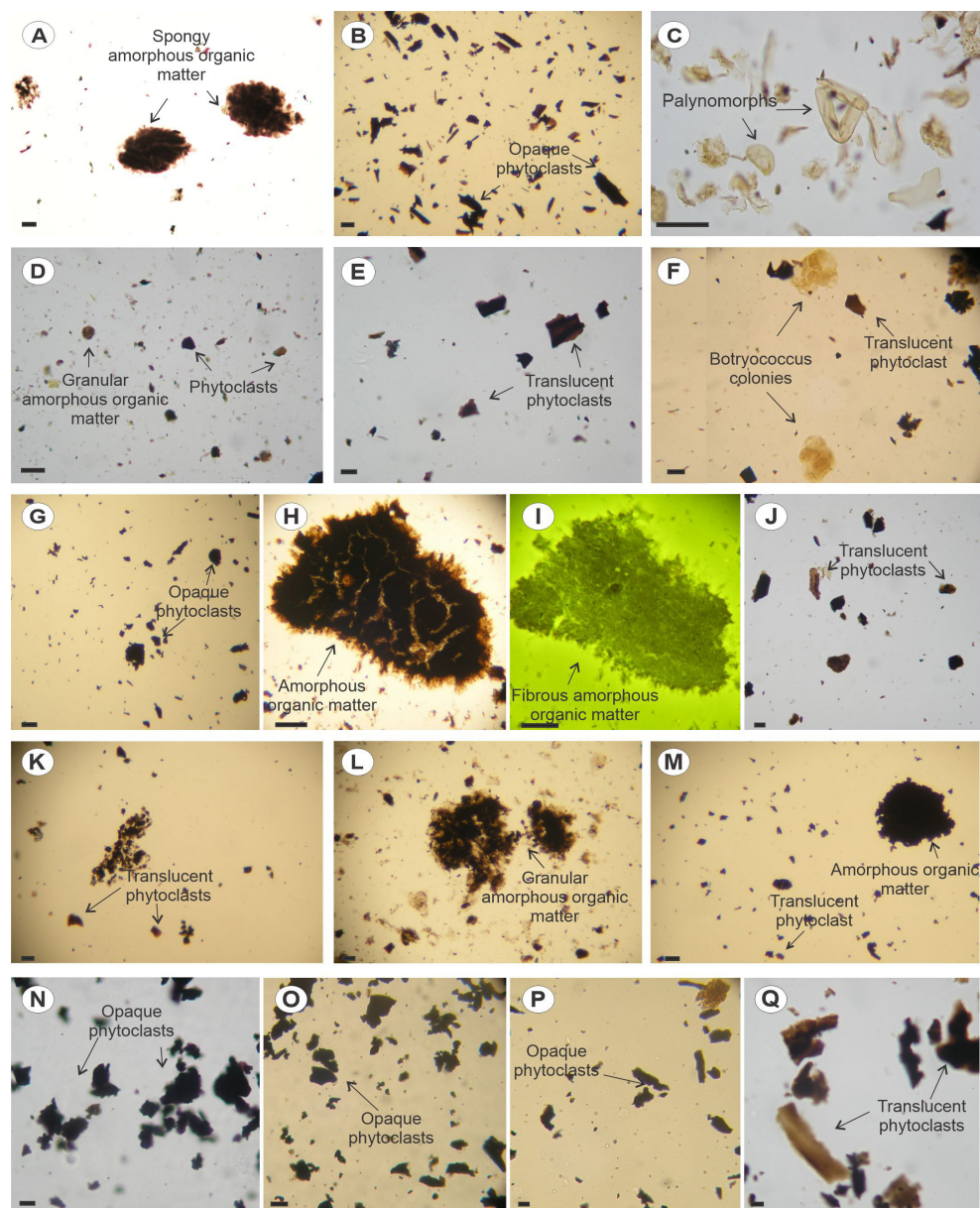


FIG. 5. Palynofacies types and selected palynomorphs from the Destacamento I section samples. Lajas Formation: **A.** Spongy amorphous organic matter (palynofacies type A), sample UNSP-DI5921, EF: P31/3. **B.** Opaque phytoclasts (palynofacies type B), sample UNSP-DI5919, EF: L27. **C.** Palynomorphs (palynofacies type C), sample UNSP-DI5918, EF: M30/1. Challaco Formation: **D.** Phytoclasts and granular amorphous organic matter (palynofacies type D), sample UNSP-DI5951, EF: G44/3. **E.** Translucent phytoclasts (palynofacies type E), sample UNSP-DI5922, EF: G36/3. Bosque Petrificado Formation: **F.** Translucent phytoclasts and *Botryococcus* colonies (palynofacies type F), sample UNSP-DI5952, EF: O28/2. **G.** Opaque phytoclasts (palynofacies type G), sample UNSP-DI5955, EF: N16/2. **H.** Amorphous organic matter (palynofacies type H), sample UNSP-DI5980, EF: U33/1. **I.** Fibrous amorphous organic matter (palynofacies type H), sample UNSP-DI5980, EF: U33/1, determined under UV light. **J.** Translucent phytoclasts (palynofacies type I), sample UNSP-DI5956, EF: A22. **K.** Translucent phytoclasts (palynofacies type J), sample UNSP-DI5979, EF: U24/1. **L.** Granular amorphous organic matter (palynofacies type K), sample UNSP-DI5975, EF: H38/4. Lotena Formation: **M.** Translucent phytoclasts and amorphous organic matter (palynofacies type L), sample UNSP-DI6076, EF: F28. **N.** Opaque phytoclasts (palynofacies type M), sample UNSP-DI6077, EF: E28. **O.** Opaque phytoclasts (palynofacies type N), sample UNSP-DI6079, EF: T34/1. **P.** Opaque phytoclasts (palynofacies type O), sample UNSP-DI6243, EF: N43/2. **Q.** Translucent phytoclasts (palynofacies type P), sample UNSP-DI6238, EF: D31. EF: England Finder coordinates. Scale bars: 20 μ m.

TABLE 2. PALYNOFACIES IDENTIFIED IN THE CUYO GROUP (LAJAS AND CHALLACÓ FORMATIONS) AND IN THE LOTENA GROUP (BOSQUE PETRIFICADO AND LOTENA FORMATIONS) AT THE DESTACAMENTO I AREA. INFORMATION ABOUT THE LITHOLOGY AND COMPONENTRY, AND THE INTERPRETATION OF EACH PALYNOFACIES IS ALSO PRESENTED.

Formation	PT	Lithologies and components of the organic matter	Interpretation
Lajas	PT A	Siltstones. Phytoclasts: up to 75.4%, mainly translucent (up to 63.9%); op:tp: 0.12-0.14, eo:bo: 4.07-4.22. AOM: up to 28.8%, mainly spongy (25.3%). Palynomorphs: up to 5.8%. Cyanobacterial remains: 3.6%. Moderate fluorescence in orange colour. TAI: 1+.	Reduced input of continental organic matter, short distances and/or short source transport times.
	PT B	Sandstones. Highest percentage of phytoclasts: 98%, mainly translucent: 56.4%; op:tp: 0.25, eo:bo: 0.46. AOM: 0.8%. Palynomorphs: 0.6%. Non fluorescent.	High input of continental organic matter, short distances and/or short source transport times.
	PT C	Mudstones. High percentage of palynomorphs: 56.7%. Low percentage of phytoclasts: 20%; op:tp: 0.04, eo:bo: 1.25. AOM: 23.4%. Cyanobacterial remains: 0.4%. High fluorescence in yellow colour. TAI: 2-.	Proximal conditions.
Challacó	PT D	Siltstones. High percentage of phytoclasts: 89.2%, mainly translucent: 62.8%; op:tp: 0.42, eo:bo: 131. AOM: 10.1%. Moderate fluorescence in orange colour.	High input of continental organic matter, traction over decantation.
	PT E	Siltstones. Phytoclasts: up to 85.2%, mainly translucent (62.8%); op:tp: 0.18-0.29, eo:bo: 24.4-31.5. AOM: up to 23.5%. Palynomorphs: 0.5%. Non to moderate fluorescence in orange colour.	High input of continental organic matter, short distances and/or short source transport times. Drier conditions.
Bosque Petrificado	PT F	Siltstones. Phytoclasts: 87.7%, mainly translucent: 48.1%; op:tp: 0.823, eo:bo: 2.97. AOM: 9.4%. Palynomorphs: 2.7%. Cyanobacterial remains: 0.4%. High fluorescence in yellow to orange colours.	Short distance and/or short source transport times.
	PT G	Siltstones. High percentage of phytoclasts: up to 99.1%, mainly opaque (up to 70.9%); op:tp: 3.31, eo:bo: 5.66-10.93. AOM: up to 2.9%. Palynomorphs: up to 0.2%. Non to moderate fluorescence in orange to yellow colours.	High terrestrial input to the basin and strong oxidation.
	PT H	Siltstones. Phytoclasts: 69.4%, mainly translucent (45.5%); op:tp: 0.52, eo:bo: 7.24. AOM: 30.6%. Low fluorescence in green colour.	Reduction in freshwater supply and decrease in the terrestrial input.
	PT I	Siltstones. Phytoclasts: up to 82.2%, mainly translucent (up to 67.3%); op:tp: 0.41-1.18, eo:bo: 0-35.5. AOM: up to 17.7%. Palynomorphs: up to 1%. Cyanobacterial remains: 0.2%. Moderate to high fluorescence in orange to yellow colours.	Reduction in freshwater supply and decrease in the terrestrial input.
	PT J	Siltstones. Phytoclasts: up to 88.9%, mainly translucent (up to 61.7%); op:tp: 0.16-0.4, eo:bo: up to 24.22. AOM: up to 28.9%. Palynomorphs: up to 0.8%. Cyanobacterial remains: 0.4%. High fluorescence in green colour.	Short distance and/or short source transport times. Reduction in freshwater supply and decrease in the terrestrial input.
	PT K	Siltstones. Phytoclasts: 55.4%, mainly translucent (39.8%); op:tp: 0.39, eo:bo: 16.11. Highest percentage of AOM: 44.2%. Palynomorphs: 0.2%. Moderate fluorescence in yellow colour.	Short distance and/or short source transport times. Reduction in freshwater supply and decrease in the terrestrial input.

table 2 continued.

