



# Incursion of tropically-distributed plant taxa into high latitudes during the middle Eocene warming event: Evidence from the Río Turbio Fm, Santa Cruz, Argentina

Damián A. Fernández<sup>a,b,e,\*</sup>, Patricio E. Santamarina<sup>c,e</sup>, Luis Palazzesi<sup>c,e</sup>,  
María Cristina Tellería<sup>d,e</sup>, Viviana D. Barreda<sup>c,e</sup>

<sup>a</sup> Laboratorio de Geomorfología y Cuaternario, CADIC, Bernardo Houssay 200, V9410 Ushuaia, Argentina

<sup>b</sup> Instituto de Ciencias Polares, Ambiente y Recursos Naturales, Universidad Nacional de Tierra del Fuego, Walanika 250, V9410 Ushuaia, Argentina

<sup>c</sup> Sección Paleopalynología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, C1405DJR CABA, Argentina

<sup>d</sup> Laboratorio de Sistemática y Biología Evolutiva, Museo de La Plata, Paseo del Bosque s/n°, B1900FWA La Plata, Argentina

<sup>e</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

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## ABSTRACT

Plant species with predominantly tropical and subtropical modern distributions (or meso-megathermal species) penetrated into the highest southern latitudes of the American continent during the global warmest periods of the Cenozoic. These species – usually phylogenetically unrelated – became fossilized typically as dispersed spores and pollen grains. Here, we describe and illustrate fossil spores and pollen grains preserved during the Middle Eocene Climatic Optimum (MECO) in Patagonian southernmost latitudes (Río Turbio Formation). We study those species that today occurred in lower latitudes (e.g. northern Argentina and Brazil) and became locally extinct from Patagonia during the subsequent cooling episodes. We also estimate their frequency in the paleofloras. Our records show the presence of: *Arecaceae*, *Cardiospermum* (Sapindaceae), *Cathedra* (Olacaceae), *Ceiba* (Malvaceae, Bombacoideae), *Cupania* (Sapindaceae), *Ilex* (Aquifoliaceae), Malpighiaceae, *Spathiphyllum* (Araceae), Trimeniaceae, and tropical ferns, as *Cnemidaria* (Cyatheaceae) and *Lygodium* (Lygodiaceae). The angiosperm families are mostly pollinated by animals, especially insects. We found that these lineages occurred more frequently during MECO samples (~40 Mya) than in older (~44 Mya) and younger (~37 Mya) samples, suggesting that the southern dispersion of tropical elements occurred in waves, following this greenhouse episode. The study of fossil forms assigned to tropical families has previously been neglected in favor of Gondwanan canopy members such as southern beeches and podocarps. Our contribution sheds light into the most underrepresented members of the paleoflora and their key role in past plant–pollinator interactions.

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## 1. Introduction

The Río Turbio Formation (RTF; Leanza, 1972) preserves a unique paleoflora that Romero (1978, 1986, 1993) referred to as “Mixed Paleoflora,” as it combines Neotropical paleofloristic elements with others typical from the sub-Antarctic cold-temperate gondwanic and warm-temperate Chaco forests (Jaramillo and Cárdenas, 2013; Barreda and Palazzesi, 2007; Barreda et al., 2020). This flora evolved during the Paleocene south of 44°S and subsequently expanded north, occupying the entire region south of 24°S, by the middle Eocene (Romero, 1986). The “Mixed Paleoflora” in the RTF developed under a warm-temperate climate, with high annual precipitation and little

seasonal variation, similar to the climate of northeastern Argentina today, but with a high latitude light regime (Panti, 2010; Hinojosa and Villagran, 2005; Jaramillo and Cárdenas, 2013).

A detailed systematic study of the continental sporomorphs from RTF by Fernández (2018) recognized 117 spore and pollen species, 76 of which were recorded for the first time in RTF, represented by 2 bryophytes, 3 lycophytes, 25 ferns, 11 gymnosperms and 76 angiosperms (Supplementary Table 1). Based on the botanical affinities of these palynomorphs, it was possible to reconstruct part of the history of the Eocene vegetation in southwestern Patagonia, as well as infer paleo-environmental conditions, suggest paleobiogeographic aspects, and analyze changes in the diversity of sporomorphs (Fernández, 2018; Fernández and Savoretti, 2020; Fernández et al., 2021). Fernández et al. (2021) recognize the “Middle Eocene Climatic Optimum” (MECO) within this sedimentary unit, based on the presence of key dinocyst species such as *Enneadocysta dictyostila*.

\* Corresponding author at: Laboratorio de Geomorfología y Cuaternario, CADIC, Bernardo Houssay 200, V9410 Ushuaia, Argentina.

E-mail address: [dafernandez@untdf.edu.ar](mailto:dafernandez@untdf.edu.ar) (D.A. Fernández).

This episode of widespread warming was marked by a rise in atmospheric CO<sub>2</sub> concentrations, biotic changes, prolonged carbonate dissolution in the deep ocean and Southern Ocean surface temperature increased as much as 6 °C (Bijl et al., 2010; Sluijs et al., 2013). Previous paleobotanical and palynological studies focused on the Gondwanan elements of the “Mixed Paleoflora” such as Nothofagaceae and Podocarpaceae (Romero, 1977, 1978, 1986, 1993), while the tropical elements have been largely overlooked. Here, we present meso-megathermic taxa recovered from marine rocks in the surroundings of the town of Río Turbio, SW of Santa Cruz province, Argentina, assigned to the RTF (Fig. 1). This contribution aims to: (1) present the taxonomy of pollen grains and spores related to extant groups that grows today mainly in tropical and subtropical areas; (2) analyze changes in the relative frequencies of these groups and their relationship with the increase in the mean annual temperature (MAT) during the MECO; (3) discuss the sensitivity that different groups of plants have as indicators of high mean annual temperatures.

## 2. Methods

### 2.1. Fossiliferous localities

Samples were collected from the shallow-marine RTF in southern Patagonia (Fig. 1). RTF preserves a thick shallow-marine and estuarine succession characterized by sandstones, limestones and conglomerates interbedded with clay horizons accumulated in coastal marine, wave- and tide-dominated shallow water environments (Furque and Caballé, 1993; Rodríguez Raising, 2010). Our high-resolution record encompasses the MECO as well as pre- and post-MECO floras. The spore-pollen bearing sediments are constrained as the mid-late Eocene (~46–34 Myr) based on foraminifera (Malumián and Nájuez, 2002) and dinoflagellate cysts (e.g. González Estebenet et al., 2016a; Fernández et al., 2021). Fernández et al. (2021) generated a CONISS diagram of the samples here studied based on their dinocyst content. Comparing their results with previous biostratigraphic schemes from RTF (González Estebenet et al., 2014, 2015; González Estebenet et al., 2016b) and Australasia (Cramwinckel et al., 2020), they manage to

locate the MECO within the unit. Overall, the RTF preserves poorly diverse dinocyst assemblages, mostly composed by endemic Antarctic (e.g. *Enneadocysta dictyostila*, *Vozzhennikovia apertura*, *Deflandrea antarctica*) and cosmopolitan (e.g. *Turbiosphaera filosa*, *Operculodinium* spp. and *Spiniferites* spp.) taxa. The cluster analysis showed three main groups of samples, with different composition. We follow the three main groups recognized by Fernández et al. (2021): (1) pre-MECO, (2) MECO and (3) post-MECO, clearly identified by dinocyst and spore and pollen grains. In addition, a thick glauconitic level was located within MECO group (between samples 19 and 20 in this paper), recognized as a Maximum Flooding Surface by Rodríguez Raising (2010) and recently dated by Fosdick et al. (2020) to the mid Eocene (41.3 Myr). These data corroborate the correspondence of samples 8–27 with the MECO for the RTF.

Here, we studied pollen samples collected from a ca 300 m thick section spanning approximately 10 million years of the Eocene, in order to better understand the relation between changes in MAT and the frequency of meso-megathermic taxa (Supplementary Fig. 1).

