Contribution to the knowledge of the fossil fungi record based on palynomycological studies from the El Foyel Group, Ñirihuau Basin, Paleogene from Patagonia Argentina

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ISSN 2469-0228

CONTRIBUTION TO THE KNOWLEDGE OF THE FOSSIL FUNGI RECORD BASED ON PALYNOMYCOLOGICAL STUDIES FROM THE EL FOYEL GROUP, ÑIRIHUAU BASIN, PALEOGENE FROM PATAGONIA ARGENTINA

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Abstract. Spores, conidiophores, and hyphae of fossil fungi recovered from nine outcropping siltstone and shale samples belonging to the Troncoso, Salto del Macho, and Río Foyel formations in the El Foyel Group at the Río Foyel Section, are described and illustrated. Representatives of 16 genera were recognized. Among the 26 species described, one is proposed as a new species, *Inapertisporites lacrimaformis*. Amerospores are the most abundant type of spores recovered. Based on the palynostratigraphical analysis of the non-pollinic (fungal) remains, a Paleogene age for the El Foyel Group is suggested. Of the three formations, Troncoso shows the highest abundance and diversity of fungal remains, which is believed to be representative of a period of optimal climatic conditions characterized as warm temperate and humid, probably related to the Middle Eocene Climate Optimum (MECO). Based on the paleoeological preferences of the specimens recovered from the El Foyel Group, a riparian or lacustrine environment in a woodland setting is inferred.

Key words. Fossil fungal spores. *Inapertisporites*. El Foyel Group. Troncoso Formation. Paleogene. MECO. Argentina.

Resumen. CONTRIBUCIÓN AL CONOCIMIENTO DEL REGISTRO FÚNGICO FÓSIL EN BASE A ESTUDIOS PALINOMICOLÓGICOS DEL GRUPO EL FOYEL, CUENCA DE ÑIRIHUAU, PALEÓGENO, PATAGONIA ARGENTINA. Se describen e ilustran esporas, conidióforos e hifas de hongos fósiles recuperados de nueve muestras de fangolitas aflorantes en la sección Río Foyel, pertenecientes a las Formaciones Troncoso, Salto del Macho y Río Foyel (Grupo El Foyel). Se reconocieron representantes de 16 géneros. Entre las 26 especies descritas, se propone una nueva especie, *Inapertisporites lacrimaformis*. Las amerósporas son el tipo de esporas más abundantes. A partir del análisis palinoestratigráfico de los restos no polínicos (fúngicos), se sugiere una edad paleógena para el Grupo El Foyel. De las tres formaciones estudiadas, la Formación Troncoso es la que muestra la mayor abundancia y diversidad de restos fúngicos. Este rasgo podría estar evidenciando un período de condiciones climáticas óptimas (templado cálido y húmedo), probablemente relacionado con el Óptimo Climático del Eoceno Medio (OCEM). En base a las preferencias paleoecológicas de los especímenes recuperados del Grupo El Foyel, se podría inferir un ambiente boscoso próximo a un cuerpo de agua fluvial o lacustre.

Palabras clave. Esporas fúngicas fósiles. *Inapertisporites*. Grupo El Foyel. Formación Troncoso. OCEM. Paleógeno. Argentina.

ALTHOUGH fossil fungi are encountered in sediments as old as the Neoproterozoic (Bonneville *et al.*, 2020), fungi did not become abundant and diverse in the palynological record until the Cretaceous, with their frequency remarkably increasing in the Paleogene when, interestingly, their diversification coincided with the diversification of angiosperms (Vermeij & Grosberg, 2010; Vajda, 2012; Saxena *et al.*, 2021). An increasing number of contributions of fossil fungi in palynological preparations have been recorded for the Cenozoic, being much less frequent in the Paleogene than in the Neogene and/or Quaternary. The El Foyel Group (Asensio *et al.*, 2005) in the Ñirihuau Basin has provided the most diverse and the best-preserved palynomycological record of the Paleogene deposits of the Argentine Patagonia and probably of South America. So far, only part of the recovered material has been published. Martínez *et al.* (2016) reported a total of 38 species of fungal spores distributed in 18 genera, with diverse modern affinities, mostly ascomycetes.

Well-preserved and diverse reproductive bodies of epiphyllous fungi have been recovered from the El Foyel Group, with preliminary results reported as the material is still under study (Bianchinotti *et al.*, 2017). Bianchinotti *et al.* (2020), using recovered fossil fungi, provided evidence that the genus *Desmidiospora* represents part of the life cycle of at least two different groups of epiphyllous ascomycetes (polyphyletic origin) and propose that fungal remains of this kind should be kept in an open allocation and treated as germlings.

The aims of this paper are: i) to present a detailed report of fossil spores and other fungal remains, with descriptions and illustrations recovered from outcropping sedimentary samples of the El Foyel Group in the Ñirihuau Basin, Argentina, ii) to integrate these recent findings with previously acquired records, facilitating a palynostratigraphical analysis of the units examined, iii) to carry out paleoecological and paleoclimatic interpretations to refine the knowledge of the El Foyel Group.

GEOLOGICAL SETTING

The Ñirihuau Basin is located in the western area of Río Negro and Chubut provinces, Argentina (Fig. 1). The stratigraphical column of this basin is comprised, from the base to the top, of the Huitrera Formation (Ravazzoli & Sesana, 1977) or its lateral equivalent the Cerro Bastión Formation (Diez & Zubia, 1981), the El Foyel Group, and the Nahuel Huapi Group (González Bonorino, 1973; González Bonorino & González Bonorino, 1978). The type section of the El Foyel Group (Fig. 2), at the Río Foyel Section (41° 44' S; 71° 30' W) is composed of outcrops in the middle valley of the river of the same name and is about 80 km south of Lago Nahuel Huapi. These outcrops are partially obscured by densely forested areas. The group consists, from the base to the top, of the Troncoso (Asensio *et al.*, 2005), Salto del Macho (Asensio *et al.*, 2005), and Río Foyel formations (Pöthe de Baldis, 1984). Together, these formations are a 2000 m thick section of volcaniclastics, thick siliciclastics, and minor limestones outcropping along the Foyel River.

The stratigraphic arrangement of the El Foyel Group formations and their respective ages remain a subject of ongoing controversy. According to Asensio *et al.* (2005),

the Río Foyel Section overlies volcanic rocks from the Cerro Bastión Formation (middle Eocene), although this contact is hidden by the dense forest cover typical of the region. The Troncoso Formation (middle to upper Eocene) constitutes the basal unit, comprising approximately 800 m of immature green sandstones with intercalations of tuffaceous shales and red shales. The Salto del Macho Formation (middle Eocene–lower Oligocene) overlies the Troncoso Formation with a sharp erosive contact. This unit is composed of thick beds of polymictic conglomerate with a maximum thickness of 560 m and with thinner layers of sandstone and intercalations of black shales and ignimbrites. The top of the section contains the lowest part of the Río Foyel Formation (Oligocene), approximately 600 m thick, predominantly composed of black shales, and occasionally interrupted by intercalations of bioclastic limestone and conglomerate.

Based on field evidence, geochemical hydrocarbon (isotopic analyses of gasses from the Arroyo de la Mina spring), and chronological data, Bernardo *et al.* (2009) proposed the existence of two petroleum systems in the Ñirihuau Basin, named Ñirihuau-Ñirihuau and Foyel-Foyel. According to this exploratory scheme, the formations comprising the El Foyel Group would span from the late Eocene to the early Oligocene. According to Asensio *et al.* (2005), the entire sequence of the El Foyel Group would have been deposited during the middle Eocene to early Oligocene.

Later, based on field data, geochronology, and calcareous nannofossils recovered from the Río Foyel Formation, Bechis *et al.* (2014) proposed a new stratigraphic framework. In this scheme, they not only relocated the El Foyel Group stratigraphically to ages as young as the Miocene, but they also modified the stratigraphic order of its constituent units. They designated the Río Foyel Formation as the basal unit, followed by the Troncoso Formation, culminating with the Salto del Macho Formation.

Here, we follow the proposal of Asensio *et al.* (2005) and Bernardo *et al.* (2009), which was reinforced by several palynological studies (Cornou, 2012; Quattrocchio *et al.*, 2012; Cornou *et al.*, 2014; Martínez *et al.*, 2016).
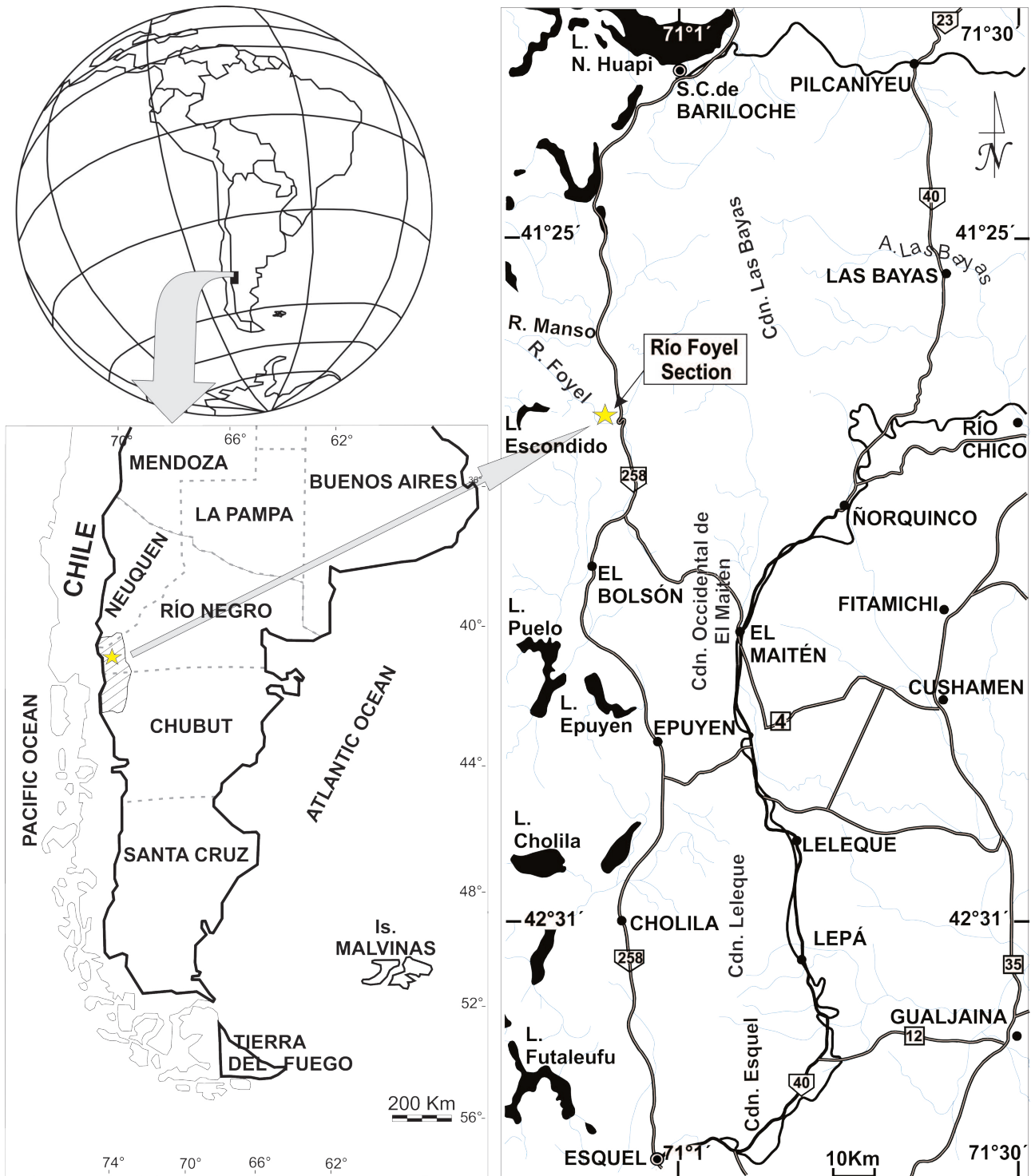
Figure 1. Location map of the Ñirihuau Basin with indication of the Río Foyel Section (modified from Cornou *et al.*, 2014).