Formation	PT	Lithologies and components of the organic matter	Interpretation
Lotena	PT L	Siltstones. Phytoclasts: 85.1%, mainly translucent (48.8%); op:tp: 0.74, eo:bo: 26.9. AOM: 14.8%. Non fluorescent.	Short distance and/or short source transport times.
	PT M	Siltstones. Phytoclasts: 98.9, mainly opaque (79.5%); op:tp: 4.09, eo:bo: 28.44. AOM: 1.1%. Non fluorescent.	High terrestrial input to the basin and strong oxidation.
	PT N	Siltstones. High percentage of phytoclasts: 99.7%, mainly opaque (65.7%); op:tp: 1.79–1.93, eo:bo: 4.06–17.3. AOM: up to 5.8%. Palynomorphs: up to 0.2. Non to low fluorescence in orange colour.	High terrestrial input to the basin and strong oxidation.
	PT O	Siltstones. Phytoclasts: 99.7%, mainly opaque (53.4%); op:tp: 0.36–1.25, eo:bo: 4.45–11.61. AOM: up to 1.2%. Moderate to high fluorescence in yellow colours.	High terrestrial input to the basin and strong oxidation.
	PT P	Siltstones. Phytoclasts: up to 87%, mainly translucent (76.9%); op:tp: 0.13–0.24, eo:bo: 4.94–9.18. AOM: up to 14.5%. Palynomorphs: up to: 3.4%. Cyanobacterial remains: up to 2.1%. Low fluorescence in orange colour.	Short distance and/or short source transport times.

PT: palynofacies type; **op:tp:** opaque:translucent ratio; **eo:bo:** equidimensional:blade-shaped ratio; **AOM:** amorphous organic matter; **TAI:** thermal alteration index.

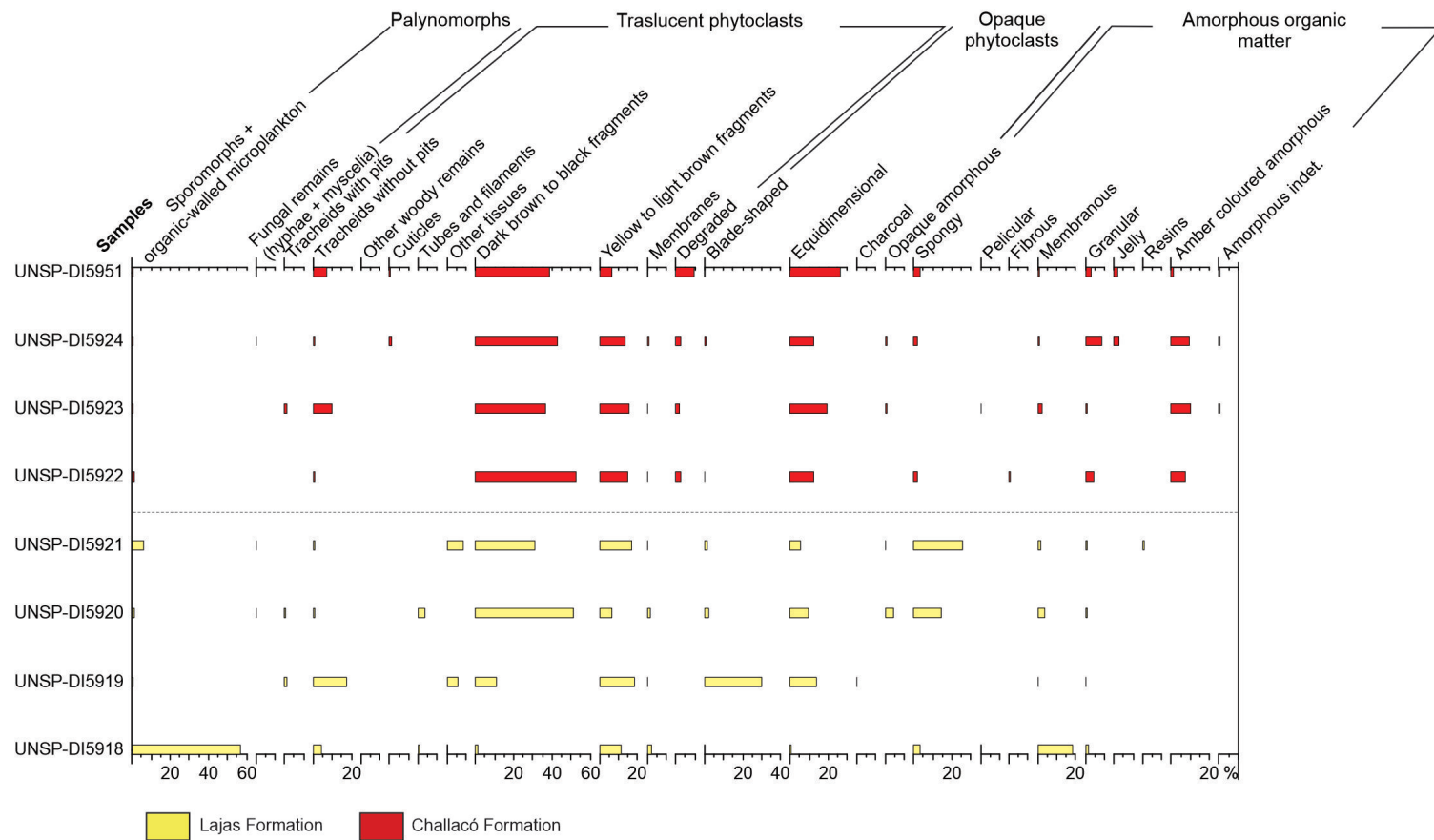


FIG. 6. Relative frequency distribution of the different recognised categories of palynological matter for the Lajas (yellow) and Challacó (red) formations at the Destacamento I section, based on the total count of at least 500 particles per sample.

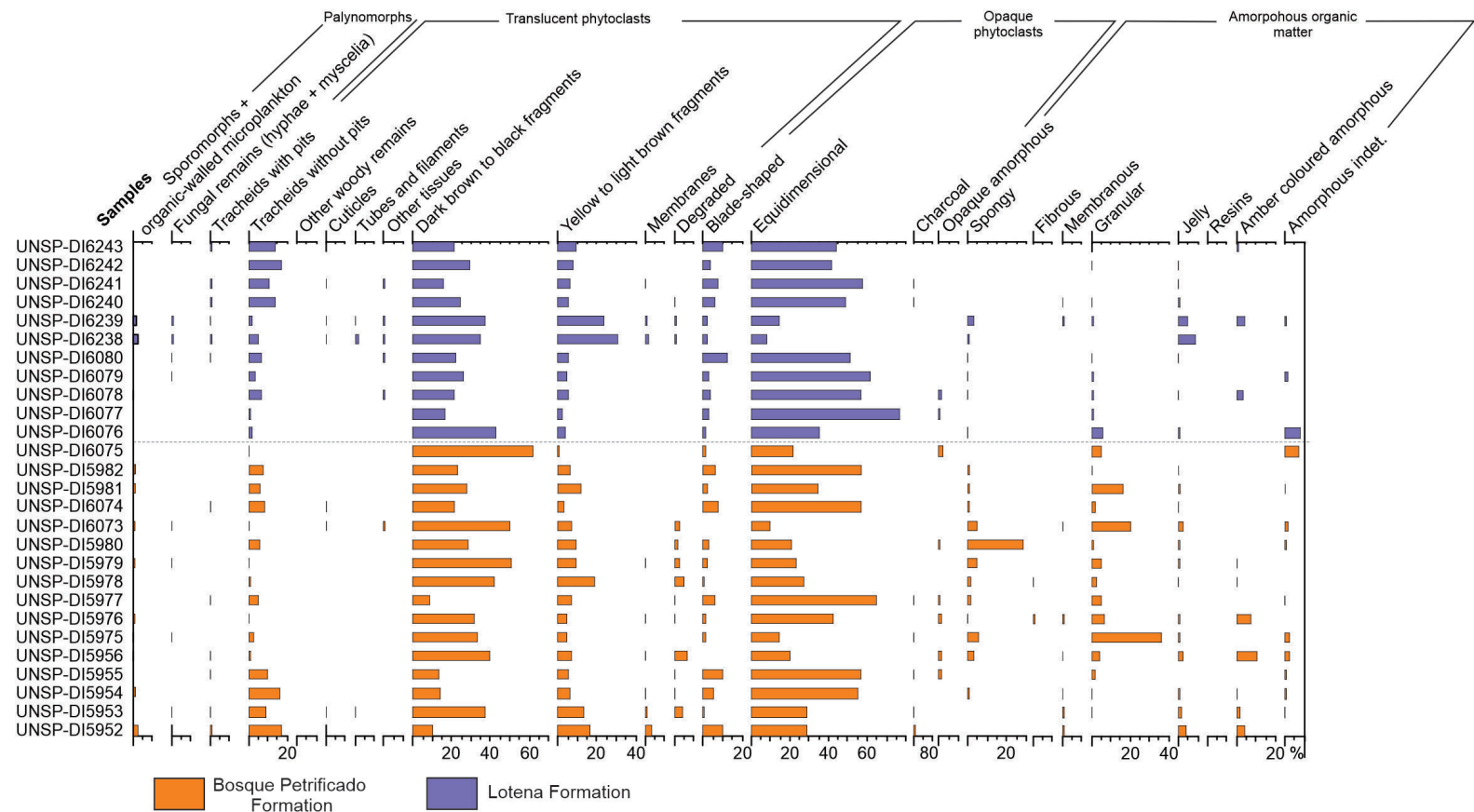


FIG. 7. Relative frequency distribution of the different recognised categories of palynological matter for the Bosque Petrificado (orange) and Lotena (violet) formations at the Destacamento I section, based on the total count of at least 500 particles per sample.

