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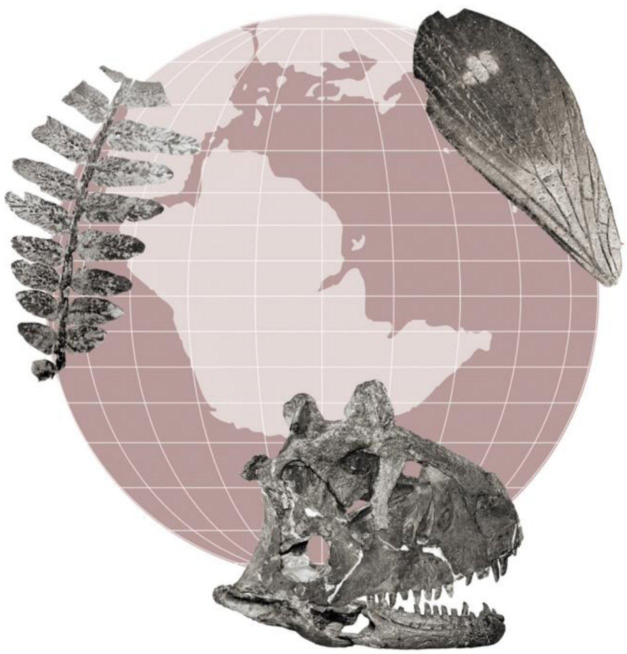

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Composition, diversity, and vegetation signals of the Eocene Río Pichileufú flora (northwestern Patagonia, Argentina), spore-pollen evidence

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- Short Description: Palynology from Río Pichileufú reveals high floral diversity, warm and increasingly seasonal conditions, and the earliest crown-group Barnadesioideae, marking major Eocene transitions.

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Abstract. The middle Eocene Río Pichileufú locality (47.7 Ma, Huitrera Formation, Río Negro Province, Argentina) preserves one of the most diverse and biogeographically significant fossil floras of the southern hemisphere. This study presents the first comprehensive palynological analysis from the site, identifying 69 spore and pollen species representing 33 plant families, including 19 newly recorded for the locality. The palynological assemblage is dominated by gymnosperms, chiefly Podocarpaceae, and by Nothofagaceae among angiosperms, accompanied by typical Gondwanan elements such as Araucariaceae, Myrtaceae, and Proteaceae. The presence of thermophilic taxa, including palms and Sapindaceae (*Cupania*), indicates warm depositional conditions, whereas the scarcity of ferns suggests seasonally dry intervals. A key finding is the fossil pollen record of Barnadesioideae (Asteraceae), representing the earliest confirmed occurrence of this crown-group lineage. Previously, Asteraceae at Río Pichileufú were known from a unique inflorescence and associated pollen related to the Mutisiodeae/Dicomeae/Oldenburgieae groups. The new evidence extends the evolutionary history of the family and demonstrates that diversification of Barnadesioideae was already underway in southern South America immediately following the Eocene Climatic Optimum. The Río Pichileufú assemblage thus offers critical evidence for the early Gondwanan diversification of the Asteraceae and records a major floristic transition in Patagonian mesothermal forests, from persistently humid conditions to increasing rainfall seasonality.

Resumen. La localidad Eocena media de Río Pichileufú (47,7 Ma, Formación Huitrera, Provincia de Río Negro, Argentina) preserva una de las floras fósiles más diversas y biogeográficamente significativas del hemisferio sur. Este estudio presenta el primer análisis palinológico exhaustivo del sitio, identificando 69 especies de esporas y polen que representan 33 familias de plantas, incluyendo 19 registradas por primera vez para la localidad. La asociación palinológica está dominada por gimnospermas, principalmente Podocarpaceae, y entre las angiospermas domina Nothofagaceae, acompañadas por elementos típicos de Gondwana como Araucariaceae, Myrtaceae y Proteaceae. La presencia de taxones termófilos, incluyendo palmeras y Sapindaceae (*Cupania*), indica condiciones cálidas de depositación, mientras que la escasez de helechos sugiere intervalos estacionalmente secos. Un hallazgo significativo es el registro fósil de polen de Barnadesioideae (Asteraceae), que representa la evidencia confirmada más antigua del grupo corona de este linaje. Anteriormente, las Asteraceae de Río Pichileufú se conocían a partir de una inflorescencia y polen asociado, perteneciente a los grupos Mutisiodeae/Dicomeae/Oldenburgieae. La nueva evidencia amplía la historia evolutiva de la familia y demuestra que la diversificación de Barnadesioideae había comenzado en el sur de Sudamérica inmediatamente después del Óptimo Climático del Eoceno. Por lo tanto, la asociación del Río Pichileufú ofrece evidencia crucial sobre la diversificación temprana de las Asteraceae en Gondwana y registra una importante transición florística en los bosques mesotérmicos patagónicos, desde condiciones persistentemente húmedas a regímenes con una creciente estacionalidad de las precipitaciones.

Key words. Palynology, Río Negro province, middle Eocene, vegetation, Asteraceae.

Palabras clave. Palinología, Provincia de Río Negro, Eoceno Medio, vegetación, Asteraceae.

INTRODUCTION

The Eocene fossil site of Río Pichileufú (Berry 1935a, b, c; 1938), located east of Bariloche city in Río Negro Province, Argentina (Fig. 1), represents one of the most taxonomically diverse and biogeographically significant plant assemblages known from the southern hemisphere. High precision $^{40}Ar/^{39}Ar$ dating of primary tuffs immediately stratigraphically above the fossiliferous layers places the deposit at 47.74 ± 0.05 Ma (Wilf et al., 2005; Wilf, 2012), capturing a key interval immediately following the Early Eocene Climatic Optimum (Hollis et al., 2012; Westerhold et al., 2020). The studied strata belong to the Huitrera Formation, a unit composed of lava flows with a bimodal composition, interbedded with volcaniclastic, often fossiliferous lacustrine sequences (Lage, 1982; Aragón & Mazzoni, 1997; Aragón & Romero, 1984; Rapela et al., 1988; Iannelli et al., 2017; Gosses et al., 2020; Hajek et al., 2025).

The Huitrera Formation extends across broad areas of northwestern Patagonia and encompasses several classic fossiliferous localities—such as Nahuel Huapi Este/Pampa de Jones (ca. 54 Ma, Wilf et al., 2010), Laguna del Hunco (ca. 52 Ma, Wilf et al., 2005), and Confluencia (middle–late Eocene, Melendi et al., 2003). Despite their age differences, all have been assigned to the Huitrera Formation (Báez et al., 1991; Melendi et al., 2003; Wilf et al., 2010; Barreda et al., 2020). These sites, renowned for their exceptionally rich megafloral, palynological, and faunal assemblages, provide key evidence for reconstructing early Paleogene vegetation, ecosystems, and environments in Patagonia.

The Río Pichileufú macroflora includes an exceptionally rich assemblage of gymnosperms, angiosperms, and ferns, many with striking biogeographic affinities to extant Australasian and Southeast Asian floras (Berry, 1938; Wilf et al., 2009, 2014, 2017a; Knight & Wilf, 2013). Noteworthy elements include the earliest fossil inflorescence of Asteraceae (Barreda et al., 2010, 2012), the last known South American ginkgophyte (Villar de Seoane et al., 2015), and several conifer lineages today mainly restricted to tropical and subtropical rainforest regions (e.g., *Agathis*, *Araucaria* Sect. *Eutacta*, *Dacrycarpus*, *Retrophyllum*, *Papuacedrus*; Wilf et al., 2009, 2014, 2017a; Wilf, 2012; Andruchow-Colombo et al., 2023; Rossetto-Harris & Wilf, 2024). These plant remains occur alongside diverse associated fauna, including insects and amphibians (Báez, 1986, 2000; Dlussky & Perfilieva, 2003; Petrulevičius & Popov, 2014; Ramírez et al., 2016; Petrulevičius, 2018), underscoring the site's exceptional paleoecological value.

Much of the early taxonomic information on fossil plants from Río Pichileufú derived from descriptions by E.W. Berry in the early 20th century (Berry, 1935a, b, c, 1938), which included numerous misidentifications that obscured the true diversity and biogeographic affinities of the flora. Recent systematic revisions (cited above) and morphotype-based analyses have clarified its composition, documenting at least 158 distinct leaf morphotypes and re-establishing Río Pichileufú as a hotspot of plant diversity during the middle Eocene (Rossetto-Harris & Wilf, 2024).

Despite its paleobotanical significance, the palynological record of Río Pichileufú remains virtually unknown, aside from rare pollen grains associated with an exceptionally preserved Asteraceae inflorescence (Barreda et al., 2010). This scarcity is largely attributable to the low palynomorph yield and poor organic preservation of the tuffaceous sediments.

Here, we present the first palynological record from the Río Pichileufú locality, evaluate its taxonomic diversity, and compare our results with the co-occurring macroflora. These analyses provide a critical framework for linking the increasingly well-documented macroflora of Río Pichileufú with its palynological record, refining reconstructions of Patagonian biodiversity dynamics and biogeographic connections during the Eocene.

MATERIALS AND METHODS

Sampling. Eleven rock samples were collected from the Huitrera Formation at the Río Pichileufú locality (Ea. Don Hipólito), Río Negro Province, Argentina (Fig. 1). The samples were obtained from two stratigraphic sections approximately 100 m apart—*Raiguenrayun* Section (RS), 41°9'26.06"S, 70°49'57.11"W, 8 samples, and *Ginkgo* Section (GS), 41°9'26.14"S, 70°50'0.67"W, 2 samples—and one additional sample (IS) from macrofloral locality RP3 of Wilf et al. (2005), 41°09'20.7"S, 70°50'04.2"W, see also Rossetto-Harris & Wilf (2024), (Figs. 2, 3).

Palynology. Samples were processed following traditional palynological techniques (Riding, 2021). Eight proved productive for palynology, including five from RS, two from GS, and one from IS. Productive samples mainly correspond to laminated tuffs and tuffaceous mudstones and sandstones (Fig. 2). Residues were mounted on microscope slides, analyzed for palynology, and counted using a Leica 2500 microscope. Slides are housed at the "Museo Paleontológico de Bariloche", under the prefix MAPBAR and catalogue numbers 12500-12507. England Finder coordinates are given for illustrated fossil morphotypes. Fossil spores and pollen grains were identified to species level whenever possible (Table 1). Terminology for pollen and spores follows Punt et al. (2007). We explored the botanical affinity of fossil morphotypes and grouped them in other taxonomic categories when feasible (i.e., families or genera). All palynomorphs were counted for each sample, yielding a total of 2108 counted specimens (Table 1).

Quantitative analysis. We arranged palynological data from the analyzed unit in an 8 × 69 matrix of samples by taxon abundance counts. We estimated diversity for samples containing more than 200 counted specimens each, while samples with lower palynomorph counts (samples RS1 and IS) were excluded from the analysis.

We estimated expected richness within samples based on our abundance matrix using the iNEXT R package (Hsieh et al., 2016). We used coverage—defined as the proportion of individuals in the assemblage that belong to species represented in the sample—to analyze diversity, as this metric has been highlighted as the most robust approach for estimating richness under conditions of incomplete sampling (Chao & Jost, 2012). By evaluating diversity at two specific coverage levels (i.e. 80% and 100%) we could identify variations in sample composition.

We compared the diversity estimates for the Río Pichileufú locality with those from other warm early and middle Eocene intervals in Patagonia. These include the Early Eocene Climatic Optimum at the Laguna del Hunco locality (52 Ma) within the Huitrera Formation, Chubut Province (Barreda et al., 2020), and the middle Eocene (ca. 40 Ma) in Río Turbio Formation, Santa Cruz Province (Fernández et al., 2021). All quantitative analyses were conducted using the open-source software R Core Team (2022), version 4.2.1.

RESULTS

Composition of the Río Pichileufú spore-pollen assemblages

Our collected samples contained moderate numbers of spores and pollen grains embedded within a matrix of well-preserved sapropelic amorphous organic matter, along with algal and fungal remains. The recovered material is relatively well-preserved, making identification at species level possible for most of the spore-pollen elements.

We identified 69 spore and pollen species (Table 1; Figs. 4–6), including nine ferns, 13 gymnosperms, and 47 angiosperms. Of these, 54 species were assigned to 33 families (2 ferns, 2 gymnosperms, 29 angiosperms), whereas the remaining 15 taxa exhibits uncertain botanical affinity. Additionally, two species of algae were recorded — (Zygnemataceae and Botryococcaceae) —.

