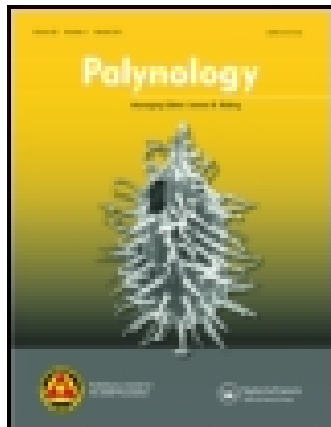


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Palynology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tpal20>

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Daniela E. Olivera^{ab}, Ana M. Zavattieri^c & Mirta E. Quattrocchio^b

^a Departamento de Geología, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Argentina

^b CONICET-INGEOSUR, San Juan 670, (8000) Bahía Blanca, Argentina

^c CONICET-IANIGLA, Centro Científico Tecnológico-Mendoza, A. Ruiz Leal s/n, Parque Gral San Martín, CC 330, 5500 Mendoza, Argentina.

Published online: 11 Mar 2015.



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To cite this article: Daniela E. Olivera, Ana M. Zavattieri & Mirta E. Quattrocchio (2015): The palynology of the Cañadón Asfalto Formation (Jurassic), Cerro Cóndor depocentre, Cañadón Asfalto Basin, Patagonia, Argentina: palaeoecology and palaeoclimate based on ecogroup analysis, *Palynology*, DOI: [10.1080/01916122.2014.988382](https://doi.org/10.1080/01916122.2014.988382)

To link to this article: <http://dx.doi.org/10.1080/01916122.2014.988382>

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The palynology of the Cañadón Asfalto Formation (Jurassic), Cerro Cóndor depocentre, Cañadón Asfalto Basin, Patagonia, Argentina: palaeoecology and palaeoclimate based on ecogroup analysis

Daniela E. Olivera^{a,b*}, Ana M. Zavattieri^c and Mirta E. Quattrocchio^b

^aDepartamento de Geología, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Argentina; ^bCONICET-INGEOSUR, San Juan 670, (8000) Bahía Blanca, Argentina; ^cCONICET-IANIGLA, Centro Científico Tecnológico-Mendoza, A. Ruiz Leal s/n, Parque Gral San Martín, CC 330, 5500 Mendoza, Argentina.

The Cañadón Asfalto Formation, Cañadón Asfalto Basin, Patagonia, Argentina, is interpreted as fluvial-lacustrine deposits. A palynological study of the lower and middle parts of the unit, at the Cañadón Lahuincó and Cañadón Caracoles sections, Cerro Cóndor Depocentre Chubut province, northwestern Patagonia, Argentina is presented. The quantitative composition of the palynofloras is characterised by the dominance of pollen produced by the conifer families Cheirolepidiaceae (*Classopollis*) and Araucariaceae (mainly *Araucariacites* and *Callialasporites*), suggesting that warm-temperate and relatively humid conditions under highly seasonal climate prevailed during the depositional times of the unit. The abundance of *Botryococcus* supports the presence of a shallow lake with probably saline conditions. Five palynomorph ecogroups (PEGs) were recognised: upland, lowland, riverside, coastal lake and aquatic. The ecological requirements of the different plant families forming the PEGs enable the inference of a sub-tropical palaeoclimate for the Cañadón Asfalto region during late Early Jurassic to mid Middle Jurassic, which is consistent with the 'seasonally dry (winterwet)' biome.

Keywords: palynology; palaeoecology; palaeoclimate; Cañadón Asfalto Formation; Patagonia; Early to Middle Jurassic; Argentina

1. Introduction

The Cañadón Asfalto Formation at Cerro Cóndor Depocentre, Cañadón Asfalto Basin, represents one of the most important records from the continental Jurassic in Extra-Andean Patagonia, Argentina. It is typically exposed in the middle valley of the Chubut River and surrounding areas, between the localities of Paso de Indios and Paso del Sapo, Chubut Province, southern Argentina (Figure 1). These deposits are known for their well-preserved biota, mainly dinosaurs and other vertebrates. The vertebrate faunas of this unit are one of the most important representatives of Gondwana by their richness, with more than 20 species from different taxonomic groups, including sauropods, theropods, ornithischians, pterosaurs, sphenodonts, mammals, fishes, frogs, turtles and crocodiles (Sterli et al. 2010). Additionally, several fossil plants, freshwater invertebrates and insect taxa were recorded from the lacustrine sediments (Escapa et al. 2008; Cabaleri et al. 2010; Monferrán et al. 2010). Despite the diversity and richness of the fossil assemblages recorded in the Cañadón Asfalto Formation, some aspects remain unresolved, such as its chronological age range and the palaeoecological and palaeoclimatic implications based on palynological data.

The earliest palynological studies on the Cañadón Asfalto Formation in the study area were carried out by Volkheimer (1971), Pöthe de Baldis (in Nullo & Proserpio 1975) and Volkheimer et al. (2001, 2008). Volkheimer et al. (2008) proposed a Middle Jurassic age (latest Early Bajocian to Early Bathonian) for a palynological assemblage recognised in the Lahuincó creek (Figure 1). Zavattieri et al. (2010) suggested an early Middle Jurassic (Late Aalenian–Middle Bathonian) age, based on its palynological content recorded in a partial section of the Cañadón Asfalto Formation.

This paper focuses on the palynological study of the Cañadón Asfalto Formation outcropping in the Cerro Cóndor area (Figure 1), where three stratigraphical sections were measured. Two of them were sampled at Lahuincó creek, which is located 15 km south of Cerro Cóndor village (Figure 1), named Cañadón Lahuincó 'A' (S43°30'59", W69°8'20") and Cañadón Lahuincó 'B', situated about 250 m west of the former (Figure 2). The third section is located 11 km north of Cerro Cóndor village, at Cañadón Caracoles creek (S43°24'8.01", W69°9'34.79") (Figures 1 and 2). The detailed palynological study of these stratigraphical sections increases the palaeofloristic knowledge on the

*Corresponding author. Email: daniela.olivera@uns.edu.ar

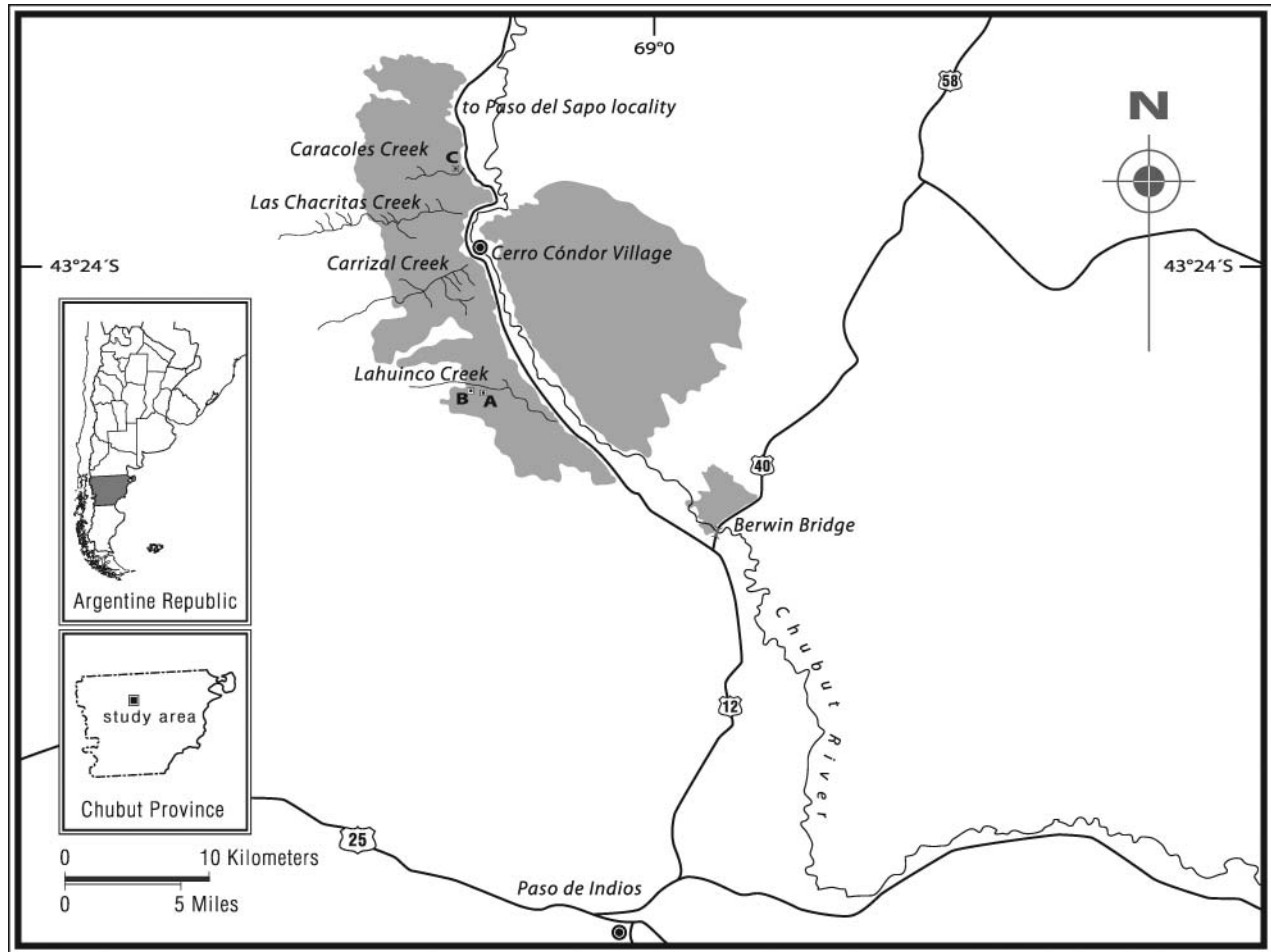


Figure 1. Location of the outcrops of the Cañadón Asfalto Formation and the three sections (A, B and C) studied, Cerro Cóndor Depocentre, area of the middle Chubut River valley. Patagonia, Argentina. A: Cañadón Lahuinco 'A'; B: Cañadón Lahuinco 'B' and C: Cañadón Caracoles.

Cañadón Asfalto Formation, at Cerro Condor Depocentre.

In order to understand plant distribution and evolution through time, we used sporomorph ecogroups (SEGs), a term introduced by Abbink (1998) and Abbink et al. (2004), with some modifications. This concept is based on particular taxa with broadly similar ecological preferences that characterise distinctive habitats or palaeocommunity types. The total types of dispersed spores and pollen of land plants reflect, partially, the composition of an individual terrestrial source community. In the present analysis, we also take into account the distribution of aquatic palynomorphs (Charophyta, Chlorophyta algae and acritarchs) in order to propose an integrated palaeoenvironmental setting recorded for the Jurassic Cañadón Asfalto Formation deposition. Therefore, the term 'sporomorph ecogroup' is herein substituted by 'palynomorph Ecogroup' (PEG). Cluster analysis

was applied to analyse the present palynological data in order to characterise different ecosystems on the bases of the palynomorph groups. The aim of this paper is to assess the palaeoecological significance of the Cañadón Asfalto palynoflora and its importance in the evolution of the ecosystem.

2. Geologic setting and sedimentary environment of the Cañadón Asfalto Basin

Two interpretations were proposed for the tectono-sedimentary evolution of the Cañadón Asfalto Basin. Figari & Courtade (1993), Cortiñas (1996), Figari et al. (1996) and Figari (2005) interpreted the Cañadón Asfalto Basin as a rift developed from the Triassic through to the Late Cretaceous, related to the widespread extensional forces during the Gondwana break-up that affected Patagonia. More recently, Silva Nieto et al. (2007) and Cabaleri et al. (2010), among others,