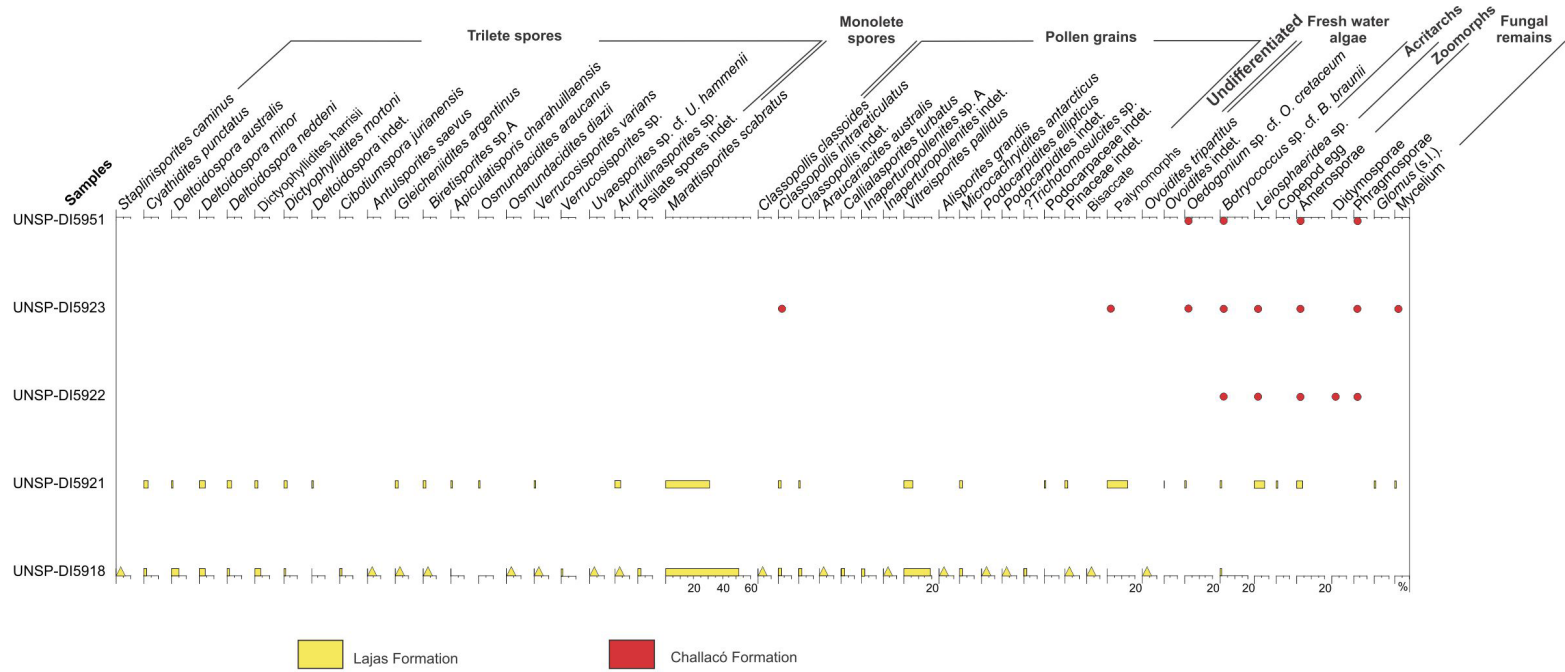


FIG. 8. Relative frequency distribution of the different recognised palynomorphs for the Lajas (yellow) and Challacó (red) formations at the Destacamento I section, based on the total count of 250 specimens per sample. Triangles indicate species with <5%. Circles indicate samples with presence.

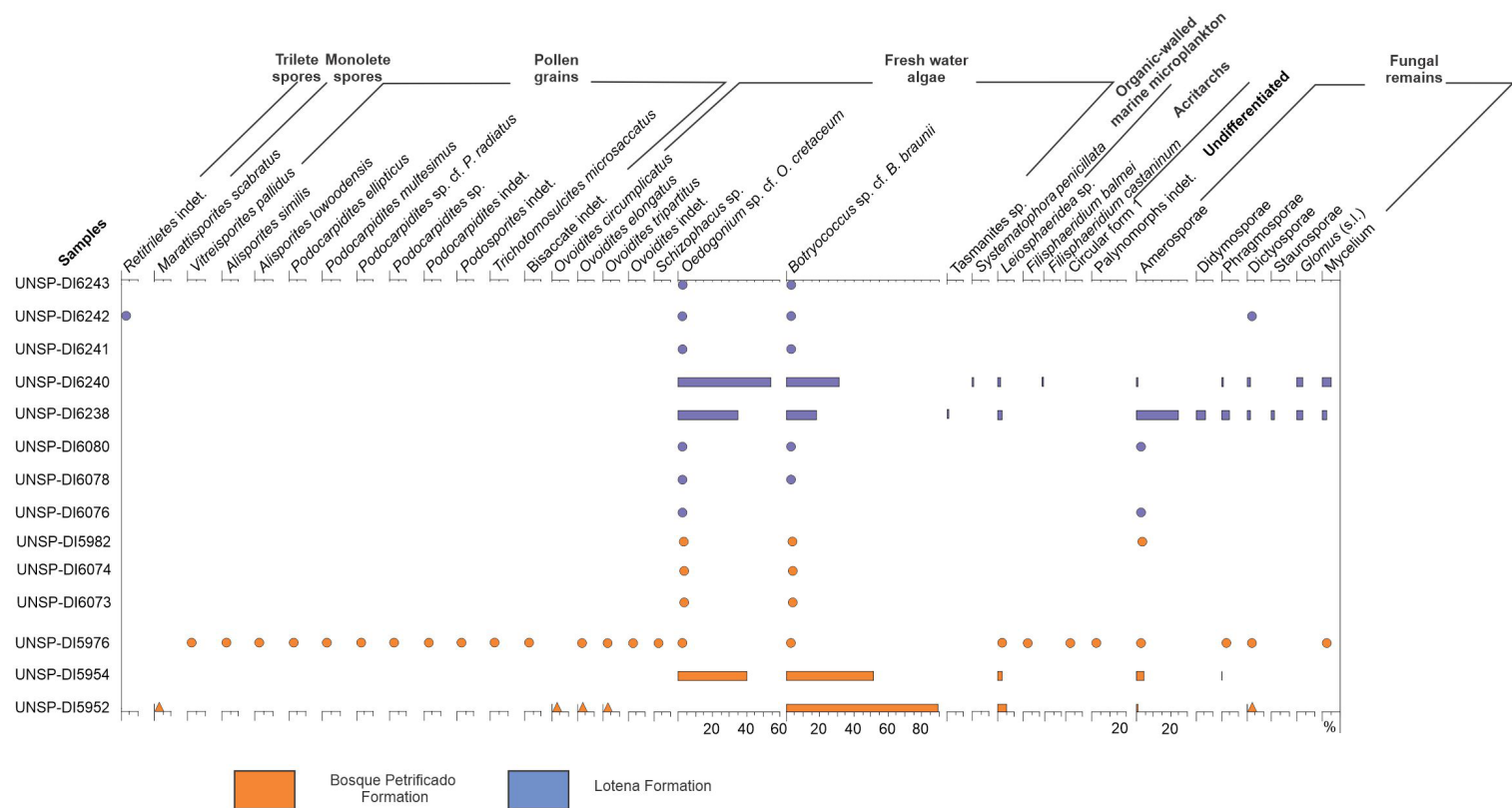


FIG. 9. Relative frequency distribution of the different recognised palynomorphs for the Bosque Petrificado (orange) and Lotena (violet) formations at the Destacamento I section, based on the total count of 250 specimens per sample. Triangles indicate species with <5%. Circles indicate samples with presence.

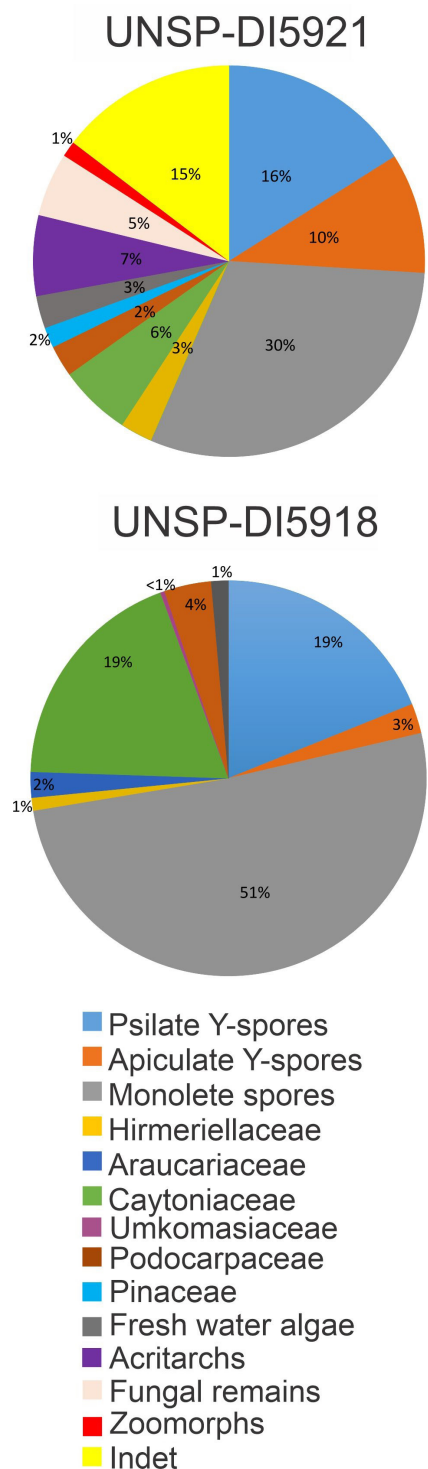


FIG. 10. Pie charts reflecting the quantitative distribution of major palynomorph groups (expressed in percentage form), for the fertile samples of the Lajas Formation.