### 2.2. Palynology

A total of 53 samples from RTF were processed. Palynomorph preparations were undertaken at the Museo Argentino de Ciencias Naturales and followed a basic procedure of maceration, chemical digestion of silicates (hydrofluoric acid), fluorosilicates (chlorhydric acid) and a light oxidation to remove excess of amorphous matter (2 min in 70% nitric acid). Residues were sieved with 25 and 10 µm meshes, and finally, concentrated and mounted onto slides following Noetinger et al. (2017) procedures. Fifty-one samples yielded abundant pollen, spores and dinoflagellate cysts. Slides were scanned under a transmitted light microscope Leica DM 500. Sporomorphs were photographed by a Leica camera ICC50 HD. A mean of 342 spores and pollen grains were counted per sample.

### 2.3. Systematic paleontology

Taxonomy, dimensions, occurrence in the RTF, previous records, botanical affinity, geographical distribution of living representatives of

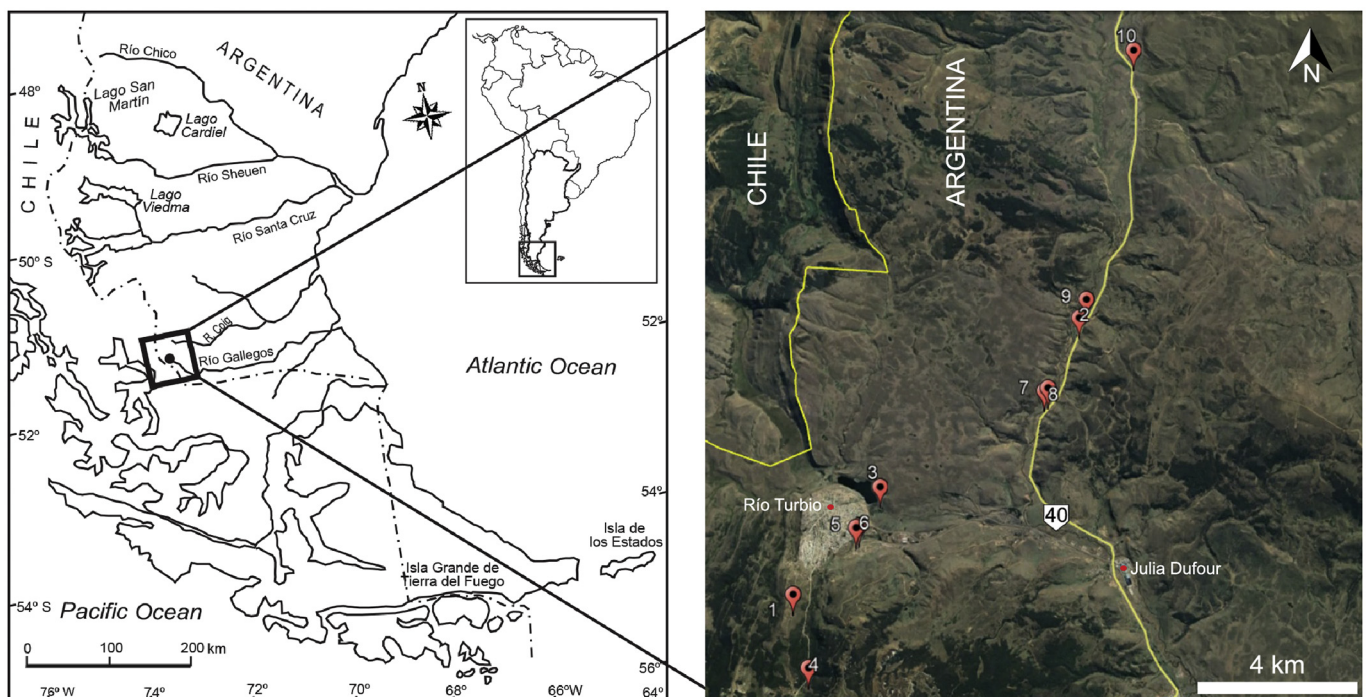


Fig. 1. Location map showing distribution of Eocene sedimentary rocks of the Río Turbio Formation, Santa Cruz Province, Patagonia, southern South America.

specimens with tropical and subtropical affinity, and pollinator and dispersion agents are given. For ferns (excluding *Cicatricosisporites* sp. 4 Archangelsky et al., 1983) only taxonomy, occurrence and their botanical affinity are presented. For more information, see Fernández and Savoretti (2020).

#### 2.4. Quantitative analysis

We arranged spore–pollen data from the RTF in a  $34 \times 117$  matrix with samples and taxa in which each cell contained count data for all taxa of the selected samples (Supplementary Table 1). We conducted a constrained cluster analysis (Q-mode) using this matrix and the ‘chclust’ function of the R package “rioja” (Juggins, 2012), that performs a constrained cluster analysis of a distance matrix, with clusters constrained by sample order. The distance matrix used was the Bray–Curtis metric (Bray and Curtis, 1957) and the agglomeration method was CONISS (Juggins, 2012). The resulting dendrogram is similar to that previously published (Fernández et al., 2021). Presence and frequency diagrams were drawn using TGView 2.0.1 program (Grimm, 2012). Occurrence records of the nearest living relatives (Supplementary Table 2) were queried using iDigBio and GBIF using ridigbio (Michonneau and Collins, 2017) and rgbif (Chamberlain et al., 2021) R packages (R Core Team, 2020), respectively. For those widely distributed taxa (e.g. *Ilex*, *Arecaceae*) we only selected those represented in the American continent. We extracted only data originally georeferenced and excluded any coordinates with zero and/or integer latitude and longitude. We downloaded the global MAT dataset from <https://www.worldclim.org/data/bioclim.html> (BIO1 5 m from BioClim), which represents historical data averaged for the years 1970–2000. We then extracted temperature from each locality record for each taxon using the “extract” function from R package raster (Hijmans, 2021), excluding any points with missing data. We then estimated the MAT for each taxon (Table 1; Supplementary Table 2).

**Table 1**

Meso-megathermal angiosperms and ferns from the RTF, WTI group, botanical affinity and their pollinators/dispersal method. \*with temperate outliers; \*\*without temperate outliers.