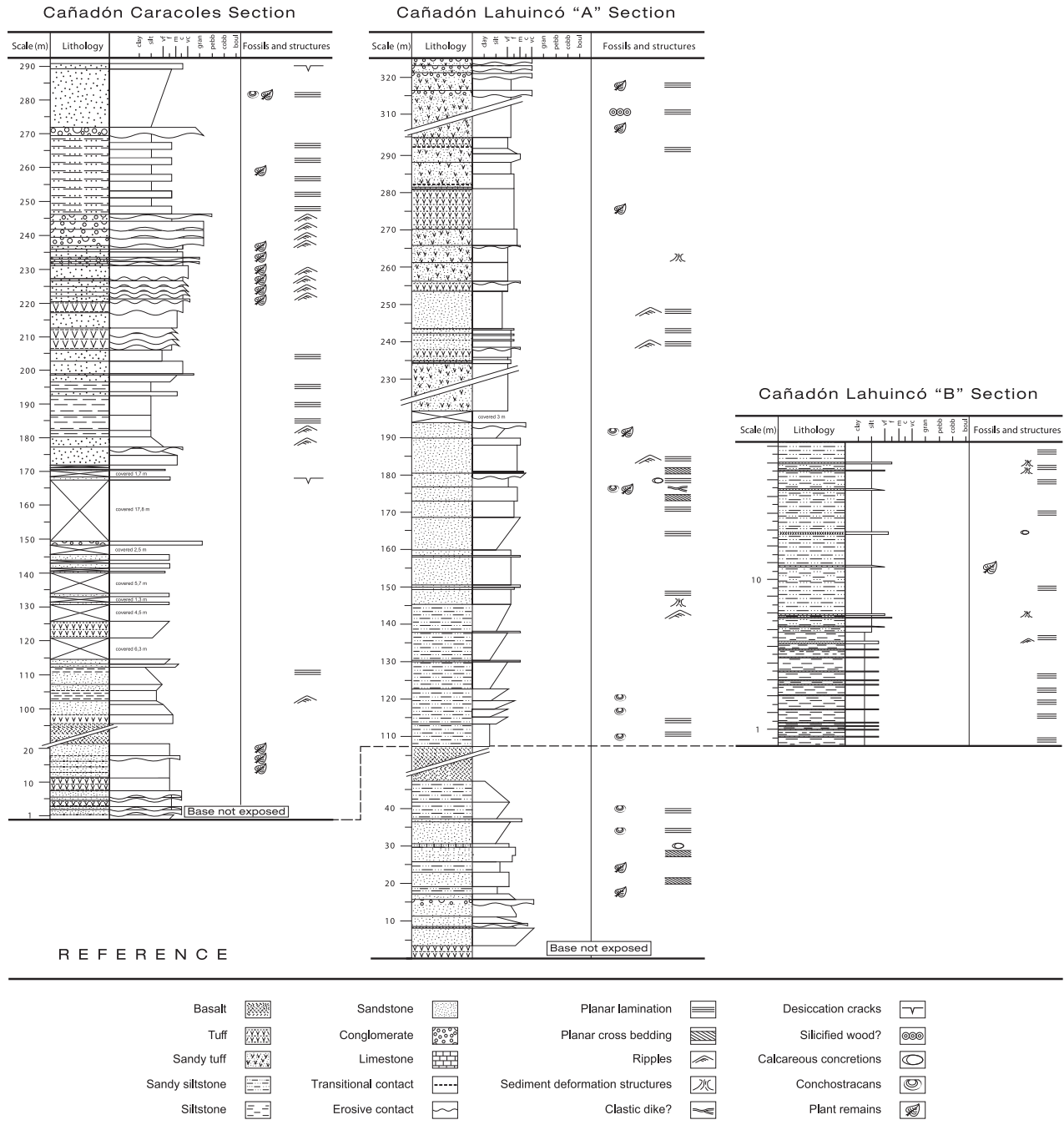


Figure 2. Stratigraphical sections of the Cañadón Asfalto Formation at Cañadón Lahuincó and Cañadón Caracoles localities. See Table 1 for sample details.

suggested that the Cañadón Asfalto Basin could have been formed by several depocentres (i.e. Cerro Cóndor, Cañadón Calcáreo, Estancia Fossati and Yanketruz) which were not strictly contemporaneous. They related them to extensional to transensional tectonism (strike-slip or pull-apart basin) and thermal subsidence. According to these authors, each Depocentre would be

composed of an isolated basin with its own evolutionary tectono-sedimentary history.

The basement of the basin exposed near the study area consists of igneous and metamorphic rocks from the Mamil Choique Formation assigned to the Early Permian (Cúneo et al. 2013). This unit is characterised by the presence of migmatites, foliated granitoids and

granitoids without deformation (Costa et al. 1996). The rocks of the Jurassic basin overlie this basement. The sequence starts with a thin unit of volcanoclastic and fluvial sediments named the Las Leoneras Formation (and its correlatives), assigned to the Early Jurassic, most probably the latest Sinemurian (Cúneo et al. 2013). The Lonco Trapial Formation overlies this unit; it is composed of a thick (up to 300 m) sequence of brecciated andesitic lavas, dacitic and andesitic tuffs, conglomerates and fine to medium tuffaceous sandstone intercalations, lahar deposits and poorly stratified volcanic agglomerates (Cabaleri & Armella 2005). This unit has been recently assigned to an age range between 188.95 and 178.77 Ma (Pliensbachian–Toarcian) (Cúneo et al. 2013). The Cañadón Asfalto Formation overlies the Lonco Trapial Formation by concordant or gradational contact (Figari 2005). This unit is composed of fluvio-deltaic lacustrine sediments, with basaltic intercalations in the lower part of the sequence and tuffites at the top. Cúneo et al. (2013) proposed an Early/Mid Toarcian–Aalenian/ Bajocian age to the Cañadón Asfalto Formation, based on the analysis of six tuff samples by the Uranium–Pb (lead) analyses of zircon (chemical abrasion-thermal ionization mass spectrometry [CA-TIMS] method). Silva Nieto et al. (2003) and Cabaleri et al. (2010) identified two members in this unit: the Las Chacritas Member in the lower part of the sequence and the Puesto Almada Member in the upper section. The former consists of lacustrine sediments with volcanic intercalations at the base, while the latter is mainly siliciclastic and represents a prograding fluvial system on the previous lacustrine deposits. In this study, we do not recognise such a subdivision for the Cañadón Asfalto Formation (Olivera 2012; Olivera et al. 2014). This formation is unconformably overlain by fluvial to lacustrine deposits of the Cañadón Calcáreo Formation. The deposition of the Cañadón Calcáreo Formation started prior to ca. 158 Ma, probably in the Oxfordian, and continued during the Late Jurassic (Cúneo et al. 2013). The previously mentioned formations are unconformably overlain by continental Cretaceous deposits of the Chubut Group (Cabaleri & Armella 2005).

3. Materials and methods

3.1. Sampling and laboratory treatments

A total of 114 outcrop samples of very fine sandstones, siltstone and mudstone were collected from the lower and middle parts of the Cañadón Asfalto Formation (Figure 2; Table 1). Fifty-one palynologically productive samples were studied. The physical and chemical extraction of palynomorphs was carried out at the Palynological Laboratory of the Instituto Geológico del Sur

Table 1. List of 51 palynologically productive samples from the Cerro Cóndor area used for the present study.

Stratigraphical sections	Field number	Lab code	Depth from base (m)
Cañadón Lahuincó ‘A’	CL06	MPEF-PALIN104	29.0
	CL08	MPEF-PALIN106	30.8
	CL18	MPEF-PALIN116	45.3
	CL21	MPEF-PALIN119	111.0
	CL22	MPEF-PALIN120	114.4
	CL23	MPEF-PALIN121	116.2
	CL24	MPEF-PALIN122	116.3
	CL25	MPEF-PALIN123	116.45
	CL26	MPEF-PALIN124	117.8
	CL27	MPEF-PALIN125	121.0
	CL28	MPEF-PALIN126	122.3
	CL29	MPEF-PALIN127	124.1
	CL30	MPEF-PALIN128	125.1
	CL31	MPEF-PALIN129	126.1
	CL32	MPEF-PALIN130	127.1
	CL33	MPEF-PALIN131	128.6
	CL34	MPEF-PALIN132	133.1
	CL35	MPEF-PALIN133	134.8
CL36	MPEF-PALIN134	136.5	
CL38	MPEF-PALIN136	140.9	
Cañadón Lahuincó ‘B’	28032008 01	MLP 551	0.10
	28032008 02	MLP 552	1.00
	28032008 03	MLP 553	1.80
	28032008 04	MLP 554	2.30
	28032008 05	MLP 555	4.30
	28032008 06	MLP 556	5.60
	28032008 07	MLP 557	7.00
	28032008 09	MLP 559	9.50
	28032008 10	MLP 560	11.0
	28032008 11	MLP 561	14.3
28032008 14	MLP 564	15.3	
Cañadón Caracoles	CC01	MPEF-PALIN154	0.00
	CC02	MPEF-PALIN155	0.15
	CC05	MPEF-PALIN157	0.45
	CC08	MPEF-PALIN161	103.2
	CC13	MPEF-PALIN166	114.5
	CC15	MPEF-PALIN168	136.9
	CC16	MPEF-PALIN169	139.4
	CC18	MPEF-PALIN170	165.9
	CC20	MPEF-PALIN172	170.1
	CC22	MPEF-PALIN174	177.4
	CC23	MPEF-PALIN175	177.6
	CC24	MPEF-PALIN176	178.9
	CC26	MPEF-PALIN178	180.7
	CC27	MPEF-PALIN179	181.1
	CC29	MPEF-PALIN181	182.3
CC30	MPEF-PALIN182	183.0	
CC32	MPEF-PALIN183	185.0	
CC35	MPEF-PALIN186	186.0	
CC43	MPEF-PALIN194	205.08	
CC49	MPEF-PALIN200	214.08	

(INGEOSUR)/Universidad Nacional del Sur (UNS)-Bahía Blanca and at Paleopalynological Laboratory of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA)/Centro Científico Tecnológico (CCT)-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)-Mendoza. Standard palynological extraction techniques involved treatments with hydrochloric and hydrofluoric acids (Volkheimer & Melendi 1976). The slides were examined using transmitted light and differential interference contrast (DIC) microscopes (Olympus BX40 and Nikon Eclipse 80i). In addition, scanning electron microscopy (SEM) was used on samples selected for their well-preserved palynomorphs. The palynological slides are housed in the Paleontological Museum Edigio Feruglio Repository, Trelew city, Chubut province, Argentina. They are identified by a catalogue number preceded by the abbreviations MLP (= Muestra Laboratorio Palinología) and MPEF (Museo Paleontológico Edigio Feruglio), respectively. Specimen locations are referred to England Finder coordinates (EFco). The natural affinities of the dispersed palynomorphs are summarised in Table 2, and the relative abundances of major palynomorph groups are expressed in the form of percentage diagrams in Figure 3.

3.2. Statistical analysis

The distribution of each species in the studied sequences is based on counts of 250–400 palynomorph specimens per sample. The relative frequencies (%) diagrams were calculated using TGview 2.0.2 (Grimm 2004).

Palynological data were interpreted using the multivariate statistical program PAST (Palaeontological Statistics) by Hammer & Harper (2009). Cluster analysis was selected as the most appropriate technique for this study. It was performed with the Euclidean distance and the unweighted pair group method (UPGM). The relative abundances of some plant families are important in these data sets; some plant communities are dominant and characteristic of a specific ecosystem (Kovach 1989). So, this analysis was chosen to identify groups of taxa that characterise each environment. The three cluster analysis graphics indicate the cophenetic correlation coefficient as a measure of the relation degree between the original distances and the final transformed distances, following Anderberg (1973) and Kovach (1989). The magnitude of this value should be close to 1 for a high-quality solution.

4. Palaeoecological requirements of the plant families present in the Cañadón Asfalto palynoflora

The association of taxa in a palynofloral assemblage reflects plant palaeocommunities, whose evolution

may show palaeoclimatic trends. The upland plant communities (mainly represented by saccate pollen grains) provide a long-distance influx (allochthonous elements) to the depositional setting, reflecting a wider diversity of the regional vegetational influence to the autochthonous coastland and lowland plant communities. However, as mentioned by many authors (e.g. Battén 1974; Quattrocchio et al. 1996), the distribution of palynomorphs is related to the sedimentary facies. Thus, in the same sequence, in different positions of a transect, the composition of the palynological assemblages can change in a lateral direction.

The botanical affinities of spores, pollen grains and organic-walled microplankton from the Cañadón Asfalto Formation are given in Table 2.

The high frequencies of *Classopollis* (Cheirolepidiaceae) may be the product of many factors, such as transportational sorting, allowing an enrichment of this pollen type in the assemblages (Volkheimer et al. 2008; Schrank 2010), a possible high productivity of the parent plants and/or the habitat in which they were developed (marginal vegetation) near the site of deposition.

The palaeoecological significance of *Classopollis* and its parental plant has been widely discussed. Many authors have considered that they were drought resistant (seasonal climate) thermophilous shrubs and trees (Sajjadi & Playford 2002b). However, this condition may vary within quite broad limits (Alvin 1982). Vakhrameev (1981) suggested that, if the Araucariaceae grow together with the Cheirolepidiaceae, the climate conditions might be warm to moderate-warm and relatively humid. The majority of the current araucariacean plants are developed in rainy forests under subtropical-temperate climate (mesothermal) and, less frequently, under temperate to temperate-cold conditions (microthermal climate) (Panti et al. 2012). However, Abbink (1998) interpreted that their thick-cuticled leaves, which characterise their foliage, allow them to develop in regions submitted to periodic dry seasons. Quattrocchio et al. (2001) observed that this group actually grows in the Planalto of southern Brazil (mountain region up to 1000 m above sea level) where they are associated with the podocarpaceans. When an increase in temperature occurred, the Podocarpaceae disappeared, and the araucariaceans migrated to the lower part of the valleys (with high humidity levels). Caccavari (2003) demonstrated that, due to the morphological and structural features of araucariacean pollen, such as the large size and the exine structure, they have a weak capacity for long-distance transport, especially wind transport. Therefore, it is suggested that rivers and/or runoff were the main transportation agents of these pollen types.

The extant Podocarpaceae comprise trees or shrubs that occupy a wide range of ecological niches, from

Table 2. Botanical affinities of spores, pollen and organic-walled microplankton from the Cañadón Asfalto Formation. Principal source of information concerning the natural relationships of dispersae palynomorphs, based on Dettmann (1963), Filatoff (1975), de Jersey & Raine (1990), Balme (1995), Sajjadi & Playford (2002a, 2002b), McKellar (1998) and Martínez et al. (2008).