A total of 19 plant families are newly recorded from RP (six tentatively assigned), and 14 family occurrences corroborate previous megafossil evidence (Table 2). Combined with the 31 families known exclusively from megafossils (Rossetto-Harris & Wilf, 2024), the RP assemblage comprises 58 confidently documented plant families.

The spore-pollen assemblages are dominated by gymnosperm pollen (ca. 49–72 %), followed by angiosperms (ca. 19–42%), whereas fern spores constitute a minor component (ca. 1–3.5%). Algal remains are represented primarily by zygospores or aplanospores of Zygnemataceae and colonies of Botryococcaceae (ca. 1–2.5%); fungal spores are consistently present, accounting for approximately 3.5–16% of grains in the assemblages. Among gymnosperms, Podocarpaceae predominate (ca. 43–70%), followed by Araucariaceae (ca. 2–6%) and trace occurrences of Cycadaceae/Ginkgoaceae. Podocarpaceae include pollen types comparable to those of extant *Podocarpus/Prumnopitys* (*Podocarpidites* spp.), *Dacrydium* (*Lygistepollenites florinii*), *Dacrycarpus* (*Dacrycarpites australiensis*), and *Microcachrys* (*Microcachrydites antarcticus*). Araucariaceae are represented by fossil species closely resembling those of extant *Araucaria* (*Araucariacites australis*) and *Wollemia/Agathis* (*Dilwynites granulatus*). Although angiosperms exhibit considerable taxonomic richness, they comprise relatively few specimens within the assemblage. The dominant family is Nothofagaceae (*Nothofagidites* spp.), primarily corresponding to the subgenera *Fuscospora* and *Nothofagus* (ca. 7–35%), accompanied by rare occurrences of *brassii*-type pollen (*N. acromegacanthus, N. fuegiensis*). Other angiosperms include Arecaceae (*Arecipites* sp.), Juglandaceae (*Plicatopollis wodehousi*), Sapindaceae

(*Cupanieideites reticularis*), Ulmaceae (*Ulmoideipites patagonicus*), and Chloranthaceae (*Clavatipollenites* sp.). Asteraceae include pollen assignable to the Mutisieae/Dicomeae/Oldenburgieae (*Mutisiapollis telleriae*) and Barnadesioideae (*Quilembaypollis* sp. aff. *Q. stuessy*) subfamilies. Gondwanan representatives such as Proteaceae (*Proteacidites* sp., *Propylipollis* sp.) and Myrtaceae (*Myrtaceidites* sp.) are also represented, together with pollen tentatively attributed to Araliaceae (*Rhoipites* cf. *sphaerica*), Lardizabalaceae (*Rhoipites* sp. 1), Rosaceae (*Striatricolporites* sp. 1), Ranunculaceae (*Polycolpites* sp.), Fabaceae (*Rhoipites* sp. 2), and Malvaceae (*Retistephanocolporites* sp., *Baumannipollis* sp.). Ferns are mainly represented by Cyatheaceae (*Cyathidites* spp., *Kuylisporites waterbolkii*, *Trilites tuberculiformis*, *Trilites parvallatus*, *Ischyosporites* sp.).

Diversity

Diversity estimates indicate consistently high relative values across all analyzed samples (Table 3). Within the local dataset, sample GS2 represents the richest assemblage in terms of total estimated richness (Chao1 = 76.18), though RS3 displays the highest richness when samples are standardized to 80% coverage (14.08).

In a broader regional context, the overall diversity of the middle Eocene (47.5 Ma) Río Pichileufú assemblages (coverage 80% = 10.70; Chao1 = 57.88) is comparable to, though lower than, the values recorded for the Early Eocene (52 Ma) Laguna del Hunco within the Huitrera Formation (coverage 80% = 18.58; Chao1 = 64.70). Similarly, the Río Pichileufú richness is slightly lower than that of the middle Eocene (~40 Ma) portion of the Río Turbio Formation in Santa Cruz Province, particularly at the 80% coverage level (17.26), despite sharing a nearly identical asymptotic richness (57.71) (Table 4; data from Fernández et al., 2021).

SYSTEMATIC PALEONTOLOGY

Taxonomy —notes on selected taxa

Genus *Kuylisporites* Potonié, 1956

Type species. *Kuylisporites waterbolkii* Potonié, 1956

Kuylisporites waterbolkii Potonié, 1956

Fig. 4C

Comments. Despite being represented by a single specimen, the distinctive triad of large symmetrically arranged pits in the interradial equatorial region enables a confident assignment to this species. Affiliation with the extant genus *Cyathea* (Cyatheaceae) links it to scaly tree ferns inhabiting warm, humid tropical and subtropical regions of Central and South America and the Caribbean. *K. waterbolkii* has been previously recorded from the Eocene (Fernández & Savoretti, 2020) and early to middle Miocene deposits of southern Patagonia (Zamaloa, 1999; Zetter et al., 1999).

Dimensions (1 specimen measured). Equatorial diameter: 30 µm.

Genus *Dilwynites* Harris, 1965

Type species. *Dilwynites granulatus* Harris, 1965

Comments. *Dilwynites* was originally defined by Harris (1965) to encompass fossil pollen grains characterized by a comparatively coarse sculpture and thicker exine than those assigned to *Araucariacites* Cookson (1947). The genus shows morphological similarities to the pollen of the extant genera *Wollemia* and *Agathis* (Macphail et al., 2013; Macphail & Carpenter, 2014). More recently, Seyfullah et al. (2023) conducted a detailed study of pollen from extant *Wollemia* and documented notable morphological variability, including specimens with thinner sculpture and a ring-like subequatorial feature—both traits that are typical of extant *Araucaria* (Del Fueyo et al., 2008). On this basis, they proposed that fossil pollen assigned to *Dilwynites* may not exclusively represent *Wollemia* but could also correspond to other members of the Araucariaceae. Although extant *Wollemia* pollen may exhibit morphological features overlapping with more than one fossil genus (i.e., *Dilwynites* and *Araucariacites*), the reverse does not necessarily apply. In particular, studies of extant *Araucaria* pollen (Del Fueyo et al., 2008) have not documented sculpture as coarse as that consistently observed in fossil *Dilwynites*. Therefore, in this study we retain the affinity of *Dilwynites* with extant *Wollemia* and *Agathis*, as both genera are characterized by relatively coarse exine ornamentation, consistent with the fossil material recorded here.

Dilwynites granulatus Harris, 1965

Figure 4G

Dimensions (6 specimens measured). Diameter: 49–60 μm.

Genus *Striamonocolpites* Mathur & Mathur, 1969

Type species. *Striamonocolpites longicolpatus* Mathur & Mathur, 1969

Striamonocolpites sp. 1

Figure 4O

Description. Pollen grain monocolpate, ellipsoidal; colpus long, reaching poles, with open ends, marginate close to the ends; exine tectate, 1 μm thick, nexine thinner than sexine; sexine striate and infrareticulate, striae thin, less than 0.5 μm thick.

Dimensions (1 specimen measured). Polar diameter (length): 29 μm.

Comparisons. Only one poorly preserved specimen was recovered. It shows broad similarities with *Striamonocolpites paludosus* D'Apolito et al. defined from the Miocene of Amazonia (D'Apolito et al., 2024), particularly by the presence of striate-reticulate sexine and a long colpus with open and marginated ends. However, it is much larger and the pitted nexine that characterized the species was not observed in the Patagonian specimen.

Striamonocolpites sp. 2

Figure 4P

Comments. A single monocolpate, striate pollen grain, with a long colpus, which differs from *Striamonocolpites* sp. 1 in not having an infrareticulate pattern, and open colpus ends.

Dimensions (1 specimen measured). Polar diameter (length): 35.5 µm.

Botanical affinity. Unknown

Genus *Striatopollis* Krutzsch, 1959

Type species. *Striatopollis sarstedtensis* Krutzsch, 1959

Comments. Several form-genera have been established to accommodate tricolpate, striate pollen grains. The first was *Tricolpites* subgenus *Striatricolpites* Van der Hammen (1956), based on a modern pollen grain of *Acer platanoides* (Aceraceae). González Guzmán (1967) subsequently elevated *Striatricolpites* to generic rank while retaining the original type species; however, this action rendered the genus invalid. Krutzsch (1959) later erected *Striatopollis* to include tricolpate, striate pollen grains. Rouse (1962) proposed *Striopollenites* for similar material, but this taxon was subsequently regarded as a junior synonym of *Striatopollis* by Potonié (1966). Likewise, *Rutihesperipites*

Srivastava (1977) was later considered a junior synonym of *Striatopollis* (Ward, 1986). Furthermore, Singh (1971) and Dettmann (1973) expanded the circumscription of *Striatopollis* to include both striate and striate-reticulate pollen grains. In the present study, we adopt *Striatopollis* in a broad sense to encompass all tricolpate, striate pollen grains, with additional diagnostic characters applied at the species level to refine taxonomic distinctions.

Striatopollis sp. 1

Figures 6I, M

Description (Observation under SEM). Pollen grain small, spheroidal, with circular outline in equatorial view, tricolpate; colpi occupies 2/3 of the polar diameter; exine surface showing a striate-rugulate pattern; striae-rugulae short (1.5 –2.4 µm) and narrow (0.3 µm), irregularly arranged on the grain surface and ornamented with transverse ridges.

Dimensions (1 specimen measured). Diameter: 23.5 µm.

Comments and comparisons. Only one specimen was observed under SEM, which shows broad resemblance with some pollen of the Simaroubaceae (Sapindales), particularly with the genus *Picramnia*. Both are tricolpate, small, striate (*Picramnia* subtype of Anzótegui & Caccavari, 2001), and particularly have the striae ornamented with transverse ridges (Anzótegui & Caccavari, 2001). However, pollen in *Picramnia* is prolate to subprolate and has the striae arranged longitudinally (Anzótegui & Caccavari, 2001; Da Luz et al., 2025), rather than in an irregular pattern as in the Patagonian specimen.

Striatopollis sp. 2

Figure 4Q

Description. Pollen grain of medium size, spheroidal to suboblate, with subcircular amb, tricolpate; colpi long, occupying more than 2/3 of the equatorial ratio, apocolpia small; exine 1–1.5 µm thick, clearly stratified, sexine thicker than nexine; sexine infrarreticulate and supraestriate; striae are anastomosing and oriented sub-parallel to colpi.

Dimensions (1specimen measured). Equatorial diameter: 36 µm.

Botanical affinity. Unknown eudicot

Genus *Tricolpites* Cookson, 1947

Type species. *Tricolpites reticulatus* Cookson, 1947

Tricolpites anguloluminosus Anderson, 1960

Figure 4T

Comments. This species was previously reported in Argentina from several Paleocene and Eocene sites (e.g., Archangelsky, 1973; Romero & Zamaloa, 1985; Melendi et al., 2003; Barreda et al., 2020).

Dimensions (1 specimen measured). Polar diameter: 30 µm.

Tricolpites sp.1

Figures 4U, V

Description. Pollen grain of medium size, suboblate to spheroidal, with circular amb, tricolpate; colpi short, occupying 1/3 of the equatorial ratio, with diffuse margins; apocolpia large 14 µm; exine thin, less than 1 um thick, sexine slightly thicker than nexine, rugulate to microreticulate; rugulae short and narrow, arranged on the grain surface forming an irregular microreticulum.

Dimensions (5 specimens measured). 22–29 µm.

Comparison. To date, no similar forms exhibiting this distinctive rugulo-reticulate sculpture have been recorded.

Tricolpites sp. 2

Figures 4W, 6A

Description. Pollen grain, small, suboblate to spheroidal, isopolar, tricolpate; colpi short occupying ½ of polar diameter, apocolpia large, ca. 6 µm width; colpal membrane covered by free standing columellae; exine 0.7-1 µm thick, stratified, columellae distinct, sexine slightly thicker than nexine; sexine reticulate, reticulum homobrochate, lumina small, 0.4–0.6 µm in diameter, subpolygonal to irregular, muri thin, less than 0.3 µm thick, with undulate margin for the slight projection of the columellae over the muri surface.

Dimensions (1 specimen measured). Subpolar diameter: 12 µm.

