# Quantitative Analysis of Cenozoic Palynofloras from Patagonia, Southern South America

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# Quantitative analysis of Cenozoic palynofloras from Patagonia, southern South America

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The statistical analysis of published Paleocene–Late Miocene palynological data from Patagonia supports several major stages of vegetation. These stages represent distinctive floral assemblages, both in composition and structure. Detrended correspondence analysis shows that during the Paleocene, southern South America was dominated by Australasian, Neotropical and Pantropical phytogeographical elements (Gondwanic paleoflora). The climate was warm and very humid. The Early Eocene was dominated by Neotropical and Pantropical taxa (Subtropical Gondwanic Paleoflora) and a reduced proportion of Australasian and a low proportion of Antarctic elements. The Middle Eocene and Oligocene were characterized by the 'Mixed Paleoflora' with the exception of the Sloggett Formation. The climate was less humid due to the onset of the Antarctic glaciation. The presence of Antarctic palynomorphs (Nothofagaceae, Podocarpaceae, Proteaceae) in Patagonia is consistent with the global cooling trend during the Late Eocene and Early Oligocene. By the Late Oligocene–Early Miocene, warm climates allowed the southward dispersal of Neotropical elements (palms, *Cupania*, *Alchornea*, Rubiaceae, Combretaceae), adding megathermal elements to the local Gondwanic floras. The appearance of some Neotropical families (Symplocaceae, Euphorbiaceae *Alchornea*) may indicate the Late Oligocene global warming event. The rise of xerophytic and halophytic shrubby-herbaceous elements (Convolvulaceae, Asteraceae, Poaceae, Chenopodiaceae and Ephedraceae) during the Late Oligocene, becoming more abundant during the Early Miocene began to give a modern appearance to plant communities. The Early–Middle Miocene corresponds to the Transitional Paleophytogeoprovince of central and southeastern Argentina, defined by a mix of Neotropical and Austral components. The Middle–Late Miocene was characterized by the final demise of megathermal elements in Patagonia, coupled with an increasing diversity and abundance of xerophytic adapted taxa, including Asteraceae, Chenopodiaceae and Convolvulaceae. Late Miocene vegetation was similar to the present vegetation, with the steppe expanded across extra-Andean Patagonia and the forest restricted to western areas where rainfall was still abundant.

**Keywords:** Cenozoic; southern South America; Patagonia; palynofloras; statistics

## 1. Introduction

The evolution of Patagonian floras was characterized by major and often abrupt changes during the Cenozoic. Here we review the compositional changes of Cenozoic palynomorph assemblages in Patagonia, the succession of phytogeographical scenarios and some evolutionary key events using modern information and multivariate statistical analysis.

Our analysis supports several major stages of vegetation over the Cenozoic. These stages represent distinctive floristic assemblages, both in composition and structure. The present paper discusses the phytogeographical areas that could have existed during the Cenozoic, and the climate under which they developed. Marine transgressions during that time in Patagonia are also considered.

Patagonia corresponds to the geographical region east of the Andean Range extending between the Río Colorado (35°–36° S), a major river descending from the eastern side of the Andes to the Atlantic Ocean, and Cape Horn, the southernmost point of South America (56° S) (Figure 1).

Patagonia is a unique region as it is the only landmass in the world (except Antarctica) that extends south of ~40° S, completely surrounded by sea (Cavallotto et al. 2011). Geologically, the area is characterized by a mosaic of Paleozoic cratons and Mesozoic rift basins related to the opening of the South Atlantic Ocean, and it is bounded to the west by the Patagonian Andes, of highly complex lithological, structural and geomorphological nature and history (Rabassa 2008).