Division	Class	Order	Family	Genera-Palynoflora	
Bryophyta	Anthocerotopsida	Anthocerotales	Anthocerotaceae	<i>Nevesisporites</i>	
			Sphagnaceae	<i>Stereisporites</i> , <i>Antulsporites</i>	
Tracheophyta	Lycopsida	Selaginellales/ Lycopodiales	Selaginellaceae/ Lycopodiaceae	<i>Retitriletes</i> , <i>Ceratosporites</i> , <i>Neoraistrickia</i> <i>Staplinisporites</i>	
			Marattiales	Marattiaceae	<i>Biretisporites</i>
	Filicopsida	Filicales	Cyatheaceae/Dicksoniaceae Dipteridaceae/ Matoniaceae	<i>Deltoidospora</i> <i>Dictyophyllidites</i> , <i>Trilobosporites</i>	
			Dicksoniaceae	? <i>Granulatisporites</i>	
			Gleicheniaceae	<i>Gleicheniidites</i>	
			Osmundaceae	<i>Todisporites</i> , <i>Verrucosisporites</i>	
			Schizaeaceae	<i>Klukisporites</i> , <i>Ischyosporites</i>	
			Undifferentiated (<i>Incertae sedis</i>)	<i>Cadargasporites</i>	
	Gymnospermopsida	Cycadales/ Benettiales		<i>Cycadopites</i> , <i>Monosulcites</i>	
			Pteridospermales	Corystospermaceae Caytoniaceae	<i>Alisporites</i> <i>Vitreisporites</i>
		Coniferales	Araucariaceae	<i>Inaperturopollenites</i> , <i>Araucariacites</i> , <i>Callialasporites</i>	
			Cheirolepidiaceae	<i>Classopollis</i>	
			Pinaceae	<i>Indusiisporites</i> , <i>Cerebropollenites</i>	
			Podocarpaceae	<i>Podocarpidites</i> , <i>Microcachryidites</i> , <i>Podosporites</i> , <i>Trisaccites</i>	
		Charophyta	Zygnematophyceae	Zygnematales	Zygnemataceae
Chlorophyta		Trebouxiophyceae		Botryococcaceae	<i>Botryococcus</i>

lowland heaths to forests and subalpine vegetation (Scholtz 1985). They especially develop in mountainous areas of tropical and subtropical regions (Schrank 2010). Sajjadi & Playford (2002b, p.152), by analogy with the modern *Microcachrys* – a shrubby podocarp inhabiting the present Tasmanian subalpine region – suggested that the ancient taxon might have grown in cool-temperate conditions in upland situations. In general, most of the fossil-genera representatives of

pinacean plants lived in temperate and relatively dry environments under cool conditions, at least in upland situations (Abbink 1998).

Pteridosperms are represented by the genera *Alisporites* and *Vitreisporites*. The parental family of the fossil genus *Alisporites* presents xeromorphic features, and they are common under seasonal climates (Artabe et al. 2001). The producers of *Vitreisporites* pollen grains (Caytoniaceae) are thought to have

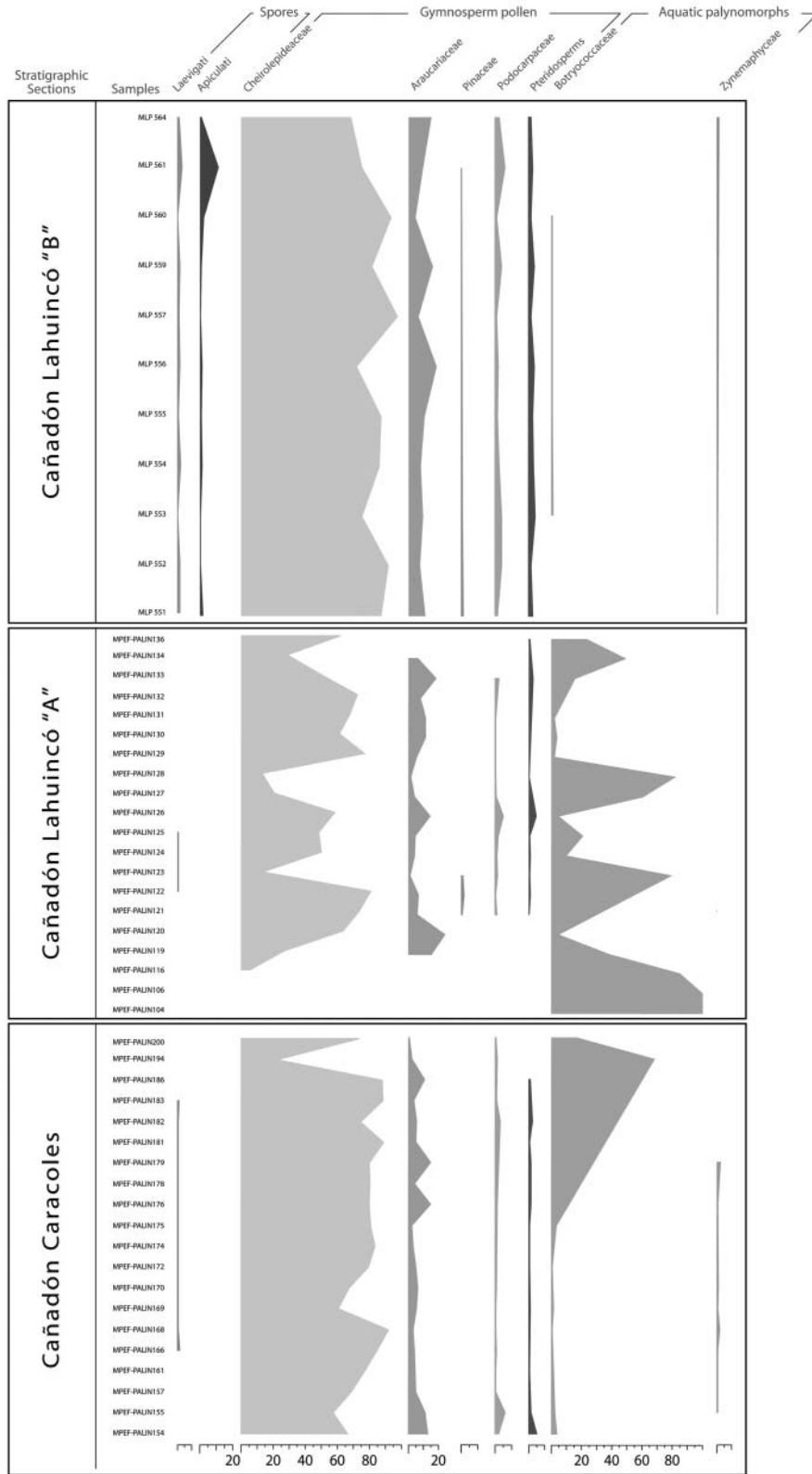
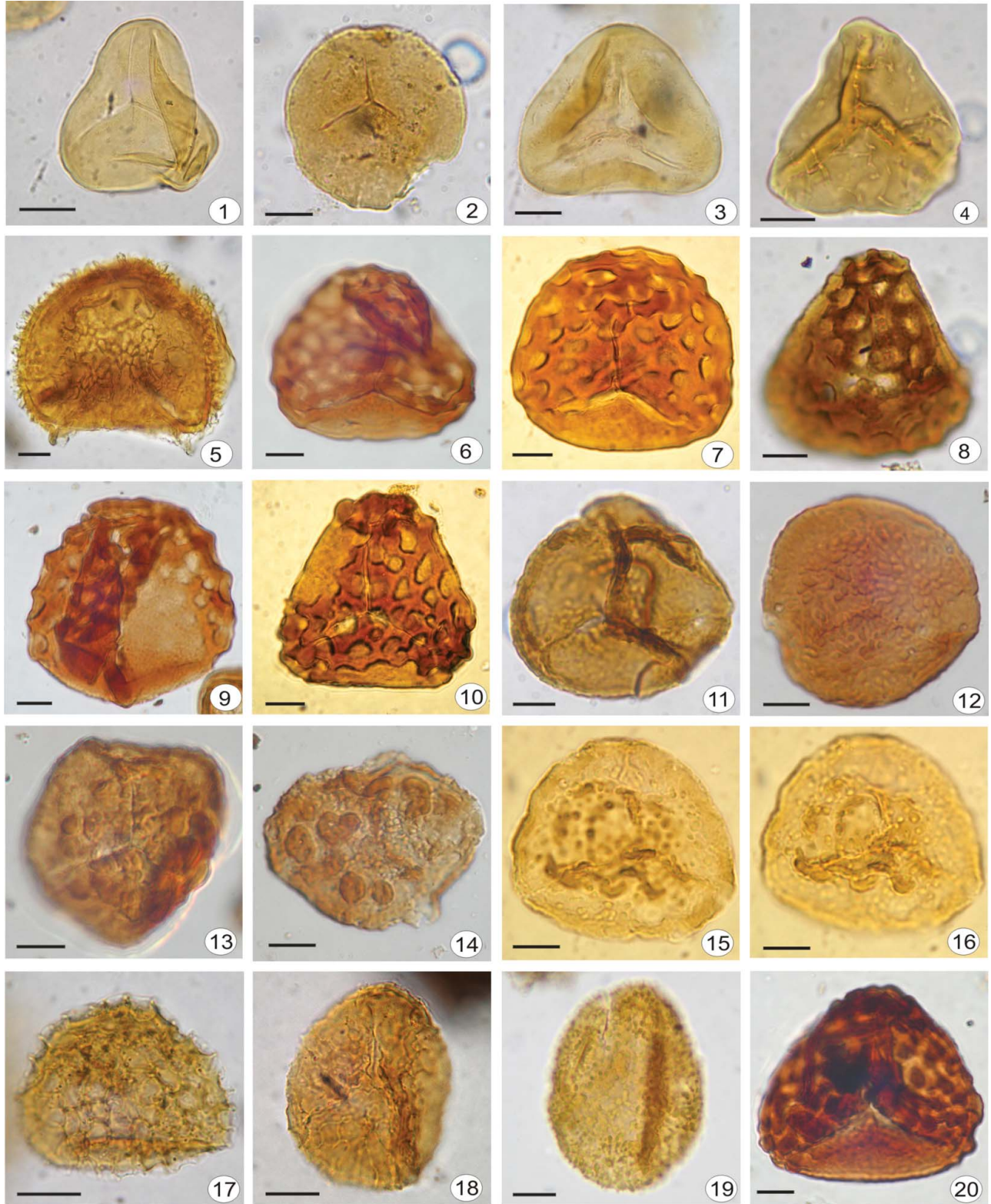


Figure 3. Quantitative distribution of major palynomorph groups in the Cañadón Asfalto Formation, expressed in percentages of total palynoflora based on 51 selected samples.



grown in deltaic, flood plain to backswamp and/or other moist environments (Schränk 2010).

Bryophyte, lycophyte and fern spores grow in different environments under humid conditions. However, some bryophytes and lycophytes are capable of enduring dry periods (Sajjadi & Playford 2002b; Berg 2007). Ferns develop successfully in woodlands under low-light conditions created by forest canopy (Sharpe et al. 2010). Only a few taxa can grow under full sunlight (e.g. Gleicheniaceae).

Botryococcus sp. cf. *B. braunii* (Botryococcaceae) is a successful coloniser in shallow, alkaline water (e.g. inland saline lakes), in areas of relatively low rainfall but with a wide range of climate conditions throughout the year (Guy-Ohlson 1992; Zippi 1998). It commonly forms water-blooms in oligotrophic lakes where other Chlorococcales algae cannot grow (Ottone & Mancuso 2006). Other freshwater algae, such as *Ovoidites* spp. (Zygnemataceae), and some palynomorphs provisionally recorded as Acritarch (leiospheres), are recognised in the present study in low proportions. The extant zygnemataceans are found in many freshwater habitats but proliferate in stagnant and oxygen-rich water bodies like shallow pools, paludal areas, rims of lakes or in areas where waters may be ephemeral (Zippi 1998; Lindström 2013).

5. Results

5.1. Composition of the Cañadón Asfalto palynoflora

The studied strata interval contains taxonomically diverse spore assemblages, pollen grains and organic-walled microplankton from freshwater environments, comprising 71 species (see Table 2; Appendix 1). The trilete spores (Plate 1, figures 1–20) are represented by 24 species belonging to 20 genera. Pollen grains (Plate 2; Plate 3, figures 1–12) record 41 species allocated in 12 genera and four aquatic species of Zygnemataceae and Botryococcaceae families' algae (Plate 3, figures 13–15) and acritarchs (*Leiosphaeridia* spp.) (Plate 3, figure 16).

In this section, we analyse the most important palynomorph groups that contributed to the composition

of the Cañadón Asfalto Formation palynoflora. The three studied sections are characterised by a high diversity of vegetation sources; the coniferophytes were clearly the most abundant component as indicated by the palynological record (Figure 3). The most conspicuous feature of this palynoflora is the dominance of Cheirolepidiaceae (*Classopollis*), reaching up to 95% of the total spectrum of palynomorphs (Figure 3). This family is associated to araucariacean pollen, which constitutes the numerically second most important sporomorph group (Figure 3).

The distribution of the palynomorphs in the three studied sections is thoroughly analysed below, based on applied statistical methods.