MATERIALS AND METHODS

All the outcrop samples (17) of siltstone and shales from the Troncoso, Salto del Macho, and Río Foyel formations in the El Foyel Group at the Río Foyel Section contain fossil fungi (Fig. 2). This contribution presents findings from nine of those samples, which complements previous results
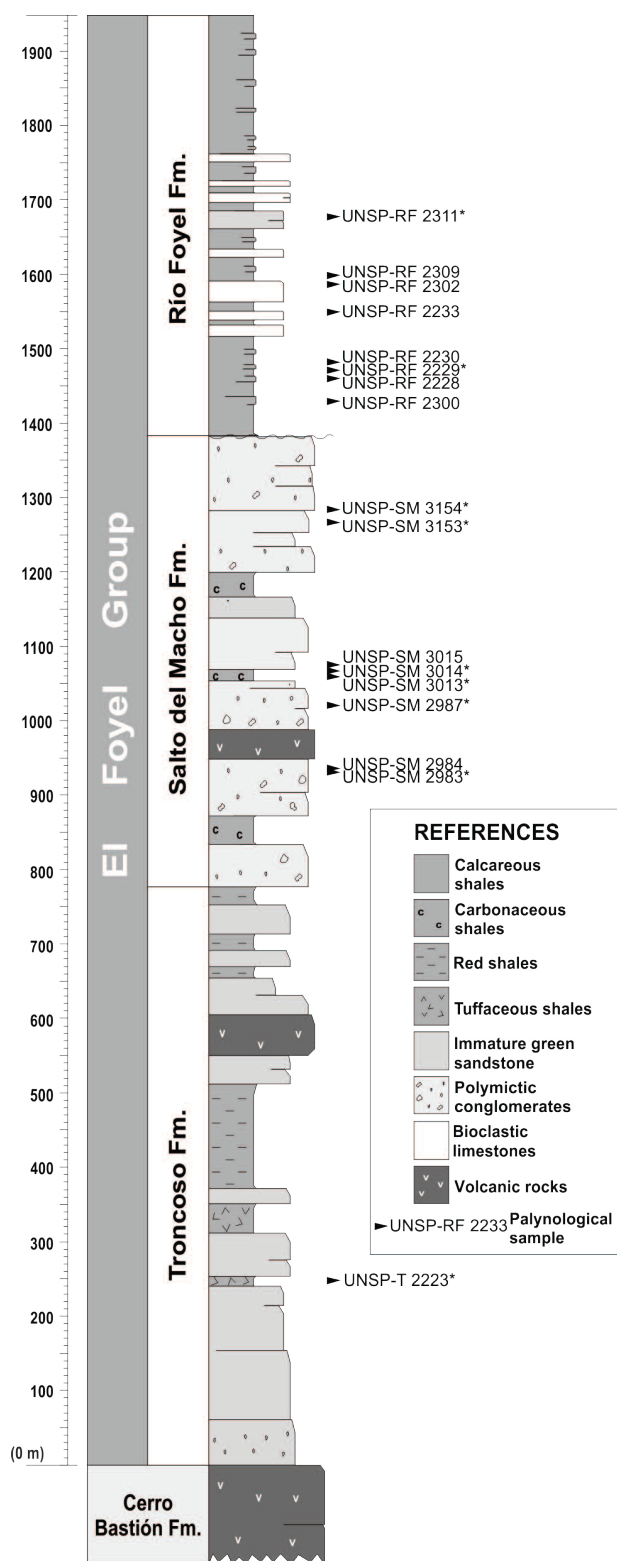
Figure 2. Río Foyel Section and distribution of palynological samples. Samples with asterisks indicate those with results presented in this contribution; the remaining samples provided palynomycological information as presented in Martínez *et al.* (2016) (modified from Martínez *et al.*, 2016).

published in Martínez *et al.* (2016). Fungal remains were extracted from the rocks using mineral-acid palynological techniques involving treatments with hydrochloric and hydrofluoric acids (Volkheimer & Melendi, 1976). The slides were examined using a transmitted light microscope (Olympus BX40A) equipped with an Olympus CAMEDIA C-5060 digital camera. The slides are housed in the Universidad Nacional del Sur-Instituto Geológico del Sur, Bahía Blanca, Buenos Aires Province, Argentina. They are identified by the abbreviation UNSP (Universidad Nacional del Sur, Palynology) and a catalog number followed by letters denoting each formation: T (Troncoso), SM (Salto del Macho), or RF (Río Foyel). Specimen locations on sample slides are noted with England Finder coordinates. In the descriptions, we indicate measurements as minimum-(mean)-maximum values. All recognized fungal spores are listed in Table 1, including both the records belonging to this contribution (taxa with asterisk and empty circles) and those coming from Martínez *et al.*, 2016 (taxa indicated with "X"), grouped by type of fungal structure.

PALYNOMYCOLOGICAL REMAINS: FUNGAL REMAINS RECOVERED FROM PALYNOLOGICAL STUDIES

Although we agree with the idea that it is necessary to attempt an approximation to the natural classification and adhere to what has previously been proposed (O'Keefe *et al.*, 2021), as long as we describe forms that are not clearly assignable to modern genera we used the morph-species approach, using pre-existing fossil names or eventually pro-posing new ones (especially for fungal spores), following the traditional approach of a morphological-based artificial classification. We chose this strategy as it allowed us to make comparisons and establish biostratigraphic correla-tions. However, we chose to describe some remains, like hyphae and conidiophores, without formal assignment, as they are common vegetative or reproductive structures that cannot be referred to a particular taxon.

Abundant and diverse remains of fungi have been previously recovered from the El Foyel Group and published by Martínez *et al.* (2016) and Bianchinotti *et al.* (2017, 2020).

TABLE 1 – Distribution of species in the studied samples. Taxa with asterisk and empty circles are records from this contribution.

		2223	2983	2984	2987	3013	3014	3015	3153	3154	2300	2228	2229	2230	2233	2302	2309	2311
Amerosporae (28)	*Diporisporites elongatus*				X													
	Diporisporites sp. cf. *D. psilatus*	X											X					
	Exesisporites sp. cf. *E. neogenicus*	X																
	Foveodiporites elegans	X		X														
	Rhizophagus sp. 1*				O				O	O								
	Hypoxylonites ater						X											
	Hypoxylonites chaiffetzii														X			
	Hypoxylonites vicksburgensis	X																
	Hypoxylonites foyelensis	X																
	Hypoxylonites sp. cf. *H. wolfei*	X					X											
	Hypoxylonites sp.						X											
	Inapertisporites circularis	X				X												
	Inapertisporites lacrimaformis sp. nov.*	O																
	Inapertisporites ovalis	X																
	Inapertisporites subovoideus	X																
	Inapertisporites sp. 1*	O																
	Inapertisporites sp. 2*		O		O		O											
	Lacrimasporonites cupuliformis																	X
	Lacrimasporonites fusoides																	X
	cf. *Lacrimasporonites* sp.																	X
	Monoporisporites minutus	X																
	Monoporisporites singularovalis					X												
	Monoporisporites sp. cf. *M. traversii*	X																
	Monoporisporites sp. 1*	O																
	Spirotremesporites simplex	O																
	Spirotremesporites sp. cf. *S. duenasii*	O																
	Spirotremesporites sp. 1*	O																
	Spirotremesporites sp. 2*	O																
Didymosporae (9)	*Cercophora*-type*	O																
	Dicellaesporites septoconstrictus	O																
	Dicellaesporites sp. cf. *D. suborbicularis*	O																
	Dicellaesporites disphaericus	O																
	Didymoporisporonites panshanensis	X																

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TABLE 1 – Continuation

		2223	2983	2984	2987	3013	3014	3015	3153	3154	2300	2228	2229	2230	2233	2302	2309	2311
Didymosporae (9)	*Dyadosporites annulatus*						X								X			
	Dyadosporites elsikii																	X
	Dyadosporites subovalis	X																
	Hilidicellites normalis*	O																
Phragmosporae (21)	*Anatolinites subcapsilaris*	X																
	Anatolinites sp. 1*	O																
	cf. *Anatolinites alaskaensis**																	O
	Brachysporisporites opimus*	O																
	Brachysporisporites sp. cf. *B. pyriformis**	O																
	Brachysporisporites sp. cf. *B. atratus**	O																
	Clasterosporium eocenicum*	O																
	Diporicellaesporites elongatus	X																
	Diporicellaesporites incurviusculus										X							
	Diporicellaesporites sp. 1									X								
	Diporicellaesporites sp. 2										X							
	Diporicellaesporites sp. 3*	O																
	Diporicellaesporites sp. 4*																O	
	Diporicellaesporites sp. 5*									O								
	Multicellites ellipticus	X			X													
	Multicellites sp. aff. *M. leptaleus*															X		
	Multicellites sp. cf. *M. tener**	O																
	Multicellites sp.	X																
	Pluricellaesporites patagonicus	X													X			
	Pluriseptata spore indet.*					O												
	Spores indet.	X										X						
Dictyosporae (7)	*Dictyosporites* sp. cf. *D. dictyosus*	X																
	Dictyosporites sp.				X													
	cf. *Dictyosporites* sp.*	O																
	Papulosporonites enormis	X																X
	Papulosporonites sphaeromorphus*	**O**																
	Polycellaesporonites sp.				X													
	Staphlosporonites sp.							X										

Ascospores and conidia

Ascospores are spores derived from sexual reproduction, formed inside a cell called an ascus (pl. asci), which are extremely variable in size, shape, color, and other morphological features. Conidia, spores of asexual origin, on the other hand, can be distinguished from ascospores by the presence of diverse marks derived from their ontogeny, like attachment scars, pores, denticules, and others. It is not always easy to distinguish between ascospores and conidia, especially in a case as this, where palynological remains are recovered as dispersed entities. Additional characters would be needed to differentiate conidia from ascospores correctly. Therefore, the artificial morphological system proposed originally by Saccardo (1877) and modified by Pirozynski & Weresub (1979) was adopted; it is based on the number of cells, disposal of septa, and presence/absence of apertures. Following this scheme, fungal spore types were named as amerospores, didymospores, and so on (Nuñez Otaño *et al.*, 2021).

SYSTEMATIC PALEONTOLOGY

Kingdom FUNGI

AMEROSPORAE

Unicellular spores (without septa), with or without visible apertures (pores). One, two, or more pores, some with a visible hilum.

Genus *Rhizophagus* P. A. Dang., 1896

Type species. *Rhizophagus populinus* P. A. Dang., 1896. Holocene, France.

Rhizophagus sp. 1
Figure 3.1–2

Studied material. UNSP-SM 2987b: F59/3, N58/2, U28/4; UNSP-SM 3153c: W48/4; UNSP-SM 3154c: V46/4.
Description. Spores subspherical, pyriform to very irregular. Wall smooth (occasionally perforated by fungal/bacterial attack), light brown, single or double walled, 1(1.2)2 µm. Subtending hyphae straight to curved, constricted, swollen or irregular, sometimes with lateral protrusions (knobbed),

many times slightly thickened at the point of juncture, but without a definite occlusion, wall wide 0.5(0.83)1 µm.
Dimensions. 68(82.8)94 x 78(117.6)175 (5 specimens).
Remarks. The morphology of the spores and subtending hyphae closely resembles that of a species of *Rhizophagus*, *R. aggregatu*s (N. C. Schenck & G. S. Sm.) C. Walker, which is regularly found in lacustrine and maritime dunes (Koske, 1985; Walker *et al.*, 2018). This spore is one of the "Glomoid spores". The concept refers to spores typical of a group of mycorrhizae-forming genera from which *Glomus* is the most emblematic representative. Obligate biotrophs, arbuscular mycorrhizae (AM) are the main drivers of most terrestrial ecosystems, living in mutualistic symbiosis with most vascular land plants to which they provide water and inorganic nutrients (Schüßler *et al.*, 2011). The AM fungi produce a few characteristic structures, of which the most easily distinguishable are the spores that are frequently recovered in palynological samples. The group is ancient, with a traceable fossil record in the Early Devonian, but presumably older, as several reports postulate its origin in the Neoproterozoic (Taylor *et al.*, 2015; Walker *et al.*, 2018). Regardless of the date, its morphology has remained virtually unchanged since its origin. This makes it easier to recognize glomalean spores in fossil samples. They were often given fossil names, such as *Palaeomycites*, which were widely used in older literature. Modern trends suggest that it is preferable to try to assign them to extant genera. From the Mesozoic and Cenozoic, the records of spores are few and isolated (Taylor *et al.*, 2015). But Kar (1979) defined a Cenozone from the Maniyara Fort Formation (Oligocene) of Kutch, Gujarat, India on the basis of the abundant presence of spores named there as *Aplanosporites robustus* [= *Palaeomycites robustus* (Kar) Kalgutkar & Janson, 2000]. He was also able to recognize this assemblage zone in the borehole Tripura sequences in North-east India (Kar, 1990). In Argentina, García-Massini *et al.* (2012) recorded *Glomus*-like spores from San Agustín, Deseado Massif, southern Patagonia Argentina, a Jurassic hot spring ecosystem. In most modern ages, occurrence of spores of AM fungi has been considered indicative of active soil erosion processes and their presence has been used as an indicator of soil conditions associated with aridity and stressed environments (Taylor *et al.*, 2015).