Botanical affinity. The specimen exhibits morphological similarities to pollen of the Brassicaceae, being spheroidal to suboblate, tricolpate, reticulate, and characterized by an ornamented colpal membrane. In particular, some species of the genus *Ischnocarpus* (Moar, 1993) display a homobrochate reticulum and comparable dimensions.

However, tricolpate, microreticulate pollen grains are present in several unrelated families, and other genera sharing similar morphological features cannot be excluded. Therefore, the proposed affinity with *Brassicaceae* should be considered tentative.

Genus. *Polycolpites* Couper, 1953

Type species. *Polycolpites clavatus* Couper, 1953

Polycolpites sp.

Figure 4X

Description. Pollen grain subespheroidal, isopolar, pericolpate; colpi short, 8–12 µm length, sometimes indistinct; exine 1–1.5 µm thick, clearly stratified, columellae distinct, sexine slightly thicker than nexine; sexine ornamented with variable spaced spinules, commonly less than 1 µm high; spinules frequently fused at the basis forming ridges with two or more spinules, leaving an undulate outline.

Dimensions (2 specimens measured). Diameter: 31–32 µm.

Comments. These specimens show broad similarities with pollen of the Ranunculaceae, particularly with species of *Ranunculus* (Moar, 1993; Garralla & Cuadrado, 1998).

Genus *Echitricolporites* Van der Hammen, 1956

Type species. *Echitricolporites spinosus* Van der Hammen, 1956

Echitricolporites sp. 1

Figures 5A, 6E,

Description. Pollen grain small, spheroidal to suboblate, with circular amb, tricolporate; colpi long, occupying 2/3 of the equatorial ratio, ora circular to subcircular, 1.5–2 µm in diameter, apocolpia small; exine thin, less than 1 µm thick, stratification obscure; exine ornamented with microspines, less than 1 µm high, thicker at the base and with pointed ends; microspines scattered on the grain surface.

Dimension (5 specimens measured). Equatorial diameter:15–22.5 µm.

Botanical affinity. This species exhibits broad similarities to the pollen of the extant *Latua venenosa* Phil. (Solanaceae), particularly in overall shape, exine thickness, and sculptural pattern. The main distinction lies in grain size, as the modern species is substantially larger (34–43 × 26–38 µm; Heusser, 1971). *Latua venenosa* is endemic to southern Chile, where it inhabits humid environments of the Coastal Range from Valdivia to Chiloé (Region X), occurring within Coihue–Raulí–Tepa and Evergreen forest types. If confirmed, this identification would represent the first evidence of Solanaceae at Río Pichileufú, a family whose oldest South American fossil records are the exceptionally preserved lantern fruits from Laguna del Hunco (Wilf et al., 2017b; Deanna et al., 2020).

Genus *Quilembaypollis* Palazzesi & Barreda, 2009

Type species. *Quilembaypollis gamerroi* Palazzesi & Barreda, 2009

Quilembaypollis sp. cf. *Q*. *stuessyi* Palazzesi & Barreda, 2009

Figures 5E, 6D, H

Description. Tetrad composed of four tricolporate, microechinate pollen grains. Individual grains of medium-size, subprolate, elliptical in equatorial view; colpi long, with acute ends; endoapertures not clearly discernible, but appear lalongate; exine tectate, 3–6 µm thick, with the sexine approximately four times thicker than nexine (observation under LM); in the best preserved areas of the grains, three sexine sublayers can be inferred: an ectosexine (~1 µm), a thicker middle layer (~3 µm) of compacted, tightly packed columellae? and a thin endosexine; three pronounced intercolpal depressions are present (ca. 3 µm x 7 µm in diameter); tectum distinctly microechinate and perforate (observation under SEM); microspines with broad-bases and blunt tips.

Dimensions (2 specimens measured). Polar diameter of individual grains: 23–29 µm.

Comparisons. These specimens are tentatively assigned to *Q. stuessyi* due to the incomplete preservation of the diagnostic sexine stratification —particularly the three columellate sublayers— that characterized both the fossil species (Palazzesi et al., 2009) and the related extant genus *Schlechtendalia* (Urtubey & Tellería, 1998). Despite these uncertainties, the combination of diagnostic characters—including a thick exine, microechinate ornamentation, and well-defined intercolpal depressions— supports their assignment to the subfamily Barnadesioideae. *Dasyphyllum* is the only other genus in this subfamily with three intercolpal equatorial depressions, although its species possess a thinner exine and less defined depressions.

Remarks. This material represents the oldest known record of the crown Barnadesioideae worldwide. Moreover, the specimen described here potentially represents the only known fossil record of Barnadesioideae pollen preserved as a tetrad. However, the material is limited to a single, poorly preserved specimen, and we cannot unequivocally exclude the alternative possibility that it represents a pollen clump (De Benedetti et al., 2024). All extant representatives of Barnadesioideae release pollen exclusively as monads (Urtubey & Tellería, 1998), and no previous fossil evidence has documented tetrad dispersal within the subfamily (Palazzesi et al., 2009).

Genus *Rhoipites* Wodehouse, 1933

Type species. *Rhoipites bradleyi* Wodehouse, 1933

Comments. *Rhoipites* are restricted to tricolporate, subprolate to spheroidal pollen grains with reticulate, microperforate to scabrate sculpture, whereas *Tricolporites* is here confined to oblate forms or to grains with non-reticulate exine sculpture that do not conform to *Rhoipites*.

Rhoipites cf. *sphaerica* (Cookson) Pocknall & Crosbie, 1982

Figures 5G–I

Description. Pollen grain, isopolar, subprolate; tricolporate, colpi long extending to ⅔ of the polar diameter, margins straight, ora distinct, lalongate, 1 µm wide and up to 2.5 µm long, protruding; exine clearly stratified; nexine 0.4–0.5 µm thick; sexine reticulate thickened at the intercolpal and polar regions (1.9–2 µm thick) and thinning gradually towards colpi (0.4–0.8 µm thick); lumina of maximum diameter at the poles and intercolpal regions (0.7–1.1 µm in diameter) diminishing in size towards colpi (0.16–0.26 µm in diameter); lumina subpolygonal to subcircular, muri 0.4–0.6 µm wide underlain by a single row of columellae.

Dimensions (7 specimens measured). Polar diameter: 23–37 µm.

Comparison. These distinctive specimens, also recorded at the LH site, fit well with the diagnosis of *R. sphaerica*, mainly considering the variability of the species in shape, size of the mesh of the reticulum and thickening of the exine (Stover & Partridge, 1973). The Patagonian specimens have a thinner nexine and smaller, more protruding ora than the type material.

Comments. These specimens exhibit notable similarities to pollen of the Araliaceae, particularly the genus *Pseudopanax* (cf. *P. arboreus*; Moar, 1993). They share a comparable overall shape and exine features, characterized by a thickened exine at the poles and a reticulate heterobrochate pattern, with larger lumina in the polar and mesocolpial regions and smaller lumina along the colpus margins. This finding aligns with the recent macrofossil record of the family from Laguna del Hunco (leaves and an infructescence) and potential leaf occurrences at Río Pichileufú (Wilf, 2025).

Rhoipites sp. aff. *R. muehlenbeckiaformis* Macphail &Truswell, 1993

Figures 6B, F

Description (Only observed under SEM). Pollen grain isopolar, tricolporate, spheroidal, with circular outline in equatorial view; colpi long, almost reaching to poles, ora present, ca. 2.5 – 3 µm high; apocolpia small; exine thin, ca. 1 µm thick, tectate; exine surface ornamented with ridges of variable width, arranged in a striate-rugulate pattern, densely perforated.

Dimensions (1 specimen measured). Polar diameter: 18 µm.

Comparison. *R. muehlenbeckiaformis* Macphail & Truswell (1993) exhibits close correspondence with our specimen in overall morphology, dimensions, and particularly in exine sculpture. Given that only a single specimen is available, and the diagnostic diamond-shaped ora is not clearly discernible, we tentatively assign this material to the Australian species.

Botanical affinity. The specimen shows morphological affinity with the pollen of *Muehlenbeckia australis* (Polygonaceae; Moar, 1993), particularly in its sculptural pattern. *Muehlenbeckia australis* pollen grains are larger, but exine stratification and ora morphology could not be compared as the specimen was observed only under SEM. *Muehlenbeckia* comprises vines and shrubs distributed along the Pacific margins, including Australia, New Zealand, Papua New Guinea, and Chile (POWO).

Rhoipites sp. 1

Figure 5K

Description. Pollen grain spheroidal to suboblate, tricolporate; colpi long almost reaching poles, apocolpia small; ora lalongate; exine 1.5–1.7 µm thick, sexine thicher than nexine, reticulate, heterobrochate, lumina larger at mesocolpia (1–1.5 µm), and small at poles and colpi magins.

Dimension (1 specimen measured). Equatorial diameter: 29.5 µm.

Comparisons. This specimen differs from *R.* cf. *sphaerica* described herein by its oblate shape, uniform thickness of the exine across the grain, and by having larger lumina restricted to the mesocolpial regions.

Botanical affinity. Tricolporate, reticulate pollen grains occur in several eudicot families. Among those currently represented in the Patagonian flora, this specimen most closely resembles pollen of *Lardizabala* (Lardizabalaceae), sharing similarities in shape, size, and the presence of heterobrochate reticulum with enlarged lumina in the mesocolpia. Comparable features are also observed in some members of the Araliaceae.

Rhoipites sp. 2

Figure 5L

Description. Pollen grain tricolporate, subspheroidal, with circular outline in equatorial view; colpi long almost reaching poles; ora lalongate, very narrow (5 µm wide, 0.5–1 µm high); exine thin (ca. 1 µm) stratified, sexine of the same thickness than nexine, psilate to microperforate.

Dimensions (1 specimen measured). Subpolar diameter: 31 µm.

Comments. No fossil species was found with comparably narrow ora.

Botanical affinity. Unknown eudicot

Genus *Senipites* Srivastava, 1969

Type species. *Senipites drumbellerensis* Srivastava, 1969

Senipites sp.

Figures 5M, N, 6C, G

Description. Pollen grain isopolar, tricolporate, oblate to suboblate, with subcircular amb; colpi occupying 2/3 of equatorial ratio, ora lalongate, narrow, 4–5 µm by 2–2.5 µm; vestibule not always observed, apocolpia small; exine thin, ca. 1 µm thick, stratified, sexine of the same thickness as nexine, columellae observed; sexine ranging from semitectate (microreticulate - with lumina less than 0.5 µm in diameter) to tectate (microperforate); tectum supraornate with densely distributed verrucae, spines and bacula with mucronate bases (observed under SEM). Under light microscopy, the surface appears rugose to microreticulate.

Dimensions (3 specimens measured). Equatorial diameter: 18–24 µm.

Comparisons. The most similar specimens are those reported as *Senipites* sp. from the Miocene of central Patagonia (Panti et al., 2025), which differ mainly by displaying reduced ornamentation along the muri and a more clearly defined vestibule. *Senipites patagonica* Barreda 1997, does not exhibit a truly reticulate surface; its muri lack ornamentation with spines and bacula, and its colpi are shorter.

Botanical affinity. Our specimens share several features with extant Symplocaceae, particularly overall shape, the vestibulate nature of the apertures (although not consistently observable in all specimens), and aspects of the exine sculpture (Barth, 1979, 1982; Premathilake et al., 1999). However, the colpi in our material are comparatively longer than those typically reported for living representatives of the family. In view of these differences, we assign the specimens to Symplocaceae with caution and consider the familial affinity to be tentative.

Genus *Striatricolporites* (van der Hammen, 1956) Leidelmeyer, 1966

Type species. *Striatricolporites pimulis* Leidelmeyer, 1966

Striatricolporites sp. 1

Figures 5Q–S

Description. Pollen grain isopolar, tricolporate, subprolate to spheroidal, with oval outline; colpi long, occupying ⅔ to ¾ of the equatorial diameter, apocolpia of medium size, ora lalongate, 3x5 µm, protruding; exine 1–1,5 µm thick, stratified, sexine of the same thickness as nexine; sexine infra-reticulate and supra-striate; striae formed by elongate rugulae arranged longitudinally to the grain and around the ora.

Dimensions (4 specimens measured). Polar diameter: 27–28 µm. Equatorial diameter: 17–23 µm.

Comments. These specimens differ from other types of *Striatricolporites* reported from the RP assemblages by the presence of protruding ora. They show similarities with pollen of the Rosaceae, particularly with the genus *Rubus* (Moar, 1983).