5.2. Cañadón Lahuincó 'A' section

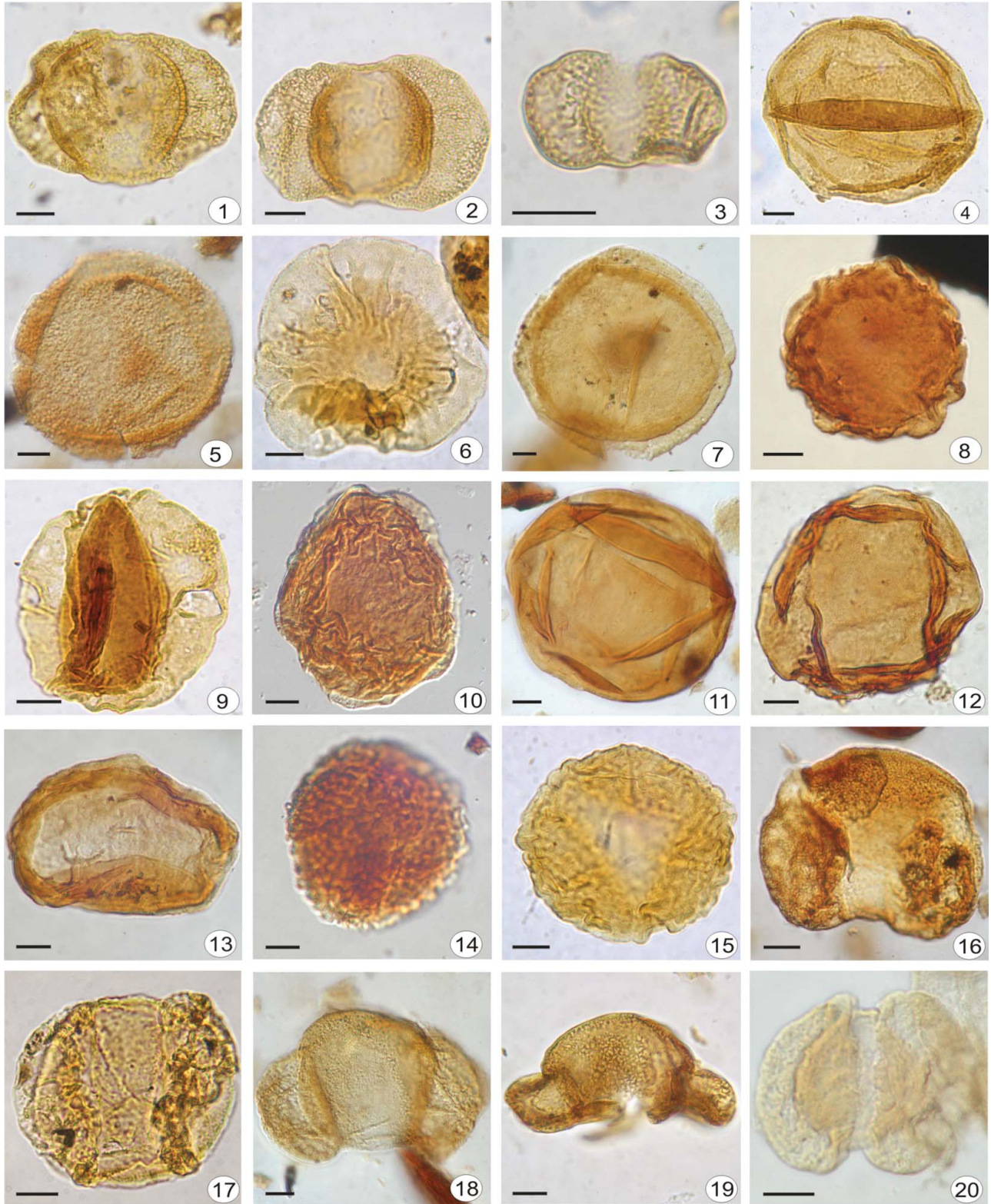
The palynological assemblages recorded in this section are characterised by the greatest abundance and diversity of conifer pollen grains and the lowest frequencies of spores of the three studied sections (Figure 3). In the cluster analysis, four groups of samples, designated A–D (Figure 4), are recognised. The cophenetic correlation coefficient of the cluster analysis is 0.8831.

Samples MPEF-PALIN104 and MPEF-PALIN106, of claystone and siltstone lithologies, were excluded from this analysis due to the fact that the palynomorph content is only represented by *Botryococcus* colonies. These palynological associations contain the highest percentages of this alga identified in the three studied sections (Figure 3). The assemblages are characterised by colonies with an excellent preservation state, where 'growth rings' are recognised, without autospores, and by skeletal colonies with the tendency to form structureless masses (Plate 3, figures 13 and 15). These palynofloras are assigned to the Aquatic PEG (Table 3; Figure 5).

5.2.1. Group A (Figure 4)

This group of two siltstone samples has high percentages of *Botryococcus* colonies (46.5 to 57%), and the terrestrial component is represented by the association

Plate 1. Scale bars: 10 μ . 1. *Deltoidospora minor* (Couper) Pocock 1970, MLP559: W32/0. 2. *Todisporites minor* Couper 1958, MLP561: Q14/2. 3. *Dictyophyllidites harrisii* Couper 1958, MLP564: E43/3. 4. *Obtusisporis modestus* (McKellar) McKellar 1998, MLP555: G30/3. 5. *Cadargasporites* sp. cf. *C. reticulatus* de Jersey & Paten 1964, MLP561: N29/4. 6. *Klukisporites labiatus* (Volkheimer) Baldoni & Archangelsky 1983, MLP561: K15/0. 7. *Klukisporites lacumus* Filatoff 1975, MLP561: V12/0. 8. *Klukisporites* sp. cf. *K. scaberis* (Cookson & Dettmann) Dettmann 1963, MLP561: V14/1. 9. *Klukisporites variegatus* Couper 1958, MLP561: H21/0, equatorial view. 10. *Ischyosporites marburgensis* de Jersey 1963, MLP561: O20/0. 11. *Nevesisporites* cf. *undatus* Backhouse 1988, MLP551: U44/0. 12–16. *Nevesisporites vallatus* de Jersey & Paten emend. McKellar (1998), 12–14 were taken with differential interference contrast (DIC) illumination; 12. MLP561: C14/2; 13. MLP561: F38/0; 14. MLP561: V36/3; 15–16, MLP561: E12/1: 15. proximal view, 16. distal view. 17. *Retitriletes austroclavatidites* (Cookson) Döring, Krutzsch, Mai & Schulz in Krutzsch 1963, MLP561: H43/1. 18. *Retitriletes* sp. 1, MLP561: X30/2. 19. *Verrucosiporites varians* Volkheimer 1972, MPEF-PALIN154: Y35/0. 20. *Trilobosporites* sp., MLP561: J44/0.



of cheirolepideacean and araucariacean pollen (Figures 3 and 4). In the two levels, *Classopollis* pollen shows similar frequencies (ca. 35%), but in MPEF-PALIN119, araucariacean grains are particularly prominent (18%). These characteristics are mainly indicative of coastal and lowland vegetation (e.g. Alvin 1982). These conditions are in accordance with the Coastal Lake and Lowland PEGs (Table 3; Figure 5). In addition, the abundant presence of chlorophytic algae indicates an important development of Aquatic PEG (Table 3).

5.2.2. Group B (Figure 4)

This group comprises four siltstone samples (Table 1 and Figure 2). These associations are characterised by high percentages of *Botryococcus* colonies (96 to 70%) indicating the predominance of the Aquatic PEG (Table 3; Figure 5). However, Upland (mainly Podocarpaceae and Pinaceae and in part Araucariaceae), Coastal Lake (Cheirolepidiaceae) and Riverside (bryophyte, lycophyte and fern spores, Crystospermaceae, Caytoniaceae, Cheirolepidiaceae and Araucariaceae) PEG components are also present (Table 3; Figure 3). The association of pinacean and podocarpacean pollen (Upland PEG) reflects the incoming of the upland forest by air and/or runoff to the basin (Table 3).

5.2.3. Group C (Figure 4)

This group of siltstone samples and thin coal presents the highest percentages of *Classopollis* pollen grains in the Cañadón Lahuincó 'A' section (81.45 to 91.75%; Figures 3 and 4), showing a strong contribution of the Coastal Lake PEG to these associations. In these assemblages, araucariacean pollen is present in all studied samples. The co-occurrence of these two conifer groups suggests the development of Riverside and/or Lowland PEGs. Caytoniacean pollen (up to 0.8%) reinforces the existence of these PEGs (Table 3). The presence of *Botryococcus* colonies (2 to 4.7%) in

three of the six samples grouped here points to the development of the Aquatic PEG in these levels (Figures 3 & 5).

5.2.4. Group D (Figure 4)

5.2.4.1. *Subgroup D₁*. Three samples of siltstone and very fine sandstone define this cluster (Table 1; Figure 2). Although these assemblages have high frequencies of *Classopollis* (57 to 70%), they also show the highest percentages of araucariacean pollen of all the samples studied (14 to 25%; Figure 3). Stukins et al. (2013, p. 120) interpreted the association of Cheirolepidiaceae and Araucariaceae pollen as a vegetal community that commonly grows on floodplains with mature and well-drained soils. Therefore, the Araucariaceae is mainly related to the Riverside and/or Lowland PEGs (Table 3; Figures 3 and 5). However, the Araucariaceae also grow in mixed forests with Podocarpaceae and Pinaceae in upland regions. Consequently, part of this material may arrive to the basin by runoff and fluvial currents from the Upland PEG, particularly in samples in which araucariaceans, podocarpaceans and/or pinaceans occurred together (Table 3; Figure 5). The presence of chlorophytic algae, especially in MPEF-PALIN133 (16.6%), may be suggesting the development of the Aquatic PEG (Table 3; Figures 3 and 5).

5.2.4.2. *Subgroup D₂*. This cluster comprises siltstone and very fine sandstone samples (Table 1; Figure 2). The palynological assemblages are dominated by *Classopollis* pollen grains (71.25% on average) and show the common presence of *Botryococcus* colonies (14 to 25.6%) and Caytoniaceae pollen (0.4 to 1.1%). Podocarpaceae (2.2 to 3%) and Araucariaceae (ca. 5%) were identified in the two lower samples, and Pinaceae in the upper sample (1.8%; Table 1; Figures 2–4). Podocarpaceae and Pinaceae, and part of the Araucariaceae pollen, constitute long-distance fluvial and/or atmospheric inputs

Plate 2. Scale bars: 10 µm; figures 7, 9–10, 12–13, 16 and 19 were taken with differential interference contrast (DIC) illumination. 1. *Alisporites lowoodensis* de Jersey 1963, MPEF-PALIN121: D48/0. 2. *Alisporites similis* (Balme) Dettmann 1963, MLP561: L55/0. 3. *Vitreisporites pallidus* (Reissinger) Nilsson 1958, MPEF-PALIN123: K38/1. 4. *Araucariacites australis* Cookson ex Couper 1953, MPEF-PALIN122: B52/2. 5. *Araucariacites* sp. cf. *A. pergranulatus* Volkheimer 1968, MPEF-PALIN122: C40/0. 6. *Callialasporites dampieri* (Balme) Sukh Dev 1961, MLP557: K25/0. 7. *Callialasporites microvelatus* Schulz 1966, MLP551: N26/0. 8. *Callialasporites minus* (Tralau) Guy 1971, MLP551:H25/0. 9. *Callialasporites turbatus* (Balme) Schulz 1967, MLP561: B20/0. 10. *Callialasporites* sp. 1, MLP561: B7/0. 11. *Inaperturopollenites giganteus* Góczán 1964, MPEF-PALIN125: F45/0. 12. *Inaperturopollenites* sp. 1, MPEF-PALIN122: H28/2. 13. *Inaperturopollenites* sp. 2, MLP551: G27/4. 14. *Cerebropollenites carlylensis* Pocock 1970, MLP561: P49/0. 15. *Cerebropollenites* sp. 1, MLP566: Y43/1. 16. *Pinuspollenites globosaccus* Filatoff 1975, oblique equatorial view, MPEF-PALIN122: B38/4. 17. *Indusiisporites* sp. 1, equatorial view, MLP553: X46/0. 18. *Indusiisporites* sp. 2, oblique polar view, MPEF-PALIN122: T30/0. 19. *Indusiisporites* sp. 3, equatorial view, MPEF-PALIN123: O43/0. 20. *Podocarpidites astrictus* Haskell 1968, MLP561: P21/0.