Species	Botanical affinity	MAT $\pm$ sd	MAT min - max	Pollinator	Reference
<i>Arecipites minutiscabratus</i>	<i>Arecaceae</i> *	23.7 $\pm$ 2.6	14.6–26.9	Beetles, bees, flies, among others	Barfod et al. (2011)
<i>Arecipites regio</i>	<i>Arecaceae</i> *	23.7 $\pm$ 2.6	14.6–26.9	Beetles, bees, flies, among others	Barfod et al. (2011)
<i>Ilexpollenites anguloclavatus</i>	<i>Ilex</i> sp.*	21.2 $\pm$ 2.9	14.1–26.6	Bees, Diptera	Giberti (1999)
<i>Ilexpollenites cliffdenensis</i>	<i>Ilex</i> sp.*	21.2 $\pm$ 2.9	14.1–26.6	Bees, Diptera	Giberti (1999)
<i>Ilexpollenites megagemmatus</i>	<i>Ilex</i> sp.*	21.2 $\pm$ 2.9	14.1–26.6	Bees, Diptera	Giberti (1999)
<i>Periporopollenites demarcatus</i>	<i>Trimeniaceae</i> *	20.8 $\pm$ 4	13.7–24.4	Hover-flies, sawflies, bees	Bernhardt et al. (2003), Thien et al. (2009)
<i>Psilamonocolpites medius</i>	<i>Arecaceae</i> *	23.7 $\pm$ 2.6	14.6–26.9	Beetles, bees, flies, among others	Barfod et al. (2011)
<i>Anacolisidites diffusa</i>	<i>Cathedra</i> sp.**	25.4 $\pm$ 1	23.9–25.9	Bees and other insects	Lai et al. (2008)
<i>Araceae</i> sp. 1	<i>Spathiphyllum</i> sp.**	24 $\pm$ 1.4	22.2–26.6	Bees, beetles, flies	Dressler (1968), Montalvo and Ackerman (1986), Gibernau (2003), Díaz Jiménez et al. (2019), Hentrich et al. (2010)
<i>Bombacacidites isoreticulatus</i>	<i>Ceiba</i> sp.**	22.4 $\pm$ 1.7	18.8–24.4	Bats, birds, monkeys	Gribel et al. (1999), - Lobo et al. (2005), - Arias et al. (2011)
<i>Cupanieidites insularis</i>	<i>Cupanieae</i> **	23.9 $\pm$ 1.8	20.2–26.8	Bees	Bawa (1977)
<i>Cupanieidites reticularis</i>	<i>Cardiospermum</i> sp.**	22.4 $\pm$ 1	21.1–23.5	Bees and other insects	Morellato and Leitao-Filho (1996)
<i>Perisyncolporites pokorny</i>	<i>Malpighiaceae</i> , <i>Banisteroid</i> group**	23.4 $\pm$ 2.7	23.1–27.1	Bees	Vogel (1990), Sigrist and Sazima (2004)
Species	Botanical affinity			Dispersal	Reference
<i>Crassoretitriletes vanraadshooveni</i>	<i>Lygodium</i> sp.*	21.9 $\pm$ 4.6	12.6–25.5	Wind	Wu et al. (2006), Perrie and Brownsey (2007)
<i>Cicatricosisporites</i> sp.	<i>Anemiaceae</i> **	21.6 $\pm$ 2	18.3–24.1	Wind	Perrie and Brownsey (2007), de la Cruz et al. (2018)
<i>Kuylisporites waterbolkkii</i>	<i>Cnemidaria</i> sp.**	23.4 $\pm$ 1.7	19.7–26.4	Wind	Gómez-Nogues et al. (2017), Perrie and Brownsey (2007)

#### 2.5. Data availability

Slides are housed at the Museo “Padre Jesús Molina” under the catalog numbers 21,647–21,699, prefixed MPM-PB. The authors declare that the data that support the findings of this study are available within this paper and its supplementary information files, and are available from the corresponding author on reasonable request.

### 3. Results

We found 16 (13 angiosperms and 3 ferns) meso-megathermal species preserved in the mid Eocene strata of the RTF. We describe, characterize and illustrate these species and conduct a quantitative analysis to constrain the MAT of the nearest living relatives to support our interpretations. We further present their changes in frequency throughout the entire RTF.

#### 3.1. Systematic paleontology

Ferns

Family: ANEMIACEAE Link, 1841

Genus: *Cicatricosisporites* Potonié and Gelletich emend. Dettmann and Clifford, 1992

Type species: *Cicatricosisporites dorogensis* Potonié and Gelletich, 1933.

*Cicatricosisporites* sp. 4 Archangelsky et al., 1983

Plate 1, 1

Description: LM: Spore, trilete, amb triangular with convex sides. Laesurae straight, extend almost to equator. The radial regions present thickening beyond the ends of the laesurae. In the proximal and distal faces, three to four ribs in each interradial region are observed, parallel to the sides of the spore.

Dimensions: Equatorial diameter 40  $\mu$ m; ribs width 3  $\mu$ m; grooves width 1.5  $\mu$ m; exine 2  $\mu$ m.

**Studied material:** Sample 11 (belonging to the MECO interval).

**Stratigraphic distribution:** This species and related forms have been widely recorded in Argentina (Melendi et al., 2003; Barreda et al., 2012; Clyde et al., 2014) and Colombia (González-Guzmán, 1967; Jaramillo and Dilcher, 2001).

**Botanical affinity:** This morphotype is comparable to the spores of family Anemiaceae (formerly Schizaeaceae) by having trilete laesura and canaliculate exospore with irregular ribs (Dettmann, 1963; Archangelsky et al., 1983; Duarte et al., 2014). Similar morphological features are present in some modern spores of Anemia Swartz (e.g., *A. jaliscana* Maxon and *A. dregeana* Kunze) (Dettmann, 1963). The Anemiaceae are primarily distributed in the neotropics, with a few species in Africa and Madagascar and one in south India and islands in the Indian Ocean (Mickel, 2016; Moran, 2019).

**Remarks:** This fossil species is commonly associated with other meso-megathermal taxa (e.g., Arecaceae, Bombacoideae, *Cupania*, *Ilex*). Goncalves Duarte et al. (2021), analyzed the paleoclimatic and paleoenvironmental conditions in which Anemiaceae grew in the past,

and found that even when the family was documented in a wide range of climates, it prevailed mainly under warm and humid conditions. The spores of the Anemiaceae are dispersed by wind (Table 1).