Striatricolporites sp. 2

Figure 5T

Description. Pollen grain, isopolar, tricolporate, of medium size, oblate to spheroidal, with circular amb; colpi long, almost reaching poles, apocolpia small, ora obscure; exine 2–2.8 µm thick, stratified, sexine three times thicker than nexine; sexine infra-reticulate and supra-striate; reticulum homobrochate, striae thin, meridionally arranged.

Dimensions (1 specimen measured). Equatorial diameter: 27 µm.

Botanical affinity. The specimen exhibits broad similarities with pollen of the Gentianaceae, particularly resembling the type morphology *Zygostigma australe sensu* Pire and Dematteis (2006).

Striatricolporites sp. 3

Figure 5U

Comments. Only a single tetrad of tricolporate, striate pollen grains was recovered from these assemblages. It resembles *S.* sp. 2 described herein, but differs in that each monad is smaller, with a thinner exine, and with a sexine that is nearly equal in thickness to the nexine, rather than distinctly thicker as in *S.* sp. 2.

Dimensions (2 specimens measured): Equatorial diameter of individual grains: 17–20 µm.

Botanical affinity. Unknown eudicot.

Genus *Tricolporites* Cookson, 1947

Type species. *Tricolporites sphaerica* Cookson, 1947

Comments. Refer to the remarks provided for the genus *Rhoipites*.

Tricolporites sp. 1

Figure 5V

Description. Pollen grain of medium size, subprolate, with sub-rectangular outline, tricolpate, each colpus apparently diorate; colpi long, occupying 3/4 of the polar diameter, ora narrow, slit-like, lalongate; exine 1 um thick, stratification obscure; sexine psilate or faintly scabrate.

Dimensions (1 specimen measured). Polar diameter: 26 µm.

Comparisons and botanical affinity. This specimen shows broad similarities to pollen of Scrophulariaceae, particularly the *Capraria* type of Sosa & Salgado (2013) and *Myoporum debile* (Anderson) R. Br. (Moar, 1993). Both taxa possess tricolpate pollen with two ora per colpus, comparable size, and relatively reduced sculpture. However, extant representatives of the *Capraria* type are typically spheroidal rather than subprolate, and *M. debile* exhibits a finely reticulate exine. Because our material consists of a single specimen and the diorate condition of the colpi cannot be clearly confirmed, we consider the available evidence insufficient for a confident assignment and therefore maintain the botanical affinity as uncertain.

Tricolporites sp. 2

Figure 5W

Description. Pollen grain, small, oblate to suboblate, isopolar, tricolporate; colpi short occupying 1/3 of polar diameter, apocolpia large; exine 1 µm thick, stratified, columellae distinct, sexine slightly thicker than nexine; sexine reticulate, reticulum homobrochate, lumina small, less than 0.5 µm in diameter, subpolygonal.

Dimensions (1 specimen measured)**.** Equatorial diameter: 16.5 µm.

Comparison. The specimen closely resembles *Tricolporites* sp. 2 from the LH section, affiliated with extant *Weinmannia*, but differs in exhibiting shorter colpi and a homobrochate rather than heterobrochate reticulum.

Botanical affinity. Unknown eudicot.

Tricolporites sp.3

Figure 5X

Description. Pollen grain tricolporate, subromboidal, colpi long, ora large (4x6 µm), subcircular with diffuse margins, slightly protruding; exine very thin with obscure stratification, surface ornamented with sparsely distributed microgranules or spines, not observe in optical section.

Dimensions (2 specimens measured). Polar diameter: 30–32 µm.

Comments. These specimens show similarities to pollen of the Papilionoideae (Fabaceae), particularly *Indigofera* (Heuser, 1971). *Indigofera* includes shrubs, subshrubs, perennial herbs, and occasionally small trees, many of which are adapted to seasonally dry habitats. With more than 700 species, it represents one of the largest genera of Fabaceae, distributed mainly across tropical and subtropical regions.

Genus *Retistephanocolporites* van der Hammen & Wijmstra, 1964

Type species. *Retistephanocolporites quadriporus* van der Hammen & Wijmstra, 1964

Retistephanocolporites sp.

Figure 5CC

Comments. This specimen conforms well to the generic diagnosis of *Retistephanocolporites*, characterized by zonocolporate pollen grains with reticulate sculpture.

Description. Pollen grain tetracolporate, oblate, with subcircular to subquadrangular outline and convex sides; colpi short (brevicolporate) extending 1/3 of the equatorial radius; ora endannulate, endannuli 2 µm thick; exine 1 µm thick, distinctly stratified, with the sexine slightly thicker than nexine; sexine columellate, semitectate, reticulate; reticulum homobrochate, with lumina 0.3–0.4 µm in diameter, muri supported by single columellae.

Dimensions (1 specimen measured). Equatorial diameter: 29 µm.

Comparisons. *Janduforia seamrogiformis* Geermeraad et al. 1968, originally defined from the Eocene of the Caribbean area, shows broad similarities with the present specimen. However, it differs in being larger and tectate, with a densely perforated tectum.

Botanical affinity. The overall morphology closely resembles the pollen of extant Bombacoideae (Malvaceae).

Zygnemataceae Kützing, 1843

Genus *Spyrogyra* Link, 1820

Type species. *Spirogyra porticalis* (Müller) Cleve, 1868

Spyrogyra type A in Zamaloa, 1996

Figure 5DD

Description. Zygospore or aplanospore oval or ellipsoidal in shape, with rounded or occasionally pointed ends; wall smooth, with a longitudinal aperture that nearly encircles the spore.

Dimensions (7 specimens measured)**.** Diameter: 64–81 µm x 34–35 µm.

Comments. Van Geel (1976) proposed that ellipsoidal, smooth-walled zygospores attributed to *Spirogyra* most likely represent a complex of species, as they lack diagnostic features that permit reliable identification at the species level. In Argentina, *Spirogyra* type A has been recorded from the Miocene Cullen Formation (Tierra del Fuego), where it was compared with the morphospecies *Ovoidites parvus* (Cookson & Dettmann) Nakoman 1966. Comparable morphotypes (i.e., *Spirogyra* type A or *O. parvus*) have also been documented in Cretaceous deposits of the Lagarcito Formation (San Juan Province;

Prámparo et al., 2005) and in Miocene strata of the Valles Calchaquíes, including the San José, Chiquimil, and Palo Pintado formations (Salta, Tucumán, and Catamarca provinces; Mautino, 2007). Martínez et al. (2008) reported seven species of *Spirogyra* from Paleogene–Neogene deposits of the Ñirihuau Basin (Río Negro Province), with *S.* sp. 6 considered comparable to *O. parvus* and to *Spirogyra* type A sensu Zamaloa. More broadly, additional zygospores attributable to Zygnemataceae have been reported from Triassic deposits of the Potrerillos and Cacheuta formations (Mendoza Province; Zavattieri & Prámparo, 2006), indicating a long stratigraphic history of this algal group in Argentina.

Extant *Spirogyra* typically colonize shallow, oxygenated, neutral-pH lentic waters under mesotrophic conditions and spring temperatures of 20–25 °C (Van Geel, 1976; Van Geel & Van der Hammen, 1978).

DISCUSSION

The first palynological record from the classic Río Pichileufú locality confirms the presence of several plant families previously identified from macrofossil assemblages and expands the known taxonomic diversity with new elements (Table 2).

The analyzed assemblages reveal a highly diverse vegetation that is broadly comparable to other key warm intervals of the Patagonian Eocene, such as the Early Eocene Climatic Optimum (EECO) at Laguna del Hunco (52 Ma) and the middle Eocene portion of the Río Turbio Formation (~40 Ma). Specifically, the Río Pichileufú assemblages align with the high-diversity signatures characteristic of these Eocene greenhouse floras (Tables 3, 4). Despite the regional significance of these findings, the palynological fertility at both Río Pichileufú and Laguna del Hunco is remarkably low. Interestingly, the palynological yield at both sites differs significantly from their respective macrofossil records. Both localities are renowned for their exceptionally preserved and abundant macrofloras, which have yielded some of the richest Eocene megafloral assemblages globally (Wilf et al., 2005; Rossetto-Harris & Wilf, 2024). The discrepancy is further highlighted by the gap between observed richness (coverage 80%) and estimated asymptotic richness (Chao1). For instance, in sample GS2, the high Chao1 value of 76.18 compared to its richness at 80% coverage of 12.56 suggests that the presence of many rare taxa (or singletons) drives the total richness estimate upward. This indicates that current palynological counts capture only a small fraction of the original standing vegetation, probably due to taphonomic biases and the "low-fertility" nature of the sediments, which favor the preservation of specific robust grains over more delicate ones. Consequently, although the palynological data broadly support the high-diversity patterns seen in the megaflora, they represent a heavily filtered snapshot of these diverse Eocene communities.

The spore-pollen assemblages indicate rainforests dominated by podocarps followed by southern beeches (Nothofagaceae), and accompanied by other Gondwanan elements such as Araucariaceae, Myrtaceae, and Proteaceae. Podocarps and araucariacean taxa are also well represented in the macrofossil record of the Río Pichileufú flora, whereas Nothofagaceae have not yet been formally identified from leaves or reproductive structures (e.g., Rossetto-Harris & Wilf, 2024). This discrepancy between the macrofossil and palynological records (also seen at Laguna del Hunco) most likely reflects differences in pollen production and dispersal. Extant Nothofagaceae are predominantly wind-pollinated and produce abundant, easily dispersed pollen that may travel well beyond the source vegetation, potentially leading to their overrepresentation in palynological assemblages. Accordingly, although the pollen record clearly demonstrates their presence in the regional vegetation, the absence of macrofossils suggests that southern beeches were probably not a dominant component of the plant communities growing immediately around the depositional site. Additional components of the assemblages are consistent with warm but somewhat seasonal conditions. Thermophilic angiosperms such as palms, *Cupania* (Sapindaceae), and Malvaceae (Bombacoideae) are consistently recorded. Ferns are notably scarce, although tree-fern lineages (*Cyathea*) are present. The low abundance of ferns (ca. 1–3.5%) contrasts strongly with the early Eocene Laguna del Hunco flora (Barreda et al., 2020), where fern spores are five times more abundant and includes a much broader diversity of families—Cyatheaceae, Pteridaceae, Polypodiaceae, Osmundaceae, and Gleicheniaceae—consistent with ever-wet environments. In contrast, the relatively fern-poor assemblage at Río Pichileufú suggests that subhumid or seasonally dry areas were present on the landscape. However, the prevalence of podocarp pollen and diverse podocarp macrofossils at Río Pichileufú, along with other macrofossil rainforest indicators such as *Papuacedrus*, *Agathis*, and Atherospermataceae, indicate the persistence of large areas of rainforest. Comparable patterns, characterized by low fern abundance, have also been documented in the middle Eocene Río Turbio Formation (ca. 40 Ma; Fernández et al., 2021), suggesting that similar environmental constraints may have affected several Patagonian basins during the middle Eocene.

Together with sedimentological evidence, the palynological data support deposition in a well-oxygenated, mesotrophic lake system. The presence of the zygnematacean alga *Spyrogyra* suggests spring lake surface-water temperatures of approximately 20–25 °C (van Geel, 1976; van Geel & van der Hammen, 1978), consistent with warm, but seasonally dry conditions. The exceptional preservation of the RP megafloristic assemblages could have been favored by rapid burial of plant material by episodic, high-sedimentation-rate events associated with landslides from the steep hillslopes of volcanic caldera lakes, as proposed for Laguna del Hunco (Hajek et al., 2025).

Among the most significant taxa recorded is pollen attributable to Barnadesioideae (Asteraceae). Previously, Asteraceae at Río Pichileufú were represented only by a unique inflorescence with associated pollen (Barreda et al., 2010, 2012). The new record represents the oldest known occurrence of crown-group Barnadesioideae, whereas earlier Late Cretaceous occurrences from Antarctica correspond to the stem lineage (Barreda et al., 2015). This finding therefore extends the fossil history of the subfamily and indicates that an early phase of diversification within Asteraceae was underway shortly after the Eocene Climatic Optimum.