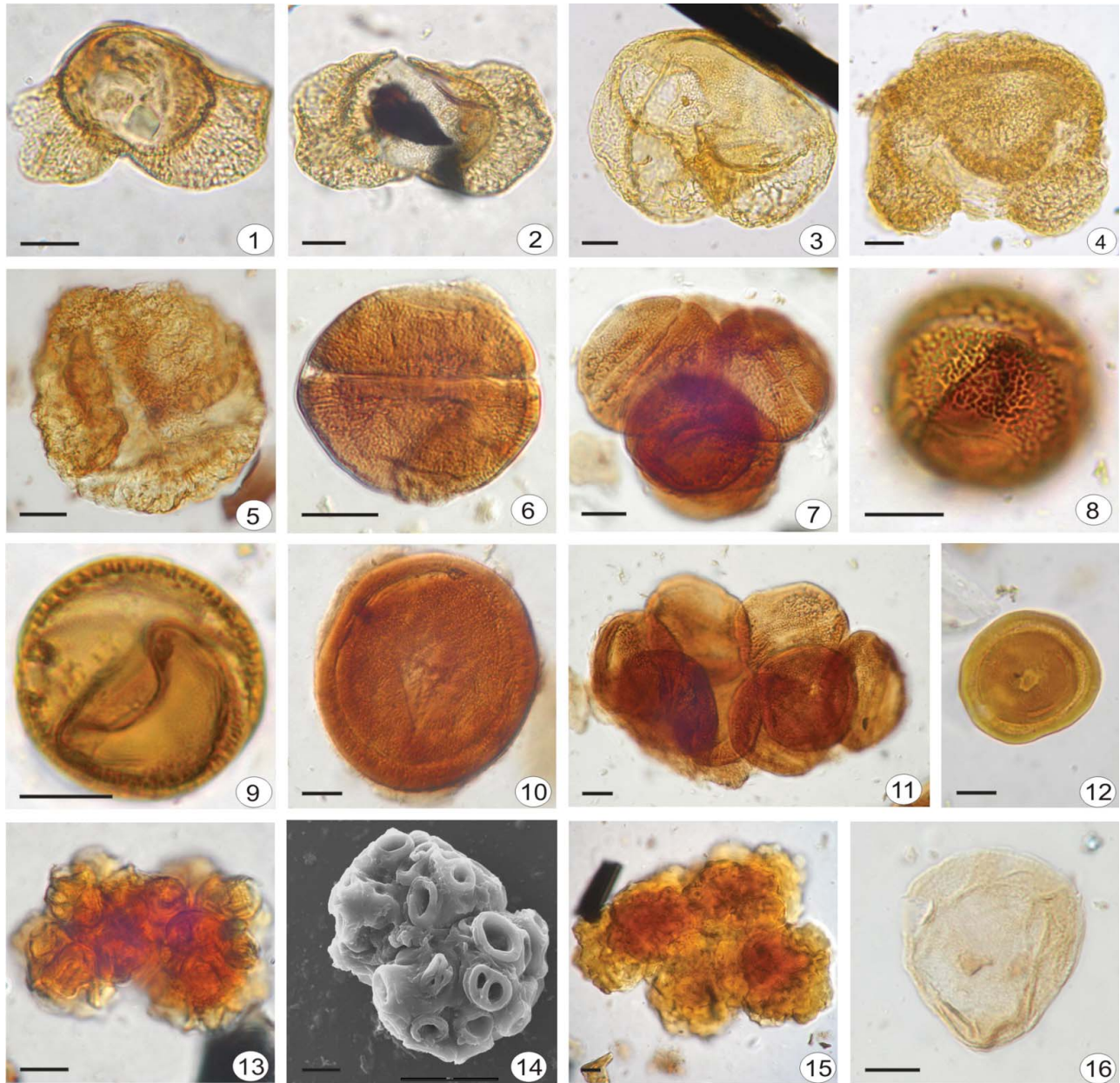


Plate 3. Scale bars: 10 μm ; figures 2, 5–7, 10–11, 13 and 15 were taken with differential interference contrast (DIC) illumination. 1–2. *Podocarpidites* sp. cf. *P. radiatus* Brenner 1963, 1. MPEF-PALIN123: U27/4: oblique equatorial view; 2. MPEF-PALIN123: B29/2: equatorial view. 3. *Microcachrydites antarcticus* Cookson 1947, MPEF-PALIN169: T38/1. 4. *Podosporites variabilis* Sukh Dev 1961, MPEF-PALIN121: Y24/2. 5. *Podosporites* sp. 1, MPEF-PALIN121: W40/4. 6–7. *Classopollis classoides* (Pflug) Pocock & Jansonius 1961, 6. MPEF-PALIN122: D46/2, single grain; 7. PALIN122: D46/2, tetrad. 8–9. *Classopollis intrareticulatus* Volkheimer 1972, MPEF-PALIN168: D38/0: 8. oblique distal view with rimula and pore, note detail of the anastomosing system of baculate exine; 9. detail of the inner central body generated by the separation of the nexine from the sexine. 10–11. *Classopollis itunensis* Pocock 1962, MPEF-PALIN122: S42/0: 10. proximal side of a single grain with vestigial adherence structure; 11. polyad MPEF-PALIN122: G27-2. 12. *Classopollis simplex* (Danzé-Corsin & Laveine) Reiser & Williams 1969, MPEF-PALIN121: M45/2: distal view with rimula and pore. 13–15. *Botryococcus* sp. cf. *B. braunii* Kützing 1849, 13–14. simple colonies, 13. MPEF-PALIN123: B34-1, 14. MPEF-PALIN123: scanning electron photomicrograph; 15. MPEF-PALIN123: B34/1: compound colony with partially structureless matrix. 16. *Leiosphaeridia* sp.1, PALIN121: B34/1.

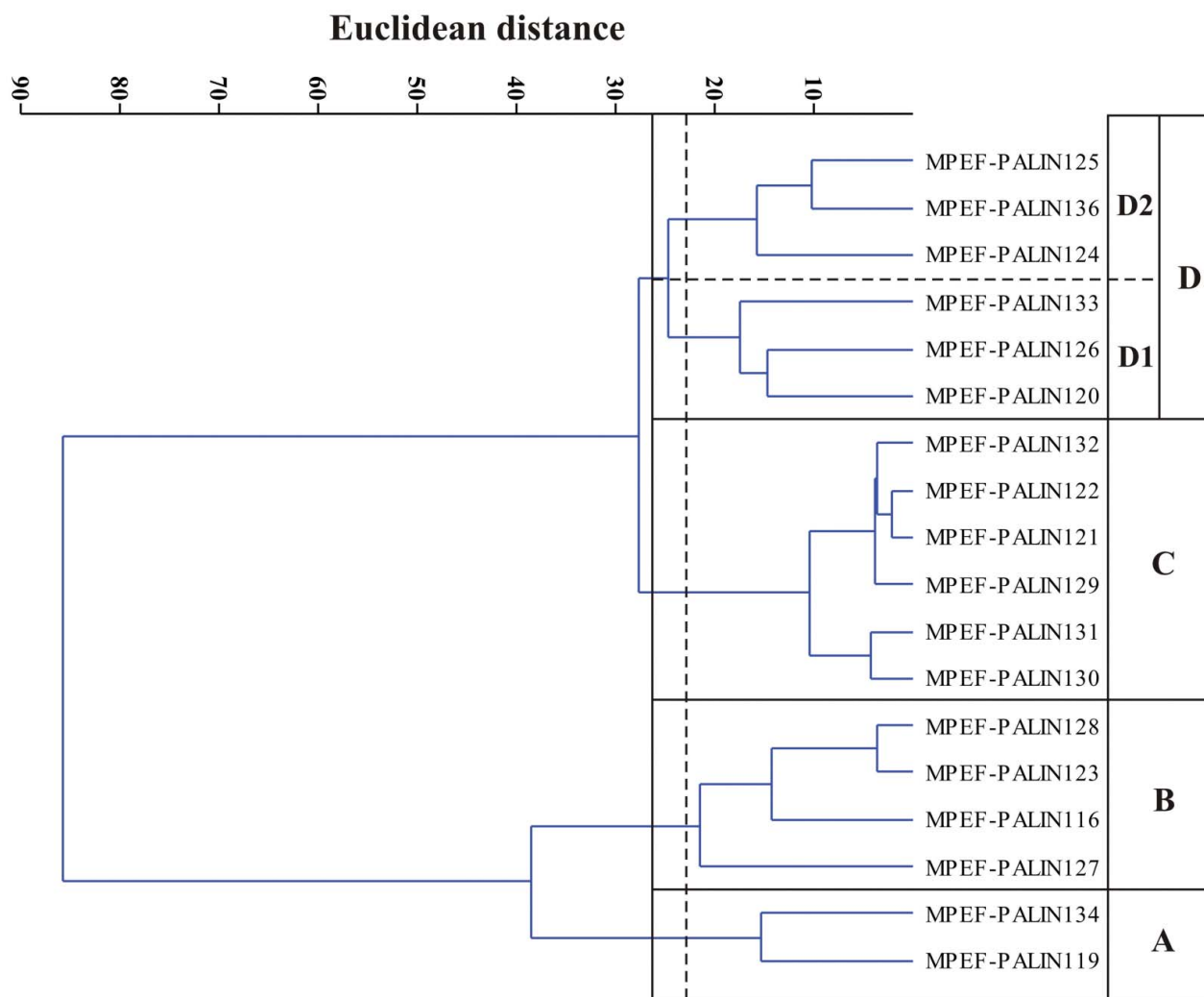


Figure 4. Cluster analysis, using Euclidean distance and the unweighted pair group method (UPGM), showing the grouping of the identified palynological assemblages in the Cañadón Lahuincó 'A' section.

mainly originating from the terrestrial vegetation of adjacent uplands (Upland PEG). The coexistence of Cheirolepidiaceae, Caytoniaceae and Botryococcaeae in the three levels suggests a littoral lacustrine environment with an important fluvial influx in the lacustrine sediments (Coastal Lake, Riverside and Aquatic PEGs; Table 3; Figure 4).

5.3. Cañadón Lahuincó 'B' section (Figures 1 and 2)

Although the Cheirolepidiaceae is the most conspicuous element in the Cañadón Asfalto palynoflora, comparatively, these assemblages show the greatest abundance and diversity of bryophyte, lycopsid and filicopsid spores of the three studied sections. The

planktonic material is scarce; few colonies of *Botryococcus* in a poor state of preservation and some spores of *Ovoidites* (related to the extant Zygnemataceae family) (Zippi 1998) are registered (Figure 3). Cluster analysis recognised three groups of samples and one outlier (MLP561), with the cophenetic correlation being 0.8085 (Figure 6). Sample MLP561 of siltstones with wavy lamination (Table 1; Figure 2) shows a long association distance in cluster analysis (Figure 6). The main difference from the other assemblages is the relatively high percentage of trilete spores (14.2%), among which ferns represent the most abundant group. They are associated with the higher percentages of pinacean, podocarpacean and araucariacean pollen of the studied section. The other components (except *Classopollis*

Table 3. Schematic classification of the proposed palynomorph ecogroups (PEGs) with an overview of the common sporomorphs and phytoplankton recorded in the present study and considered to be characteristic of the various PEGs (modified from Abbink 1998). Principal source of climatic inferences: Abbink (1998), Guy-Ohlson (1992), Quattrocchio et al. (2001) and Martínez et al. (2008). Bryophyte spores are included in the PEGs, indicating local humid conditions.

Palynomorph ecogroups (modified from Abbink 1998 and Abbink et al. 2004)	Genera	Palaeoclimate indicators
Upland (UpL)	<i>Inaperturopollenites</i> <i>Araucariacites</i> <i>Callialasporites</i>	?Warm to temperate, relatively wet
	<i>Microcachryidites</i> <i>Podocarpidites</i> <i>Podosporites</i> <i>Indusiisporites</i>	Temperate, relatively dry
	<i>Neoraistrickia</i> <i>Obtusisporis</i> <i>Deltoidospora</i> , <i>Dictyophyllidites</i> <i>Trilobosporites</i> <i>Todisporites</i> <i>Klukisporites</i> <i>Ischyosporites</i> <i>Cadargasporites</i>	Warm to temperate, relatively wet
	<i>Nevesisporites</i> <i>Stereisporites</i> <i>Antulsporites</i> <i>Todisporites</i> <i>Verrucosisporites</i>	Can withstand long periods of drought; seasonal climate
Lowland (LoL)	<i>Biretisporites</i> <i>Deltoidospora</i> , <i>Dictyophyllidites</i> <i>Trilobosporites</i> , <i>Granulatisporites</i> <i>Gleicheniidite</i> <i>Klukisporites</i> <i>Ischyosporites</i> <i>Cadargasporites</i> <i>Retitriletes</i> <i>Ceratosporites</i> <i>Neoraistrickia</i> <i>Staplinisporites</i>	Warm to temperate, relatively wet
	<i>Inaperturopollenites</i> <i>Araucariacites</i> <i>Callialasporites</i>	?Warm to temperate, relatively wet
	<i>Classopollis</i>	Warm to temperate, can withstand long periods of drought; seasonal climate
Riverside (RS)	<i>Retitriletes</i> <i>Ceratosporites</i> <i>Neoraistrickia</i> <i>Staplinisporites</i> <i>Biretisporites</i> <i>Deltoidospora</i> <i>Dictyophyllidites</i> <i>Trilobosporites</i> <i>Granulatisporites</i> <i>Gleicheniidites</i> <i>Klukisporites</i> <i>Ischyosporites</i> <i>Cadargasporites</i>	Warm to temperate, relatively wet
	<i>Nevesisporites</i> <i>Stereisporites</i> <i>Antulsporites</i>	Can withstand long periods of drought; seasonal climate
	<i>Alisporites</i>	Warm, can withstand long periods of drought; seasonal climate
	<i>Vitreisporites</i> .	Warm, relatively wet
	<i>Inaperturopollenites</i> <i>Araucariacites</i> <i>Callialasporites</i>	?Warm to temperate, relatively wet
Coastal lake (CL)	<i>Classopollis</i>	Warm to temperate, can withstand long periods of drought; seasonal climate
Aquatic (A)	<i>Botryococcus</i>	Highly seasonal climate
	<i>Ovoidites</i>	Temperate to warm; seasonal climate