Challacó Formation

The palynomorphs recovered from this unit are very scarce (Fig. 8). The palynological assemblage is characterised by a predominance of Chlorophyta (*Botryococcus* and *Oedogonium*) and very few pollen grains. This unit also contains fungal spores dominated by the Amerosporae and Phragmosporae types.

4.3.2. Lotena Group

Bosque Petrificado Formation

In this formation, only two samples have enough material to be statistically significant (Fig. 9). These are mostly dominated by *Botryococcus* and *Oedogonium* algae, reaching up to 92.2%, followed by *Leiosphaeridea* sp. and fungal spores. A notable feature is the presence of zygnematacean algae (sample UNSP-DI5976), showing the highest diversity of this group among the studied samples. Fungal spores, when present, are dominated by Amerosporae (up to 4.5%) and Phragmosporae (up to 0.6%).

Lotena Formation

Eight samples belonging to this unit have palynomorph content (two fertile samples and six with “presence”) (Fig. 9). The fertile samples have high percentages of *Botryococcus* and *Oedogonium* algae, reaching up to 84.9%. These algae are associated with fungal spores (up to 44.6%). Dinoflagellate cysts are present in a very small proportion (0.7%). The other samples also show predominance of Chlorophyta algae and fungal spores, the latter dominated by Amerosporae and Didymosporae.

4.4. X-Ray diffraction and petrographic analysis

The Lotena Formation samples were analysed by XRD and petrography. In this contribution, results are presented for a couple of samples: UNSP-DI6238 and UNSP-DI6240, selected because of their mineral content. The rest of the dataset will be part of a forthcoming work.

Sample UNSP-DI6238 corresponds to a dark grey mudstone from the middle part of the Lotena Formation (Fig. 2). The XRD analysis shows the presence of quartz, feldspar, calcite, gypsum, glauconite, and clay minerals as illite (Fig. 13A). Petrographically, there is abundant quartz with undulose extinction, K-feldspar blades, illite, calcite (grains and veins), gypsum, chlorite, altered lithic fragments, montmorillonite, and glauconite (Fig. 13C). The matrix is microcrystalline with quartz and calcite.

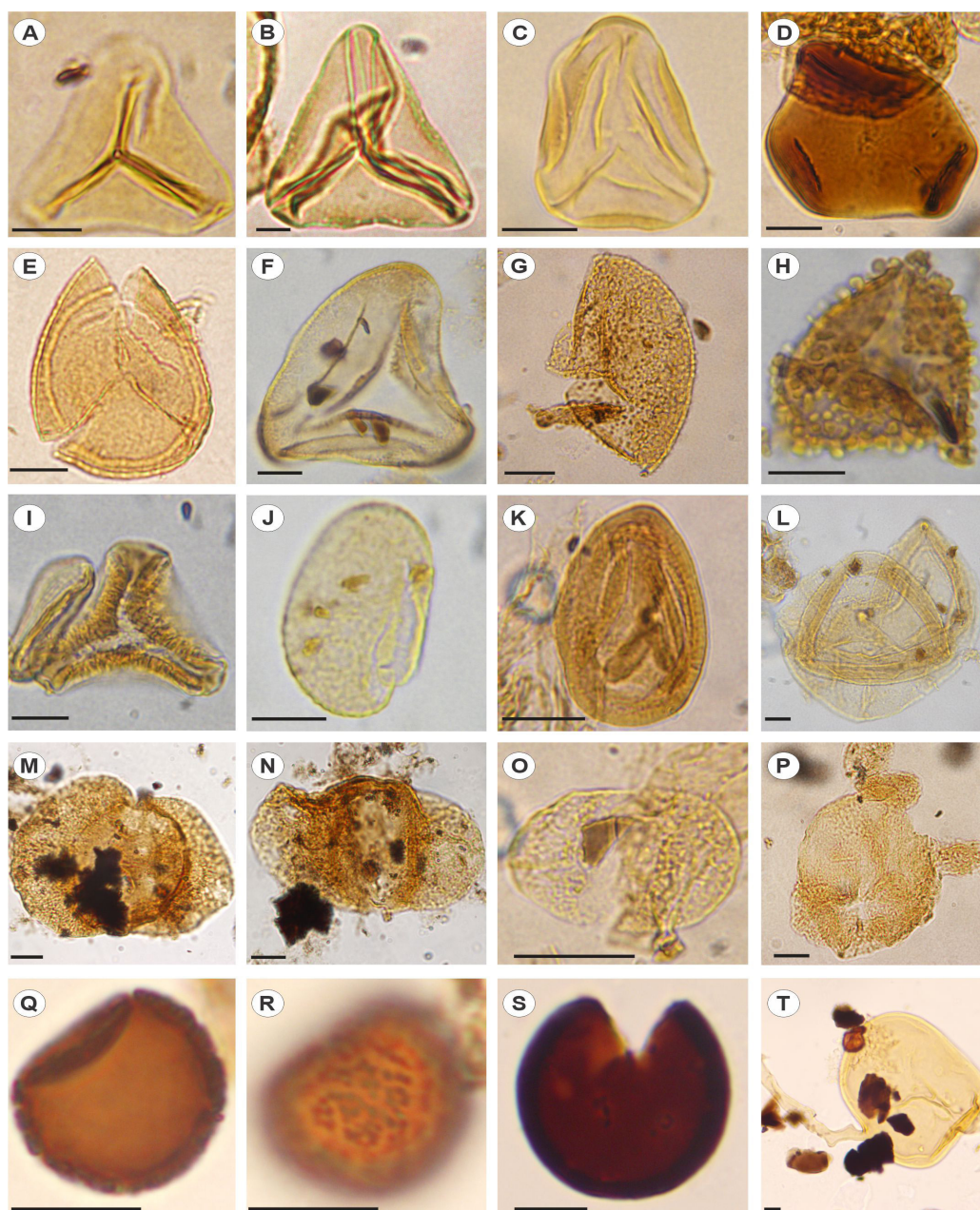


FIG. 11. Selected palynomorphs from the Destacamento I section samples. Lajas Formation: **A.** *Biretisporites* sp. A (in Volkheimer 1974), sample UNSP-DI5918, EF: K31/2. **B.** *Dictyophyllidites mortoni*, sample UNSP-DI5918, EF: Z36/2. **C.** *Gleicheniidites argentinus*, sample UNSP-DI5918, EF: Z16/2. **D.** *Cibotiumspora jurienensis*, sample UNSP-DI5918, EF: N29/3. **E.** *Staplinisporites caminus*, sample UNSP-DI5918, EF: X29/4. **F.** *Cyathidites punctatus*, sample UNSP-DI5918, EF: N30. **G.** *Osmundacidites diazii*, sample UNSP-DI5918, EF: G16. **H.** *Uvaesporites* sp. cf. *U. hammenii*, sample UNSP-DI5918, EF: P34/4. **I.** *Auritulinasporites* sp., sample UNSP-DI5918, EF: W29. **J.** *Marattisporites scabratus*, sample UNSP-DI5918, EF: Z43/4. **K.** *Classopollis classoides*, sample UNSP-DI5918, EF: E40. **L.** *Callialasporites turbatus*, sample UNSP-DI5918, EF: C15/4. Bosque Petrificado Formation: **M.** *Alisporites similis*, sample UNSP-DI5976, EF: T36/3. **N.** *Podocarpidites multesimus*, sample UNSP-DI5976, EF: O36/4. Lajas Formation: **O.** *Vitreisporites pallidus*, sample UNSP-DI5918, EF: E40/2. **P.** *Microcachrydites antarcticus*, sample UNSP-DI5918, EF: M15. Bosque Petrificado Formation: **Q-R.** Amerosporae, sample UNSP-DI5976, EF: N38. Lotena Formation: **S.** Amerosporae, sample UNSP-DI6238, EF: R34/2. **T.** *Glomus* (s.l.), sample UNSP-DI6238, EF: Q24/3. EF: England Finder coordinates. Scale bar: 10 μ m.