Within this framework, the relatively high abundance of Nothofagaceae pollen at Río Pichileufú provides an important signal of broader regional vegetation change. Pollen assignable to the subgenera *Fuscospora* and *Nothofagus* are common, whereas the *brassii*-pollen type occurs only rarely. In the middle Eocene Río Pichileufú flora (ca. 47.5 Ma), the family reaches notable abundances (10–35%), contrasting with its absence in early Eocene assemblages from Nahuel Huapi Este and Pampa de Jones (ca. 54 Ma; Melendi et al., 2003; Wilf et al., 2010). These values exceed those recorded at the early Eocene Laguna del Hunco locality (ca. 52 Ma; ~5%; Barreda et al., 2020) but remain lower than those reported from the apparently younger Confluencia assemblage (middle–late Eocene?, >40%; Báez et al., 1991; Melendi et al., 2003). This progressive increment most likely reflects regional cooling and increasing seasonality following the Early Eocene Climatic Optimum, indicating a gradual expansion of temperate elements in Patagonian vegetation and the transition from ever-wet mesothermal communities toward cooler forest ecosystems.

The presence of Araliaceae, represented by *Rhoipites* cf. *sphaerica*, aligns with the recent macrofossil record of the family from Laguna del Hunco (leaves and an infructescence) and potential leaf occurrences at Río Pichileufú (Wilf, 2025). These fossils, most likely from shrubs or small trees, highlight the persistence of thermophilic rainforest elements and the development of a complex understory within the Eocene Patagonian forests.

Together, the macrofossil and palynological records illustrate complementary aspects of Eocene floristic evolution in Patagonia. The emergence of Barnadesioideae reflects evolutionary innovation and diversification of new lineages under warm conditions, whereas the expansion of Nothofagaceae signals the increasing ecological dominance of temperate Gondwanan elements after the EECO. The occurrences of Araliaceae and several conifers such as *Agathis, Papuacedrus, Dacrycarpus,* and *Retrophyllum* bridge these patterns, indicating the survival of rainforest components amid growing seasonality.

Collectively, these trends emphasize the transitional nature of the Río Pichileufú flora, which captures both the final expression of everwet mesothermal communities and the onset of subhumid, seasonally dry forests that would later dominate southern South America.

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Figure legends

Figure 1. A, B) Location map showing the geographic position of the sampled sections. C) Satellite image of the study area, with the red star marking the location of the outcrops. Image from Landsat/Copernicus 2025; Google Earth, accessed October 2025.

Figure 2. Schematic stratigraphic sections of the Huitrera Formation at the Río Pichileufú locality, showing the location of sampled levels in the two local sections (*Raiguenrayun* (SG) and *Ginkgo* (SG), and correlations (dashed line). Sample (IS) is from the macrofloral locality RP3 of Wilf et al. (2005).

Figure 3. Panoramic view of the Río Pichileufú locality showing the valley and the locations of two sampled stratigraphic sections: *Raiguenrayum* (RS) and *Ginkgo* (GS).

Figure 4. Light microscope (LM) images of selected spores and pollen grains of the Huitrera Formation, Río Pichileufú locality. A) *Biretisporites* sp. MAPBAR 12503b: G32-1. B) *Cyathidites australis* MAPBAR 12506a: G49-2. C) *Kuylisporites waterbolkii* MAPBAR 12504b: W44. D) *Trilites parvallatus* MAPBAR 12505a: P30-3/Q30-1. E) *Trilites tuberculiformis* MAPBAR 12503b: R42. F) *Araucariacites australis* MAPBAR 12505d: J30-4, LM image of specimen in Fig 6J. G) *Dilwynites granulatus* MAPBAR 12506a: E27-3. H) *Dacrycarpites australiensis* MAPBAR 12506a: N40-2. I) *Microcachrydites antarcticus* MAPBAR 12506b: D43. J) *Lygistepollenites florinii* MAPBAR 12506a: R37-2. K) *Podocarpidites* cf. *exiguus* MAPBAR 12505a: J39-2. L) *Podocarpidites marwickii* MAPBAR 12505a: L37. M) *Arecipites minutiscabratus* MAPBAR 12504b: F40-1. N) *Liliacidites regularis* MAPBAR 12506b: S45-4. O)

Striamonocolpites sp. 1 MAPBAR 12503b: X30-2. P) *Striamonocolpites* sp. 2 MAPBAR 12506b: K31-4/K32-3. Q) *Striatopollis* sp. 2 MAPBAR 12506a: R31-3. R) *Psilatricolpites patagonicus* MAPBAR 12502a: P42-1. S) *Psilatricolpites* sp. 1 MAPBAR 12504b: N41-2. T) *Tricolpites anguloluminosus* MAPBAR 12506b: L50-3. U, V) *Tricolpites* sp. 1, U) MAPBAR 12506a: M56-4, V) MAPBAR 12506b: S30-4. W) *Tricolpites* sp. 2 MAPBAR 12506e: M43-1, LM image of specimen in fig. 6A. X) *Polycolpites* sp. MAPBAR 12506b: E56-1, arrows showing the colpi. Y) *Cicotriporites* sp. MAPBAR 12504b: X32. Z) *Plicatopollis wodehousi* MAPBAR 12502a: G40-2. AA) *Propylipollis* sp. MAPBAR 12506a: J28. BB) *Proteacidites* sp. MAPBAR 12506b: O31-4. CC) *Ulmoideipites patagonicus* MAPBAR 12504b: Z49-4. DD) *Cupanieidites reticularis* MAPBAR 12506b: R57-1. Scale bars equal 5 µm, except in figures A, E, F, G, H, J, K, L, and R (10 µm) and figure W (3 µm).

Figure 5. Light microscope (LM) images of selected palynomorphs of the Huitrera Formation, Río Pichileufú locality. (A) *Echitricolporites* sp. 1 MAPBAR 12506b: W48-3, arrow showing os. (B) *Ericipites microtectatum* MAPBAR 12502a: N49-3. (C), (D) *Favitricolporites australis* MAPBAR 12506b: D55-3, same specimen at two focus levels. (E) *Quilembaypollis* sp. aff. *Q. stuessyi* MAPBAR 12506d: O44-2, LM image of specimen in fig 6D. (F) *Rhoipites baculatus* MAPBAR 12502a: N51-1. (G) to (I) *Rhoipites* cf. *sphaerica*, (G) MAPBAR 12506b: S43-4, (H) MAPBAR 12504b: Z58-4, (I) MAPBAR 12506b: N41-3. (J) *Rhoipites* cf. *romeroi* MAPBAR 12505a: K38-4. (K) *Rhoipites* sp. 1 MAPBAR 12504b: W59-3/X59-1. (L) *Rhoipites* sp. 2 MAPBAR 12506b: S47. (M), (N) *Senipites* sp., (M) MAPBAR 12502a: E34-3, (N) MAPBAR 12506d: S40-2, LM image of specimen in fig 6C. (O), (P) *Striatricolporites* cf. *gamerroi* (O) MAPBAR 12506b: M56, (P) MAPBAR 12506d: M41-1, LM image of

specimen in fig. 6N. (Q) to (S) *Striatricolporites* sp. 1, (Q) MAPBAR 12506b: Q56-4, (R) MAPBAR 12506b: S43-1, (S) MAPBAR 12504b: R26-4. (T) *Striatricolporites* sp. 2 MAPBAR 12506a: O34. (U) *Striatricolporites* sp. 3 MAPBAR 12506b: T24-2. (V) *Tricolporites* sp. 1 MAPBAR 12502b: R56-2. (W) *Tricolporites* sp. 2 MAPBAR 12502b: N55-3. (X) *Tricolporites* sp. 3 MAPBAR 12506a: K49-3. (Y) *Nothofagidites fueguiensis* MAPBAR 12502a: U48. (Z) *Nothofagidites flemingii* MAPBAR 12505a: L39-4. (AA) *Nothofagidites saraensis* MAPBAR 12506b: W31-2. (BB) *Baumannipollis* sp. MAPBAR 1256a: U39-4. (CC) *Retistephanocolporites* sp. MAPBAR 12506a: J50-4. (DD) *Spyrogyra* type A of Zamaloa 1996 MAPBAR 12504a: N41-1. Scale bars equal 5 µm, except in figures B–D, S, and W (3 µm) and figures F and DD (10 µm).

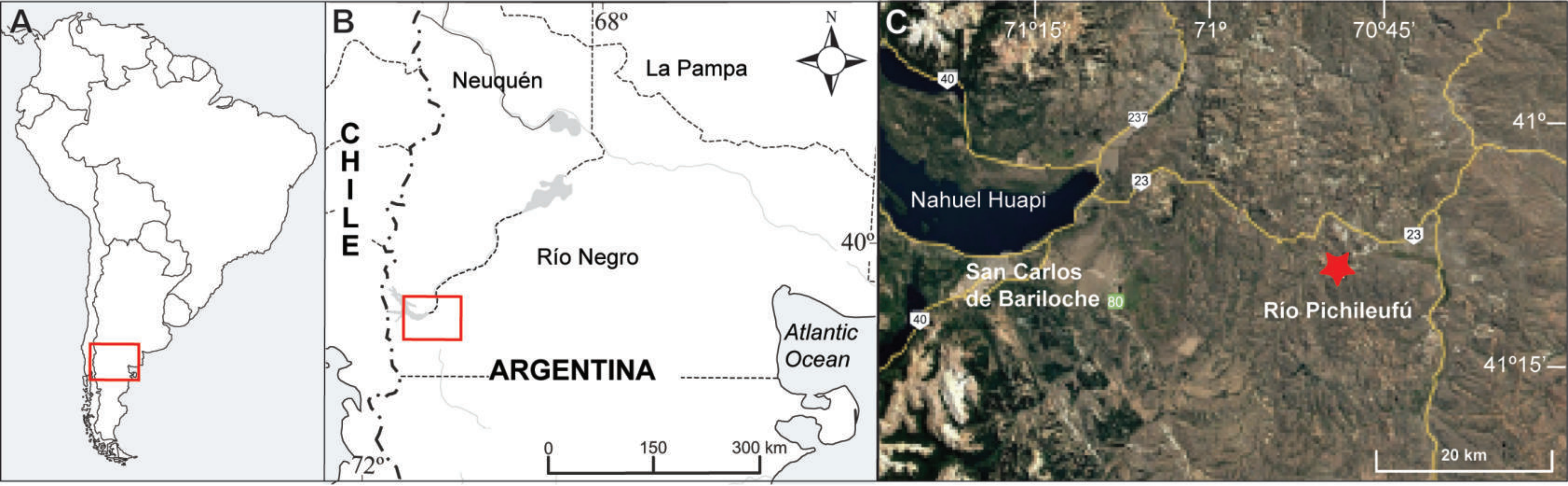
Figure 6. SEM images of selected pollen grains of the Huitrera Formation, Río Pichileufú locality. (A) *Tricolpites* sp. 2. (B), (F) *Rhoipites* sp. aff. *R. muehlembeckiaformis*, (B) general view, (F) details of aperture and sculpture. (C), (G) *Senipites* sp., (C) general view, (G) details of the sculpture. (D), (H) *Quilembaypollis* sp. aff. *Q. stuessyi*, (D) general view of the tetrad, (H) details of a grain with a marked intercolpal depression. (E) *Echitricolporites* sp. 1. (I), (M) *Striatopollis* sp. 1, (I) general view, (M) details of the characteristic segmented muri. (J) *Araucariacites australis*. (K), (P) *Liliacidites regularis*, (K) general view, (P) detail of the reticulate sculpture. (L), (Q) *Arecipites minutiscabratus* (L) general view, (Q) detail of the perforate/ microreticulate sculpture. (N), (O) *Striatricolporites* cf. *gamerroi*, (N) general view, (O) details of the suprastriate/infrareticulate sculpture. Scale bars equal 3 µm in figures A–D and L; 5 µm in figures E, I, K, and N; 1 µm in figures F–H, M, O–Q; and 10 µm in figure J.

Table 1. Species list, nearest living relatives, stratigraphic distributions, counts and frequencies.

Table 2. Palynological and megafloral records from the RP locality. First column: botanical affinity (family, genus); second column: palynomorphs taxa here recorded (only those palynomorphs identified to family or genus level are listed in this table); third to fifth columns: megafossil records —including fossil taxa, fossil type, and references— Only megafossils also identified by palynomorphs are included in the table. Shaded areas indicate absence of fossil record. For further information on megafossils not identified through palynomorphs, in addition to the references cited above, see summaries in Rossetto-Harris & Wilf (2024).

Table 3. Diversity estimates for the analyzed samples from the Huitrera Fm., Río Pichileufú locality, based on spore pollen assemblages (Chao1= Chao richness estimator, SC=1; Expected richness at coverage, SC=0.8).