**Family:** CYATHEACEAE Kaulfuss, 1827

**Genus:** *Kuylisporites* Potonié, 1956

**Type species:** *Kuylisporites waterbolkii* Potonié, 1956

*Kuylisporites waterbolkii* Potonié, 1956

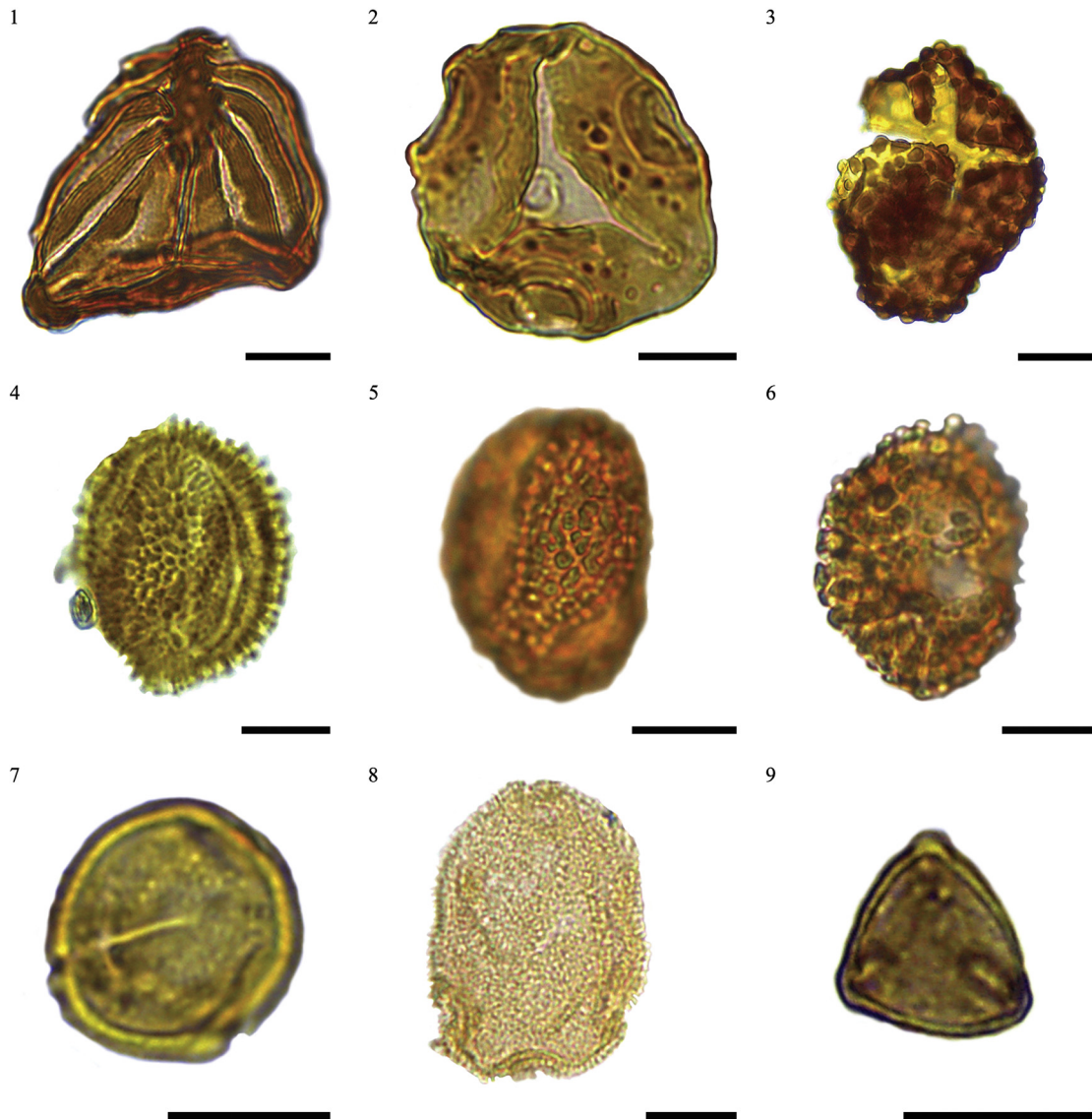
Plate 1, 2

**Description:** LM: Spore, trilete, amb round to triangular-round. Laesurae straight, almost reaching equator. Laevigate. Three large pits are found at the center of the equator of the interradial zones.

**Studied material:** Samples 9 and 22 (all belonging to the MECO interval).

**Stratigraphic distribution:** This species has been found in the southern Gondwanan realm from Late Cretaceous to early Miocene (Mohr and Lazarus, 1994; Fernández and Savoretti, 2020).

**Botanical affinity:** This morphotype is comparable to the spores of genus *Cnemidaria* (Cyatheaaceae) by having trilete laesurae and three



**Plate I.** Meso-megathermal spore-pollen species from the RTF. 1. *Cicatricosisporites* sp. 4, sample 11 E55(2); 2. *Kuylisporites waterbolkii*, sample 09 D18(2); 3. *Crassoretitriletes vanraadshooveni*, sample 12S11(4); 4. *Ilexpollenites anguloclavatus*, sample 13M56(2); 5. *Ilexpollenites cliffdenensis*, sample 16S27(3); 6. *I. megagemmatus*, sample 25 D31(2); 7. *Perisyncolporites pokorny*, sample 3 H11(1); 8. *Bombacacidites isoreticulatus*, sample 16 X38(4); 9. *Anacolosidites diffusa*, sample 30W52(1). Scale bar is 10  $\mu$ m. Taxonomic names are followed by the slide number and England Finder coordinates.

large pits (diameter about 5–7 µm) symmetrically arranged at the center of the spore sides (Mohr and Lazarus, 1994). The geographic range of living *Cnemidaria* covers the area of Central America, the Greater Antilles and the northern part of South America (Mohr and Lazarus, 1994). *Cnemidaria* spores are dispersed by wind (Table 1).

Family: LYGODIACEAE Roemer, 1840

Genus: **Crassorettriletes** Germeraad et al., 1968

Type species: *Crassorettriletes vanraadshooveni* Germeraad et al., 1968

*Crassorettriletes vanraadshooveni* Germeraad et al., 1968

Plate 1, 3

Description: LM: Spore, trilete, amb round. Laesurae straight. Exine heavily verrucate.

Material studied: Samples 8–14; 24–25; 27–28; 34.

Stratigraphic distribution: Species cosmopolite, recorded since Aptian (see White, 2006).

Botanical affinity: This morphotype is comparable to the spores of genus *Lygodium* (Lygodiaceae), by having trilete laesura, medium-large size (50 µm or more), and a sporoderm composed of perispore and exospore. Surface sculpture of *Lygodium* spores ranges from smooth to scabrate, verrucate, rugulate or reticulate (Rozefelds et al., 2017). The spores found in the RTF have a thin scabrate perispore and a ruguloreticulate exospore. *Lygodium* species mainly grow in tropical regions; but there are a few temperate outliers in North America and Japan (Tryon and Tryon, 1982; Wikström et al., 2002). Most living species prefer moist environments, although a few are found in areas with a pronounced dry season (Hanks, 1998). *Lygodium* spores are dispersed by wind (Table 1).

Dicotyledoneae

Family: AQUIFOLIACEAE Bercht. and J. Presl 1825

Genus: **Ilexpollenites** Thiergart, 1937

Type species: *Ilexpollenites iliacus* (Potonié) Thiergart, 1937

Botanical affinity: Genus *Ilexpollenites* is comparable to the pollen grains of actual *Ilex* (Aquifoliaceae) by having tricolporate apertures with poorly defined pores, conspicuous gemmae and clavae of variable size (Martin, 1977b). In present days, most species of the Aquifoliaceae grow in the tropics and subtropics, with a wide distribution in temperate areas of Asia, Europe, Africa (a single species), North and South America, where endemism are prominent (Heywood et al., 2007; Macphail et al., 1994). In Argentina, *Ilex* is restricted to subtropical areas (Zuloaga et al., 2009).

*Ilexpollenites anguloclavatus* McIntyre, 1968

Description: LM: Pollen grain, prolate, amb elliptical. Tricolpate, colpi long and obscured by sculptural elements. Exine sculptured with prominent and thin clavae, with necks slightly narrower than their heads.

Dimensions: Equatorial diameter 23–26 µm; polar diameter 24(32) 37 µm; exine thickness 3–4 µm; clavae height 1(1,6)2,7 µm.

Material studied: Samples 5; 7–18; 20–22; 25–27; 30.

Stratigraphic distribution: This fossil species has been widely recorded from Late Cretaceous to early Neogene in Argentina (Romero and Castro, 1986; Anzótegui and Acevedo, 1995; Povilaukas, 2013), Australia (Macphail, 1999; Stover and Partridge, 1982; Tulip et al., 1982; Truswell and Owen, 1988; Alley and Benbow, 1989; Dettmann and Jarzen, 1990; Martin, 1991; Martin, 1977b; Pocknall, 1991) and New Zealand (Pocknall and Mildenhall, 1984; Raine, 1984; Mildenhall and Pocknall, 1989; Pocknall, 1990, 1991), when tropical climates were more widespread (Pearson et al., 2001; Jenkyns et al., 2004).

*Ilexpollenites clifdenensis* McIntyre, 1968

Description: LM: Pollen grain, prolate, amb elliptical. Tricolpate, colpi long. Exine sculptured with clavae, heads rounded in surface view.

Dimensions: Equatorial diameter 20–29 µm; polar diameter 17(26) 32 µm; exine thickness 1,5(1,6)2 µm; clavae height 0,5(1)1,75 µm.

Material studied: 1; 3; 6; 8; 13; 16–19; 21; 23–24; 28; 32.

Stratigraphic distribution: This species was recorded in Argentina from Eocene to late Pliocene (Romero and Castro, 1986; Anzótegui

and Acevedo, 1995) and in Australia (Martin, 1977a; Owen, 1988; Alley and Benbow, 1989) and New Zealand (Pocknall and Mildenhall, 1984; Raine, 1984) from Eocene to Miocene.

*Ilexpollenites megagemmatus* McIntyre, 1968

Description: LM: Pollen grain, prolate, amb elliptical. Tricolpate, obscured by dense sculptural elements. Exine sculptured by short and strong clavae, with wide necks and broad heads.

Dimensions: Equatorial diameter 28(30)32 µm; polar diameter 30 (33)36 µm; exine thickness 3–3,5 µm; clavae height 1,5–2 µm.

Material studied: 10; 15; 25 (all belonging to the MECO interval).

Stratigraphic distribution: This is the first record of the species for Argentina. *I. megagemmatus* was previously registered in Australia from late Eocene to early Oligocene (Alley and Benbow, 1989) and in New Zealand from late Oligocene to early Miocene (Pocknall, 1982; Pocknall and Mildenhall, 1984; Raine, 1984; Mildenhall and Pocknall, 1989).