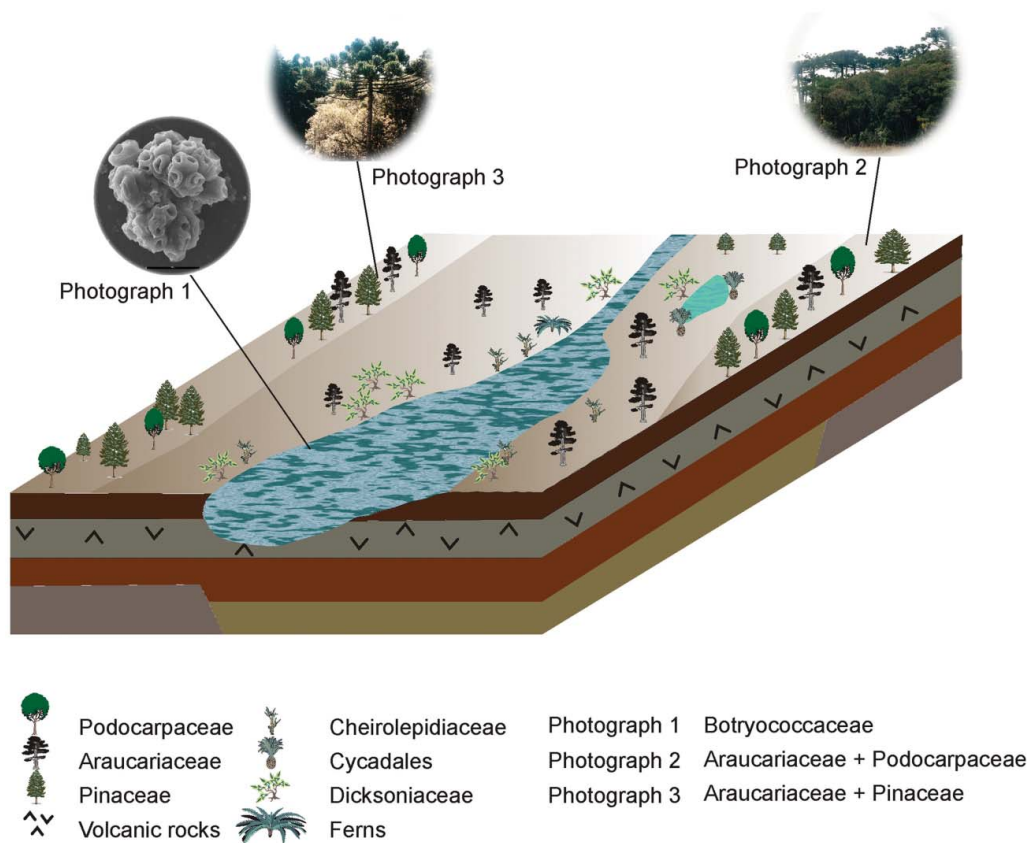


Figure 5. Palaeoenvironmental scenario for the Early to Middle Jurassic of the Cañadón Asfalto Formation, Cerro Córdor depocentre, Chubut province, Argentina.

pollen) are present in lower proportions (Figure 3). Stukins et al. (2013, p. 120) interpreted the co-occurrence of Podocarpaceae conifers and ferns as possibly indicative of an upland ecosystem. Consequently, the Upland PEG is considered an important component of this association.

5.3.1. Group A (Figure 6)

The palynological associations have been recorded in laminated siltstones and massive claystones (Table 1; Figure 2). Although the *Classopollis* pollen is the most abundant taxon (69.5 to 73.5%), these assemblages also present the highest percentages of Araucariaceae pollen (16 to 19.5%) in the studied section (Figure 3). The other gymnosperm families and spores recognised in the Cañadón Asfalto palynoflora are regularly present in the three samples (Figure 3). These features suggest an important presence of the Riverside, Lowland and Coastal Lake PEGs. Conversely, the common presence in these assemblages of pinacean and podocarpacean pollen associated with the araucariacean suggests some influence of long-distance fluvial and/or atmospheric supply originating from forest regions in

upland situations (Upland PEG component) (Table 3; Figure 5).

5.3.2. Group B (Figure 6)

Group B comprises five laminated siltstones samples. This cluster shows a strong influence of the Riverside, Lowland and Coastal Lake PEGs (Table 3; Figure 5), as indicated by the co-occurrence of Cheirolepidiaceae and Araucariaceae families (Figures 3 and 6). The common presence of pteridosperms and spores reinforces this inference. The development of wood communities in the upland regions is represented in the palynological assemblages by the association of podocarpacean and pinacean pollen (Figures 3). Although zygospores of *Ovoidites* are scarce (between 0.4 and 1%), they are regularly present in these samples, suggesting the development of a water fluvial-paludal environment that may be ephemeral (Zippi 1998).

5.3.3. Group C (Figure 6)

These assemblages have been recorded from laminated siltstone samples (Table 1; Figure 2). They show the

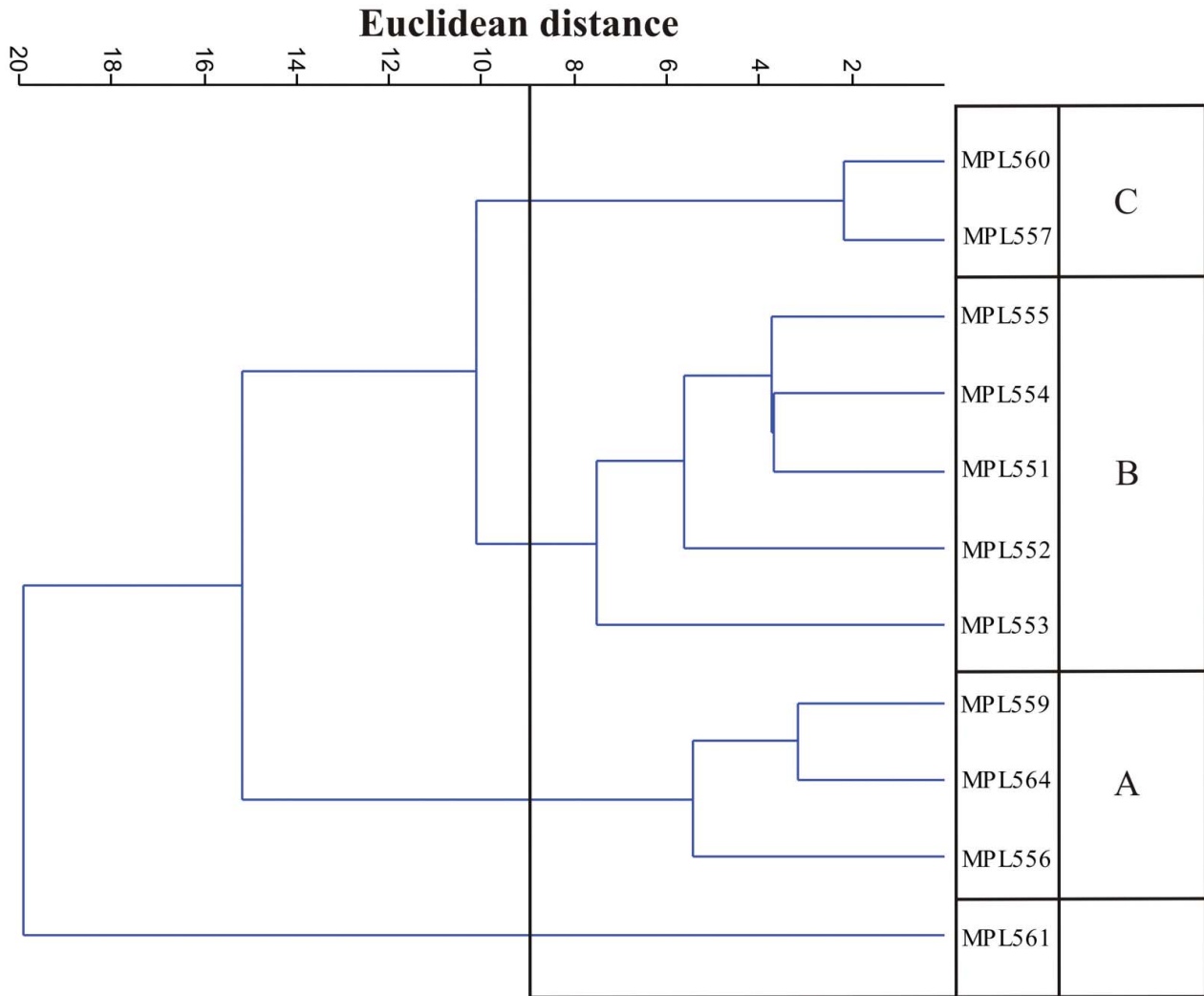


Figure 6. Cluster analysis, using Euclidean distance and the unweighted pair group method (UPGM), showing the grouping of the identified palynological assemblages in the Cañadón Lahuincó 'B' section.

highest percentages of *Classopollis* (89.6–89.7%) and the lowest percentages of araucariacean pollen in the whole studied section (4.4–6.3%; Figure 3). These characteristics suggest a strong influence of Riverside, Lowland and Coastal Lake PEGs in the ecosystem. The presence of Araucariaceae and Podocarpaceae in very low frequencies could indicate the development of forest communities relatively far from the site of deposition, the scarce representation of these communities or a decrease in runoff which may indicate a dry season (Figure 5).

5.4. Cañadón Caracoles section (Figures 1 and 2)

The palynoflora identified in this section shows high percentages of Cheirolepidiaceae associated with the common presence of Araucariaceae pollen (Figure 7).

Trilete spores are represented by lycophytes and ferns. Riverside, Lowland and Coastal Lake are the PEGs with stronger representation in these palynological associations, suggesting more proximity to the terrestrial source in this part of the basin.

Two groups of samples and two outliers (MPEF-PALIN194 and MPEF-PALIN200) emerged when the palynological data were transferred into a cluster analysis (Figure 7). The cophenetic correlation is 0.9918.

5.4.1. Group A (Figure 7)

This group comprises siltstone samples (Table 1; Figure 2). These associations are characterised by the highest percentages of Araucariaceae (13.8 to 15.13%), associated with important frequencies of *Classopollis* (73 to 81.6%; Figure 3).

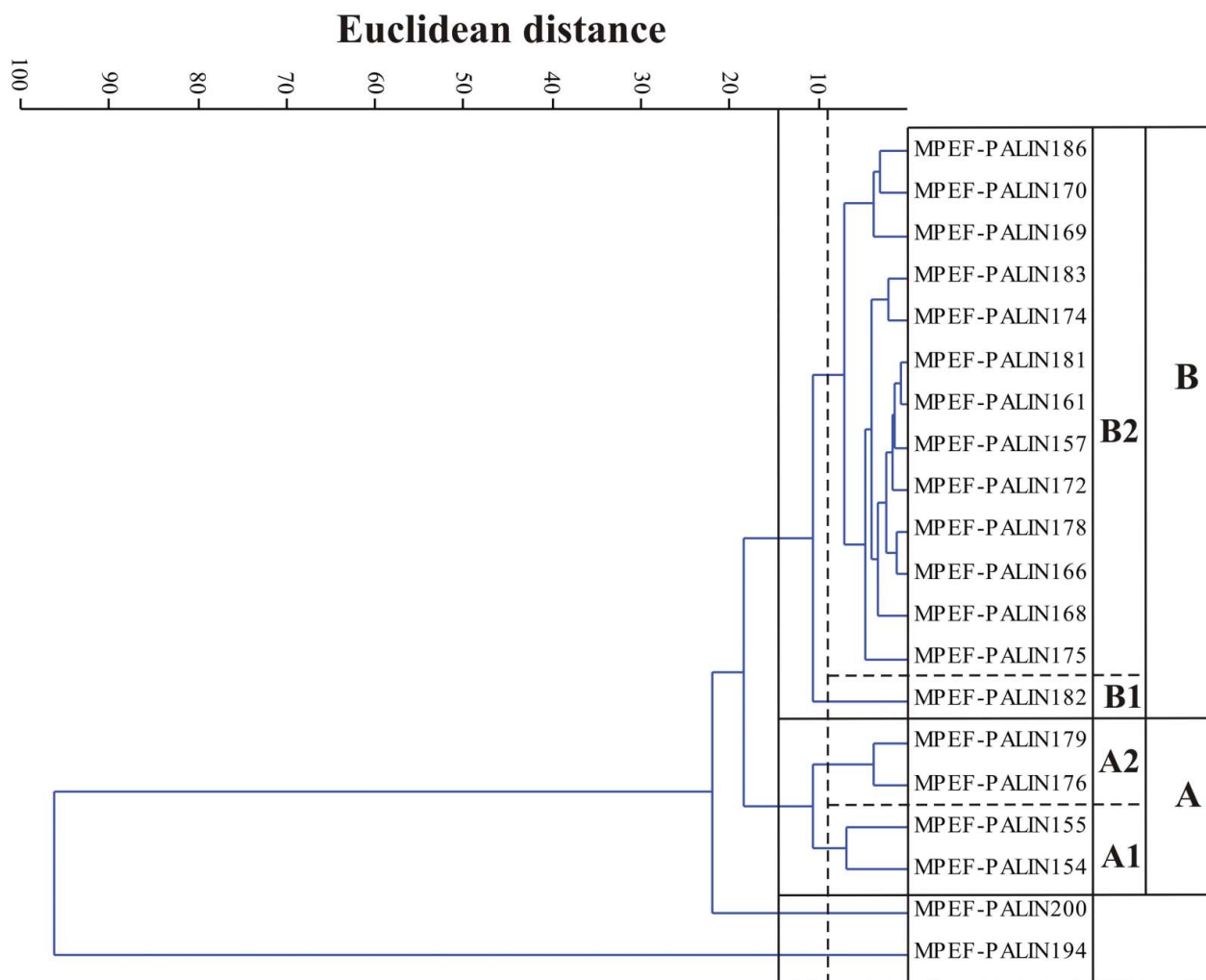


Figure 7. Cluster analysis, using Euclidean distance and the unweighted pair group method (UPGM), showing the grouping of the identified palynological assemblages in the Cañadón Caracoles section.