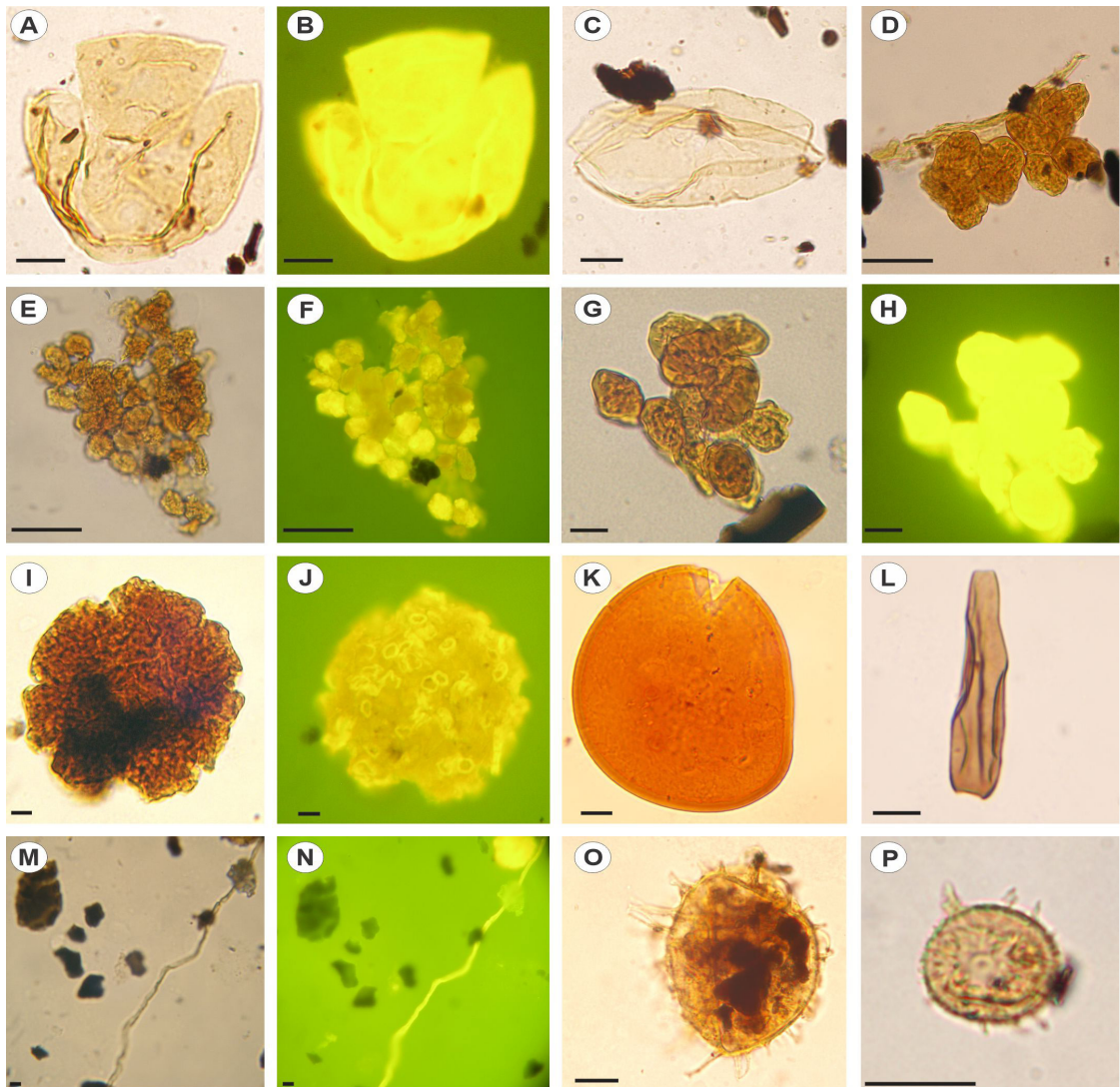


FIG. 12. Selected palynomorphs from the Destacamento I section samples. Bosque Petrificado Formation: **A-B.** *Ovoidites tripartitus*, sample UNSP-DI5952, EF: P33, transmitted and UV light. **C.** *Ovoidites elongatus* sample UNSP-DI5952, EF: O34. Lotena Formation: **D.** *Oedogonium* sp. cf. *O. cretaceum*, sample UNSP-DI6238, EF: Y19. **E-F.** *Oedogonium* sp. cf. *O. cretaceum*, sample UNSP-DI6238, EF: T24, transmitted and UV light. **G-H.** *Oedogonium* sp. cf. *O. cretaceum*, sample UNSP-DI6238, EF: X40, transmitted and UV light. **I-J.** *Botryococcus* sp. cf. *B. braunii*, sample UNSP-DI6238, EF: T24, transmitted and UV light. **K.** *Tasmanites* sp., sample UNSP-DI6238, EF: M20. **L.** Cyanobacterial sheath, sample UNSP-DI6238, EF: M28. **M-N.** Cyanobacterial filament, sample UNSP-DI6238, EF: L24, transmitted and UV light. **O.** *Systematophora penicillata*, sample UNSP-DI6240, EF: N20. **P.** *Filisphaeridium castaninum*, sample UNSP-DI6240, EF: U17/4. EF: England Finder coordinates. Scale bars: 10 μ m.

Sample UNSP-DI6240 is a green to grey mudstone from the middle-upper part of the Lotena Formation (Fig. 2). The XRD analysis identified quartz, calcite, and minor glauconite and illite (Fig. 13B). The petrographic study revealed irregular particles of

quartz, elongated K-feldspar, lithic fragments, calcite, illite, limonite, chlorite, gypsum, and glauconite (Fig. 13D). The matrix has microcrystalline calcite, quartz, and iron oxides. The lithic fragments correspond to volcanic particles with mineral alteration.

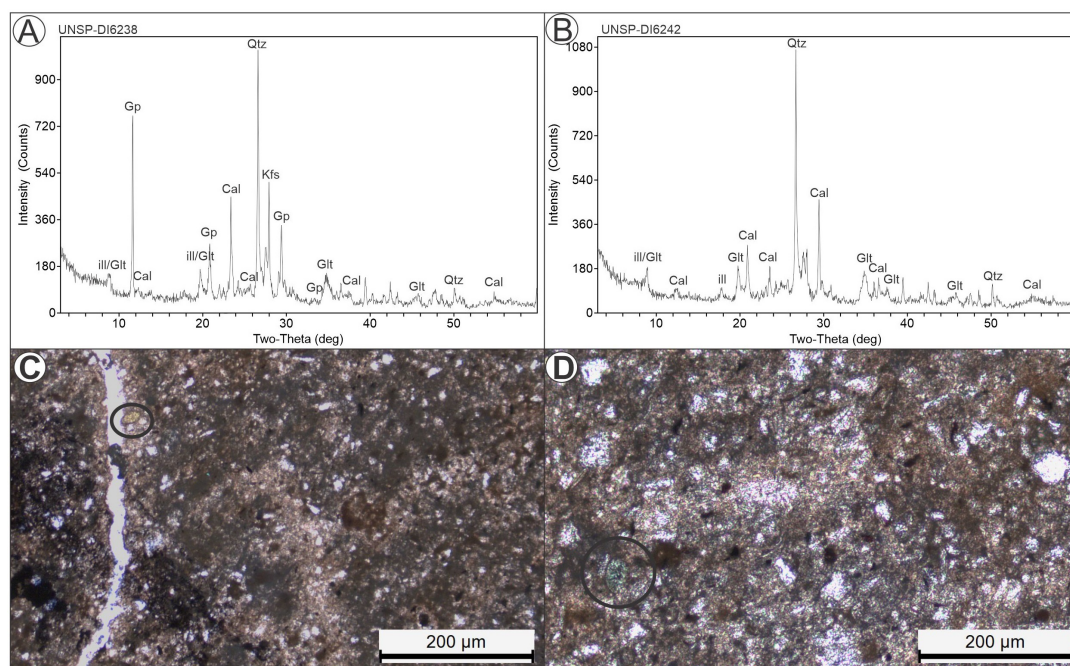


FIG. 13. Lotena Formation. Upper row. X-Ray diffractograms of samples UNSP-DI6238 (A) and UNSP-DI6242 (B) with peaks of quartz (Qtz), K-feldspar (Kfs), illite (ill), calcite (Cal), gypsum (Gp), and glauconite (Glt). Lower row. Photomicrographs of samples UNSP-DI6238 (C) and UNSP-DI6242 (D); black circles show the presence of detritic glauconite in each.

5. Palaeoecological requirements of the Destacamento I palynoflora

The palaeoecological requirements of the main groups of palynoflora recognised in this study are presented below.

5.1. Spores

Marattiaceae. Fern monolete spores, mainly *Marattisporites* (= *Punctatosporites* following McKellar, 1998), are typically found in ground cover lowland, mire or wet (hygrophyllous) environments (Petersen *et al.*, 2013; Lindström, 2015; Lindström *et al.*, 2017), although Alaug *et al.* (2007) reported the adaptive capacity of these spores to thrive in dry conditions. Ilyna (1986) and Ilyna and Shurygin (2000) linked the palynozone association of *Marattisporites scabratus*-*Klukisporites variegatus*-*Dictyophyllidites Classopolis* with the Early Toarcian climatic warming.

5.2. Pollen grains

Caytoniaceae. Several authors (*e.g.*, Schrank, 2010; Kujau *et al.*, 2013; Olivera *et al.*, 2015) have

associated the parental plant of these pollen grains (mainly *Vitreisporites*) with deltaic, flood plain to backswamp, swamp and/or other wet environments and wet climates (Abbink *et al.*, 2004).

5.3. Freshwater algae

5.3.1. Botryococcaceae

Extant *Botryococcus* are cosmopolitan algae that grow in fresh to brackish waters such as lakes and marshes (*e.g.*, Zalesky, 1926; Tyson, 1995), in tropical and temperate climates, although they can also tolerate seasonal cold weather (Batten and Grenfell, 1996). Furthermore, modern algae grow mainly in oligotrophic to mesotrophic lakes (*e.g.*, Komárek and Marvan, 1992; Ottone *et al.*, 2005), in areas with relatively low rainfall but with a wide range of climatical conditions throughout the year (*e.g.*, Guy-Ohlson, 1992; Zippi, 1998; Olivera *et al.*, 2015).