The rising Andes Range had a marked influence on climate patterns, and has a profound influence on biotic distributions (Hinojosa & Villagrán 1997; Villagrán & Hinojosa 1997; Sepulchre et al. 2010; Folguera et al. 2011; Le Roux 2012). Andean uplift and a drop in global temperature contributed to the development of extreme aridity, and climates with stronger seasonality in eastern areas. This deeply differentiated the Andean from the

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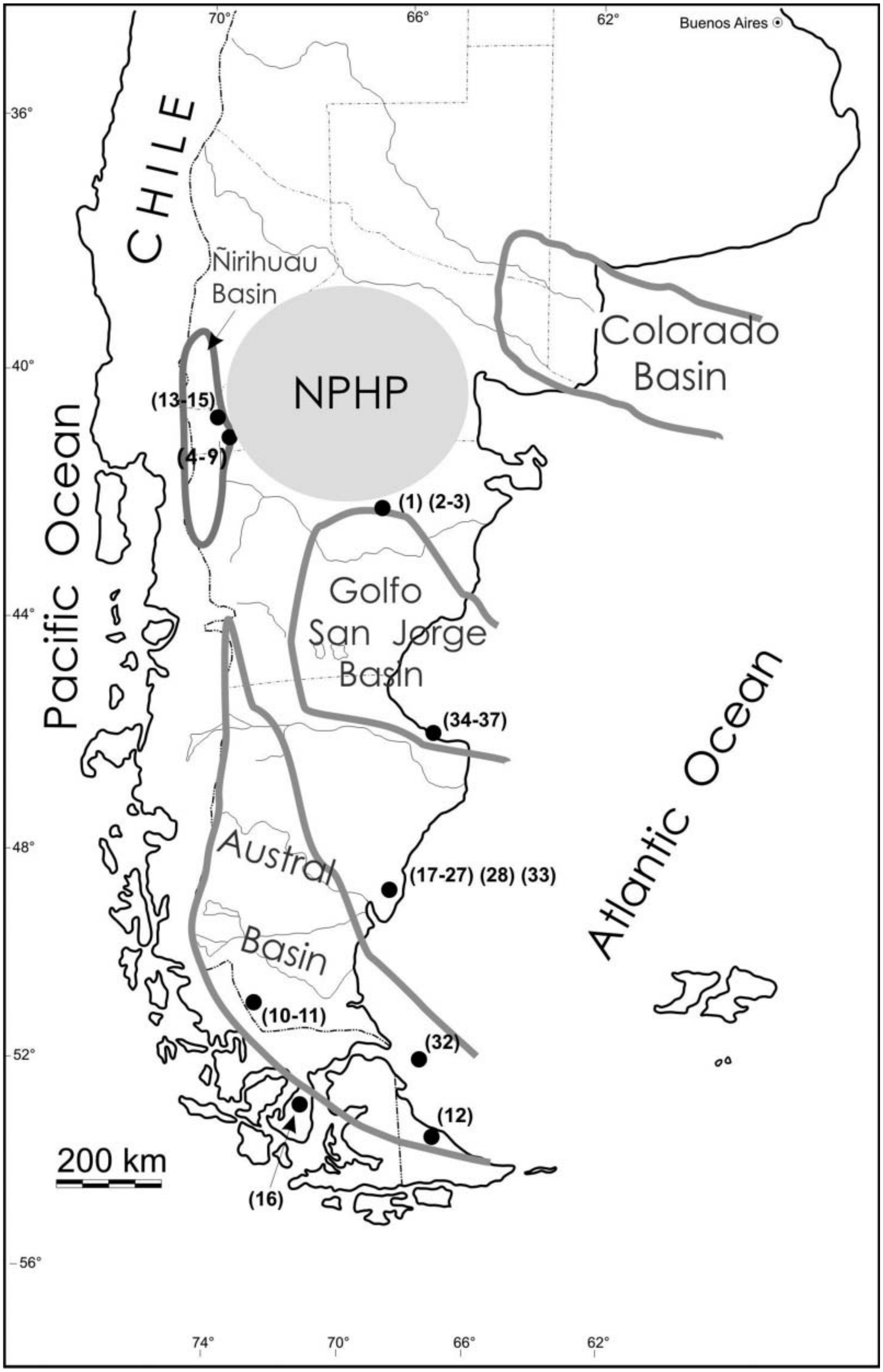

Figure 1. Map of Argentina indicating the sedimentary basins and localities described in the text. NPHP: North Patagonian High Plateau.

Extra-Andean regions with a spinose steppe in the Extra-Andean region and cold temperate forests restricted to more humid heights at the foot of the Andes.