5.4.1.1. *Subgroup A₁*. This group is characterised by the highest representation of Podocarpaceae (2.3–8%; UpL PEG) in the studied section. The presence of Botryococcaceae and Zygnemataceae indicates the Aquatic PEG.

5.4.1.2. *Subgroup A₂*. The main difference between this subgroup and the upper (A₁) is the low frequencies of podocarpacean pollen (1%; Upland PEG). The presence of Zygnemataceae suggests the development of ephemeral water bodies that may be related to fluvial environments. The abundant presence of Araucariaceae and Cheirolepidiaceae, associated with pteridosperms and spores, is indicative of Riverside, Lowland and Coastal Lake PEGs (Table 3; Figure 5).

5.4.2. *Group B* (Figure 7). This group comprises mostly siltstone and very fine sandstone samples

(Table 1; Figure 2). The most conspicuous feature of this cluster is the high contribution of the Cheirolepidiaceae to these assemblages, reaching up to 95% of the total palynomorph spectrum (Figure 3). The long-distance component (sporomorphs from upland regions), mainly represented by bissacate pollen grains of podocarpaceans and pinaceans, is scarce or absent (Figure 3).

5.4.2.1. *Sugroup B₁*. This subgroup comprises one sample and presents the highest percentages of spores (4.8 %) in the studied section, associated with araucariacean, podocarpacean and pteridosperm (mainly corytosperms) pollen grains (Figure 3). These assemblages are indicative of Lowland, Coastal Lake and Upland PEGs (Table 3).

5.4.2.2. *Sugroup B₂*. The Riverside, Lowland and Coastal Lake PEGs are well represented, and the

Aquatic PEG is characterised by the presence of Botryococcaceae and Zygnemataceae (Figure 3).

5.4.3. *Outlier samples (Figure 7)*. The high frequencies of *Botryococcus* in samples MPEF-PALIN194 and MPEF-PALIN200 produce the separation of these levels in the cluster analysis (Figure 7). In the former, the algae represent about the 76% of the total spectrum of palynomorphs, and in the latter, this chlorophytic alga reaches 19%, indicating an important development of the Aquatic PEG (Figures 3 and 5). In these assemblages, the terrestrial material was represented by cheiralepidiacean, podocarpacean and araucariacean pollen (Figure 3), suggesting a coastal lake and upland supply to the lacustrine environment.

5.5. *Palynological correlation of the studied stratigraphical sections in the Cañadón Asfalto Formation*

Biostratigraphic units, particularly those defined by the first occurrences of taxa, allow drawing correlation lines that generally coincide with time lines (Boggs 1987). The chronostratigraphic correlation of the three studied sections (Olivera 2012) was based on the first occurrence of *Callialasporites turbatus* (*Callialasporites turbatus* Subzone of Neuquén Basin, Late Toarcian; Quattrocchio et al. 1996) and the first appearance of *Microcachryidites antarcticus* (basal boundary of *Ischyosporites marburgensis* Subzone of Neuquén Basin, Early Bajocian age; Quattrocchio et al. 1996) in the studied sections. The last occurrence of *Ischyosporites marburgensis* in two of the three sections (Cañadón Lahuincó 'B' and Cañadón Caracoles) suggests a Late Bajocian age by comparison with the upper boundary of *Ischyosporites marburgensis* Subzone of the Neuquén Basin (Quattrocchio et al. 1996) (Table 1; Figures 2 and 8).

It is important to remark the presence of an erosional surface (paraconcordance) in the Cañadón Lahuincó 'A' section (Olivera et al. 2013), below and above which the incoming of *C. turbatus* (MPEFPALIN121) and *M. antarcticus* (MPEFPALIN123) is registered in 25 cm of thickness of this section.

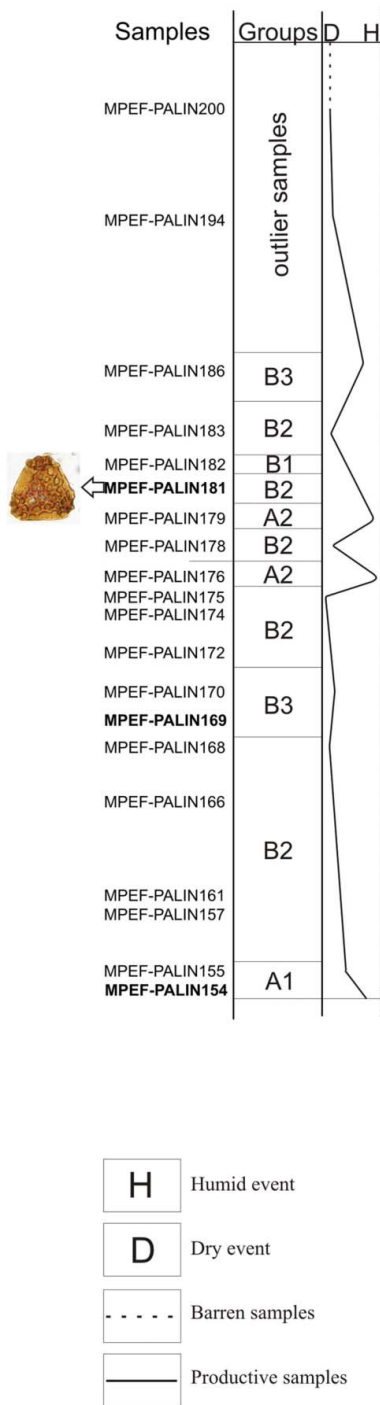
6. Palaeoecological evolution of the Cañadón Asfalto palynoflora

Figure 8 shows the chronostratigraphic correlation of the Cañadón Asfalto Formation at Cañadón Caracoles, Cañadón Lahuincó 'A' and 'B' sections, based on palynological data. The palaeoenvironmental trend (D: dry; H: humid) of Figure 8 is based on the PEGs (Table 3).

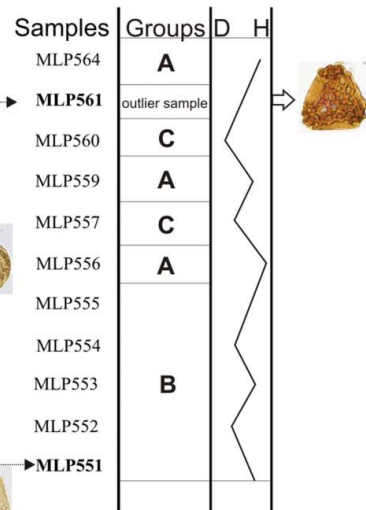
The lowest stratigraphical part of the Cañadón Asfalto Formation is only identified in the Cañadón Lahuincó 'A' section (Table 1; Figures 2 and 8). It corresponds to a clastic sequence (siltstones and very fine sandstones) intercalated between two basaltic flows (Table 1; Figure 2). These sediments are characterised by the presence of monotypic *Botryococcus* assemblages (Figure 3). This chlorophytic algae suggests shallow-water conditions (Guy-Ohlson 1992; Guy-Ohlson & Lindström 1994). Bryant et al. (1994) suggested that the absence of sporomorphs in palynological associations could be related to alkaline pH, relatively oxidant Eh and biogenic activity. Therefore, the absence of sporomorphs in these samples may be the result of a selective preservation of the more resistant algal material. This notion is reinforced by the presence of the abundant taphoflora in lateral chronocorrelation levels (Escapa 2008) located on the opposite side of the Lahuincó creek. Despite this, the Aquatic PEG appears as the dominant ecosystem in this part of the sequence. The presence of simple and compound colonies showing different development stages in a single association suggests that variable seasonal conditions of the environment existed for a long time (Guy-Ohlson & Lindström 1994). Sporomorphs are gradually incorporated into the associations in the three subsequent samples included in groups B, A and D₁. (Table 1; Figures 2–4), which may be in response to a relative increase in humidity, especially for MPEFPALIN120 (Group D₁), presenting a high frequency of araucariacean pollen. This enables the inference of a higher water supply in the system, which would cause the increase in the runoffs and/or ephemeral rivers. Consequently, higher percentages of araucariacean pollen and a gradual decrease of *Botryococcus* colonies are observed. These may be result of a eutrophication process (Ottone & Mancuso 2006), which could be related to a higher input of nutrients to the lake. Although the Araucariaceae family is mainly related to Lowland and Riverside PEGs, when it is associated to the Podocarpaceae and the Pinaceae, part of this group may have an upland forest source (Upland PEG).

Upwards in the Cañadón Lahuincó 'A' section, the incoming of *Callialasporites* is registered (Figure 8). In this part of the sequence, it was possible to identify group C, which was related to a relatively dry period and an important presence of Riverside, Lowland and Coastal Lake PEGs. Although *Classopollis* is the most abundant component of the assemblage, the influence of regional vegetation is represented by pinacean and podocarpacean pollen (Upland PEG; Figure 3). North of this locality (Figure 1), in the Cañadón Caracoles section, it was also possible to recognise dry conditions (Subgroups A₁ and B₂) and an important contribution of the regional plant communities, especially in

Cañadón Caracoles



Cañadón Lahuincó "B"



Cañadón Lahuincó "A"

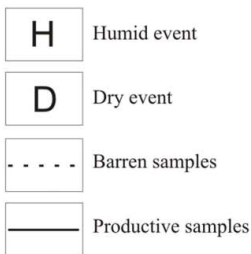
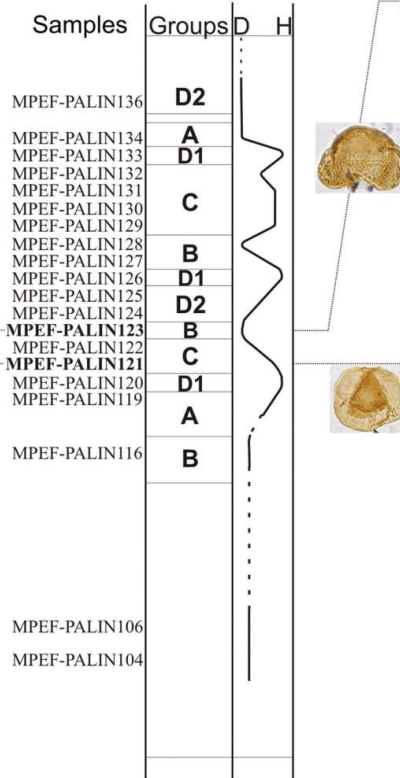


Figure 8. Inter-section chronostratigraphic correlation based on palynological data.

subgroup A₁ (Figure 8). The extensive representation of upland forests may suggest a lower position of ecotones, bringing these communities into closer proximity to the lowland site of deposition (Quattrocchio et al. 1996, p. 479), probably because cooler and dry

conditions prevailed. During this dry period, the incoming of *M. antarcticus* in the Early Bajocian is registered (Figure 8, Groups B and B₃).

In Cañadón Lahuincó 'A', Group B, a *Botryococcus* bloom and an important decrease of the local

input (Cheirolepidiaceae and Araucariaceae) were identified. A negative correlation between the Cheirolepidiaceae and Araucariaceae and the Botryococcaceae (Table 2; Figure 3) was observed. The high percentages of this alga are recorded in limestones and finely laminated pelites and marls, which also yield abundant conchostracan valves (Figure 2). The numerous conchostracan assemblages were interpreted by Cabaleri et al. (2010) as episodes of mass mortality when living conditions turned unfavourable, probably due to a decrease in the water level of the palaeolake under drying conditions. The high percentages of *Botryococcus* and the corresponding lower values of Cheirolepidiaceae and Araucariaceae (Figures 2 and 3) agree with a dry season and consequently a reduction of water transport palynomorphs in the depositional site. In these levels, the pteridosperms are mainly represented by the fossil genus *Alisporites*, reinforcing the suggested drought conditions.

In the Cañadón Caracoles section, Subgroup B₂, it was also possible to recognise this dry event, without the Botryococcaceae bloom. Pteridosperms in this part of the sequence are also represented by the fossil genus *Alisporites*. The difference between Cañadón Caracoles, north of the studied area, and Cañadón Lahuincó 'A' at the south is the higher presence of planktonic material and regional vegetation input (Upland PEG; Podocarpaceae/Pinaceae) in the second section in comparison to the records from the former. Remarkably, both sections end with abundant *Botryococcus* and low percentages of Cheirolepidiaceae and Araucariaceae pollen grain content, suggesting dry conditions and a return to an oligotrophic palaeolake. Fluctuations between relatively dry and relatively wet conditions are registered after the incoming of *C. turbatus* (Figure 8).

The Cañadón Lahuincó 'B' section represents the lateral facies towards the west of the sequence studied in the Cañadón Lahuincó 'A' section (Figures 1, 2 and 8). These palynological assemblages show local conditions yielding higher percentages of spores than in the other two profiles (Figure 3). Only a few *Botryococcus* colonies in a poor state of preservation were recognised in this sequence. Conversely, Zygnemataceae has more participation in these palynological associations. This may be related to local conditions of water bodies, e.g. stagnant ponds. Except for the MLP561 level, the Riverside, Lowland and Coastal Lake PEGs are the ecosystems with more representation in this sequence. In the mentioned sample, the high frequencies of ferns associated with long-distance pollen suggest an important influence of regional vegetation in this assemblage (Upland PEG). In fact, this level

registered the first appearance of *Microcachryidites antarcticus* (Figure 8).