Family: MALPIGHIACEAE Jussieu, 1789

Genus: **Perisyncolporites** Germeraad et al., 1968

Type species: *Perisyncolporites pokorny* Germeraad et al., 1968

*Perisyncolporites pokorny* Germeraad et al., 1968

Plate 1, 7

Description: LM: Pollen grain, oblate, amb circular. Tricolporate, with straight colpi and elliptical pores. Exine microreticulate.

Dimensions: Equatorial diameter 21–23 µm.

Material studied: Samples 3 and 23.

Stratigraphic distribution: *P. pokorny* is a species recognized in fossil assemblages from South America and the Caribbean during warm periods from the middle Eocene to Pleistocene (Germeraad et al., 1968; De Porta, 1974; Regali et al., 1974; Doubinger, 1976; de Lima and Salard-Cheboldaeff, 1981; de Lima and Dino, 1984; Escobar, 1984; de Lima et al., 1985; Dueñas-Jimenez, 1986, 1999; Fasola and Paredes De Ramos, 1991; Colmenares and Teran, 1993; Hoorn et al., 1994; Rull, 1997; Jaramillo and Dilcher, 2000). This species was also identified in the late Neogene of Africa (Partridge, 1978; Salard-Cheboldaeff et al., 1992) and the early Oligocene to late Miocene of Australia (Macphail and Truswell, 1989; Macphail and Stone, 2004).

Botanical affinity: The material analyzed resembles species of living Malpighiaceae, especially those of the Banisteroid group (Davis and Anderson, 2010). Fossil forms are similar to some species of the Tetrapterid clade within the Banisteroid, currently present in Northern and central Argentina. They are characterized by a circular to subcircular outline, thin colpoids and a similar number of pores (Fernández et al., 2012). The center of diversity of Malpighiaceae is tropical South America (Anderson, 2004). *Gallardoia fischeri* Hicken (clade Cordobioide also included within the Banisteroide) represents the southernmost penetration of the family in the world, reaching 41° S. That species differs from the specimens here analyzed by showing verrucate sculpture (Fernández et al., 2012). Dispersal of Malpighiaceae pollen grains is by bees (Table 1).

Family: MALVACEAE Juss. 1789

Genus: **Bombacacidites** Couper, 1960

Type species: *Bombacacidites bombaxoides* Couper, 1960

*Bombacacidites isoreticulatus* McIntyre, 1965

Plate 1, 8

Description: LM: Pollen grain, oblate, amb round to triangular. Tricolporate, with short colpi and circular pores. Exine microreticulate.

Dimensions: Equatorial diameter 24(29.7)36 µm; pore diameter 1.5–3 µm; costa 1.5–3 µm; exine thickness 1–2 µm.

Material studied: Samples 9–12; 14; 19; 23 (all belonging to the MECO interval).

Stratigraphic distribution: This fossil species was found in Argentina (Barreda et al., 2012) and New Zealand during warm peaks of the Paleogene (Mildenhall, 1978; Raine, 1984; Raine and Wilson, 1988; Pocknall, 1990). This is the first record of the species for the Eocene of Argentina.

Botanical affinity: These morphotypes are comparable to the pollen grains of genus *Ceiba* (Malvaceae, Bombacoideae) by having circular

amb, tricolporate aperture with short ectoapertures, narrow and circular endoapertures; reticulate exine more or less homobrochate, and muri less than 1  $\mu\text{m}$  wide, simplibaculate. In southern South America *Ceiba* is represented by four species restricted to subtropical areas. *C. speciosa* (A. St.-Hil.) Ravenna is the southernmost species, growing at warm-temperate latitudes, reaching 29°S, in central Argentina (Zuloaga et al., 2009). Dispersal agents of *Ceiba* pollen grains are diverse, including bees, birds and monkeys (Table 1).

Family: OLACACEAE Brown, 1818

Genus: **Anacolosidites** Cookson and Pike ex Krutzsch, 1959

Type species: *Anacolosidites efflatus* (Potonié) Erdtman ex Krutzsch, 1959

*Anacolosidites diffusa* Archangelsky, 1973

Plate I, 9

Description: LM: Pollen grain, oblate, amb triangular. Triporate, pores radially elongated, located near the equator. Exine scabrate.

Dimensions: Equatorial diameter 10  $\mu\text{m}$ .

Material studied: Sample 32.

Stratigraphic distribution: Fossil species commonly found in Argentina during warm peaks ranging from the Late Cretaceous to the Paleocene (Archangelsky, 1976; Papú, 1989; Ruiz and Quattrocchio, 1993, 1996, 1997).

Botanical affinity: The fossil species presents general similarities with the pollen types recognized in *Cathedra* (Olacaceae) by having rounded-triangular amb, tri-diporate (i.e. the apertures comprise three pairs of pores, and the two members of each pair face each other on opposite hemispheres, without any suggestion of an ectocolpus), elliptic pores close to the corner of the grain in polar view, and scabrate exine (Malécot and Lobreau-Callen, 2005). Species of the genus *Cathedra* are exclusively neotropical. Among the five recognized species, only one is

known from wet forests, the other ones are recorded from drier ecosystems (restinga) (Malécot and Lobreau-Callen, 2005). *Cathedra* pollen grains are dispersed by different insect groups, including bees (Table 1).

Family: SAPINDACEAE Juss. 1789

Genus: **Cupanieidites** Cookson and Pike, 1954

Type species: *Cupanieidites mayor* Cookson and Pike, 1954

*Cupanieidites insularis* Mildenhall and Pocknall, 1989

Plate II, 1

Description: LM: Pollen grain, oblate, amb triangular. Tricolpate, colpi bifurcate and unite with adjacent colpi isolating a polar island. Exine reticulate in the mesocolpia, fading to a punctate pattern towards the colpi and poles.

Dimensions: Equatorial diameter 15(15.7)18  $\mu\text{m}$ ; exine thickness 0.6–1  $\mu\text{m}$ .

Material studied: Samples 4; 14; 21; 23; 27; 32.

Stratigraphic distribution: Previously described for the early to middle Miocene of New Zealand (Mildenhall and Pocknall, 1989).

Botanical affinity: The analyzed fossil pollen presents general similarities with the pollen of *Cupania* (Sapindaceae), both being peroblate, isopolar, with 3-syncolporate aperture, and triangular outline in polar view. *Cupania* is distributed mainly in tropical regions (Acevedo-Rodríguez et al., 2017). In southern South America, *Cupania vernalis* Cambess. is the southernmost species of the genus, growing in north-eastern (30°S), Argentina (Zuloaga et al., 2009). Dispersal of *Cupania* pollen grains is carried out by bees (Table 1).

Remarks: This is the oldest record for the species and the first record for South America.

*Cupanieidites reticularis* Cookson and Pike, 1954

Plate II, 2



**Plate II.** Meso-megathermal spore-pollen species from the RTF. 1. *Cupanieidites insularis*, sample 19 C12(2); 2. *Cupanieidites reticularis*, sample 14L19(4); 3. *Periporopollenites demarcatus*, sample 13 I44(4); 4. Araceae sp. 1., sample 5 O34(1); 5. *Arecipites minutiscabratus*, sample 3 Q39(3); 6. *Arecipites regio*, sample 25L36(3); 7. *Psilamonocolpites medius*, sample 6 R30(3). Scale bar is 10  $\mu\text{m}$ . Taxonomic names are followed by the slide number and England Finder coordinates.

**Description:** LM: Pollen grain, oblate, amb triangular. Tricolpate, colpi extend from the equator to the poles, where they fuse. Polar island absent. Exine regularly microreticulate.

**Dimensions:** Equatorial diameter 21(24)26 µm; exine thickness < 1 µm.

**Material studied:** Samples 9; 14; 21 (all belonging to the MECO interval).

**Stratigraphic distribution:** This fossil species has been widely recorded both in Argentina (Barreda and Caccavari, 1992; Barreda, 1996; Barreda, 1997; Barreda and Palamarczuk, 2000; Palamarczuk and Barreda, 2000) and Brazil (Regali et al., 1974; de Lima and Boltenhagen, 1981; Hengreen, 1981; Beurlen and Regali, 1987; Viviers and Regali, 2018) during warm periods of the Late Cretaceous to early Neogene.