The structure of the living Patagonian flora, dominated by the steppe, is a direct consequence of past climatic and tectonic events. These arid-adapted communities were widespread during the Late Neogene, but their origin in Patagonia can be traced back to the Paleogene (Barreda & Palazzesi 2007).

Despite past tectonic changes throughout the last 250 Ma, Patagonia has generally been situated within the latitudes influenced by the westerlies. Now, this area is bounded by both semi-permanent Pacific and Atlantic anticyclones to the north, and a low pressure belt centered at approximately 60° S (Campagnucci 2011). Due to the orographic effect of the Patagonian Andes, the flux of the westerlies (which advect moist air from the Pacific Ocean and bring precipitation) discharges water on the western sector of the Cordillera (up to 7000 mm at the coast) leaving dry air to the east, where precipitation is less than 400 mm (Campagnucci 2011; Le Roux 2012).

In the present contribution we compile and quantitatively analyze the palynological record of Patagonia during the Cenozoic, and compare it with both climatic and paleobotanical models proposed for the southern South American biotas.

## 2. Methods

The palynological data analyzed was taken from a vast area, ranging from 38° S to 54° S. The assemblages considered in the matrixes (see Appendix 1, supplemental online material) includes the Cerro Bororó and Salamanca formations (Danian); the Huitrera and Río Turbio formations (Eocene); the Sloggett, Loreto and Troncoso formations (Late Eocene–? Early Oligocene); the Salto del Macho and Río Foyel formations, the 'basal muddy section' of the San Julián Formation (Oligocene); the San Julián Formation (playa La Mina) and the Río Leona Formation (Late Oligocene); the Aries x-1 well, (Late Oligocene–Early Miocene; and the Monte León and Chenque formations (Early–Middle Miocene). Only sporomorphs which are well described and illustrated were considered, and comprise a total of 224 species. Detrended Correspondence Analysis (DCA) was then used to relate the presence/absence of sporomorphs from different localities throughout the Cenozoic (ter Braak & Smilauer 1998). A range-through analysis was done to avoid distortion by facies control on fossil abundances.

The axis positions for each locality obtained from the first two DCA axes were then incorporated into a cluster analysis. Cluster analysis was performed with a Euclidean distance between localities, constrained by age. A bootstrap analysis (Manly 1991) and 1000 permutations to estimate the significance of each main clade were carried out.

Finally, we discuss the cluster results compared with paleoclimatic (mean annual temperature, MAT) estimates obtained by Leaf Margin Analysis (LMA), using the equations of Peppe et al. (2011) and Hinojosa et al. (2011). We used both equations as they represent the minimum and maximum estimates of MAT, because they consider the phylogenetic constraints associated with leaf margin character (Hinojosa et al. 2011). Leaf margin data used for LMA are from several sites including Ligorio Marquez, Laguna del Hunco and Palacio de los Loros among others (Hinojosa 2005; Wilf et al. 2005; Hinojosa et al. 2006; Iglesias et al. 2007.

## 3. Results

### 3.1. *Detrended Correspondence Analysis*

The total inertia (sum of all eigenvalues) for the DCA was 3.0, and the first two DCA axes explained 25.2% of the total variance (Figure 2). Paleocene palynofloras (1–3) comprise the association of Podocarpaceae, Olacaceae, Ulmaceae, Symplocaceae and Pandanaceae, among others. Early Eocene palynofloras (4–9, Figure 2) are characterized by the co-ocurrence of Olacaceae, Proteaceae and Juglandaceae. There is an important shift during the Middle Eocene with the common presence of *Nothofagus* in several localities including Río Turbio (10–11), and the association with Aquifoliaceae. Late Eocene to Oligocene palynofloras (12–32) represent a stable association composed of Podocarpaceae, Nothofagaceae, Myrtaceae and Proteaceae. Finally, Late Oligocene–Miocene palynofloras (33–37) are characterized by Rosaceae (e.g. *Psilatricolporites quenua* (*Polylepis*/*Acaena*); Asteraceae (e.g. *Tubulifloridites antipodica* and *Poluspissusites puntensis*) and Malvaceae (e.g. *Baumannipollis chubutensis*).