7. Palaeoclimatic considerations

Global palaeobiogeographic patterns are mainly dependent on climate and continental tectonics. Rees et al. (2000, p. 12) emphasised that 'the effects of continental motion can be pronounced and must be considered when interpreting paleoclimates'. During the Jurassic, Argentina was located in the mid-palaeolatitudes of southwestern Gondwana. Palaeomagnetic data analyses (Iglesias Llanos et al. 2006) show that the Cañadón Asfalto Basin shifted from its highest palaeolatitude (ca. 56°) by the end of the Triassic to the end of the Sinemurian. During the Pliensbachian–Toarcian, the region moved northward, reaching the lowermost palaeolatitudes (ca. 30°) and subsequently, during the Middle to Late Jurassic, the area moved south again and eventually attained a similar position to the present day (ca. 43°).

The high proportion of Cheirolepidiaceae and Araucariaceae associated with components from upland forest ecosystems, mainly Podocarpaceae and Pinaceae which represent plants morphologically and physiologically adapted to greater moistures stress (Graham 2012), in several levels of the studied sections, suggests that the Cañadón Asfalto palynoflora accumulated under a warm-temperate climate with strong seasonality. These climatic characteristics are in agreement with the climate zone named the 'seasonally dry (winterwet) biome' *sensu* Rees et al. (2000), recording relatively dry summers and wet winters under warm-temperate climates. This biome has also been inferred by Escapa (2008) on the basis of the Cañadón Asfalto taphoflora at the Lahuincó Creek. The climatic inferences based on palynological data herein presented are supported by other proxies, such as the abundant presence of turtles and biothermal belts (Sterli 2008; Cabaleri & Armella 2005).

Abundant plant remains were also recorded in the Cañadón Lahuincó creek, mainly represented by conifers (about 90%) belonging to Araucariaceae and Cupressaceae *sensu lato* families and minor amounts of equisetaleans and ferns (Escapa 2008). Palynological evidence also shows a dominance of conifer pollen grains over sphenophyte, bryophyte, lycophyte and fern trilete spores. The vegetation diversity recorded in this unit provides a broad testimony to the existence of profuse late Early to mid Middle Jurassic flora, allowing the development of spectacular dinosaurs and other vertebrate faunas registered in the Cañadón Asfalto Formation (Figure 5).

8. Conclusions

The present palynological research on the Cañadón Asfalto Formation, Cerro Cóndor depocentre, Cañadón Asfalto Basin, allows the following conclusions to be drawn:

- The present study increases the palynological knowledge of the Cañadón Asfalto Formation, at Cerro Cóndor Depocentre. Seventy-one species of spores, pollen grains and organic-walled microplankton were recognised.
- The incoming of *C. turbatus*, in the sample MPEF-PALIN121 located above the second basaltic flow at Cañadón Lahuincó 'A' section, indicates a Late Toarcian age. The last occurrence of *I. marburgensis*, registered in Cañadón Lahuincó 'B' and Cañadón Caracoles sections, suggests a late Bajocian age. Thus, the palynoflora of the lower and middle part of the Cañadón Asfalto Formation outcropping in the surrounding area of the Cerro Cóndor locality between those levels has a Late Toarcian to Late Bajocian age. Below these levels, an Early/Mid Toarcian age was proposed by Cúneo et al. (2013) based on the analysis of one tuff sample by the U–Pb analysis of zircon (CA-TIMS method).
- Five palynomorph ecogroups (PEG) were recognised: Upland, Lowland, Riverside, Coastal Lake and Aquatic. Their distribution in the three studied sections is provided. A greater representation of the Lowland and Coastal Lake PEGs at the north of the studied area (Cañadón Caracoles section) suggests the development of a littoral zone in this sector. The higher presence of planktonic material (mainly *Botryococcus* colonies, Aquatic PEG) and long-distance transported pollen grains (Podocarpaceae and Pinaceae, Upland PEG) in the assemblages of the Cañadón Lahuincó 'A' sections may indicate the presence of a more distal situation in this part of the depocentre.
- Fluctuations between relatively dry to relatively wet conditions are registered after the incoming of *C. turbatus* (Late Toarcian). The Cañadón Lahuincó 'A' section and the Cañadón Caracoles section end with important frequencies of Botryococcaceae and low percentages of terrestrial palynomorphs (Cheirolepidiaceae and Araucariaceae pollen grains), suggesting the presence of a dry period during the Middle Jurassic (Late Bajocian) in this region.
- The palynological evidence suggests a highly seasonal, warm-temperate palaeoclimate for the

Cañadón Asfalto region during late Early to mid Middle Jurassic time, which is consistent with the 'seasonally dry (winterwet) biome', *sensu* Rees et al. (2000).

- The Cañadón Asfalto Formation is interpreted as accumulated in a dominantly lacustrine environment, characterised by carbonatic and siliciclastic facies associations, interfingering with volcanic and volcanoclastic deposits. From a palynological viewpoint, the development of a shallow, saline and oligotrophic palaeolake is supported by the presence of abundant Botryococcaceae in a good state of preservation in several of the studied associations. The different inferred ecosystems show the distribution of the late Early to mid Middle Jurassic vegetation in the Cañadón Asfalto Formation, Cerro Cóndor Depocentre.

Acknowledgements

The authors thank Dr. Eckart Schrank, two anonymous reviewers and the Editor for their helpful suggestions which improved the final version of the manuscript. The authors kindly acknowledge Eugenia Zavattieri for their help with graphics. The authors are grateful to Lic. Eugenia Soreda for field assistance and contributing resources in the field work. Dr. Ignacio Escapa and Dr. Rubén Cúneo are also kindly acknowledged for their help during fieldwork. The logistic support in the field work provided by the Edigio Feruglio Museum is greatly appreciated.

Funding

This work was supported by the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) under the following Research Projects [PICT 2006-01516 and PICT 2012-1520, BID 1728/OC-AR to R.N. Cúneo and PICT 2011-2546 BID 1728/OC-AR to A.M. Zavattieri]; Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) [under Grant PIP 11220090100605-A.M. Zavattieri] and Secretaría General de Ciencia y Tecnología de la Universidad Nacional del Sur (SEGcyT) [under Grant PGI-24/H126.-M.A. Martínez].

Author biographies



DANIELA E. OLIVERA is a postdoctoral fellow at the Consejo Nacional de Investigaciones Científicas y Técnicas (CCT-CONICET) in Bahía Blanca, Argentina and is also a teaching assistant in palaeontology at the Universidad Nacional del Sur, Bahía Blanca, Argentina. She obtained a PhD in 2012 from the Universidad Nacional del Sur.

Daniela's research interests include palynofacies analysis and the palynostratigraphy of Argentinian Mesozoic and Cenozoic successions.



ANA M. ZAVATTIERI is an independent researcher for the National Research Council of Argentina. She specialises on the Upper Permian to Lower Jurassic biostratigraphy, palaeontology and palynology of Argentina and surrounding areas.



MIRTA E. QUATTROCCHIO specialises in terrestrial and marine palynomorphs as applied to Mesozoic and Cenozoic biostratigraphy and sedimentary basin analysis in Argentina. She is a researcher for the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bahía Blanca, Argentina.

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Appendix 1

Alphabetical list of identified species and illustration references.

Trilete spores

- Antulsporites saevus* (Balme) Archangelsky & Gamero emend. [= *A. baculatus* (Archangelsky & Gamero) Archangelsky & Gamero, 1966]
- Cadargasporites* sp. cf. *C. reticulatus* de Jersey & Paten 1964
- Biretisporites* sp. A (in Volkheimer 1974)
- Cadargasporites* sp. cf. *C. reticulatus* de Jersey & Paten 1964 (Plate 1, figure 5)
- Clavatisporites* spp.
- Deltoidospora australis* (Couper) Pocock 1970
- Deltoidospora minor* (Couper) Pocock 1970 (Plate 1, figure 1)
- Diptyophyllidites harrisii* Couper 1958 (Plate 1, figure 3)
- Ischyosporites marburgensis* de Jersey 1963 (Plate 1, figure 10)
- Klukisporites labiatus* (Volkheimer) Baldoni & Archangelsky 1983 (Plate 1, figure 6)
- Klukisporites lacunus* Filatoff 1975 (Plate 1, figure 7)
- Klukisporites variegatus* Couper 1958 (Plate 1, figure 9)
- Klukisporites* sp. cf. *K. scaberis* (Cookson & Dettmann) Dettmann 1963 (Plate 1, figure 8)
- Neoraistrickia* cf. *suratensis* McKellar 1974
- Nevesisporites* cf. *undatus* Backhouse 1988 (Plate 1, figure 11)
- Nevesisporites vallatus* de Jersey & Paten emend. McKellar 1998 (Plate 1, figures 12–16)
- Obtusisporis modestus* (McKellar) McKellar 1998 (Plate 1, figure 4)
- Retitriletes austroclavitudites* (Cookson) Döring, Krutzsch, Mai & Schulz in Krutzsch 1963 (Plate 1, figure 17)
- Retitriletes semimuris* (Danzé-Corsin & Laveine) McKellar 1974
- Retitriletes* sp. 1 (Plate 1, figure 18)
- Stereisporites* sp. cf. *S. psilatus* (Ross) Pflug 1953
- Todisporites minor* Couper 1958 (Plate 1, figure 2)
- Trilobosporites* sp. (Plate 1, figure 20)
- Verrucosisporites varians* Volkheimer 1972 (Plate 1, figure 19)

Gymnosperm pollen grains

- Alisporites lowoodensis* de Jersey 1963 (Plate 2, figure 1)
- Alisporites similis* (Balme) Dettmann 1963 (Plate 2, figure 2)
- Araucariacites australis* Cookson ex Couper 1953 (Plate 2, figure 4)

- Araucariacites fissus* Reiser and Williams 1969
- Araucariacites pergranulatus* Volkheimer 1968
- Araucariacites* sp. cf. *A. pergranulatus* Volkheimer 1968 (Plate 2, figure 5)
- Araucariacites* sp. A (in Volkheimer 1972)
- Calliasporites dampieri* (Balme) Sukh Dev 1961 (Plate 2, figure 6)
- Calliasporites microvelatus* Schulz 1966 (Plate 2, figure 7)
- Calliasporites minus* (Tralau) Guy 1971 (Plate 2, figure 8)
- Calliasporites segmentatus* (Balme) Srivastava 1963
- Calliasporites turbatus* (Balme) Schulz 1967 (Plate 2, figure 9)
- Calliasporites* sp. 1 (Plate 2, figure 10)
- Classopollis classoides* (Pflug) Pocock and Jansonius 1961 (Plate 3, figures 6–7)
- Classopollis intrareticulatus* Volkheimer 1972 (Plate 3, figures 8–9)
- Classopollis itunensis* Pocock 1962 (Plate 3, figures 10–11)
- Classopollis simplex* (Danzé-Corsin & Laveine) Reiser and Williams 1969 (Plate 3, figure 12)
- Classopollis torosus* (Reissinger) Balme 1957
- Cerebropollenites macroverrucosus* (Thiergart) Schulz 1967
- Cerebropollenites mesozoicus* (Couper) Nilsson (in Couper, 1958)
- Cerebropollenites carlylensis* Pocock 1970 (Plate 3, figure 14)
- Cerebropollenites* sp. 1 (Plate 2, figure 15)
- Inaperturopollenites indicus* Srivastava 1966
- Inaperturopollenites giganteus* Góczán 1964 (Plate 2, figure 11)
- Inaperturopollenites microgranulatus* Volkheimer 1972
- Inaperturopollenites* cf. *reidi* (de Jersey) de Jersey 1964
- Inaperturopollenites* sp. 1-2 (Plate 2, figures 12–13)
- Indusiisporites parvisaccatus* (de Jersey) de Jersey 1963
- Indusiisporites* sp. 1-3 (Plate 2, figures 17–19)
- Microcachrydites antarcticus* Cookson 1947 (Plate 3, figure 3)
- Pinuspollenites globosaccus* Filatoff 1975 (Plate 2, figure 16)
- Podocarpidites astrictus* Haskel 1968 (Plate 2, figure 20)
- Podocarpidites ellipticus* (Cookson) Couper 1953
- Podocarpidites multesimus* (Bolkhovitina) Pocock 1962
- Podocarpidites verrucosus* Volkheimer 1972
- Podocarpidites* sp. cf. *P. radiatus* Brenner 1963 (Plate 3, figures 1–2)
- Podocarpidites* sp. cf. *P. verrucosus* Volkheimer 1972
- Podosporites variabilis* Sukh Dev 1961 (Plate 3, figure 4)
- Podosporites* sp. 1 (Plate 3, figure 5)
- Vitreisporites pallidus* (Reissinger) Nilsson 1958 (Plate 2, figure 3)

Algae

- Botryococcus* sp. cf. *B. braunii* Kützing 1849 (Plate 3, figures 13–15)
- Ovoidites* spp.

Acritarch

- Leiosphaeridia* sp. 1 (Plate 3, figure 16)