**Botanical affinity:** The fossil pollen is similar to that of *C. grandiflorum* (Sapindaceae). Both types are heteropolar, 3-syncolporate, with subtriangular or triangular outline in polar view, and microreticulate exine (Bellonzi et al., 2020). In South America, *C. grandiflorum* is the southernmost species of Sapindaceae, growing in the northern Buenos Aires province, Argentina (Zuloaga et al., 2009). Dispersal of *C. grandiflorum* pollen grains is carried out by bees and other insects (Table 1).

**Family:** ?TRIMENIACEAE Gibbs, 1917

**Genus:** **Periporopollenites** Thomson and Pflug, 1953

**Type species:** *Periporopollenites stigmosus* Thomson and Pflug, 1953

*Periporopollenites demarcatus* Stover and Partridge, 1973

Plate II, 3

**Description:** LM: Pollen grain, spherical, amb round. Pantoporate. Exine microreticulate.

**Dimensions:** Equatorial diameter 28.5(31.2)36 µm.

**Material studied:** 7; 10; 13; 17; 19–21; 27 (most of them belonging to the MECO interval).

**Stratigraphic distribution:** This fossil species has been widely recorded from Maastrichtian to early Miocene in Argentina (Romero and Zamalao, 1985; Romero and Castro, 1986; Baez et al., 1990; Mautino and Anzótegui, 1998; Melendi et al., 2003) and Australia (e.g., Hill, 1984, 1991; Taylor et al., 1990; Carpenter et al., 2007) during warm periods.

**Botanical affinity:** The fossil–pollen resembles those of *Trimenia papuana* Ridley and *T. weimanniifolia* Seeman (Trimeniaceae) by having small pollen grains, spheroidal, with approximately 20 apertures, and a slightly punctate exine (Sampson and Endress, 1984). Extant Trimeniaceae species are distributed in eastern Australia and an island chain stretching from Celebes to the Moluccas, New Guinea, New Caledonia, Fiji, Samoa, and the Marquesas. The family prefers a tropical climate moderated by oceanic influence (Yamada et al., 2008). Trimeniaceae pollen grains are dispersed by a diversity of Hymenoptera groups, including hover-flies, sawflies and bees (Table 1).

Monocotyledoneae

**Family:** ARACEAE Juss., 1789

Araceae sp. 1.

Plate II, 4

**Description:** Pollen grain, subspherical to prolate. Inaperturate. Exine with 20–24 longitudinal ribs, sometimes bifurcated, that converge at the poles.

**Dimensions:** Equatorial diameter 22–24 µm; polar diameter 28–30 µm; ribs width 1 µm; exine thickness 1 µm.

**Material studied:** Samples 5 and 16 (all belonging to the MECO interval).

**Botanical affinity:** The RTF material presents most of the diagnostic features proposed by Hesse and Zetter (2007) for the genus *Spathiphyllum*: sphericity degree and thin and bifurcated ribs. The specimens studied do not have more than 15 ribs per side. Genus *Spathiphyllum* includes 50 species that exhibit a tropical distribution: 47 species are restricted to the Neotropics and the three remaining to the Philippines and Indonesia (Cardona, 2004). A diversity of insect groups are recorded as dispersal agents of Araceae pollen grains, including bees, beetles, and flies (Table 1).

**Family:** ARACEAE Berchtold and Presl, 1823

**Genus:** **Arecipites** (Wodehouse) Nichols et al., 1973

**Type species:** *Arecipites punctatus* Wodehouse, 1933

*Arecipites minutiscabratus* (McIntyre) Milne, 1988

Plate II, 5

**Description:** LM: Pollen grain, prolate, amb elliptical. Colpate, colpus long. Exine scabrate.

**Dimensions:** Greater equatorial diameter 47(52)58 µm; lesser equatorial diameter 31(35)39 µm.

**Material studied:** Sample 6; 13; 22–23 (most of them belonging to the MECO interval).

**Stratigraphic distribution:** Previous fossil records are from Argentina (Romero and Castro, 1986; Herbst et al., 2000; Barreda et al., 2012) and Australia (Milne, 1988; Martin, 1998) during warm periods from Maastrichtian to late Miocene.

**Botanical affinity:** The tectate exine is clearly noted in intermediate focus in *Arecipites* (Plate II, 5). The extended sulcus with pointed apices, as long as the long axis, has high systematic value (Harley, 2006; Harley and Baker, 2001), and broadly links these morphotypes with some living subfamilies in the palm family as Coryphoideae, Calamoideae and Arecoideae. This family grows mainly in tropical regions of the world (Africa, India, China, Taiwan, Vietnam, Indonesia, Sumatra, Thailand, Philippines, Brazil, Central America and Caribbean isles, Colombia, Bolivia, Peru, Argentina). In South America *Trithrinax campestris* (Burmeist.) Drude and Griseb reaches 32°S (Zuloaga et al., 2009) and *Jubaea chilensis* (Molina) Baill reaches 35°S (Gonzalez et al., 2009), growing south of the sub-tropical areas. Dispersal agents of Arecaceae pollen grains include beetles, bees and flies, among other groups (Table 1).

*Arecipites regio* (Van der Hammen and Garcia) Jaramillo and Dilcher, 2001.

Plate II, 6

**Description:** LM: Pollen grain, prolate, amb elliptical. Colpate, colpus long, marginate. Exine foveolate.

**Dimensions:** Greater equatorial diameter 20(25.4)33 µm; lesser equatorial diameter 12(16.5)18 µm.

**Material studied:** Sample 3; 9; 14; 16; 23; 27.

**Stratigraphic distribution:** Fossil species found from late Paleocene to late Eocene of Colombia (González-Guzmán, 1967; Jaramillo and Dilcher, 2001).

**Botanical affinity:** This morphotype is comparable to the pollen grains of family Arecaceae by having tectate exine, monosulcate aperture and finely foveolate surface (Harley, 2006; Nichols et al., 1973).

**Remarks:** This is the first record for Argentina.

**Genus:** **Psilamonocolpites** Van der Hammen and Garcia de Mutis, 1966

**Type species:** *Psilamonocolpites medius* Van der Hammen, 1954

*Psilamonocolpites medius* Van der Hammen, 1954

Plate II, 7

**Description:** LM: Pollen grain, prolate, amb elliptical. Colpate, colpus long. Exine psilate to scabrate.

**Dimensions:** Greater equatorial diameter 15(26.8)40 µm; lesser equatorial diameter 5.5(13)28 µm; polar diameter 6(16.8)22 µm; exine thickness < 1–1 µm.

**Material studied:** Samples 2–4; 6; 8–23; 25–28; 30–34.

**Stratigraphic distribution:** Widely recorded species in South America and Africa (see White, 2006) during warm periods from Early Cretaceous to Pleistocene.

**Botanical affinity:** This morphotype is comparable to the pollen grains of family Arecaceae by having a tectate exine and monosulcate aperture (Harley, 2006).

### 3.2. Quantitative analysis

#### 3.2.1. MAT preference of the taxa analyzed (Table 1)

Taxa here assigned as meso-megathermal include plants whose extant representatives grow today mainly in the tropics and subtropics, although in some cases their range extends beyond these regions. We corroborate that all the taxa analyzed prefer MAT above 20 °C according

to our analysis (Table 1). This temperature corresponds with the meso-megathermal interzone (20–24 °C) according to Nix (1982) and Greenwood (1994), and with the subtropical climate (C) according to Belda et al. (2014) and Reichgelt et al. (2018). Based on the MAT values calculated for each taxa two groups were distinguished: taxa that grow today only in places with MAT above 16 °C (temperate limit sensu Reichgelt et al., 2018) and taxa with some species that grow in areas with MAT lower than 16 °C (Table 1).