### 3.2. *Cluster analysis*

Cluster analysis (Figure 3) also recognized the groups discerned by the DCA analysis with bootstrap values above 74. The first cluster with Euclidean distance (EC) of 2.6 and bootstrap of 100 segregates the Paleocene–Early Eocene palynofloras from the rest. In this cluster, it is possible to distinguish Paleocene palynofloras from Eocene palynofloras with an Euclidean distance of 1.4 and a bootstrap value of 74. Middle Eocene palynofloras (10–11) cluster together with an EC of 1.8 and a bootstrap value of 74. Late

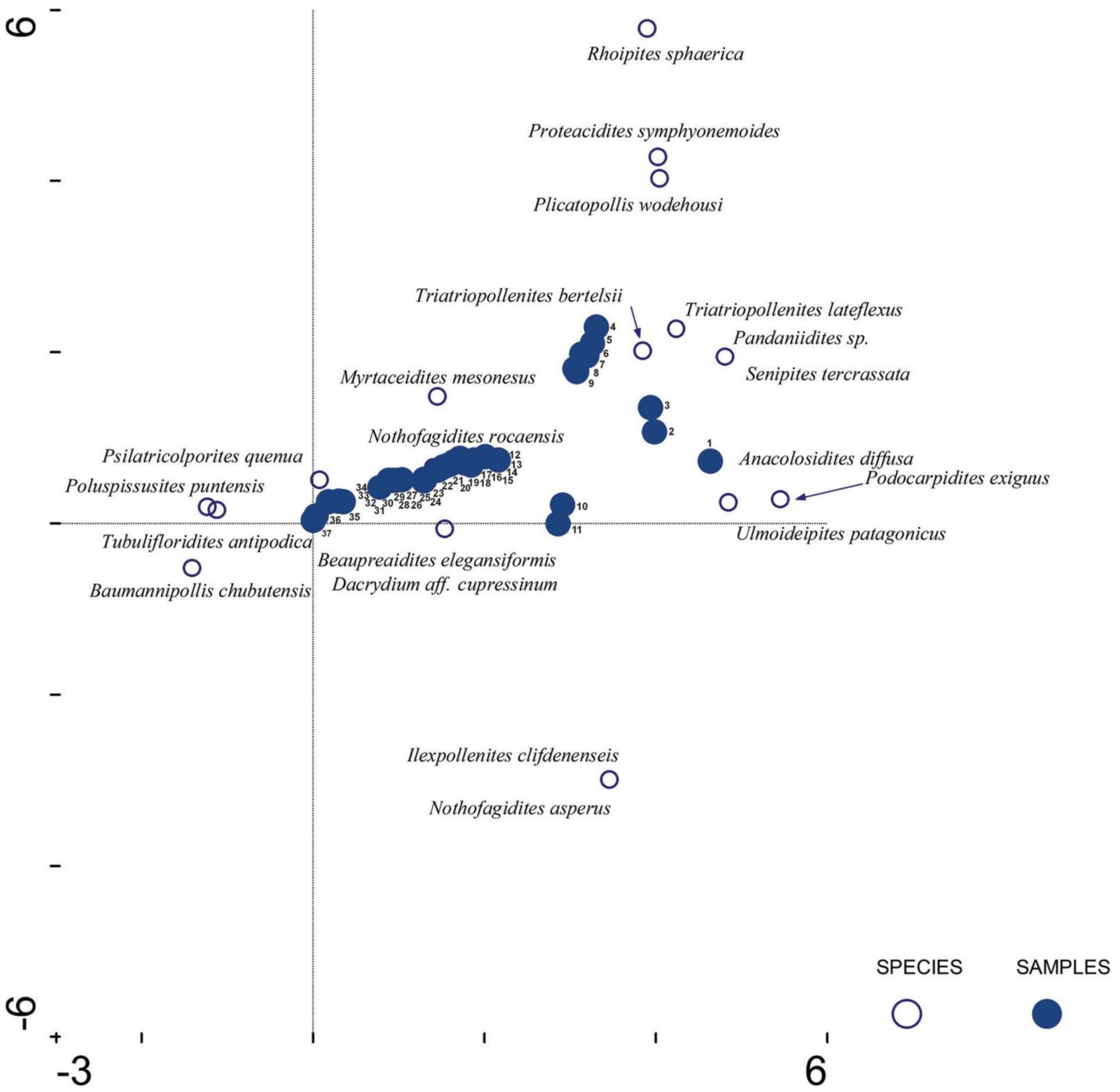

Figure 2. The first two axes of Detrended Correspondence Analysis (DCA) of Patagonian palynological data, with the recognized Paleofloras (I–IV). The first two axes explain 25.2% of the total variance. Eigenvalues sum = 3.001.