5.3.2. Oedogoniaceae

Several authors have reported modern species of *Oedogonium* in freshwater habitats worldwide (*e.g.*, Tiffany, 1930; Fritsch, 1961). There are currently no records of marine species, and only four out of

the 205 species have been reported from brackish water in Europe: *O. capilare* (Bousedra marsh, Benchabane Razika, 2015; salt lakes, Cambra, 1989), *O. howei* (Spanish salt lakes, Cambra, 1989), and *O. intermedium* (salt and littoral lakes, Cambra, 1992). Zippi (1998) established the following order for the preferred habitats for *Oedogonium*: permanent ponds, lakes, temporary ponds and streams. Sexual reproduction of this alga is seasonal, occurring once or twice a year, and requires elevated alkalinity and nitrogen deficiency (Fritsch, 1961; Zippi, 1998). Although fossil specimens of *Oedogonium* are rare (Tappan, 1980; Zippi, 1998; Martínez *et al.*, 2008a), a widespread palaeoecology is interpreted for the fossil oospores (zygotes) of *Oedogonium* algae: low-moving or still, shallow, freshwater with an alkaline pH and nitrogen deficiency in a region that is somewhat seasonal (Zippi, 1998). Martínez *et al.* (2008a) stated that the development of these resistant spores in Oedogoniaceae is a reproductive strategy to resist the imminent drying up of the water body and then germinate when environmental conditions become favourable.

5.3.3. Zygnemataceae

Modern zygnematacean algae grow mainly in freshwater environments as a part of the macrobenthos and macroplankton. They thrive in shallow, oxygen-rich, lentic environments with a pH close to neutral, or acidic in the case of *Zygonium*. Few species habit brackish lacustrine environments and there are no marine representatives. Zippi (1998) observed that the fossil genus *Ovoidites* and zygospores of modern zygnematacean genera, such as *Spirogyra* and *Sirogonium*, are almost indistinguishable.

The fossil algae, mainly the genus *Ovoidites*, are restricted to freshwater environments such as paludal, stagnant, low-gradient fluvial deposits, lake margins or shallow freshwater lacustrine deposits where the water may have been ephemeral and oxygen-rich (Zippi, 1998; Martínez *et al.*, 2008a; Worobiec, 2014; Olivera *et al.*, 2015; Zavattieri *et al.*, 2020). The limited range of habitat preferences exhibited by these algae suggests that *Ovoidites* could serve as a useful indicator of ancient freshwater coal deposits (Rich *et al.*, 1982). The habitat preferences of living *Spirogyra*-producing algae, include “stagnant, shallow, and more or less mesotrophic freshwater habitats” (van Geel and van der Hammen, 1978, p. 379). The presence of Zygnemataceae spores indicates a seasonal or ephemeral habitat, during

which the water body (probably a waterlogged or ephemeral lagoon) was seasonally subjected to intense evaporation under temperate climatic conditions, even reaching temperatures above 20 °C (predominance of *Spirogyra*, according to van Geel and van der Hammen, 1978, and Martínez *et al.*, 2008a).

5.4. Fungal remains

Fungal spores. The high diversity of fungal spores and remains suggests a high humidity climate (Taylor *et al.*, 2015). Romero *et al.* (2021) linked the dominance of Amerosporae forms to a wet environment with structurally closed vegetation, and associated this morphological type with saprophytic fungi, which have air dispersal strategies and reach longer distances.

6. Discussion

6.1. Palynostratigraphy

The Lajas Formation records the presence of *Microcachrydites antarcticus*, a very useful biostratigraphical taxon (Figs. 8 and 11; Supplementary Table S1). In the Neuquén Basin, the first appearance of this taxon indicates the base of the *Ischyosporites marburgensis* Subzone (latest Early Bajocian-Late Bajocian; Quattrocchio *et al.*, 1996). Therefore, at the Destacamento I section, an age no older than latest Early Bajocian is suggested for the uppermost part of the Lajas Formation. Due to the wide biochrons exhibited by the species recorded in this palynoflora assemblage, the youngest age of the Lajas Formation cannot be constrained; however, a minimum Late Bathonian age is suggested based on the Challacó Formation palynological record (see below). The presence of *Cyathidites punctatus* in this formation is also worth mentioning, as this taxon has been recorded in Argentina for Aptian and younger rocks only, so this new evidence would extend the first appearance of *Cyathidites punctatus* to much older strata in Argentina.

The Challacó Formation does not seem to have biostratigraphically useful taxa (Fig. 8; Supplementary Table S1). However, at the Quebrada Álvarez section, situated 5.7 km northeast from the Destacamento I section, Chalabe *et al.* (2024) proposed for this unit a Late Bathonian-Early Callovian age based on the palynological biomarkers identified. In addition, Zavala *et al.* (2020, and references therein)

recognised, from a sedimentological perspective, the intra-Callovian Unconformity (Early Callovian) as the boundary between the Challacó and Bosque Petrificado formations.

In the Bosque Petrificado Formation, the presence of *Alisporites lowoodensis* in sample UNSP-DI5976 implies an age not younger than Early Callovian for the strata that contain this taxon (Figs. 2 and 9). Although elsewhere this taxon has been recognised up to the Tithonian (e.g., McKellar, 1974; Burger, 1996; Filatoff, 1975; El Afty *et al.*, 2013), in Argentina its record is no younger than Early Callovian (Chalabe *et al.*, 2024). Another noteworthy feature in this unit is the presence of zygnematacean algae previously unregistered in the Neuquén Basin literature, such as the freshwater specimens *Ovoidites elongatus* and *O. circumplicatus*. In Argentina, *O. elongatus* (= *Spirogyra* sp. Type A; Zamaloa, 1996) has so far been reported in the Triassic of the Cuyana Basin (Zavattieri *et al.*, 2020; Gutiérrez and Zavattieri, 2023), in the Cretaceous of the Cañadón Asfalto Basin (Tomas *et al.*, 2022), in the Paleogene of the Ñirihuau Basin (Martínez *et al.*, 2008a), and in the Neogene of Tierra del Fuego (Zamaloa, 1996). Outside Argentina, this taxon has mentions only in the Cenozoic (e.g., Herrmann, 2010; Worobiec, 2014; Denk *et al.*, 2019). *O. circumplicatus* (= Gen. et sp. indet. Martínez *et al.*, 2008a), on the other hand, has been reported in the Triassic of the Cuyana Basin (Zavattieri *et al.*, 2020; Gutiérrez and Zavattieri, 2023) and in the Paleogene of the Ñirihuau Basin (Martínez *et al.*, 2008a), with no records outside Argentina.

Finally, in the Lotena Formation no palynological biomarkers were found, although the stratigraphical position of this unit in a regional context suggests a maximum Late Callovian age. A notable feature of the Lotena Formation assemblages studied in this contribution is the record of the acritarch *Filisphaeridium castaninum*. This taxon has so far only been identified in the Los Molles Formation, with an estimated Late Aalenian to Early Bajocian age, so the specimens recognised in the Lotena Formation would constitute the youngest register of *F. castaninum* in Argentina.

6.2. Palaeoenvironmental and palaeoclimatic interpretations

Many variables are involved in the deposition of palynological matter, such as its source of origin,

the depositional lithology and location, sea level fluctuations, palaeoclimate, and palaeoproductivity (e.g., Oboh-Ikuenobe *et al.*, 1997; Borronei *et al.*, 2018). The palynological, petrographic, sedimentological, and XRD information, combined with the identification of some useful ichnotaxa, fossil molluscs, and microbial mat remains, were integrated into a coherent framework to allow interpretations on the depositional environments of the Cuyo and Lotena groups at the Destacamento I section.

6.2.1. Cuyo Group Lajas Formation

The upper part of the Lajas Formation contains thin carbonaceous sandstone beds with evidence of tidal action (e.g., sigmoidal tidal bundles and tidal rhythmites) and terrestrial fossil plant leaves (Fig. 2). The palynofacies defined for this unit (palynofacies types A to C; Figs. 2 and 5A-C; Table 2) are strongly dominated by continental organic matter. Palynofacies types A and B are mainly composed of translucent phytoclasts, while in the palynofacies type C the terrestrial palynomorphs (sporomorphs + fungal spores) build most of the continental organic matter (Table 2). Both the palynological organic matter and the plant remains present in these levels, reflect an elevated continental supply to the basin associated with high water availability in a coastal marine palaeoenvironment. A noteworthy feature of the palynomorph content is the lack of marine components. Several authors have proposed that a high turbidity, mixed water column can make the marine setting a very unfavourable environment for the development of microplankton, such as dinoflagellates (e.g., García *et al.*, 2006; Franco Arias, 2018). These conditions are often associated with strong fluvial discharges into the marine basin, and although these currents are an effective mechanism for the basinward transport of very high quantities of nutrients, they are sometimes charged with clastic material, producing variations in water salinity. In these cases, the high sediment load impacts light penetration and limits microplankton growth and biological productivity (e.g., Alpine and Cloern, 1988). Thus, the proxies studied in the Lajas Formation may suggest tide-modified, deltaic shallow marine conditions, consistent with the depositional setting proposed for this unit by Zavala *et al.* (2020) and Chalabe *et al.* (2024) in other locations. The presence of cyanobacterial remains in palynofacies types A and C (Table 2) reinforce

the interpretation of above, as they are commonly associated with shallow coastal environments (e.g., Rodríguez *et al.*, 2023). Palynofacies type A also shows a higher percentage of amorphous organic matter, that alongside an apparent reduction in the phytoclasts abundance could indicate a relatively low freshwater supply to the system and a consequent decrease in the terrestrial input to the basin towards the top of the unit (Table 2).