Genus *Inapertisporites* van der Hammen, 1954

Type species. *Inapertisporites variabilis* van der Hammen, 1954. Maastrichtian, Colombia.

Inapertisporites lacrimaformis sp. nov.

Figure 3.3–5

MycoBank: 851481

Derivation of name. The specific name derives from Latin, in reference to the tear-drop shape of the spores.

Studied material. UNSP-T 2223f2: E48/4, X41, K34; UNSP-T 2223f3: M37/1; UNSP-T 2223f4: O34/2 (holotype), M39/1, M39/2, N42/4, Q47/4; UNSP-T 2223f8: K28/3, L49/1, S21/1.

Description. Spores 1-celled, with a tear-drop outline, broadly rounded at one end, but slightly pointed with a conical protuberance at the other, with no apertures. Wall black, smooth, looking rigid, fractured in some specimens.

Dimensions. 36(46.8)60 x 39(51.4)62 µm (12 specimens). Holotype: 48 x 51 µm.

Remarks. *Inapertisporites lacrimaformis* sp. nov. is characterized by its tear-drop outline and large size. Its shape resembles that of *I. conicus* Song & Li from the late Oligocene of Dongying Formation, China (in Song *et al.*, 1989), although is consistently smaller (20 x 23 µm). *Inapertisporites solidus* Song & Cao from the Late Cretaceous of King George Island, Antarctica (Song & Cao, 1994) also has a similar morphology and black wall, but it also is smaller (18–22 x 28–32 µm) than ours. We were unable to reliably assign this species to any extant genus. Due to the color and opacity of the spores, it was difficult to study some features of the wall and ornamentation; however, in the optical section, they did not show any evidence of ornamentation. The obscure color, size, and shape are features representative of several species of aquatic hyphomycetes, such as some in *Parafuscosporella* or *Vanakripa* (Yang *et al.*, 2020). No species of the first genus has been mentioned yet from outside East Asia, while species of the second are known from freshwater and terrestrial environments worldwide (Yang *et al.*, 2020). The huge size of these spores is suggestive of dispersion through water, so we infer that they are representative of the biota of an aquatic environment within the forest.

Inapertisporites sp. 1

Figure 3.6

Studied material. UNSP-T 2223f2: A52/4.

Description. Spores 1-celled, rounded, with no apertures. Wall black, smooth.

Dimensions. 46 x 48 µm (1 specimen).

Remarks. No assignment could be made to this spore. Its opacity and dark color preclude its study. From its shape and dimensions, it could be compared to *I. globatus* Sah & Kar, 1974, a species described from the early Eocene of India (Saxena & Tripathi, 2011). *Inapertisporites* sp. 1 is similar to UAB-7, a specimen illustrated and described by Revelles *et al.* (2016) from the Early Neolithic Settlement of La Daga, Girona, Spain; however, they differ in size (20 x 30 µm).

Inapertisporites sp. 2

Figure 3.7–11

Studied material. UNSP-SM 2983d: T19/1; UNSP-SM 2987b: O32; UNSP-SM 3014b: J49/3.

Description. Spores globose, circular in outline, irregularly ornamented by clavae, baculae, and granules of low height (0.5–1 µm). The ornamentations are gathered forming groups, causing their irregular distribution throughout the surface.

Dimensions. 12(14.67)17 x 14(15.57)17.5 µm, including ornamentation (3 specimens).

Remarks. This morphotype shows high similarity with several fossil and extant spores. They coincide with HdV-1061 (van Geel *et al.*, 2011), recovered from Holocene deposits from Lake Challa, Kenya. Among the extant ones, it resembles the conidia of a species belonging to *Hypomyces* (Ascomycota, Order Hypocreales) fungus, *H. microspermus* Rogerson & Samuels. This mycoparasitic fungus shows host specificity with some boletes, mainly with members of the *Xerocomus chrysenteron* group (Sahr *et al.*, 1999; Douhan & Rizzo, 2003). Besides, our fossil spores also are comparable to basidiospores of several species, *e.g.*, to several different Sclerodermatales species included within Boletales as illustrated in Guzman *et al.* (2013) and Wu *et al.* (2023).

Genus *Monoporisporites* van der Hammen, 1954

Type species. *Monoporisporites minutus* van der Hammen, 1954. Maastrichtian, Colombia.

Monoporisporites sp. 1
Figure 3.12–13

Studied material. UNSP-T 2223f2: G43/2, X41/4; UNSP-T 2223f7: Y29/3.

Description. Spores 1-celled, outline tear-drop-shaped up to lemon-shaped, monoporate, one end broadly rounded, other end pointed bearing a simple pore, 2–3 μm in diameter (Fig. 3.12–13, red arrows). No ornamentation is observed in the optical section; therefore, it is assumed that the wall is psilate, up to 2 μm wide.

Dimensions. 40(47.7)55 x 43(50.7)57 μm (3 specimens).

Remarks. It is comparable to *Monoporisporites koenigii* Elsik (20–22 x 24–30 μm, pore: 0.5 μm in diameter) from the Paleocene of Texas, USA (Elsik, 1968); *Monoporisporites* sp. 3 (23.5 x 25 μm, pore: 3 μm in diameter) from the middle Eocene of Chubut, Argentina (Sepúlveda, 1980); and *Monoporisporites* cf. *traversii* Ediger & Alisan (32 x 34 μm, pore up to 3 μm in diameter) from the middle to late Eocene of Maracaibo Lake, Venezuela (Ramírez, 2004).

Genus *Spirotremesporites* Dueñas-Jiménez, 1979 *emend*. Elsik, 1990

Type species. *Spirotremesporites simplex* Dueñas-Jiménez, 1979. Pleistocene, Colombia.

Remarks. *Spirotremesporites*, like *Hypoxylonites*, are genera of forms comprising species with aseptate, elongated spores that have a long scar or furrow, and are without pores. The furrow in the first genus forms an angle with the axis of the spore and may be straight, curved to S-shaped, sigmoidal in outline, or spiral around the spore axis, while in the second is straight and parallel to the long axis of the spore (Elsik, 1990).

These spores could be related to modern ascospores, mainly those of some genera belonging to Xylariomycetidae, which have germ slits. Germ slits are believed to be an ancient trait that appeared during Cretaceous times, being considered one of the stable characters to discriminate among modern genera (Samarakoon *et al*., 2022). In these, straight slits are mostly the rule, while curved ones are less common, being typical of all the species of a few genera, such as *Helicogermslita* Hawks. & Lodha and *Yuea* O. E. Erikss. But, the trait could also be present in some species of several other genera in the group. In most cases, the assignment of a fossil spore to an extant species is risky, because most features used in modern taxonomy are not preserved or observable in ancient sediments. Among fossil ascospores, *Spirotremesporites* has been less recorded than *Hypoxylonites*, which sometimes constitutes 20% of the palynological association (Elsik, 1990) and even its abundance allowed the establishment of an early Oligocene biozone in the northwest Gulf of Mexico (Elsik & Yancey, 2000).

So far, we have only recovered spores of *Hypoxylonites* from samples of the El Foyel Group: Troncoso and Salto del Macho formations (3 species each) and one from the Río Foyel Formation (Martínez *et al*., 2016). In this contribution, we report *Spirotremesporites* for the first time from the Ñirihuau Basin, in the Troncoso Formation.

Spirotremesporites simplex Dueñas-Jiménez, 1979 *emend*. Elsik, 1990
Figure 3.14

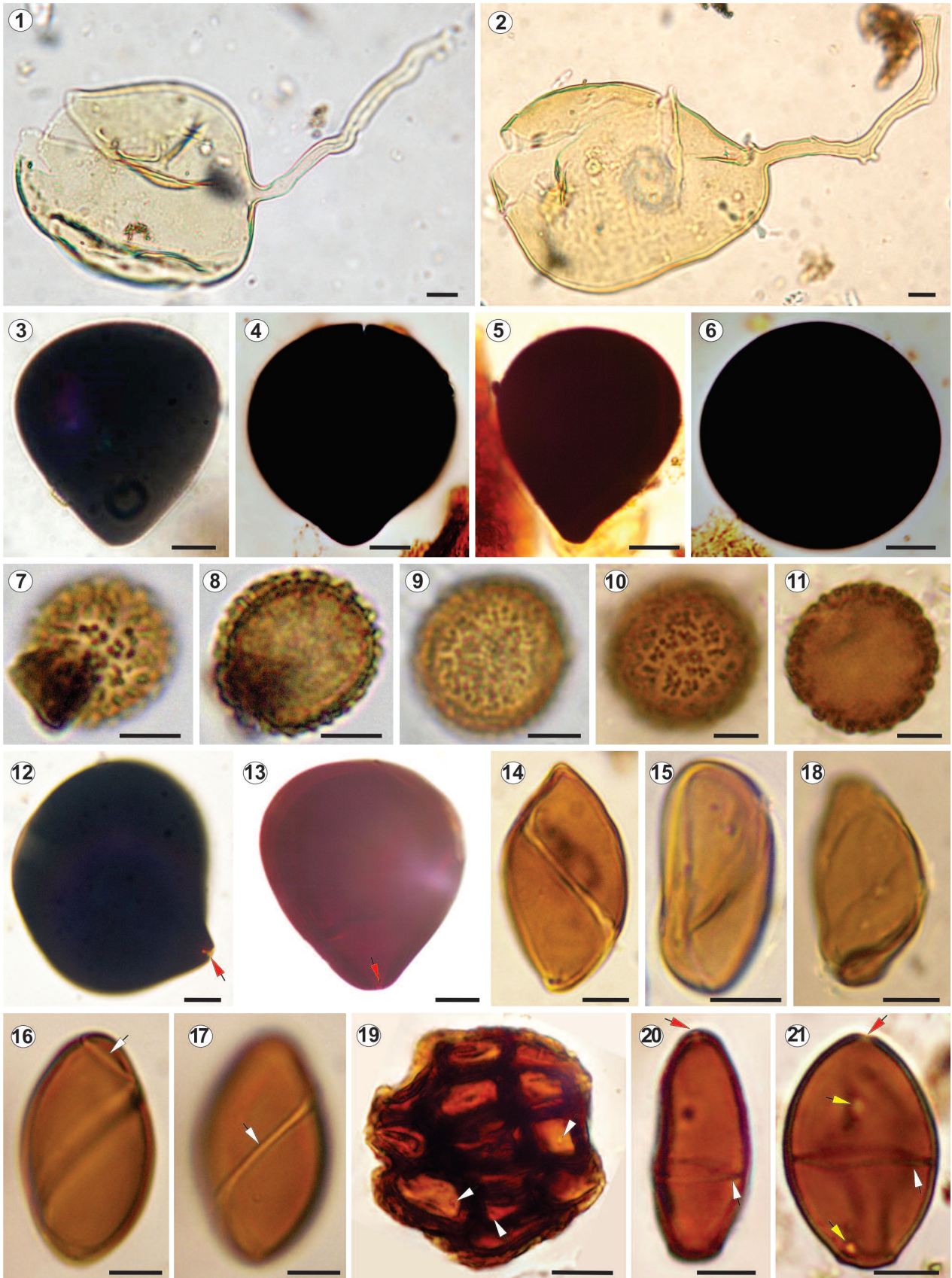**Studied material.** UNSP-T 2223e1: U26/1.