Table 4. Mean diversity estimates from the RP locality and other units from Patagonia, representing warm climatic intervals. These are: LH locality, Huitrera Fm., Chubut province, —Early Eocene Climatic Optimum—, and Río Turbio Fm. Santa Cruz province, —middle Eocene—, (Chao1= Chao richness estimator, SC=1; Expected richness at coverage, SC=0.8).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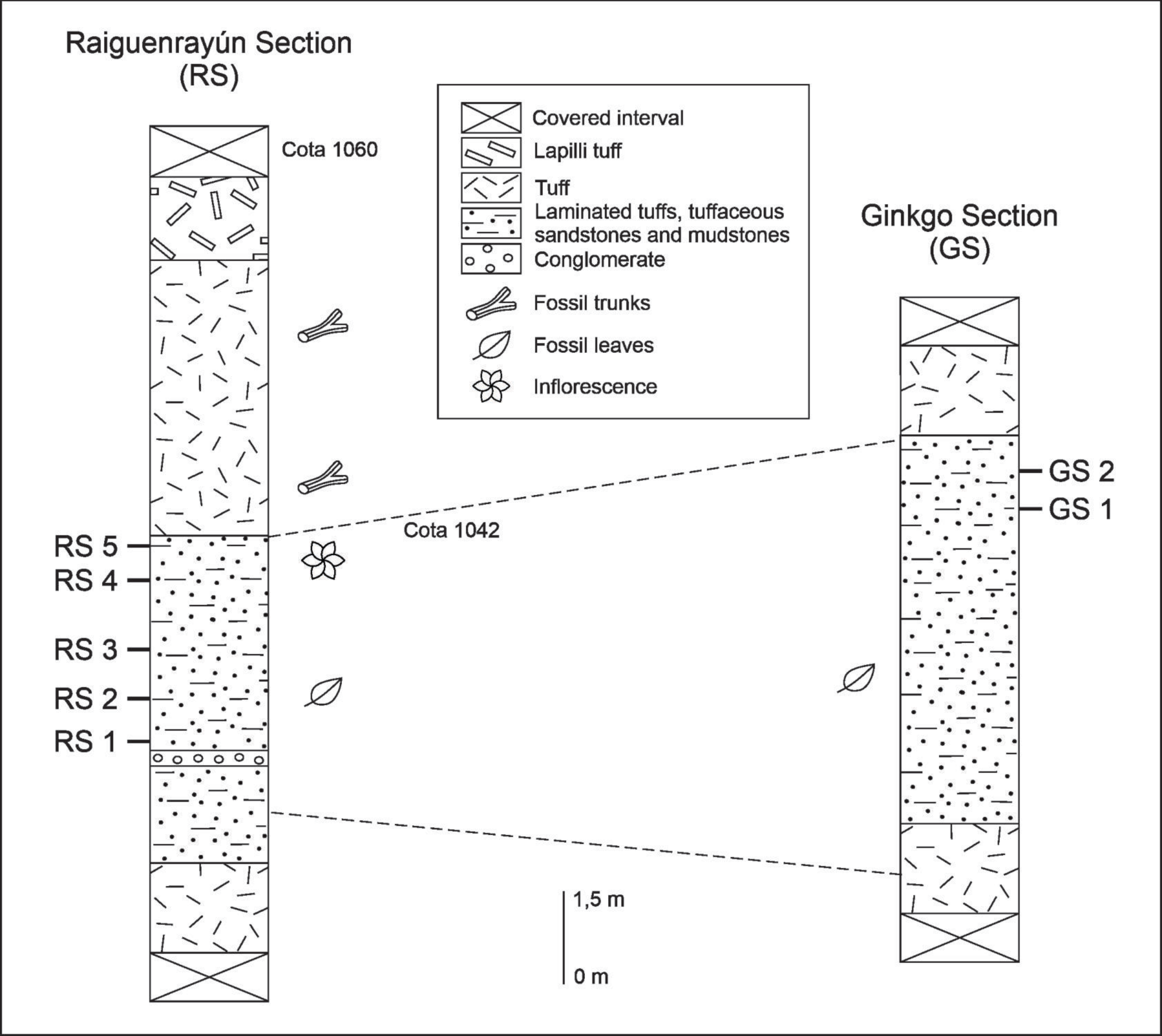
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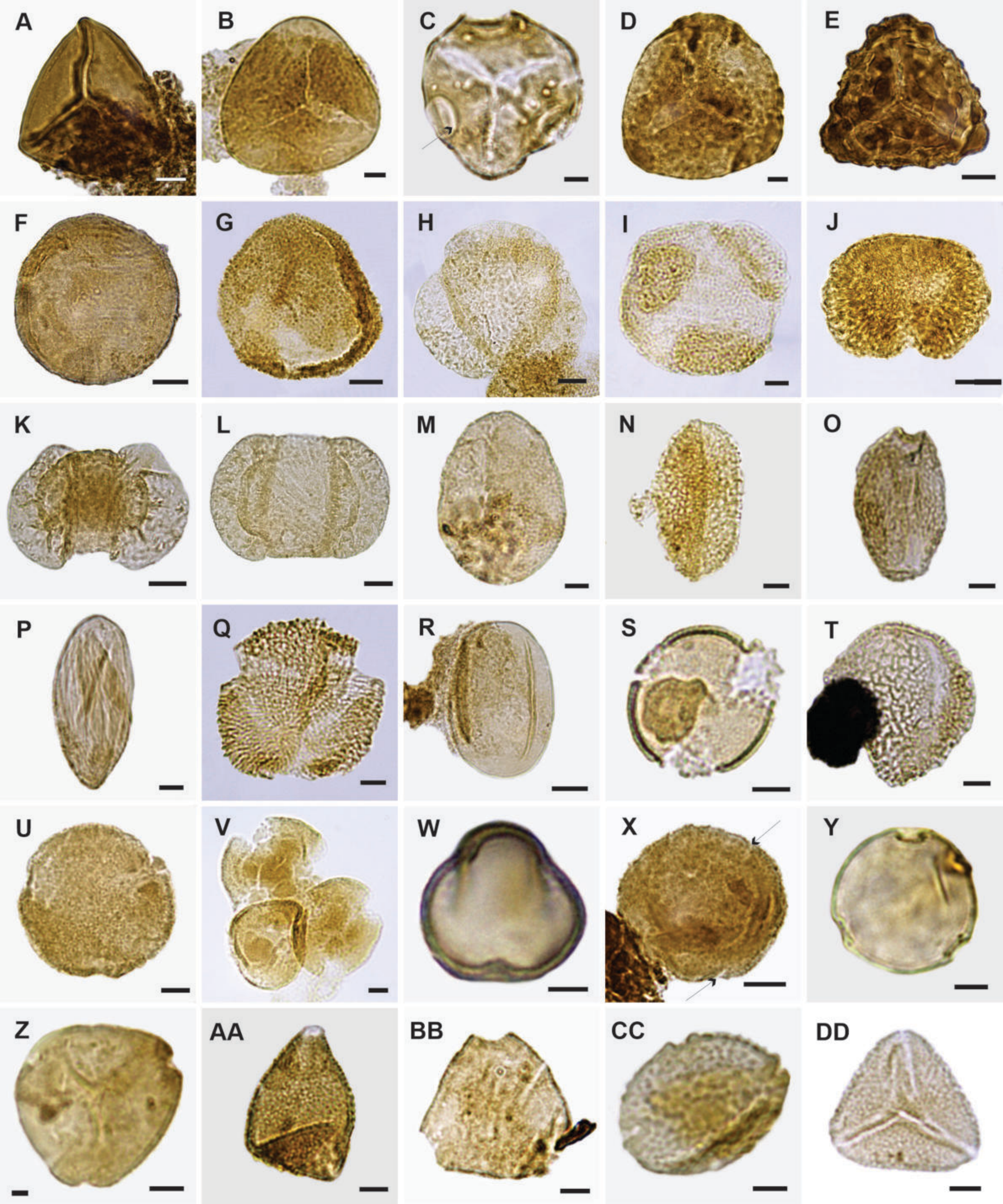
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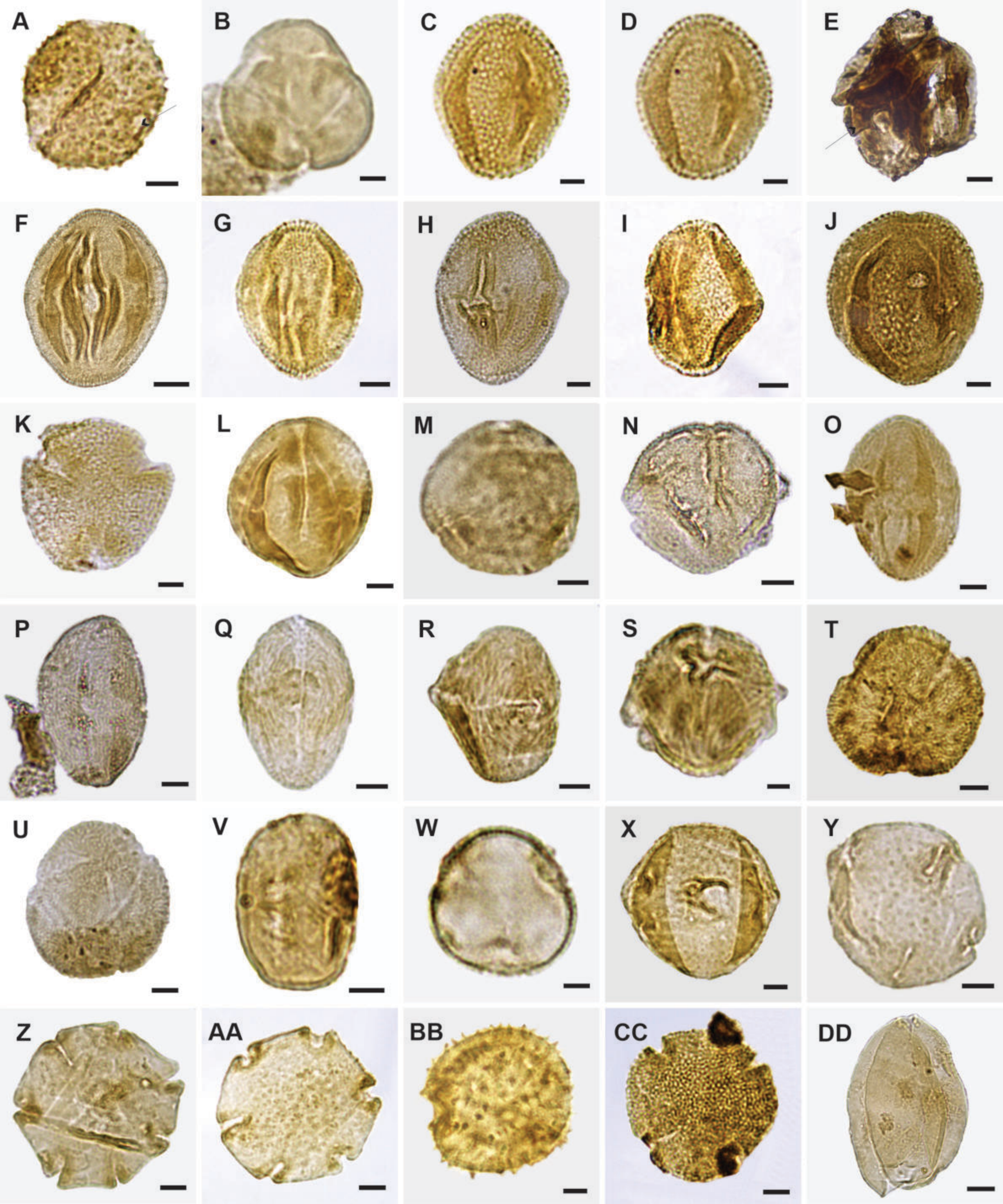
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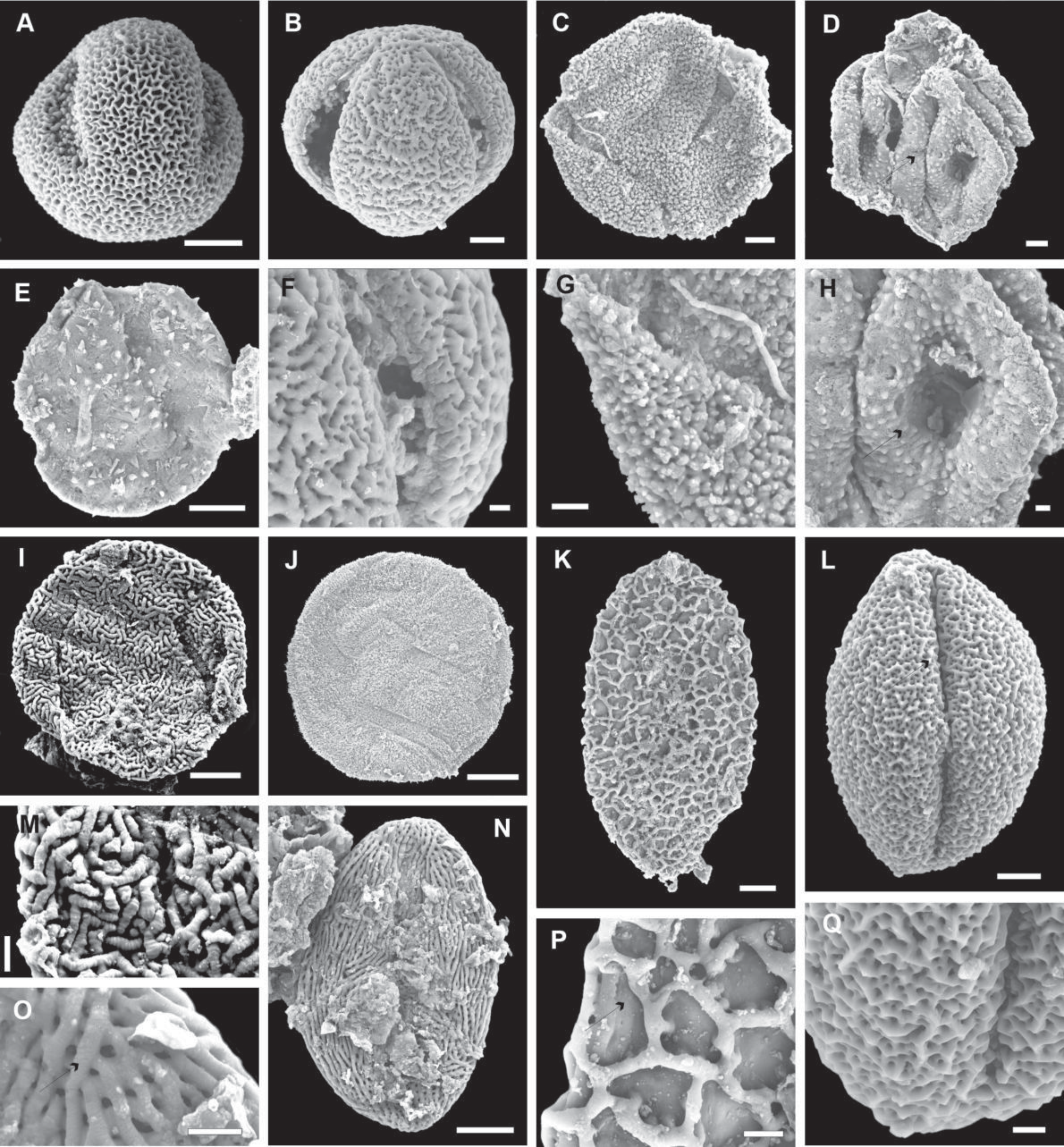
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Fossil taxon	Nearest living relatives	RS1		RS2		RS3		RS4		RS5		GS1		GS2		IS	
		MAPBAR 12500		MAPBAR 12501		MAPBAR 12502		MAPBAR 12503		MAPBAR 12504		MAPBAR 12505		MAPBAR 12506		MAPBAR 12507	
		N°	%	N°	%	N°	%	N°	%	N°	%	N°	%	N°	%	N°	%
Pteridophyte																	
Biretisporites sp. (Fig. 4A)	Schizaeaceae	0	0	0	0	0	0	1	0,26	0	0	0	0	0	0	0	0
Cyathidites australis Couper 1953 (Fig. 4B)	Cyatheaceae?	0	0	0	0	0	0	3	0,78	0	0	3	1,38	8	1,76	0	0
Cyathidites minor Couper 1953	Cyatheaceae?	0	0	2	0	5	1,56	0	0	10	3,01	0	0	5	1,1	0	0
Deltoidospora sp.	Unknown fern	0	0	0	0	3	0,93	0	0	0	0	1	0,46	0	0	2	2,2
Ischyosporites sp.	Cyatheaceae	0	0	0	0	1	0,31	0	0	0	0	0	0	1	0,22	0	0
Kuylisporites waterbolkii Potonié 1956 (Fig. 4C)	Cyatheaceae (*Cyathea*)	0	0	0	0	0	0	0	0	1	0,3	0	0	0	0	0	0
Laevigatosporites ovatus Wilson & Webster 1946	Blechnales	0	0	0	0	0	0	1	0,26	0	0	0	0	2	0,44	0	0
Trilites parvallatus Krutzsch 1959 (Fig. 4D)	Cyatheaceae	0	0	0	0	0	0	1	0,26	0	0	1	0,46	0	0	0	0
Trilites tuberculiformis Cookson 1947 (Fig. 4E)	Cyatheaceae (*Dicksonia*)	0	0	0	0	0	0	3	0,78	0	0	0	0	0	0	0	0
spores total sum and %		0	0	2	0,7	9	2,8	9	2,3	11	3,3	5	2,3	16	3,5	2	2,2
Gymnospermophyta																	
Araucariacites australis Cookson 1947 (Figs. 4F, 6J)	Araucariaceae (*Araucaria*)	0	0	4	1,4	15	4,67	8	2,08	14	4,22	9	4,13	27	5,95	1	1,1
Cycadopites sp.	Cycadaceae/Ginkgoaceae	0	0	0	0	2	0,62	0	0	0	0	0	0	0	0	0	0
Dacrycarpites australiensis Cookson & Pike 1953 (Fig. 4H)	Podocarpaceae (*Dacrycarpus*)	0	0	3	1,05	2	0,62	2	0,52	4	1,2	0	0	5	1,1	0	0
Dilwynites granulatus Harris 1965 (Fig. 4G)	Araucariaceae (*Agathis/Wollemia*)	0	0	1	0,35	2	0,62	2	0,52	2	0,6	0	0	1	0,22	0	0
Lygistepollenites florinii (Cookson & Pike) Stover & Evans 1973 (Fig. 4J)	Podocarpaceae (*Dacrydium*)	0	0	18	6,29	22	6,85	27	7,03	11	3,31	9	4,13	30	6,61	2	2,2
Microcachrydites antarcticus Cookson 1947 (Fig. 4I)	Podocarpaceae (*Microcachrys*)	3	13,6	18	6,29	61	19	30	7,81	36	10,8	19	8,72	29	6,39	7	7,69
Podocarpidites elegans Romero 1977	Podocarpaceae (*Podocarpus*)	5	22,7	53	18,5	41	12,8	64	16,7	48	14,5	32	14,7	67	14,8	13	14,3
Podocarpidites cf. *exiguus* Harris 1965 (Fig. 4K)	Podocarpaceae	0	0	6	2,1	6	1,87	0	0	7	2,11	0	0	0	0	0	0
Podocarpidites ellipticus Cookson 1947	Podocarpaceae (*Podocarpus*)	0	0	34	11,9	0	0	0	0	0	0	0	0	3	0,66	0	0
Podocarpidites marwickii Couper 1953 (Fig. 4L)	Podocarpaceae (*Podocarpus*)	0	0	33	11,5	16	4,98	10	2,6	5	1,51	1	0,46	10	2,2	1	1,1
Podocarpidites microreticuloidatus Cookson 1947	Podocarpaceae (*Podocarpus*)	0	0	22	7,69	57	17,8	68	17,7	35	10,5	38	17,4	44	9,69	1	1,1
Podocarpidites rugulosus Romero 1977	Podocarpaceae	0	0	9	3,15	0	0	9	2,34	3	0,9	0	0	0	0	0	0
Trisaccites microsaccatum (Couper) Couper 1960	Podocarpaceae	0	0	4	1,4	14	4,36	5	1,3	1	0,3	3	1,38	6	1,32	44	48,4
gymnosperms total sum and %		8	36	205	72	238	74	225	59	166	50	111	51	222	49	69	76
Magnoliophyta																	
Arecipites minutiscabratus (McIntyre) Milne 1988 (Figs. 4M, 6L, Q)	Arecaceae	0	0	0	0	0	0	5	1,3	1	0,3	0	0	0	0	0	0