Samples UNSP-DI5918 and UNSP-DI5921 exhibit high percentages of *Marattisporites scabratus*, a thermophilic taxon. High frequencies of this species have previously been related to warm climatic conditions (e.g., Ilyna, 1986). The high content of *M. scabratus* is a noteworthy feature of this palynoflora as Marattiaceae spores are typically abundant in the Aalenian but become less abundant in the Bajocian and Bathonian (Alaug *et al.*, 2007), so its high presence in the uppermost part of the Lajas Formation could suggest a local warming during the Late Bajocian. The high proportion of these monolete spores is accompanied by Caytoniaceae pollen grains (*Vitreisporites pallidus*) and other spore ferns (Fig. 8). According to Lindström (2015), the presence of *M. scabratus* is associated with lowland, mire or wet environments, while the high abundance of the caytoniacean pollen (mainly *V. pallidus*) accompanying the peak of fern spores, is evidence of the establishment of swamps, backswamps and/or the dominance of deltaic environments (Kuajú *et al.*, 2013; Chalabe *et al.*, 2024). In contrast to the palynological record identified to the north of the Huicul Arch, the Hirmeriellaceae pollen grain record is sparse (Fig. 8). This supports the idea of swampy and deltaic environments, as the conifers that produced *Classopollis* pollen grains avoided swampy and watery areas (Vakhrameev, 1981; Chalabe *et al.*, 2024). In these assemblages, Podocarpaceae and Araucariaceae pollen occur in low proportions (4 and 2% in average, respectively). Their presence could be related to what is known as regional or extra-regional pollen (see Holmes, 1994), with these palynomorphs probably representing long-distance sporomorphs (*i.e.*, travel distances of more than a few hundred metres from their source plants). Assuming these two pollen types came from the same forested upland ecosystem, the slightly higher abundances of Podocarpaceae may be attributed to its morphology, as Podocarpaceae is more easily transported by the wind.

The dominance of continental organic matter (*i.e.*, translucent organic particles, well-preserved palynomorphs and plant remains) allows for short distances and/or short source transport times to be inferred for the Lajas Formation, indicating proximal conditions and a rapid burial of these organic particles, inhibiting their deterioration (Table 2).

Palynofacies can also be used to assess the hydrocarbon potential of a given unit (e.g., Batten, 1983; Tyson, 1995). For the studied samples from the Lajas Formation, the thermal alteration index, which helps to determine the thermal maturity of the rock, is provided in table 2. The thermal alteration index values observed range from 1+ to 2-, corresponding to an immature state of hydrocarbon generation. Fluorescence is also an important method for determining the maturity of the kerogen by assessing the intensity and colour of the organic matter components when irradiated with UV light (Kemp *et al.*, 2019). Qualitative fluorescence is intense in immature samples and decreases during diagenesis and catagenesis, disappearing completely at the end of catagenesis (Mendonça Filho *et al.*, 2012). In the Lajas Formation, fluorescence colours are orange to yellow, consistent with an immature state (Table 2).

Challacó Formation

This formation is characterised by massive grey siltstones (Fig. 2). Two palynofacies types were defined for this formation (D and E; Table 2). The high equidimensional to blade-shaped particle ratio (eo:bo ratio) recorded in the palynofacies type D could indicate a predominance of traction over decantation processes (e.g., Martínez *et al.*, 2005a; Olivera *et al.*, 2020; Chalabe *et al.*, 2022) (Fig. 5D), whereas the low opaque to translucent phytoclasts ratio (op:tp ratio) of palynofacies type E could mean short distances and/or short source transport times. In addition, palynofacies type E shows an increase in the amorphous organic matter content, which could indicate relatively drier conditions with a reduction in the surface runoff and therefore a lower terrigenous input to the basin (Chalabe *et al.*, 2024) (Fig. 5E; Table 2).

Although none of the Challacó samples had more than 250 palynomorphs, there are three samples with presence (UNSP-DI5922, 5923 and 5951; see section 3.2). Among the recognised palynomorphs in these samples, the Chlorophyta algae are the dominant, mainly *Botryococcus* and *Oedogonium*. This last taxon has not been identified in the Neuquén Basin

to date and has very few mentions in the fossil record worldwide (e.g., Martínez *et al.*, 2008a). The modern Chlorophyta algae *Oedogonium* has been found mainly in freshwater environments, with few species in brackish environments (see section 5.3.2). Thus, the presence of both Chlorophyta algae (*Oedogonium* and *Botryococcus*) suggests lacustrine conditions (freshwater to brackish) for the Challacó Formation, in accordance with other studies (e.g., Zavala and González, 2001; Zavala, 2002; Martínez *et al.*, 2005a; Zavala *et al.*, 2020; Chalabe *et al.*, 2024).

6.2.2. Lotena Group

Bosque Petrificado Formation

This unit is composed of siltstones to conglomerates, interbedded with sandstone levels with plant debris, broken clasts, imbricated clasts, clay chips, rust spots, and siderite nodules (Fig. 2). Syntedimentary precipitation of siderite can occur when there is mixing of seawater and freshwater under reducing conditions, as it does in coastal marshes (e.g., Nichols, 2009). At around 158 m in the section, the ichnogenus *Skolithos* isp. was recognised (sample UNSP-DI6075, palynofacies type J). Classified as *Domichnia* in the ichnological literature, this ichnogenus is produced by suspension-feeding and deposit-feeding organisms. It is associated with shallow, high-energy environments, usually marine, such as coastal or subtidal zones (Desjardins *et al.*, 2010; Knaust, 2017). All the palynofacies of the Bosque Petrificado Formation (Table 2), apart from palynofacies type G, display high percentages of translucent phytoclasts, which are indicative of short distances and/or short source transport times (Fig. 5F, J, K; Table 2). Palynofacies types H and K also exhibit higher percentages of amorphous organic matter, which could be attributed to a reduction in freshwater supply to the system and a resulting decrease in the terrestrial input to the basin (Fig. 5H, I, L; Table 2). Similar palaeoenvironmental conditions were inferred for the Challacó Formation by Chalabe *et al.* (2024) in the Quebrada Álvarez section.

The palynoflora of this formation exhibits a high proportion of *Botryococcus* and *Oedogonium* algae, accompanied by *Leiosphaeridea* sp., *Ovoidites* algae and fungal spores. As mentioned above, *Botryococcus* and *Oedogonium* are associated with freshwater to brackish lacustrine conditions, while *Ovoidites* is a valuable indicator of ancient freshwater deposits and temperate climates. This palynomorph content could be related to the development of freshwater coastal

ponds with a periodical influence of marine waters (e.g., coastal marshes). The bloom of *Botryococcus* and *Oedogonium* identified at the bottom of the Bosque Petrificado Formation could represent a period of disconnection of the marine system and the development of mainly freshwater bodies. In addition, the acritarch *Filisphaeridium balmei* was recognised (sample UNSP-DI5976; palynofacies type I), a taxon previously found in shallow marine environments (e.g., Martínez *et al.*, 2005b, 2008b; Quattrocchio *et al.*, 2008), so its presence and that of the *Skolithos* ichnogenus is probably associated with periods of seawater advance.

Lotena Formation

The Lotena Formation includes fine-grained marine sediments containing abundant small benthonic bivalves belonging to the fossil-genus *Bositra*. These molluscs probably thrived in a shallow environment and may have been killed by an abrupt input of continental waters (Parent *et al.*, 2023). *Trichichnus* isp. and *Skolithos* isp. represent the ichnological content of this unit. *Trichichnus* consists of straight to sinuous, sparsely branched or unbranched, cylindrical trace fossils, less than 1 mm in diameter (Stachacz, 2012; Campetella, 2022). This trace has been interpreted either as a domichnial structure of deposit-feeders or as a chemichnial structure formed by chemosymbiotic organisms, being commonly found in both shallow and deep-marine environments, particularly in fine-grained substrates (Stachacz, 2012; Campetella, 2022).

The palynofacies types identified are mainly dominated by phytoclasts, which suggests a high terrestrial input to the basin (Table 2). Translucent phytoclasts predominate in palynofacies types L and P, indicating short distances and/or source transport times, with a predominance of traction over decantation (Martínez *et al.*, 2005a; Chalabe *et al.*, 2024) (Fig. 5M, Q; Table 2). Conversely, palynofacies types M and O are dominated by opaque phytoclasts indicating a strong oxidation (Fig. 5N, P; Table 2). Among the opaque fragments, the equidimensional forms with rounded edges are dominant, possibly indicating reworking from older deposits and/ or long source transport distances (Tyson, 1995; Falco *et al.*, 2021; Chalabe *et al.*, 2024).

In the mid-section, there is a high proportion of well-preserved palynomorphs, with a predominance of *Botryococcus* and *Oedogonium* along with fungal spores with very scarce marine components (samples UNSP-DI6238 and UNSP-DI6240; palynofacies

types P and O). This is indicative of a freshwater to brackish lacustrine environment (e.g., Zippi, 1998; Martínez *et al.*, 2008a), while the high proportion and diversity of fungal spores has been associated with high humidity conditions (Taylor *et al.*, 2015). Sample UNSP-DI6238 shows the highest content of fungal spores, dominated by the Amerosporae type. Amerosporae is typical of wet environments, and its presence could represent a period of frequent flooding events. These floods could have been highly erosive, resuspending previously deposited material and leaving the rounded-edged equidimensional opaque phytoclasts as evidence.

The XRD and petrographic analyses show the presence of detritic glauconite grains (de Castro *et al.*, 2021) (Fig. 13C, D). Authigenic glauconite has been reported in restricted shelf to shallow-marine environments (Fernández-Landero and Fernández-Caliani, 2021; Wilmsen and Bansal, 2021). In the Neuquén Basin, it has been identified in the Los Molles Formation (e.g., Gan *et al.*, 2019; Campetella, 2022). In the studied samples at the Destacamento I section, the glauconite grains are detritic in origin, possibly indicating the erosion of tectonically exhumed marine deposits from the Huincul Arch area. Zavala and Freije (2002) reported for the Lotena Formation palaeocurrents showing a clear provenance from the northeast. Later, Zavala *et al.* (2020), based on palaeocurrent and lithological evidence, proposed that most of the conglomerates, sandstones and shales of the Bosque Petrificado Formation could represent recycled sedimentary deposits previously accumulated in the Lajas and Los Molles formations. This is supported by the presence of detritic glauconite and equidimensional opaque phytoclasts with rounded edges in the studied samples, that could only be explained if the Cuyo Group was tectonically exposed and uplifted, supplying material during the accumulation of the Lotena Formation.