Description. Spore aseptate with fusiform outline, furrow oblique to the axis of the spore (*ca*. 50 degrees to the axis), straight for most of its length except near the outline of the spore which becomes asymptotic with a S-shaped pattern, apparently located on one side of the spore. Wall smooth, medium brown, 1 μm thick.

Dimensions. 14 x 25 μm (1 specimen).

Remarks. According to Dueñas-Jiménez (1979), the spores assigned to this species have an affinity with Xylariaceae.

Stratigraphic and geographic distribution. This species has previously been reported from the Miocene to Pleistocene, Tarragona Section, Bogotá, Colombia (Dueñas-Jiménez, 1979) and Miocene Barreiras Formation, North Brazil (Guimarães *et al*., 2013). To our knowledge, this finding in the Troncoso Formation constitutes the first pre-Miocene record of this species.

Spirotremesporites sp. cf. *S. duenasii* Elsik, 1990
Figure 3.15

Studied material. UNSP-T 2223e1: P29/2.

Description. Spore aseptate with a reniform outline and S-shaped furrow. Wall smooth, medium brown, *ca.* 0.5 μm thick.

Dimensions. 8 x 16.5 μm (1 specimen).

Remarks. This material is compared but not assigned to a fossil species described from the Pleistocene of Colombia, *S. duenasii* Elsik. Although the outline is similar, our spore is smaller and the wall is thinner (overall size 9–10 x 20–22 μm, wall *ca.* 1 μm). The furrow looks similar to the one illustrated by Kalgutkar & Jansonius (2000, pl. 4, fig. 45), originally described as spiraled by Elsik (1990).

Spirotremesporites sp. 1

Figure 3.16–17

Studied material. UNSP-T 2223e2: L48.

Description. Spore aseptate with elliptical outline and rounded ends. The furrow is oblique at 43 degrees to the axis, straight in one face of the spore, but describing a helicoidal pattern at one end of the opposite side (Figs. 3.16–17, white arrows). Wall smooth, medium brown, 1 μm thick.

Dimensions. 13 x 22 μm (1 specimen).

Remarks. The elliptical rounded outline resembles that of *Spirotremesporites shahejiensis*, a spore described by Elsik (1990) from the Eocene–Oligocene Shahejie Formation, China; however, that taxon is larger (16 x 28 μm), the wall is thinner (*ca.* 0.8 μm), and the furrow is inclined at a different angle (25 degrees to the axis).

Spirotremesporites sp. 2

Figure 3.18

Studied material. UNSP-T 2223e3: P33/4.

Description. Spore aseptate with elliptical to reniform outline. At least two oblique furrows can be recognized on one face of the spore. Wall smooth, medium brown, *ca.* 0.5 μm thick.

Dimensions. 10 x 19 μm (1 specimen).

Remarks. The most similar species is *Spirotremesporites ecuatorialis* Dueñas-Jimenez, 1979 (Pleistocene of Colombia), but it differs because it has four to eight short furrows and the outline is ellipsoidal. It is probable that *Spirotremesporites* sp. 1 and *S.* sp. 2 both constitute new species; however, open allocation is preferred until additional spores are found. Because of the helicoid germ slit and similarity in shape and size, our materials (*Spirotremesporites* sp. cf. *S. duenasii* and *Spirotremesporites* sp. 1) resemble the ascospores of *Yuea chusqueicola* (Speg.) O. E. Erikss., the only species of a xylariaceous genus described from culms of *Chusquea cummingii* Nees., a bamboo species endemic to the Andes of Argentina and Chile. The temptation to assign the material to *Yuea* is great, but the problem arises when we recapitulate the history of bamboo fossil records. The origin of bamboo was largely believed to occur in Gondwana. This presumption was based on a material from Laguna del Hunco biota of southern Argentina that was described by Frenguelli & Parodi (1941) as *Chusquea oxyphylla* and dated early Eocene (52 My). Subsequently, Brea *et al.* (2013) suggested that the assignment of Frenguelli and Parodi's specimen to the extant genus of *Chusquea* was dubious, although its affinity to the Bambusoideae subfamily was not questioned (see Brea & Zucol, 2007). However, recently, Wilf (2020) reexamined the type material and concluded it should be assigned to Podocarpaceae, thus dismantling the theory of the South American origin of this group of plants. Is it possible that *Yuea*, that is only known from *Chusquea*, was present on another host during the Paleogene? Or is it possible that the finding of these spores indicates that

Figure 3. Selected palynomycological remains from the El Foyel Group samples. **1–2,** *Rhizophagus* sp. 1; **1,** UNSP-SM 3153c: W48/4; **2,** UNSP-SM 3154c: V46/4. **3–5,** *Inapertisporites lacrimaformis* sp. nov.; **3,** UNSP-T 2223f4: O34/2 (holotype); **4,** UNSP-T 2223f2: X41; **5,** UNSP-T 2223f2: E48/4. **6,** *Inapertisporites* sp. 1, **UNSP-T 2223f2: A52/4. 7–11,** *Inapertisporites* sp. 2; **7–8,** UNSP-SM 2983d: T19/1; **9,** UNSP-SM 2987b: O32; **10–11,** UNSP-SM 3014b: J49/3; **7, 9, and 10,** Details of the spore surface showing cluster of ornaments; **8 and 11,** Optical section. **12–13,** *Monoporisporites* sp. 1; **12,** UNSP-T 2223f7: Y29/3, red arrow shows the pore; **13,** UNSP-T 2223f2: G43/2, red arrow shows the pore. **14,** *Spirotremesporites simplex*, **UNSP-T 2223e1: U26/1. 15,** *Spirotremesporites* sp. cf. *S. duenasii*, **UNSP-T 2223e1: P29/2. 16–17,** *Spirotremesporites* sp. 1, **UNSP-T 2223e2: L48,** white arrows show the helicoidal furrow. **18,** *Spirotremesporites* sp. 2, **UNSP-T 2223e3: P33/4. 19,** cf. *Dictyosporites* sp., **UNSP-T 2223f7: Z17/3,** white arrow show "pores" into some cells. **20–21,** *Cercophora*-type; **20,** UNSP-T 2223e1: X23/1, red and white arrows show a terminal pore and a medium septum respectively; **21,** UNSP-T 2223d: O21/2, yellow arrows show probable effects of corrosion. Scale bars (7–11, 14–18, and 20–21)= 5 μm; scale bars(1–6, 12–13, and 19)= 10 μm.

Chusquea was present, so the Gondwanan origin of the group should not be ruled out? As the aphorism says "the absence of evidence is not evidence of absence". The scarcity of records of fossil bamboos and of detailed studies of mycobiota in the area prevents any conclusions.

DIDYMOSPORAE
Spores 1-septate, with or without pores or hilum.

Cercophora-type
Figures 3.20–21, 4.1–2

Species included in *Cercophora* can be coprophilous, xylophilous or, less frequently, recovered from soil or aquatic habitats (in Catania *et al.*, 2011). The oldest record of coprophilous fungi from land animals is known from the Permian in Russia (Bajdek *et al.*, 2016); however, the use of fossil form-names makes their recognition in the deep-time fossil record challenging (Shumilovskikh *et al.*, 2021). Both modern and fossil types have often been reported as dung indicators (Cugny *et al.*, 2010). However, while *Podospora*, *Sordaria,* and *Sporormiella* are generally regarded as being among the strongest indicators of dung in paleoecological studies, caution is needed in interpreting the presence of *Cercophora*, as this fungus is not an obligate coprophage (van Asperen *et al.*, 2020).

Studied material. UNSP-T 2223d: S15/1, O21/2; UNSP-T 2223e1: U21, X23/1.

Description. Spores ellipsoidal to lemon-shaped, medium to dark brown, two-celled. Apical cell conical, with a tiny pore, 0.5–1 μm (Figs. 3.20–21, 4.1, red arrows), basal cell with truncate base. A pale, thin, medium septum (less than 0.5 μm) can be recognized (Fig. 3.21, white arrow), although in most specimens the septum is not truly median (Figs. 3.20, 4.1–2, white arrows). Cell wall smooth, 0.5–1 μm thick. The specimen illustrated in Figure 3.21 shows additional pores, maybe due to corrosion effects (yellow arrows).

Dimensions. 8(10.5)12 x 15(18)20 μm (4 specimens).

Remarks. The specimens described as *Cercophor*a-type could not be assigned to any known fossil form-name, although similar material has previously been published from late Eocene samples of USA, as cf. *Lacrimasporonites* (Ethridge Glass *et al.*, 1986, pl. 2., figs. 11–14). Our material

shows great morphological similarity with several spores (viz. HdV-112, HdV-1013, and UG-1183) described in van Geel *et al.* (1981, 2011) and also in Gelorini *et al.* (2011). These authors considered them ascospores and postulated their affinity with *Cercophora* Fuckel; since then, a natural classification scheme has been followed for this material. According to Gelorini *et al.* (2011), this type probably represents different species, which may be attributed to diverse genera such as *Cercophora*, *Podospora*, *Triangularia*, *Tripterospora*, and *Zopfiella*. All of these genera are hardly distinguishable by their single ascospores.

Genus *Dicellaesporites* Elsik, 1968

Type species. *Dicellaesporites popovii* Elsik, 1968. Paleocene, Texas, USA.

Dicellaesporites disphaericus
Sheffy & Dilcher, 1971
Figure 4.3–4

Studied material. UNSP-T 2223d: S38/2.

Description. Spore 1-septate, with any visible pores or apertures. Outline irregularly elliptical and crenulate, slightly constricted at the septum. Septum medium, two-layered, slightly folded, dark brown, *ca.* 2 μm wide. Wall rough, micro-reticulate (Fig. 4.4, yellow arrow), with lumina *ca.* 0.5 μm, medium brown, *ca.* 1 μm thick.

Dimensions. 16 x 22 μm (1 specimen).

Stratigraphic and geographic distribution. The material agrees well with *D. disphaericus*, which was described from middle Eocene deposits of the Puryear clay pit in Tennessee, USA (Sheffy & Dilcher, 1971). This taxon was recorded in Neyveli Lignite, South India, Eocene–Late Miocene/Pliocene (Ambwani, 1983), and Pelotas Basin, Miocene, Brazil (Premaor *et al.*, 2018).

Dicellaesporites septoconstrictus Kalgutkar, 1993
Figure 4.5–6

Studied material. UNSP-T 2223e1: Y25/3; UNSP-T 2223b: L18.

Description. Spores 1-septate, both cells ellipsoidal of similar size, rounded to slightly tapering at both ends,

constricted at the septum. Septum medium, complex, 3-layered, very dark brown, 2–3 μm thick. Wall smooth, light to medium brown, *ca*. 1 μm thick. No visible pore.

Dimensions. 8–9.5 x 22–24 μm (2 specimens).

Remarks. Our material coincides with the description and illustrations presented by Kalgutkar (1993) for *D. septoconstrictus.* One of the specimens (Fig. 4.6) shows a major resemblance, while the other spore (Fig. 4.5) has the cells folded, being less constricted at the septum, so its resemblance is less. These spores are hardly assignable to any extant fungi, as Gelorini *et al.* (2011) previously quoted with respect to Type UG-1125 (plate I): "this type probably includes different species or genera". These spores show similarities with ascospores in different genera, for example, several bitunicate representatives, like some in Dacampiaceae (Akulov & Hayova, 2016) or Venturiales (Zhang *et al*., 2011).

Stratigraphic and geographic distribution. This taxon was previously reported from the late Paleocene–early Eocene of Peel River, Yukon Territory, Canada (Kalgutkar, 1993) and the Iceberg Bay Formation, at Kanguk Peninsula, Axel Heiberg Island, Arctic Canada (Kalgutkar, 1997).

Dicellaesporites sp. cf. *D. suborbicularis*
Song & Li in Song *et al.*, 1989
Figure 4.7

Studied material. UNSP-T 2223b: L45/3.