3.2.2. Presence of meso-megathermal forms (Fig. 2)

*Psilamonocolpites medius*, *Ilexpollenites anguloclavatus*, *I. clifdenensis*, *Cupanieidites insularis*: Species present in the three groups of samples (pre-MECO, MECO and post-MECO).

*Bombacacidites isoreticulatus*, *Cicatricosisporites* sp. 4, *Cupanieidites reticulatus*, *Ilexpollenites megagemmatus*, *Kuylisporites waterbolckii*: Meso-megathermal taxa present only in the MECO. *B. isoreticulatus*, *C.*

*reticulatus*, *K. waterbolckii* are forms closely related with taxa that grow today only in places with MAT above 16 °C (Table 1).

*Arecipites minutiscabratus*, *Arecipites regio*, *Crassoretitriletes vanraadshooveni*, *Arecaceae* sp. 1, *Periporopollenites demarcatus*, *Perisyncolporites pokorny*: Taxa present almost exclusively in the MECO, with few exceptions in adjacent samples.

*Anacolosidites diffusa*: Unique meso-megathermal taxa exclusive to the Post-MECO.

3.2.3. Pollen diagram. Sum of meso-megathermal forms (Fig. 3)

The sporomorph assemblage consists of abundant angiosperm pollen (25–80%) and ferns spores (10–50%), with gymnosperm pollen as a minor component of the assemblage (10%). Angiosperm pollen are dominated by *Nothofagidites* spp. (mainly *Nothofagus* sg. *Nothofagus*) and *Myrtacidites* spp. (Myrtaceae, Myrtoideae), with *Granodiporites nebulosus*, *Proteacidites* spp. and *Propylipollis* spp. (Proteaceae) as minor elements. Ferns spores are mainly represented by tree ferns

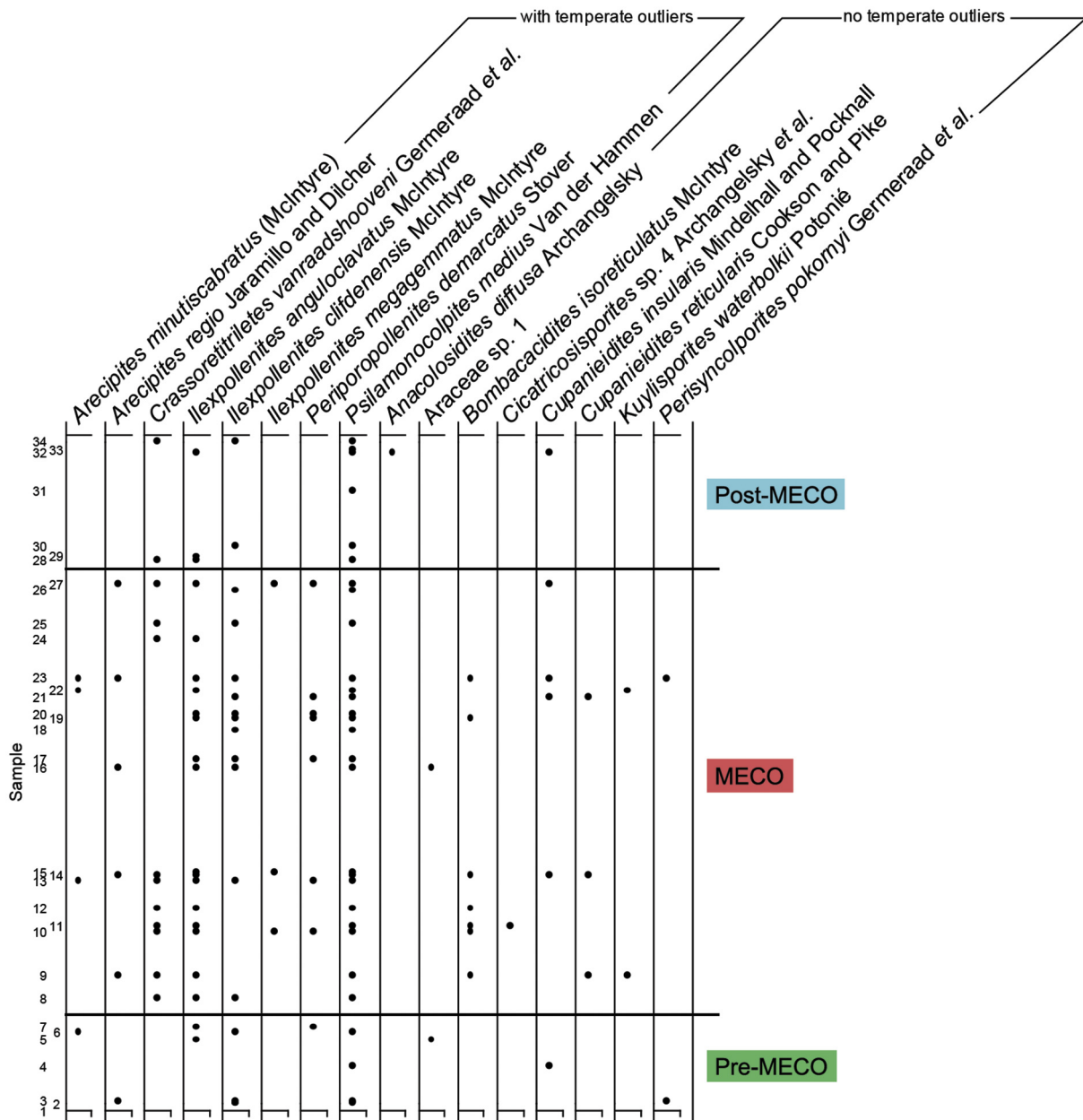


Fig. 2. Presence of meso-megathermal forms along the RTF.



(Cyatheaceae/Dicksoniaceae and Osmundaceae) which consist mainly of *Cyathidites minor* and *Trilites* spp. and to a lesser extent, of *Cyatheacidites annulatus* and *Baculatisporites* spp. Saccate pollen are mainly represented by *Podocarpidites* spp. and *Phyllocladidites mawsonii* (Podocarpaceae); other gymnosperm is *Araucariacites australis* (Araucariaceae, Araucaria). At the beginning of the MECO ferns increase from ~30% to ~60% while angiosperms decrease dramatically from ~70% to ~30%. Also Podocarpaceae increase from ~5% to ~20% and tropical groups from ~2% to ~6%. At the core of the MECO ferns drop to a minimum, while angiosperms become dominant (80%). Apart from the dominant lineages (i.e. *Nothofagus*, Podocarpaceae and Dicksoniaceae), other gondwanan families (e.g. Myrtaceae and Proteaceae) became important elements (Fig. 3). Meso-megathermal forms are present throughout the entire RTF, although in low frequency. Their higher peaks of abundance and diversity are observed only within the MECO (Figs. 2–3). At the end of the MECO (samples 18–23) ferns rise again to maximum values (ca. 60%) while angiosperms and meso-megathermal groups decrease at the same time. Post-MECO ferns decrease towards the top while Podocarpaceae remains abundant and a drop of tropical forms diversity (~40%) is recorded (Fig. 3).