7. Conclusions

The palynological assemblages recovered from the uppermost part of the Lajas Formation constitute the first palynological record for this formation in the Picún Leufú sub-basin. According to some marker species, this palynoflora would not be older than latest Early Bajocian. These deposits were accumulated in a deltaic, shallow-marine environment under a warm climate. On the other hand, freshwater to brackish lacustrine conditions are interpreted for the Challacó

Formation, in accordance with previous studies, while the Bosque Petrificado Formation shows evidence of mixing of seawater and freshwater, probably developed in coastal ponds with episodic marine influence. According to the presence of *Alisporites lowoodensis*, the Bosque Petrificado Formation would not be younger than Early Callovian. Finally, a shallow marine environment strongly influenced by fluvial discharges is interpreted for the Lotena formation, where recycled sediments are also present.

This study also reports the youngest records of the species *Filisphaeridium castaninum* and *Cyathidites punctatus* in Argentina, and the first mention of the elusive chlorophyte algae *Oedogonium*.

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Supplementary material

TABLE S1. LIST OF THE PALYNOFORMH SPECIES IDENTIFIED IN THE LAJAS, CHALLACÓ, BOSQUE PETRIFICADO AND LOTENA FORMATIONS IN THE DESTACAMENTO I SECTION. BIOLOGICAL AFFINITIES OF SPORES, POLLEN AND ORGANIC-WALLED MICROPLANKTON FROM THE UNITS.

	Biological affinities	Taxons/ Samples	UNSP-DI5918	UNSP-DI5921	UNSP-DI5922	UNSP-DI5923	UNSP-DI5951	UNSP-DI5952	UNSP-DI5954	UNSP-DI5976	UNSP-DI5982	UNSP-DI6073	UNSP-DI6074	UNSP-DI6076	UNSP-DI6078	UNSP-DI6080	UNSP-DI6238	UNSP-DI6240	UNSP-DI6241	UNSP-DI6242	UNSP-DI6243			
			Lajas Fm.	Challacó Fm.			Bosque Petrificado Fm.							Lotena Fm.										
Spores	Bryophyte	<i>Staplinisporites caminus</i> (Balme 1957) Pocock, 1962 (Fig. 11E)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
	Cyatheaceae/Dicksoniaceae	<i>Cyathidites punctatus</i> (Delcourt and Sprumont) Delcourt, Dettman and Hugues, 1963 (Fig. 11F)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
	Cyatheaceae/Dicksoniaceae Dipteridaceae/Matoniaceae	<i>Deltoidospora australis</i> (Couper) Pocock, 1970	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
		<i>Deltoidospora minor</i> (Couper) Pocock, 1970	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
		<i>Deltoidospora neddeni</i> Pflug (in Thompson and Pflug, 1953)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
		<i>Dictyophyllidites harrisii</i> Couper, 1958	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
		<i>Dictyophyllidites mortoni</i> Playford and Dettmann, 1965 (Fig. 11B)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
		<i>Deltoidospora</i> indet.	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		Dipteridaceae (?)	<i>Cibotiumspora jurianensis</i> (Balme, 1957) Filatoff, 1975 (Fig. 11D)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Gleicheniaceae	<i>Gleicheniidites argentinus</i> Volkheimer, 1972 (Fig. 11C)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
	Marattiaceae	<i>Biretisporites</i> sp.A (in Volkheimer, 1974) (Fig. 11A)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
	Uncertain Filicopsida	<i>Apiculatisporis charahuillaensis</i> Volkheimer, 1972	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
	Osmundaceae	<i>Osmundacidites araucanus</i> Volkheimer, 1972	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Osmundacidites diazii</i> Volkheimer, 1972 (Fig. 11G)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Verrucosisporites varians</i> Volkheimer, 1972	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Verrucosisporites</i> sp. (in Volkheimer, 1972)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		Selaginellaceae/ Lycopodiaceae	<i>Uvaesporites</i> sp. cf. <i>U. hamnenii</i> (Fig. 11H)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Auritulinasporites</i> sp. (Fig. 11I)		X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	<i>Retitritiles</i> sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	
	Sphagnaceae	<i>Antulsporites saevus</i> (Balme) Archangelsky and Gamarro emend. McKellar, 1998	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Undifferentiated	Psilate spore indet.	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Marattiaceae	<i>Marattisporites scabratus</i> (Couper, 1958) Singh, 1971 (Fig. 11J)	X	X	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Pollen grains	Hirmeriaceae (=Cheirolepideaceae)	<i>Classopollis intrareticulatus</i> Volkheimer, 1972	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Classopollis classoides</i> (Pflug, 1953) Pocock and Jansonius, 1961 (Fig. 11K)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Classopollis</i> indet.	X	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Araucariaceae	<i>Araucariacites australis</i> Cookson ex Couper, 1953	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Callialasporites turbatus</i> Schulz, 1967 (Fig. 11L)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Inaperturopollenites</i> sp.A (in Volkheimer, 1972)	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Inaperturopollenites</i> indet.	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		Caytoniaceae	<i>Vitreisporites pallidus</i> Volkheimer, 1972 (Fig. 11O)	X	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-
	Umkomasiaceae (=Corystospermaceae)	<i>Alisporites similis</i> (Balme) Dettmann, 1963 (Fig. 11M)	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Alisporites grandis</i> Dettmann, 1963	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Alisporites lowoodensis</i> (Balme) Dettmann, 1963	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
	Podocarpaceae	<i>Microcachrydites antarcticus</i> Cookson, 1947 (Fig. 11P)	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Podocarpidites ellipticus</i> Cookson, 1947	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Podocarpidites multesimus</i> Pocock, 1962 (Fig. 11N)	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Podocarpidites</i> sp. cf. <i>P. radiatus</i>	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Podocarpidites</i> sp.	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Podocarpidites</i> indet.	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Podosporites</i> indet.	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Trichotomosulcites microsaccatus</i> (Couper, 1953) Schrank, 2010	-	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	
		? <i>Trichotomosulcites</i> sp.	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		Podocarpaceae indet.	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
		Pinaceae	Pinaceae indet.	X	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
		Undifferentiated	Bisaccate indet.	X	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-

Table S1 continued.

			Biological affinities	Taxons/ Samples	UNSP-DI5918	UNSP-DI5921	UNSP-DI5922	UNSP-DI5923	UNSP-DI5951	UNSP-DI5952	UNSP-DI5954	UNSP-DI5976	UNSP-DI5982	UNSP-DI6073	UNSP-DI6074	UNSP-DI6076	UNSP-DI6078	UNSP-DI6080	UNSP-DI6238	UNSP-DI6240	UNSP-DI6241	UNSP-DI6242	UNSP-DI6243		
					Lajas Fm.	Challacó Fm.			Bosque Petrificado Fm.							Lotena Fm.									
Undifferentiated				Palynomorph indet.	X	X	-	X	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-		
Organic walled microplackton	Charophyta	Zygnemataceae	<i>Ovoidites circumplicatus</i> Zavattieri <i>et al.</i> , 2020	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-		
			<i>Ovoidites elongatus</i> (Hunger, 1952) Krutzsch, 1959 (Fig. 12C)	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
			<i>Ovoidites tripartitus</i> Zavattieri <i>et al.</i> , 2020 (Fig. 12A-B)	X	-	-	-	-	-	X	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
			<i>Ovoidites</i> indet.	X	X	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
			<i>Schizophacus</i> sp.	-	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
	Chlorophyta	Oedogoniaceae	<i>Oedogonium</i> sp. cf. <i>O. cretaceum</i> (in Martínez <i>et al.</i> , 2008a) (Fig. 12D-H)	-	X	-	X	X	-	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
		Botryococcaceae	<i>Botryococcus</i> sp. cf. <i>B. braunii</i> Kützing, 1849 (Fig. 12I-J)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
	Dinoflagellate cyst			<i>Systematophora penicillata</i> (Ehrenberg, 1843) Sarjeant, 1980 (Fig. 12O)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	
	Prasinophyceae			<i>Tasmanites</i> sp. (Fig. 12K)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	
	Acritarchs	<i>Leiosphaeridea</i> sp. (in Chalabe <i>et al.</i> , 2024)			-	X	X	X	-	X	X	X	-	-	-	-	-	-	-	X	X	-	-	-	
		<i>Filisphaeridium balmei</i> (Sarjeant) Sarjeant and Stancliffe, 1994			-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	
		<i>Filisphaeridium castaninum</i> (Valensi) Sarjeant and Stancliffe, 1994 (Fig. 12P)			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	
Undifferentiated				Circular form 1	-	-	-	-	-	-	-	X	-	-	-	-	-	-	-	-	-	-	-		
Zoomorphs				Copepod egg	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Fungal remains				Amerosporae (Fig.11Q-S)	-	X	X	X	X	X	X	X	X	-	-	X	-	X	X	X	-	-	-		
				Didymosporae	-	-	X	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-	
				Phragmosporae	-	-	X	X	X	-	X	X	-	-	-	-	-	-	-	X	X	-	-	-	-
				Dictyosporae	-	-	-	-	-	-	X	-	X	-	-	-	-	-	-	X	X	-	X	-	-
				Staurosporae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	-	-	-
				Glomus (s.l.) (Fig. 11T)	-	X	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	X	-	-	-
				Mycelium	-	X	-	X	-	-	-	-	-	X	-	-	-	-	-	-	X	X	-	-	-

Main source of information concerning the natural relationships of dispersed palynomorphs based on Dettmann (1963), Filatoff (1975), de Jersey and Raine (2002), Balme (1995), McKellar (1998), Sajjadi and Playford (2002a, 2002b), Martínez *et al.* (2008a), and Schrank (2010).