Description. Spore 1-septate, both cells subcircular to broadly ellipsoidal, slightly constricted at one side of the septum. Cells hemispherical of similar size. Septum medium, one-layered, flat, straight, without septal folds, dark brown, *ca*. 1μm wide. Wall smooth, medium brown, *ca*. 1 μm thick. No visible pores.

Dimensions. 8 x 11 μm (1 specimen).

Remarks. The material is compared with *D. suborbicularis*, a spore described for the late Oligocene of China (Dongying Formation), which is considerably bigger (15 x 20 μm) than ours.

Genus *Hilidicellites* Kalgutkar & Jansonius, 2000

Type species. *Hilidicellites appendiculatus* (Sheffy & Dilcher) Kalgutkar & Jansonius, 2000. Middle Eocene, Tennessee, USA.

Hilidicellites normalis (Sheffy & Dilcher)
Kalgutkar & Jansonius, 2000
Figure 4.8

Studied material. UNSP-T 2223e1: P29/4.

Description. Spore 1-septate, slightly constricted at the septum. The two cells are of similar size, with a simple pore barely discernible at one end. Septum medium, dark brown, 2 μm thick. Wall smooth, medium brown, 1μm thick.

Dimensions. 4 x 9 μm (1 specimen).

Remarks. This material agrees with *H. normalis* reported from the middle Eocene, Tennessee, USA (Sheffy & Dilcher, 1971).

PHRAGMOSPORAE

Spores transversely septate, with more than one septum, sometimes with a pore or hilum at one end.

Genus *Diporicellaesporites* Elsik, 1968

Type species. *Diporicellaesporites stacyi* Elsik, 1968. Paleocene, Texas, USA.

Remarks. Given that in Martínez *et al.* (2016) two species of *Diporicellaesporites* were illustrated and described in open assignment (as *Diporicellaesporites* sp 1. and sp. 2), we decided to follow the correlative numbering for those specimens described in the same genus.

Diporicellaesporites sp. 3
Figure 4.9

Studied material. UNSP-T 2223f7: O38/3.

Description. Spore 5-septate, fusiform to barrel shape, each end cell has a concave outline ("pore"), up to 13 μm wide. Septa straight or slightly curved. Wall smooth, medium brown, 1 μm thick.

Dimensions. 38 x 59 μm (1 specimen).

Remarks. *Diporicellaesporites* sp. 3 does not totally agree with any of the species included in the genus so far. However, as only one specimen has been recovered, we prefer to keep it in open allocation. Although similar in shape to some other species, it differs from all of them in several characteristics. *Diporicellaesporites concavus* (Kumar, 1990), from the Early–Middle Miocene of South India, is smaller (22-24 x 38-42 μm, pores ± 2 μm wide) and has less septa;
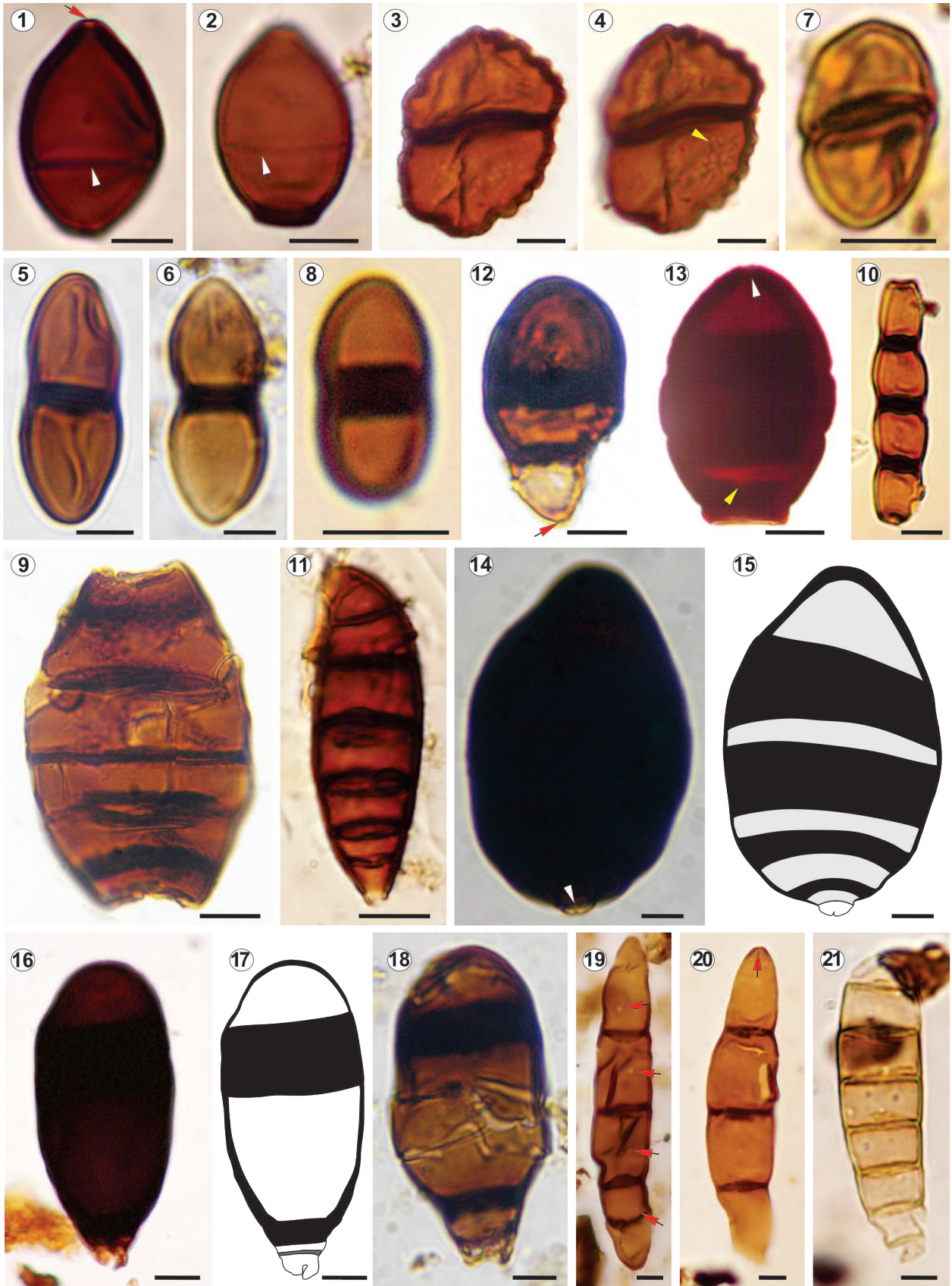
D. chitaleyae (Kalgutkar, 1993), from late Paleocene–early Eocene of Canada, has septal folds with central pores and cells are unequally colored (the two most central are larger and darker). An unnamed species, *Diporisporites* sp. (in Singh & Chauhan, 2008, pl. 1, fig. 9), from the Neogene of India, is the most similar in shape and septa, but is consistently smaller (20 x 32 µm, pores 5 µm wide).

Diporicellaesporites sp. 4
Figure 4.10

Studied material. UNSP-RF 2309c: R47.

Description. Conidia cylindrical, slightly curved, 3-septate, flattened at both ends, hila *ca.* 2 µm wide. Septa dark brown, thicker than the conidium wall, reaching 2 µm at the middle part of the septa and laterally thinning up to 1.5 µm on both sides. Conidium wall smooth, light brown, *ca.* 0.5 µm thick.

Dimensions. 6 x 30 µm (1 specimen).

Remarks. This spore looks like *Diporicellaesporites icebergi* (Kalgutkar & Sigler, 1995) from the late Paleocene–early Eocene of Iceberg Bay Formation, Canada, in morphology and dimensions (5–7 x 27–42 µm); however, *D. icebergi* has septal pores which are not visible in our material. When compared with extant species, it resembles those conidia of *Heteroconium*-like species. These hyphomycetes are foliicolous fungi with similar morphology but differ phylogenetically and in their ecology (Hughes, 2007; Cheewangkoon *et al.*, 2012). The spore described here has truncate ends, resembling the conidia that develop inter-calary in *Heteroconium s. l.*, while the terminal ones usually have more rounded ends. The terminal scars described here are termed "pores'' in most palynological papers.

Diporicellaesporites sp. 5
Figure 4.11

Studied material. UNSP-SM 3154c: X9.

Description. Spore 7-septate, elliptical outline with one end slightly curved. Hilum 2–3µm wide. Septa thin, except the three central ones, which are wider, and up to 2 µm and two-layered. Wall smooth, medium brown, 1µm thick.

Dimensions. 16 x 50 µm (1 specimen).

Remarks. This specimen is similar to the specimen described by Ferreira *et al.* (2005, fig. 2M) as *Diporicellaesporites*? from the Paleocene of Brazil. When we try to refer this spore to an extant taxon, we find it difficult to interpret whether the ends are just broken cells or whether they correspond to lost appendages, for example from genera such as *Seiridium*. In either case, this assignment would represent a genus totally different from the others to which the former species were related. This reinforces the idea that taxonomy based on fossil morphotypes is unnatural (O'Keefe *et al.*, 2021).

Genus ***Anatolinites*** Elsik *et al.*, 1990

Type species. *Anatolinites dongyingensis* (Ke & Shi) Elsik *et al.*, 1990. Oligocene, China.

cf. ***Anatolinites alaskaensis*** Elsik *et al.*, 1990
Figure 4.12

Studied material. UNSP-RF 2311c: D41/3.

Description. Spore 2-septate, smooth with obovate to slightly pyriform outline. The spore wall is *ca.* 1 µm over the proximal cell and 2-layered (2 µm) over the two distal cells, which are the most darkly pigmented (moderate to dark

Figure 4. Selected palynomycological remains from the El Foyel Group samples. **1–2,** *Cercophora*-type; red and white arrows show a terminal pore and a medium septum respectively, **1, UNSP-T 2223e1: U21, 2, UNSP-T 2223d: S15/1**; **3–4,** *Dicellaesporites disphaericus*, **UNSP-T 2223d: S38/2**, yellow arrow shows a micro-reticulate wall ; **5–6,** *Dicellaesporites septoconstrictus*; **5, UNSP-T 2223e1: Y25/3**, specimen showing folded cells; **6, UNSP-T 2223b: L18**; **7,** *Dicellaesporites* sp. cf. *D. suborbicularis*; **8,** *Hilidicellites normalis*, **UNSP-T 2223e1: P29/4**; **9,** *Diporicellaesporites* sp. 3, **UNSP-T 2223f7: O38/3**; **10,** *Diporicellaesporites* sp. 4, **UNSP-RF 2309c: R47**; **11,** *Diporicellaesporites* sp. 5, **UNSP-SM 3154c: X9**; **12,** cf. *Anatolinites alaskaensis*, **UNSP-RF 2311c: D41/3**, red arrow shows a tiny pone; **13,** *Anatolinites* sp. 1, **UNSP-T 2223f3: R38**, white arrow shows a distal pore, while yellow arrow points to a simple pore in the proximal septum; **14–15,** *Brachysporisporites opimus*, **UNSP-T 2223d: J47/2**; **14,** Specimen showing the black pigmented wall. The white arrow shows a pore enclosed by a minute "pore-cell"; **15,** Sketch based on the studied specimen, previously illuminated with false color, showing several septa; **16–17,** *Brachysporisporites* sp. cf. *B. atratus*, **UNSP-T 2223f2: A52**; Sketch based on dark brown to black pigmented specimen; **18,** *Brachysporisporites* sp. cf. *B. pyriformis*, **UNSP-T 2223b: N32**; **19,** *Multicellites* sp. cf. *M. tener*, **UNSP-T 2223b: J18/1**, red arrows show minute pores in the middle of four cells; **20,** Pluriseptata spore indet., **UNSP-SM 3013e: X66**, red arrow shows a terminal pore; **21,** *Clasterosporium eocenicum*, **UNSP-SM 2983d: D31/3**. Scale bars (1–8, 10, 12, 14–15, and 18–21)= 5 µm; scale bars (9, 11, 13, 16, and 17)= 10 µm.

brown), while the proximal cell is light brown. The septa are black varying from 1.5 to 3 μm wide. The proximal pore is tiny while the distal pore was not observed (Fig. 4.12, red arrow).