Baumannipollis sp. (Fig. 5BB)	Malvaceae	0	0	0	0	0	0	0	0	0	0	1	0,46	1	0,22	0	0
Cicotriporites sp. (Fig. 4Y)	Cannabaceae	0	0	1	0,35	0	0	0	0	1	0,3	0	0	1	0,22	0	0
Clavatipollenites sp.	Chloranthaceae (*Ascarina*)	0	0	0	0	0	0	0	0	1	0,3	0	0	0	0	0	0
Compositoipollenites sp.	Misodendraceae (*Misodendron)*	0	0	0	0	0	0	1	0,26	0	0	1	0,46	1	0,22	0	0
Cupanieideites reticularis Cookson & Pike 1954 (Fig. 4DD)	Sapindaceae (*Cupania*)	0	0	0	0	1	0,31	0	0	0	0	0	0	1	0,22	0	0
Echitricolporites sp. 1 (Figs. 5A, 6E,)	Solanaceae? (*Latua*?)	0	0	2	0,7	2	0,62	0	0	0	0	4	1,83	2	0,44	0	0
Ericipites microtectatum Archangelsky & Zamaloa 1986 (Fig. 5B)	Empetraceae (*Empetrum rubrum*)	0	0	0	0	1	0,31	0	0	1	0,3	0	0	0	0	0	0
Favitricolporites australis Archangelsky 1973 (Figs. 5C, D)	Unknown eudicot	0	0	8	2,8	2	0,62	1	0,26	4	1,2	3	1,38	2	0,44	4	4,4
Liliacidites regularis Archangelsky 1973 (Figs. 4N, 6K, P)	Liliaceae	0	0	0	0	0	0	0	0	1	0,3	0	0	1	0,22	0	0
Mutisiapollis telleriae Barreda & Palazzesi 2010	Asteraceae (Mutisieae/Carduoideae)	0	0	0	0	0	0	2	0,52	0	0	0	0	0	0	0	0
Myrtaceidites sp.	Myrtaceae	0	0	0	0	6	1,87	1	0,26	0	0	1	0,46	2	0,44	0	0
Nothofagidites acromegacanthus Menéndez & Caccavari 1975	Nothofagaceae (*Nothofagus,* extinct brassii type*)*	0	0	3	1,05	0	0	0	0	0	0	0	0	0	0	0	0
Nothofagidites fuegiensis Menéndez & Caccavari 1975 (Fig. 5Y)	Nothofagaceae (*Nothofagus,* extinct brassii type*)*	0	0	0	0	6	1,87	0	0	0	0	1	0,46	1	0,22	0	0
Nothofagidites flemingii (Couper) Potonié 1960 (Fig. 5Z)	Nothofagaceae (*Nothofagus (Nothofagus*))	2	9,09	5	1,75	7	2,18	26	6,77	8	2,41	18	8,26	57	12,6	0	0
Nothofagidites saraensis Menéndez & Caccavari 1975 (Fig. 5AA)	Nothofagaceae (*Nothofagus (Fuscospora*))	2	9,09	39	13,6	14	4,36	38	9,9	109	32,8	32	14,7	74	16,3	0	0
Plicatopollis wodehousi (Nichols) Fred. & Christ 1978 (Fig. 4Z)	Juglandaceae	0	0	1	0,35	1	0,31	0	0	1	0,3	0	0	0	0	0	0
Polycolpites sp. (Fig. 4X)	Ranunculaceae (*Ranunculus?*)	0	0	0	0	1	0,31	0	0	0	0	0	0	1	0,22	0	0
Propylipollis sp. (Fig. 4AA)	Proteaceae (*Lomatia*)	0	0	0	0	2	0,62	0	0	0	0	0	0	1	0,22	0	0
Proteacidites sp. (Fig. 4BB)	Proteaceae	0	0	1	0,35	2	0,62	0	0	0	0	0	0	2	0,44	0	0
Psilatricolpites patagonicus Freile 1972 (Fig. 4R)	Unknown eudicot	0	0	1	0,35	1	0,31	2	0,52	0	0	0	0	0	0	0	0
Psilatricolpites sp. 1 (Fig. 4S)	Unknown eudicot	0	0	0	0	0	0	1	0,26	1	0,3	0	0	0	0	0	0
Quilembaypollis sp. aff. *Q. stuessyi* Palazzesi & Barreda 2009 (Figs. 5E, 6D, H,)	Asteraceae (Barnadesioideae)	0	0	0	0	0	0	0	0	0	0	0	0	3	0,66	0	0
Retistephanocolporites sp. (Fig. 5CC)	Malvaceae (Bombacoideae)	0	0	0	0	0	0	0	0	0	0	0	0	1	0,22	0	0
Rhoipites baculatus Archangelsky 1973 (Fig. 5F)	Rutaceae?	0	0	1	0,35	2	0,62	0	0	2	0,6	0	0	1	0,22	0	0
Rhoipites cf. *sphaerica* (Cookson) Pocknall & Crosbie 1982 (Figs. 5G, H, I)	Araliaceae (*Pseudopanax*?)	3	13,6	0	0	1	0,31	5	1,3	4	1,2	1	0,46	6	1,32	0	0
Rhoipites cf. *romeroi* Baldoni 1997 (Fig. 5J)	Vitaceae (*Cissus*?)	0	0	0	0	0	0	0	0	0	0	1	0,46	0	0	0	0
Rhoipites sp. aff. *R. muehlenbeckiaformis* Macphail &Truswell 1993 (Figs. 6B, F)	Polygonaceae (*Muehlenbeckia*?)	0	0	1	0,35	0	0	0	0	0	0	0	0	1	0,22	0	0
Rhoipites sp. 1 (Fig. 5K)	Lardizabalaceae (*Lardizabala*?), Araliaceae?	0	0	0	0	0	0	0	0	1	0,3	1	0,46	0	0	1	1,1
Rhoipites sp. 2 (Fig. 5L)	Unknown eudicot	0	0	0	0	0	0	1	0,26	1	0,3	0	0	2	0,44	0	0
Senipites sp. (Figs. 5M, N, 6C, G,)	Symplocaceae?	0	0	0	0	2	0,62	0	0	0	0	0	0	2	0,44	0	0
Striamonocolpites sp. 1 (Fig. 4O)	Unknown angiosperm	0	0	0	0	0	0	1	0,26	0	0	0	0	0	0	0	0
Striamonocolpites sp. 2 (Fig. 4P)	Unknown angiosperm	0	0	1	0,35	0	0	0	0	0	0	0	0	1	0,22	0	0
Striatopollis sp. 1 (Figs. 6I, M)	Sapindales, Simaroubaceae? (*Picramnia*?)	0	0	0	0	0	0	0	0	0	0	0	0	1	0,22	0	0