#### 4. Discussion

Our work shed light into the southward dispersion events of species with tropical to subtropical modern distribution into the sub-Antarctic realm during global greenhouse periods. These dispersion events appear to have occurred more than once across the Cenozoic (Hinojosa and Villagran, 2005; Barreda and Palazzesi, 2007; Jaramillo and Cárdenas, 2013). However, from the mid Miocene and onwards, cooling and arid conditions in southern Patagonia forced these species along with others to migrate northwards (mostly megathermal species) and westwards (mostly Gondwanan species) (Barreda and Palazzesi, 2007). The presence of key species and the sum of meso-megathermal forms indicate that the group of samples accumulated during the

MECO preserves significantly more meso-megathermal species than the pre- and post-MECO group of samples (Figs. 2–3). The most direct evidence is the presence of meso-megathermal taxa, such as *Bombacacidites isoreticulatus* (Malvaceae, Bombacoideae), *Cupanieidites reticulatus* (*Cardiospermum* sp.), *Ilexpollenites megagemmatus* (*Ilex* sp.), which exclusively occur in MECO samples. Almost 67% of the meso-megathermal taxa described are exclusive or almost exclusive to the MECO sample group. This is congruent with the increase in pollen diversity (ca. 40%) reported by Fernández et al. (2021) for the MECO group of samples and with the peak of mammalian diversity described by Woodburne et al. (2014) for southern Patagonia. Interestingly, the nearest living relatives of those three meso-megathermal taxa exclusively recorded across the MECO (e.g. *Cardiospermum*, *Ceiba*, *Ilex*) co-occur today in Misiones and Yungas (Zuloaga et al., 2009) (northern Argentina, subtropical climate), about 3000 km up north from where they were found in mid Eocene sediments.

The presence of palms (Arecaceae) (preserved as *Psilamonocolpites medius*) throughout the RTF suggests that the minimum temperature of the coldest month (CMMT) was higher than 2–8 °C and most likely frost-free (Reichgelt et al., 2018). Although Papadakis (1978, 1980) considers climate without frost as “tropical” (megathermal), in more recent climate classifications frost-free does not immediately mean tropical or megathermal climate (Belda et al., 2014).

We quantitatively corroborate the MAT estimations of the groups, traditionally assumed as indicative of tropical conditions in the fossil record. We recognized two groups: one with temperate outliers (e.g. Arecaceae, *Ilex* sp., *Lygodium* sp., Trimeniaceae; MAT lower than 16 °C sensu Reichgelt et al., 2018; Table 1) and another without species from temperate areas (e.g. *Cathedra* sp., *Spathiphyllum* sp., *Ceiba* sp., Cupanieae, *Cardiospermum* sp., Banisteroid group, Anemiaceae, *Cnemidaria* sp.; Table 1). These analyses support a higher MAT in MECO samples in contrast to pre- and post-MECO sample groups.

It is important to note that all the meso-megathermal taxa belonging to angiosperms are pollinated by insects (e.g., bees, beetles, flies) and

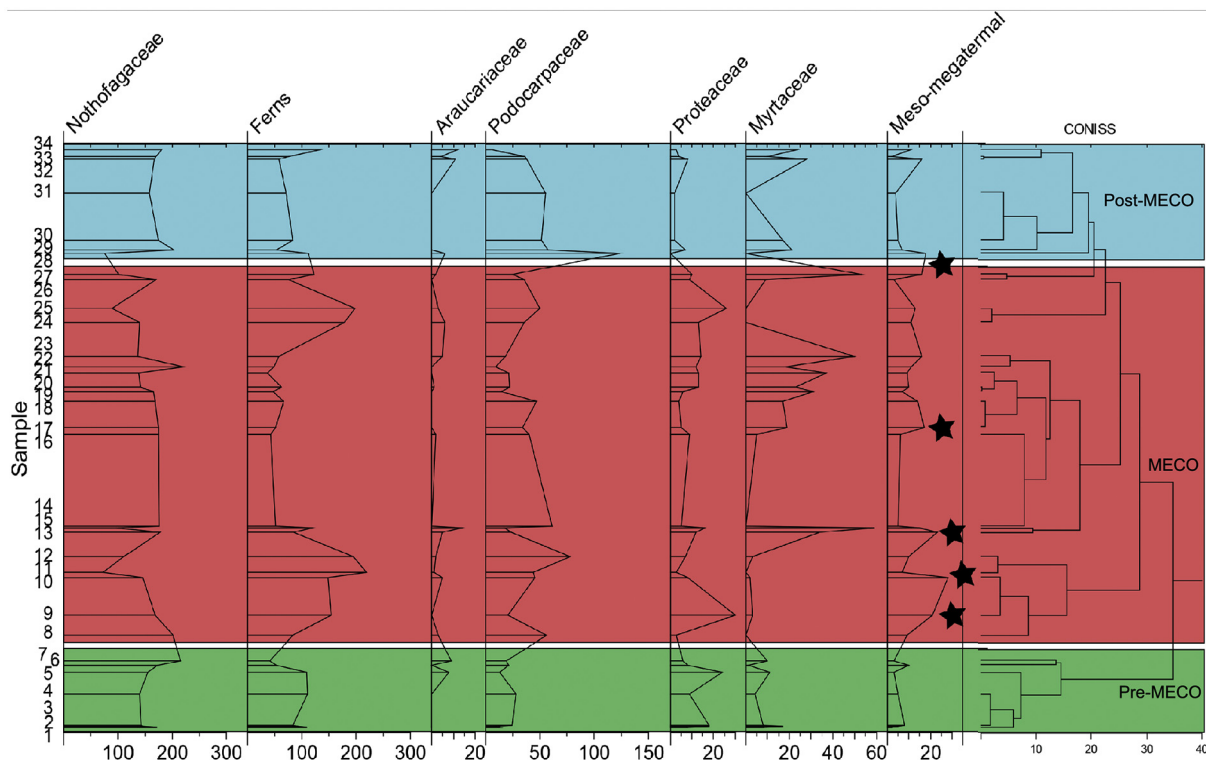


Fig. 3. Relative frequency of the most common plant groups and sum of meso-megathermal forms. Stars indicate peaks of abundance.

other animals (e.g., bats, birds). (Table 1). The great diversification of insects recorded during the Eocene (Wilf and Labandeira, 1999; Engel, 2001; Wilf et al., 2005; Curran et al., 2008; Nyman et al., 2012), may have played an important role in the dispersion of these taxa to southern latitudes. The insect diversity values recorded for the Eocene in high latitudes on both hemispheres are comparable to those in present day tropical forests (Archibald et al., 2010).

## 5. Conclusions

We present the taxonomy of pollen grains and spores related to extant groups that grow today mainly in tropical and subtropical areas. The species *Bombacacidites isoreticulatus* and *Arecipites regio* are new records for Argentina; *Ilexpollenites megagemmatus* and *Cupanieidites insularis* are new records for South America, and the record of *C. insularis* also represents the oldest record of this species.

Nearly 70% of the meso-megathermal taxa described here are exclusive or almost exclusive to the MECO. This group of samples shows peaks of abundance of meso-megathermal forms.

We consider that, among all the meso-megathermal forms studied, the ones with the greatest weight as indicators of high MAT are *Cardiospermum*, *Cathedra*, *Ceiba*, Cupanieae, Malpighiaceae (Banisteroid group) and *Spathiphyllum*. According to our estimates using the GBIF database, these taxa do not represent American species that grow with MAT below 16 °C.

The presence of pollen related to palms throughout the RTF would indicate that a climate without frosts had prevailed. The presence of an assemblage of meso-megathermal forms and their frequency support a higher MAT in MECO samples in contrast to pre- and post-MECO sample groups. This is consistent with previous studies using leaf physiognomic analyses (Hinojosa and Villagran, 2005; Panti, 2010) and paleotemperature databases (Jaramillo and Cárdenas, 2013).

RTF preserves a unique flora, evidence of an extinct biome, and also sheds light into the understanding of the relationship between past floras and paleoclimate. The study of fossil forms assigned to tropical families has previously been neglected in favor of large and more typical members of the flora such as the Gondwanan canopy members (e.g. southern beeches and podocarps) (Romero, 1977, 1978, 1986, 1993), which include anemophilous groups greatly represented in Southern Hemisphere assemblages. Our contribution also highlights the role of the underrepresented members of the paleoflora and their importance in past plant–pollinator interactions. It also increases our understanding of past southern South American biotas before the onset of the Antarctic glaciation during the early Oligocene.

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## Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Declaration of Competing Interest

None.

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