Dimensions. 12 x 21 μm (1 specimen).

Remarks. It is provisionally compared with *Anatolinites alaskaensis* from the Eocene of Alaska, due to its morphological similarity; however, that species is slightly larger (14–16 x 26–40 μm) and has a distal pore that was not seen here. When compared with extant fungi, it resembles the immature conidia of *Coryneum* as illustrated in Senwanna *et al.* (2018) or of *Endophragmiella* (Yonezawa *et al.*, 2008), both recovered from twigs and bark.

<div align="center">

Anatolinites sp. 1

Figure 4.13

</div>

Studied material. UNSP-T 2223f3: R38.

Description. Spore 2-septate (?), spatulate in shape, with a pore in the distal end (*ca.* 2 μm wide, Fig. 4.13, white arrow), hilum proximal, with a narrow basal frill. At least two septa of different thickness are observed, the proximal one bears a simple pore, *ca.* 2 μm wide (Fig. 4.13, yellow arrow) that does not traverse the septum completely. Spore wall up to 2 μm thick.

Dimensions. 30 x 44 μm (1 specimen).

Remarks. The middle black area is up to 20 μm high, making it difficult to discern more details of the septation. Sutton (1986) described several conidia with dark areas which he called "black-banded". Generally, in conidia of this type, septa are evident only in young conidia. When fully mature, septa are obscure and highly indistinguishable. The material presented here is comparable to the slightly smaller conidia of *Mucispora obscuriseptata* (Yang *et al.*, 2016), hyphomycete described as growing on wood submerged in freshwater.

<div align="center">

Genus ***Brachysporisporites*** Lange & Smith, 1971

</div>

Type species. *Brachysporisporites pyriformis* Lange & Smith, 1971. Early–middle Eocene, Australia.

<div align="center">

Brachysporisporites opimus

(Elsik & Jansonius) Norris, 1986

Figure 4.14–15

</div>

Studied material. UNSP-T 2223d: J47/2.

Description. Spore ovoidal to lemon-shaped, five-celled. The wall is black pigmented making it difficult to recognize the presence of septa; only when the image is abruptly modified with false color and brightness, four very dark septa are internally differentiated. Pore enclosed by a minute, thin-walled "pore-cell" (Fig. 4.14, white arrow). Wall smooth, medium brown, 1 μm thick. Barely visible wall up to 2 μm thick.

Dimensions. 27 x 42 μm (1 specimen).

Remarks. This taxon was reported from the Mackenzie Delta Region, District of Mackenzie, Northwest Territories, Canada by Elsik & Jansonius (1974, age: Paleogene) and Norris (1986, age: Eocene). Subsequently, Norris (1997) recognized *B. opimus* as a sporadically occurring species in the *Multicellaesporites-Pluricellaesporites* Zone (late Paleocene–early Eocene), from Adgo F-28 well, Beaufort-Mackenzie Basin, Canada.

<div align="center">

Brachysporisporites sp. cf. ***B. atratus***

Figure 4.16–17

</div>

Studied material. UNSP-T 2223f2: A52.

Description. Spore dark brown to black, clavate in outline, four-celled. The proximal two cells are paler than the distal ones. Three septa of different thickness and color can be identified: middle brown proximal septum (1.5 μm wide), middle septum black (5 μm wide) and thick distal black septum (17 μm wide). Cell wall smooth, *ca.* 1.5 μm thick.

Dimensions. 31 x 68 μm (1 specimen).

Remarks. This specimen is compared with *B. atratus* described by Kalgutkar (1993) in late Paleocene–early Eocene samples from Peel River, Yukon Territory, Canada. We refrain from assigning it to *B. atratus* because it is consistently smaller (20–25 x 40–53 μm).

<div align="center">

Brachysporisporites sp. cf. ***B. pyriformis***

Figure 4.18

</div>

Studied material. UNSP-T 2223b: N32.

Description. Spore pyriform, medium brown, four-celled. The proximal cell, paler than the distal cells, has a 3 μm wide pore. Three very dark non-equidistant septa can be

identified (proximal: 1 μm wide, middle: 3 μm wide, and distal: 6 μm wide). The middle cell is fractured, which is why the pyriform outline is somewhat deformed. Cell wall smooth, *ca*. 1 μm thick.

Dimensions. 18 x 37 μm (1 specimen).

Remarks. Although our specimen is very similar in size (15–18 x 35–40 μm) and morphology to the type species, we preferred to compare it with *B. pyriformis* (early–middle Eocene from South Australia), because this taxon has the widest ovoidal part and the septa are equidistantly arranged. Several specimens described here could be referred to what Sutton & Sellar (1966) called "black-banded conidia". These are euseptate conidia, with some septa more deeply pigmented than others. This type of spore is produced by several unrelated genera of ascomycetes, mostly hyphomycetes. Sutton (1986) discussed the ecological significance of black bands, considering them important in preservation and a way to diminish conidial collapse. *Brachyporisporites* species may refer to the extant genus *Bactrodesmium* Cooke. This genus has recently been revised by Réblová *et al.* (2020), who accepted 35 species, most with a saprobic habit on decaying plant material (mainly bark or wood). Three species have been found in Argentina, all in the Andean region (Sánchez & Bianchinotti, 2023).

Genus *Clasterosporium* von Schweinitz, 1834

Type species. *Clasterosporium caricinum* von Schweinitz, 1834. Holocene, Pennsylvania, USA.

Clasterosporium eocenicum Fritel & Viguier, 1909
Figure 4.21

Studied material. UNSP-SM 2983d: D31/3.

Description. Elongate, clavate spore, narrowing towards the base and gradually expanding toward the apex (clavate form), light brown, 7-septate. Septa thin, *ca*. 0.5 μm wide. Apical cell hemispherical, the two basal cells hyaline in color. Terminal pore up to 2 μm wide. Cells wall smooth, *ca.* 0.5 μm thick. Additional tiny pores can be observed in some cells, maybe due to corrosion effect.

Dimensions. 11 x 43 μm (1 specimen).

Remarks. Our material coincides in morphology and size with the spores described by Fritel & Viguier as *Clasterospoium*

eocenicum for the early Eocene of Brétigny et Muirancourt (Oise), France. Bippus *et al.* (2019) recovered Type three fungal spores comparable to *C. eocenicum*, from Tufolitas Laguna del Hunco, an early Eocene volcaniclastic, lacustrine caldera-fill deposit of the Huitrera Formation in the northwest of Chubut Province, Argentinean Patagonia.

Genus *Multicellites* Kalgutkar & Jansonius, 2000

Type species. *Multicellites tener* (Ke & Shi) Kalgutkar & Jansonius, 2000. Eocene–Oligocene, China.

Multicellites sp. cf. *M. tener* (Ke & Shi)
Kalgutkar & Jansonius, 2000
Figure 4.19

Studied material. UNSP-T 2223b: J18/1.

Description. Spore pluriseptate, with elliptical-elongate outline. Composed of three rectangular medium cells and two other terminals with rounded acuminate ends. Septa medium brown in color, slightly folded, up to 2μm wide. Wall smooth, light brown, *ca*. 0.5 μm thick, slightly thickened at both ends. A minute pore can be seen in the middle of four cells (Fig. 4.19, red arrows).

Dimensions. 11 x 63 μm (1 specimen).

Remarks. The recovered specimen resembles *Multicellites tener* from the Eocene–Oligocene, Panshan, China. We prefer to compare and not to assign it formally because our material has fewer septa (four instead of five for the formal species). The minute pores identified could represent both germinative structures and/or corrosion effects.

Pluriseptata spore indet.
Figure 4.20

Studied material. UNSP-SM 3013e: X66.

Description. Spore elongate, light brown, four-celled. Septa thick, dark brown, *ca*. 1 μm thick, giving the appearance of greater thickness (2 μm) by superimposing the lower focus. A terminal tiny pore (Fig. 4.20, red arrow) can be observed at one end. (*ca*. 0.5 μm diameter). Cells wall smooth, *ca.* 0.5 μm thick.

Dimensions. 13 x 58 μm (1 specimen).

Remarks. The spore is broken at one end, so it cannot be

assigned with certainty to a specific genus and may correspond to *Diporicellaesporites* or *Pluricellaesporites*, among others. Our material shows some resemblance to the UG-1145 type (Gelorini *et al.*, 2011).

DICTYOSPORAE

Muriform spores divided by few or many longitudinal and transverse or diagonal intersecting septa; variable shapes, inaperturate, or with a more or less distinct hilum, which may be a scar or protruding.

Genus ***Dictyosporites*** Felix, 1894
emend. Kalgutkar & Jansonius, 2000

Type species. *Dictyosporites loculatus* Felix, 1894. Eocene, USSR.

cf. ***Dictyosporites*** sp.
Figure 3.19

Studied material. UNSP-T 2223f7: Z17/3.
Description. Spore muriform, polygonal in shape, dark brown thick septa (up to 4 µm wide) dividing the spore into twelve cells, some of each with a small depression resembling a pore, *ca.* 0.5 µm (Fig. 3.19, white arrows).
Dimensions. 39 x 40 µm (1 specimen).
Remarks. Our material is mechanically damaged, broken, and probably secondarily deformed, so it was impossible to provide a more accurate identification.

Genus ***Papulosporonites***
Schmiedeknecht & Schwab, 1964

Type species. *Papulosporonites sphaeromorphus* Schmiedeknecht & Schwab, 1964. Middle Eocene, Germany.

Papulosporonites sphaeromorphus
Schmiedeknecht & Schwab, 1964
Figure 5.1

Studied material. UNSP-T 2223b: D16.
Description. Spore ovoidal, dark brown. Multicellate, with an indeterminate number of cells of 9 µm wide each one. Cells wall smooth, *ca.* 1 µm thick.
Dimensions. 62 x 75 µm (1 specimen).

Remarks. Our specimen coincides with the description presented in Kalgutkar & Jansonius (2000) for *Papulosporonites sphaeromorphus* from the middle Eocene of Germany. *Papulosporonites* has been widely cited from the Late Cretaceous, as in Thakur *et al.* (2015) (Late Pliocene of India), Kumar (2022) (Middle Pliocene of Tobago), Ferreira *et al.* (2005) (Paloecene of Brazil), and Sonkusare *et al.* (2021) (Maastrichtian of India). Our specimen is reminiscent of the extant reproductive structures named bulbils or gemmae. These can be produced by several unrelated fungi, being considered non-sexual reproductive structures or neotenous ascomatal propagules (Davey *et al.*, 2008).

CONIDIOPHORES

Conidiophores are specialized hyphae that carry conidiogenous cells from which conidia are formed. Some fungi form distinctive conidiophores that can be assigned to specific taxa; however, studying them in the fossil record to assign them to particular genera is challenging (O'Keefe, 2017). We recovered some conidiophores from the Troncoso Formation samples, some of these still attached to plant cuticles. These conidiophores are morphologically similar to those formed by some extant ascomycetes, the "cercosporoid", which is a species-rich group of plant pathogens that form leaf spots.

Specimen 1
Figure 5.2

Studied material. UNSP-T 2223b: G33.
Description. Conidiophores brown, mildly curved, narrowed at the apex, 2–5 septate, septa thin, barely noticeable; loci apical and lateral, somewhat refractive, *ca.* 0.5 µm wide. Stromata dark brown, poorly developed.
Dimensions. 6 x 60 µm, 7 x 65 µm, and 7 x 33 µm (the latter probably broken).
Remarks. Similar material was presented by El Atfy *et al.* (2013) from the Oligocene/Miocene boundary, Nukhul Formation, Gulf of Suez, Egypt. O'Keefe (2017, pl. 5, fig. 8) illustrated conidiophores from the Miocene Heath Formation, Tumbes Province, Perú and called them "conidiophores with unknown affinities".

Specimen 2

Figure 5.3−4

Studied material. UNSP-T 2223b: G53/4.