Striatopollis sp. 2 (Fig. 4Q)	Unknown eudicot	0	0	0	0	1	0,31	0	0	0	0	0	0	1	0,22	0	0
Striatricolporites cf. *gamerroi* Archangelsky 1973 (Figs. 5O, P, 6N, O)	Anacardiaceae	0	0	1	0,35	3	0,93	0	0	0	0	0	0	1	0,22	0	0
Striatricolporites sp. 1 (Figs. 5Q, R, S)	Rosaceae (*Rubus?*)	0	0	1	0,35	1	0,31	0	0	1	0,3	0	0	2	0,44	0	0
Striatricolporites sp. 2 (Fig. 5T)	Gentianaceae?	0	0	0	0	1	0,31	0	0	0	0	0	0	1	0,22	0	0
Striatricolporites sp. 3 (Fig. 5U)	Unknown eudicot	0	0	0	0	0	0	0	0	0	0	0	0	1	0,22	0	0
Tricolpites anguloluminosus Anderson 1960 (Fig. 4T)	Unknown eudicot	0	0	0	0	0	0	0	0	0	0	0	0	1	0,22	0	0
Tricolpites sp. 1 (Figs. 4U, V)	Unknown eudicot	0	0	0	0	0	0	0	0	2	0,6	0	0	7	1,54	0	0
Tricolpites sp. 2 (Figs. 4W, 6A)	Brassicaceae?	0	0	0	0	0	0	0	0	0	0	0	0	1	0,22	0	0
Tricolpites sp. 3	Unknown eudicot	0	0	0	0	0	0	1	0,26	0	0	0	0	0	0	0	0
Tricolporites sp. 1 (Fig. 5V)	Unknown eudicot	0	0	0	0	1	0,31	0	0	0	0	0	0	0	0	0	0
Tricolporites sp. 2 (Fig. 5W)	Unknown eudicot	0	0	0	0	1	0,31	0	0	0	0	0	0	0	0	0	0
Tricolporites sp. 3 (Fig. 5X)	Fabaceae (*Indigofera* ?)	0	0	0	0	1	0,31	0	0	0	0	0	0	1	0,22	0	0
Ulmoideipites patagonicus Archangelsky 1973 (Fig. 4CC)	Ulmaceae	0	0	1	0,35	0	0	1	0,26	2	0,6	0	0	0	0	0	0
Angiosperms total sum and %		7	32	67	23	60	19	86	22	141	42	64	29	181	40	5	5,5
Algae																	
Botryococcus sp.	Botryococcaceae	0	0	1	0,35	1	0,31	3	0,78	1	0,3	0	0	2	0,22	4	4,4
Zygnemataceae Spirogyra type A (Fig. 5DD)	Zygnemataceae	0	0	1	0,35	0	0	7	1,82	6	1,81	3	1,4	9	1,98	1	1,1
Algae total sum and %		0	0	2	0,6	1	0,3	10	2,6	7	2,1	3	1,4	11	2,4	5	5,5
Fungi																	
Fungal spores		7	31,8	10	3,5	13	4,05	54	14,1	7	2,11	35	16,1	24	5,29	10	11
Total sum of palynomorphs		22	100	286	100	321	100	384	100	332	100	218	100	454	100	91	100

Nearest living relatives	Microfossil	Megafossil		
	Fossil genus/species	Fossil genus/species	Type of fossil	References
Pteridophyta				
Blechnales	*Laevigatosporites ovatus*	*"Asplenium" incertum*	Sterile pinnule	Berry, 1938; Rossetto Harris & Wilf, 2024
Cyatheaceae: *Cyathea* , *Dicksonia*	*Kuylisporites waterbolkii, Cyathidites spp., Trilites tuberculiformis, Trilites parvallatus, Ischyosporites* sp.	*"Dicksonia" patagonica*	Sterile and fertile pinnules	Berry, 1938; Rossetto Harris & Wilf, 2024
Schizaeaceae	*Biretisporites* sp.			
Gymnospermophyta				
Araucariaceae: *Araucaria* Sect. *Eutacta*	*Araucariacites australis*	*Araucaria pichileufensis*	Leafy branches, cone scales, pollen cones	Berry, 1938; Rossetto-Harris et al., 2020
Araucariaceae: *Agathis*	*Dilwynites granulatus*	*Agathis zamunerae*	Leafy branches, single leaves, seed cones, cone scales + seeds, pollen cones	Berry, 1938; Wilf et al., 2014; Rossetto Harris & Wilf, 2024
Cycadaceae/Ginkgoaceae	*Cycadopites* sp.	Cycad, *Ginkgoites patagonica*	Leaves	Berry, 1938; Villar et al., 2015; Rossetto Harris & Wilf, 2024
Podocarpaceae: *Podocarpus*	*Podocarpidites* spp.	*Podocarpus andiniformis*	Leafy branches, peduncle of pollen cones	Berry, 1938; Rossetto Harris & Wilf, 2024
Podocarpaceae: *Dacrycarpus*	*Dacrycarpites australiensis*	*Dacrycarpus engelhardti*	Leafy branches	Berry, 1938; Wilf, 2012; Andruchow-Colombo et al., 2023; Rossetto Harris & Wilf, 2024
Podocarpaceae: *Dacrydium*	*Ligistepollenites florinii*			
Podocarpaceae: *Microcachrys*	*Microcachrydites antarcticus*			
Magnoliophyta				
Arecaceae	*Arecipites minutiscabratus*	Monocot insertae sedis	Leaves	Rossetto Harris & Wilf, 2024
Liliaceae	*Liliacidites regularis*	Monocot insertae sedis	Leaves	Rossetto Harris & Wilf, 2024
Juglandaceae	*Plicatopollis wodehousi*	Cf. Juglandaceae or Cunoniaceae	Leaves	Rossetto Harris & Wilf, 2024
Fabaceae	*Tricolporites* sp. 3	*"Cassia"* spp., *"Dalbergia" patagonica* , *"Leptolobium" prenitens, "Inga" patagonica*	Several foliage types	Berry 1938; Rossetto Harris & Wilf, 2024
Proteaceae	*Proteacidites* sp., *Propylipollis* sp.	*Lomatia preferruginea*	Leaves	Berry, 1938; González et al., 2007; Rossetto Harris & Wilf, 2024
Anacardiaceae	*Striatricolporites* cf. *gamerroi*	"*Schinopsis*" *morongifolia*	Several foliage types	Berry 1938; Rossetto Harris & Wilf, 2024
Sapindaceae: *Cupania*	*Cupanieideites reticularis*	*"Cupania" grosse-serrata, Cupania, Paulinia, "Cupania" vernaliformis*	Leaves	Berry, 1938; Rossetto Harris & Wilf, 2024
Myrtaceae	*Myrtaceidites* sp.	*"Myrcia" deltoidea*	Leaves	Berry, 1938; González et al., 2007; Rossetto Harris & Wilf, 2024
Malvaceae	*Retistephanocolporites* sp., *Baumanipollis* sp.	*"Triumfetta" irregulariter-serrata,* cf. *Malvaceae, "Buettneria" asterotrichiformis, Malvacarpus guiñazui*	Leaves, fruits	Berry, 1938; Rossetto Harris & Wilf, 2024; Siegert et al., 2024
Asteraceae: Mutisioideae/Dicomeae/Oldemburgieae	*Mutisiapollis telleriae*	*Raiguenrayun cura*	inflorescence	Barreda et al., 2010; 2012
Asteraceae: Barnadesioideae	*Quilembaypollis* sp. aff. *Q. stuessyi*			
Cannabaceae	*Cicotriporites* sp.			
Chloranthaceae	*Clavatipollenites* sp.			
Ericaceae	*Ericipites microtectatum*			
Symplocaceae?	*Senipites* sp.			
Araliaceae	*Rhoipites* cf. *sphaerica*			
Polygonaceae *Muehlenbeckia* ?	*Rhoipites sp.* aff. *R. muehlenbeckiaformis*			
Rutaceae?	*Rhoipites baculatus*			
Vitaceae: *Cissus*	*Rhoipites* cf. *romeroi*			
Misodendraceae: *Misodendron*	*Compositoipollenites* sp.			
Rosaceae: *Rubus*	*Striatricolporites* sp. 1			
Lardizabalaceae: *Lardizabala* ?	*Rhoipites* sp. 1			
Nothofagaceae: *Nothofagus (Fuscospora) N. (Nothofagus)* N. (extinct pollen brassii type)	*Nothofagidites saraensis, N. flemingii, N. fuegiensis, Nothofagidites acromegacanthus*			

Ulmaceae	*Ulmoideipites patagonicus*			
Ranunculaceae: *Ranunculus* ?	*Polycolpites* sp.			
Gentianiaceae?	*Striamonocolpites* sp. 1			
Brassicaceae ?	*Tricolpites* sp. 2			
Simaroubaceae?: *Picramnia* ?	*Striatopollis* sp. 1			
Solanaceae?: *Latua?*	*Echitricolporites* sp. 1			

Samples	Coverage=0.8	Chao1
RS2	10.73	58.14
RS3	14.08	46.36
RS4	9.46	52.92
RS5	9.42	47.94
GS1	7.99	65.75
GS2	12.56	76.18

Age (Ma)	Geologic Unit	Locality/Province	Coverage=0.8	Chao1
Early Eocene (52)	Huitrera Fm.	Laguna del Hunco, Chubut	18.58	64.70
Middle Eocene (47.5)	Huitrera Fm.	Río Pichileufú, Río Negro	10.70	57.88
Middle Eocene (ca.40)	Río Turbio Fm.	Santa Cruz	17.26	57.71