Description. Conidiophores septate, straight to slightly sinuous, diverging from a common nodose base and then branching laterally at almost right angles. At their bases the hyphae are slightly widened (up to 4 μm) and thinner distally (up to 3 μm), culminating in rounded ends, sometimes they exhibit a distal pore (broken hyphae?). The wall of the hyphae reaches up to 1 μm. A lateral pore is observed near the distal end of one of the hyphae (Fig. 5.3, red arrow).

Dimensions of hyphae. 3.5 x 37 μm, 4 x 45 μm (two measured hyphae).

Remarks. In the specimen studied, the hyphae are superimposed on different planes making it difficult to observe individual features. This material is representative of a species-rich group of plant pathogens forming leaf spots. The specimen illustrated here shows a resemblance to the extant genus *Cladosporiella* Deighton, which has a hyperparasitic habit on cercosporoid hyphomycetes and rusts (Braun *et al.*, 2013).

Specimen 3

Figure 5.5−7

Studied material. UNSP-T 2223d: S20.

Description. Fascicle of straight to sinuous conidiophores that emerge from a base (stroma) attached to a cuticle. At least up to 13 conidiophores can be recognized, medium to dark brown, becoming paler towards the apex, simple, slightly curved, proliferating percurrently, thick walled, 1−1.5 μm.

Dimensions. 5(5.3)7 x 13(57.1)87 μm (13 measured).

Remarks. The area where this material is in contact with the cuticle is darkened and looks amorphous, so the zone of insertion of the conidiophores is difficult to observe; however, some are clearly bulbous at the base. In two of the lighter colored conidiophores, integrated, terminal, broadened conidiogenous cells with marginal frills can be distinguished (Fig. 5.7, red arrows). These are reminiscent of the "caliciform" type described in the extant genus *Melanocephala* S. Hughes, an ascomycete genus of uncertain position. *Melanocephala* species are saprophytes on dead wood and bark. One conidium described here under the
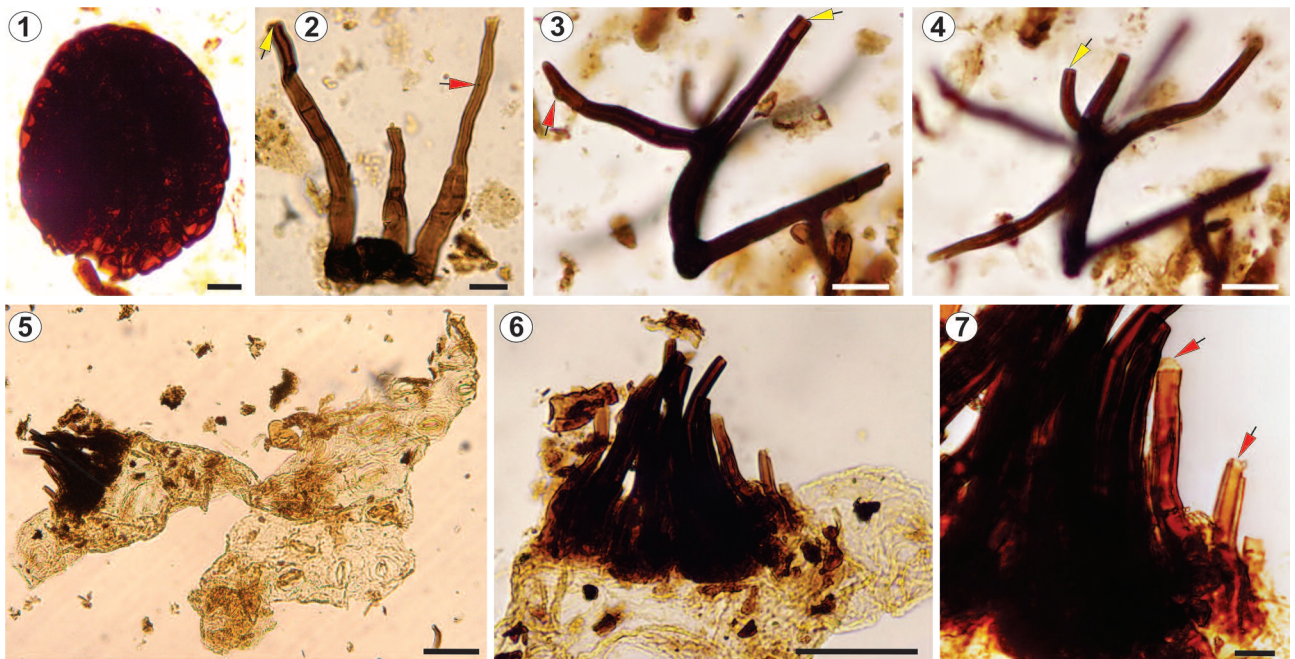

Figure 5. Selected palynomycological remains from the El Foyel Group samples. **1,** *Papulosporonites sphaeromorphus*, **UNSP-T 2223b: D16**; **2−7,** Conidiophores; **2,** Specimen 1, **UNSP-T 2223b: G33**, yellow and red arrows show apical and lateral loci respectively; **3−4,** Micrographs of the Specimen 2 in two focuses, **UNSP-T 2223b: G53/4**, yellow and red arrows show apical and lateral pores respectively; **5−7,** Micrographs of the Specimen 3 **UNSP-T 2223d: S20**, with different magnification; note in 6 and 7 how the conidiophores adheres to the surface of a plant cuticle; red arrows show terminal conidiogenous cells with marginal frills. Scale bars (1−4 and 7)= 10 μm; scale bar (5)= 50 μm; scale bar (6)= 20 μm.

name *Anatolinites* sp. 1 (Fig. 4.13) shows a fimbriate lower margin, reminiscent of conidia that separate rhexolytically from *Melanocephala*.

PALYNOSTRATIGRAPHY OF THE EL FOYEL GROUP

The distribution of different taxa of fungal spores within each of the units that compose the El Foyel Group and their respective biochrons has allowed us to delimit the age of the analyzed formation (Tab. 1, Fig. 6).

Most of the fungal taxa identified in the Troncoso Formation have a biochron that spans from early to middle Eocene. *Spirotremesporites simplex* constitutes the only

Taxon	Paleogene / Neogene (Paleocene, Eocene, Oligocene, Miocene, Pliocene — E/M/L)	References according to country or region
Inapertisporites circularis		Cosmopolitan (1)
Monosporisporites minutus		Colombia (2), India (3)
Inapertisporites subovoideus		China (4), India (5)
Inapertisporites ovalis		China (4), India (6)
Diporisporites elongatus		Colombia (2), China (4), India (7), Argentina (8), Lao PDR (9)
Didymoporisporonites panshanensis		China (4, 10), Canada (11), Lao PDR (9)
Diporicellaesporites incurviusculus		Canada (12), Argentina (13), Brazil (14)
Hypoxylonites vicksburgensis		USA (15, 16), Canada (19)
Brachysporisporites opimus		Canada (17, 18, 19)
Antolinites subcapsilaris		Canada 11), USA (20, 21)
Dicellaesporites septoconstrictus		Canada (22, 12)
Dicellaesporites disphaericus		USA (20), India (23), Brazil (14)
Foveodiporites elegans		China (10, 24)
Dyadosporites annulatus		Argentina (25)
Clasterosporium eocenicum		France (26), Argentina (27)
Hypoxylonites chaiffetzii		USA (15), India (28)
Multicellites ellipticus		USA (20, 24), Brazil (29)
Papulosporonites enormis		Turkey (24), Argentina (13)
Hypoxylonites ater		India (30), Brazil (31), Argentina (13)
Pluricellaesporites patagonicus		Argentina (13), Brazil (14), Lao PDR (9)
Dyadosporites subovalis		USA (20, 24), Lao PDR (9)
Diporicellaesporites elongatus		USA (20, 24)
Hilidicellites normalis		USA (20)
Monoporisporites singularovalis		USA (20, 24)
Papulosporonites sphaeromorphus		Germany (32)
Lacrimasporonites cupuliformis		USA (20, 33)
Dyadosporites elsikii		Cameroon (34, 24)
Lacrimasporonites fusoides		Cameroon (34, 24)
Spirotremesporites simplex		Brazil (31), Colombia (35)

Figure 6. Range chart of all fungal spores assigned to species (modified and actualized from Martínez *et al.*, 2016). References: (1) Palynodata Inc. & White (2006); (2) van der Hammen (1954); (3) Singh & Saxena (1980); (4) Song *et al.* (1999); (5) Saxena & Khare (1992); (6) Sarkar *et al.* (1994); (7) Pathak & Banerjee (1984); (8) Quattrocchio *et al.* (2003); (9) Sattraburut *et al.* (2023); (10) Ke & Shi (1978); (11) Parsons & Norris (1999); (12) Kalgutkar (1997); (13) Martínez *et al.* (2016); (14) Premaor *et al.* (2018); (15) Elsik (1990); (16) White & Ager (1994); (17) Elsik & Jansonius (1974); (18) Norris (1986); (19) Norris (1997); (20) Sheffy & Dilcher (1971); (21) Elsik *et al.* (1990); (22) Kalgutkar (1993); (23) Ambwani (1983); (24) Kalgutkar & Jansonius (2000); (25) Romero & Castro (1986); (26) Fritel & Viguier (1909); (27) Bippus *et al.* (2019); (28) Nandi *et al.* (2003); (29) Souza Silva (2015); (30) Kumar (1990); (31) Guimarães *et al.* (2013); (32) Schmiedeknecht & Schwab (1964); (33) Ethridge Glass *et al.* (1986); (34) Salard-Cheboldaeff & Locquin (1980); (35) Dueñas-Jiménez (1979).

exception, since this taxon has not been identified until now in pre-Miocene deposits. Therefore, based on this study, its basal limit would be extended to ages as old as the middle Eocene. The presence of taxa exclusive to the Eocene stands out in this unit, such as *Clasterosporium eocenicum*, *Diporicellaesporites elongatus*, *Hilidicellites normalis*, and *Papulosporonites sphaeromorphus*. In the Salto del Macho and Río Foyel formations, stratigraphic biomarker fungi taxa are less abundant than in Troncoso. Hence, based on this study, these units would tentatively be assigned to the middle to late Eocene and late Eocene to early Oligocene, respectively. The ages obtained for these different units from the fungal record do not differ significantly from those derived from the study of pollinic palynomorphs.

From the comparison of palynomorph data (spores+ pollen grains) from the El Foyel Group with others from Patagonia using multivariate statistical techniques, Quattrocchio *et al.* (2012) found strong similarities between the Troncoso Formation and the Sloggett Formation (late Eocene to ?early Oligocene); and between the Salto del Macho and Río Foyel formations with the Loreto Formation (late Eocene–Oligocene) and the San Julián Formation in the Cabo Curioso area (Oligocene). Cornou *et al.* (2014) concluded that the Salto del Macho Formation is no older than the middle Eocene, indicated by the presence of *Echitriporites trianguliformis* form A, *Graminidites* sp., *Myrtaceidites parvus* form *nesus*, *Myrtaceidites verrucosus*, *Psilatricolpites minutus*, and *Tricolpites (Psilatricolpites) lumbrerensis*; being the youngest age, the early Oligocene, evidenced by the presence of *Rousea minuscula* and *Spinizonocolpites hialinus*.

VARIABILITY OF FUNGAL COMMUNITIES AS AN INDICATOR OF PALEOENVIRONMENTAL AND PALEOCLIMATIC CHANGES

To date, the El Foyel Group, Ñirihuau Basin, has provided the richest and diverse palynomycological association of Cenozoic deposits in Argentina and probably in South America, composed of spores, remains of microthyriaceous reproductive bodies, hyphae, and conidiophores. Previous results on the fungal content recovered from palynological outcrop samples from the different units that make up the El Foyel Group can be found in Martínez *et al.* (2016) and Bianchinotti *et al.* (2017, 2020).

Martínez *et al.* (2016) reported 38 species, mostly ascomycetes, distributed in 18 genera with diverse affinities (Tab. 1, taxa indicated with "X"). In this contribution, 26
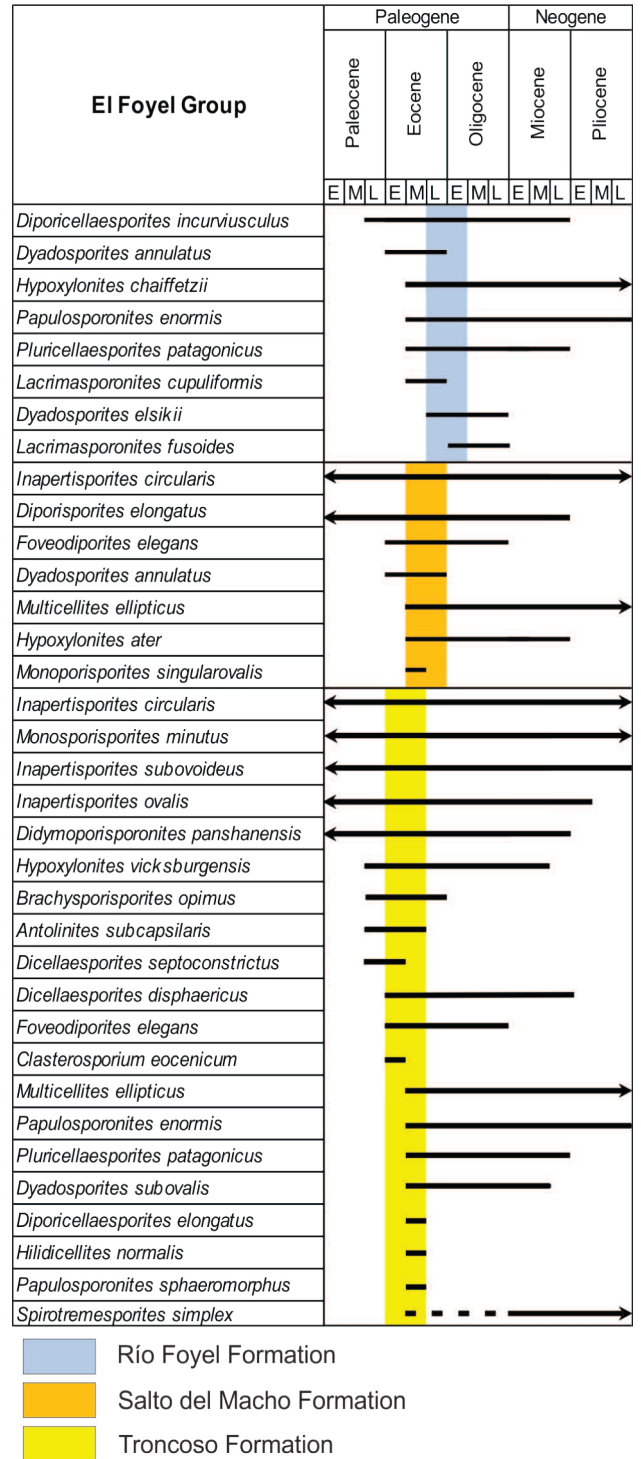

Figure 7. Inferred ages for the Troncoso, Salto del Macho, and Río Foyel formations based on palynomycological biomarkers recorded.

species distributed in 16 genera were recognized (Tab. 1, taxa with asterisk and empty circles). Therefore, the total fungal spore knowledge of the El Foyel Group has substantially increased, reaching a total of 64 species distributed in more than 25 genera.

Following the artificial morpho-taxonomic Saccardo system, from the four morphological types distinguished, the amerosporae and phragmosporae types were the best represented in all formations, while the didymosporae and dictyosporae types appeared as minor constituents. Of the three formations that make up the El Foyel Group, the Troncoso Formation is the one with the greatest abundance and diversity of fungal spores (Fig. 8), seconded by the Salto del Macho Formation. These units not only present a great abundance of spores but also of other fungal remains like hyphae, germlings (Bianchinotti *et al.*, 2020), and ascomata of epiphyllous fungi.

Fungal spores as well as other types of palynomorphs (spores, pollen grains, organic wall microplankton, etc.) have been widely used to carry out paleoecological, paleoenvironmental, biostratigraphic and paleoclimatic

interpretations (*e.g.*, van Geel, 1978; Gelorini *et al.*, 2012; Hooghiemstra, 2012; Worobiec & Worobiec, 2013; Martínez *et al.*, 2016).

Several authors have hypothesized that the composition and diversity of fungal communities are strongly shaped by ecological conditions (*e.g.* Větrovský *et al.*, 2019; Daws *et al.*, 2020; Romero *et al.*, 2021). Therefore, from an actualistic point of view, understanding the diversity of these paleo-communities enables the generation of paleoclimatic and paleoenvironmental inferences for the time period studied.

Romero *et al.* (2021) suggested that certain morphological features of fossil spores become valuable for making inferences at the community level, especially when specific identifications are challenging. In geological sections from Middle Miocene coal mines in two studied locations (Thailand and Slovakia), amerospores were identified as the predominant component, followed by phragmospores (Romero *et al.*, 2021). They interpreted this pattern as evidence of shared past climatic scenarios between both sites. The dominance of amerospores suggests humid
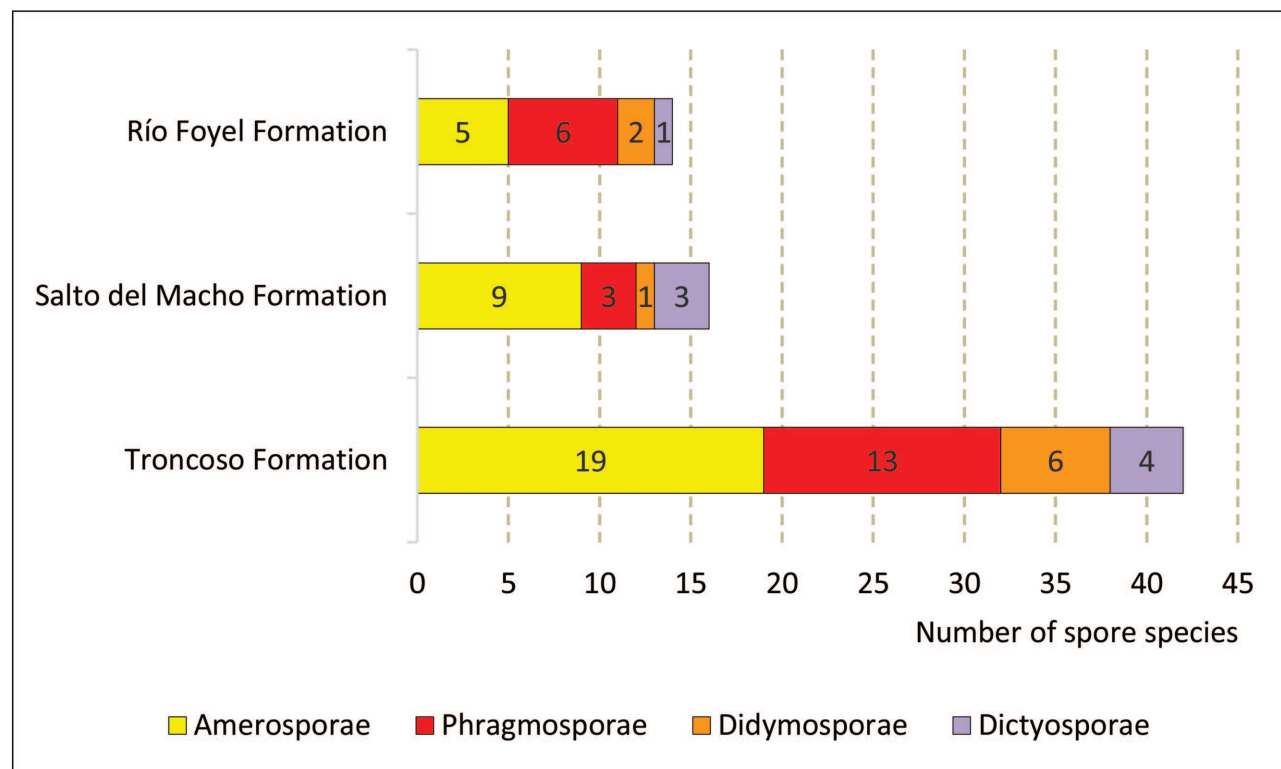

Figure 8. Histogram of fungal spores according to Saccardo's artificial morpho-taxonomic system.

conditions and a vegetation structure that is densely closed (Calhim *et al.*, 2018; Crandall *et al.*, 2020; Romero *et al.*, 2021). Amerospores were the unique type recovered from southern McMurdo Sound, Antarctica by Pilie *et al.* (2023), which related its presence to warm and humid conditions.

Besides, a significant amount of epiphyllous fungi remains were recovered in samples from the Troncoso and Salto del Macho formations (Bianchinotti *et al.*, 2017, 2020). Following Romero *et al.* (2021), these records are linked to climate settings corresponding to warm temperate, humid habitats with mixed forests.

Except for a few specimens, for example *Rhizophagus* sp. 1 and *Inapertisporites* sp. 2, a saprobic habit was inferred for the majority of the spores. Many of them have a huge resemblance to those of extant species growing on lignicolous materials submerged in fresh water. The fungal assemblage recovered from the El Foyel Group could be linked to a riparian or lacustrine environment in a woodland setting.

All the records discussed agree with the analysis of the pollinic palynomorphs of the same group. Cornou *et al.* (2018) concluded that the analysis of sporomorphs (spores + pollen grains) reflected a regional forest, represented in the three formations of the El Foyel Group, by Araucariaceae, Podocarpaceae, and Nothofagaceae. The first two families were dominant in the Troncoso Formation, together with Myrtaceae. The Nothofagaceae reached its maximum abundance in the Salto del Macho Formation, together with meso/megathermic elements, mainly Arecaceae and Bombacaceae. Pteridophytes, present in all three units, were more abundant and diverse in the Salto del Macho Formation. This led to infer that paleoclimatic conditions were relatively stable during the considered interval, ranging from a warm-temperate climate (Troncoso and Río Foyel formations) to a warm-humid climate (Salto del Macho Formation). These findings also reinforce the hypothesis of Taylor *et al.* (2015) that the high diversity of fungal remains is indicative of humid climate and the association with epiphyllous fungi would provide additional information related to conditions of high temperatures.

The presence and diversity of fungi have consistently been associated with the Middle Miocene Climate Optimum (MMCO) (Romero *et al.*, 2021; Pilie *et al.*, 2023). Although the stratigraphic classification and age assignment of formations within the El Foyel Group remain a matter of debate (whether Paleogene or Neogene, see Geological Setting), it is apparent that the diversity of pollen and non-pollen palynomorphs (fungal remains) recovered from the Troncoso Formation may indicate a period of optimal climatic conditions, where humidity and temperature played a pivotal role in the richness of terrestrial ecosystems. Remarkably, intervals of optimal climatic conditions are recognized in the Eocene and the Miocene (MECO: Middle Eocene Climate Optimum and MMCO). Therefore, the biotas of the Troncoso Formation likely represent one of these climatic events, more likely associated with MECO. Rather than being exhaustive, the study of these units calls for further research to contribute to clarifying this matter.

CONCLUSIONS

In this contribution, we present the fossil fungal content (with illustrations and descriptions) recovered from the El Foyel Group (Troncoso, Salto del Macho, and Río Foyel formations). This palynomycological association constitutes a rich assemblage mainly composed of spores and the remains of conidiophores and vegetative hyphae. Twenty-six species distributed in 16 genera were recognized here. A new species, *Inapertisporites lacrimaformis* is proposed here. Among the spores, amerospores and secondly the phragmosporae were the most recovered types in all formations, with the Troncoso Formation being the one that presented the greatest abundance and diversity of fungal spores. These findings allow us to increase substantially the fungal diversity known so far for the units of the El Foyel Group. The ages inferred for the units of the El Foyel Group, based on the palynostratigraphical analysis of the non-pollinic (fungal) remains, agree with previous information derived from pollinic biomarkers, suggesting a Paleogene age for the El Foyel Group. The high diversity of the fungal assemblage recovered from the Troncoso Formation could be representative of a period of optimal climatic conditions characterized as warm temperate and humid, probably related to the MECO. Based on the paleoeological preferences of recovered fungal remains from the El Foyel Group, a riparian or lacustrine environment in a woodland setting could be inferred.

ACKNOWLEDGMENTS

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