Eocene–Oligocene (12–32) and Late Oligocene/Miocene (33–37) palynofloras are distinguished by an EC of 1.37 and a bootstrap value of 100.

### 3.3. *Physiognomical analysis*

Figure 4 shows the difference between calculated Paleocene to Oligocene MAT and modern MAT for southern South America. The differences between the mean values obtained by the Peppe et al. (2011) and Hinojosa et al. (2011) equations range from 0.01 to 1.75 °C, within the standard error of both models (4.0 vs. 2.3 °C, respectively).

Results show MAT between 0.6–12 °C warmer than today for the Paleogene (Figure 4), with the maximum warming for the Early Eocene when MAT reached 9–12 °C relative to present values (Figure 4). From this optimum, MAT decreased greatly, reaching minimum values by the Oligocene with values 0.6–1 °C warmer than today. MAT calculations for the Miocene could not be carried out, as fossil leaf material is still too scarce.

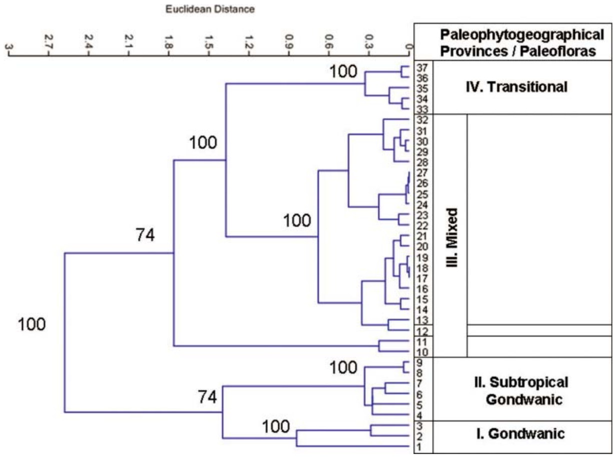

Figure 3. Cluster analysis, using Euclidean distance, showing the grouping of several palynological assemblages from different formations and/or localities (1–37). The numbers associated to the clusters represent the statistical significance of the main groups (I–IV) by bootstrap analysis (1000 permutation). References: (1) Volkheimer et al. 2007; (2–3) Archangelsky 1973, 1976; Archangelsky and Romero 1974; Archangelsky and Zamaloa 1986; (4–9) Melendi et al. 2003; (10–11) Archangelsky 1972; Romero and Castro 1986; Romero and Zamaloa 1985; Romero 1977; (12) Olivero et al. 1998; (13–15) Asensio et al. 2005; Quattrocchio et al. 2012; (16) Fasola 1969; (17–27), Náñez et al. 2009; (28) Barreda 1997; (29–31) Barreda et al. 2008; (32) Palamarczuk and Barreda 2000; (33) Barreda and Palamarczuk 2000a; (34–37) Barreda 1996; Palamarczuk and Barreda 1998; Barreda and Palamarczuk 2000c. Formations: 1, 2. Cerro Bororó (1. Las Plumas. 2 Golfo San Jorge); 3. Salamanca; 4–9 Huitrera (4–6. Pampa Jones; 7–9. Confluencia); 10, 11. Río Turbio (10. Lower; 11. Upper); 12. Sloggett; 13–15. El Foyel Group (13. Troncoso; 14. Salto del Macho; 15. Río El Foyel): 16. Loreto; 17–28. San Julián (17–27. Cabo Curioso area; 28. Playa La Mina); 29–31. Río Leona (29. Lower; 30. Middle; 31. Upper). 32. Aries x-1 borehole; 33. Monte León; 34–37 Chenque [Palynozones: A (34), B (35), C (36), D (37)].

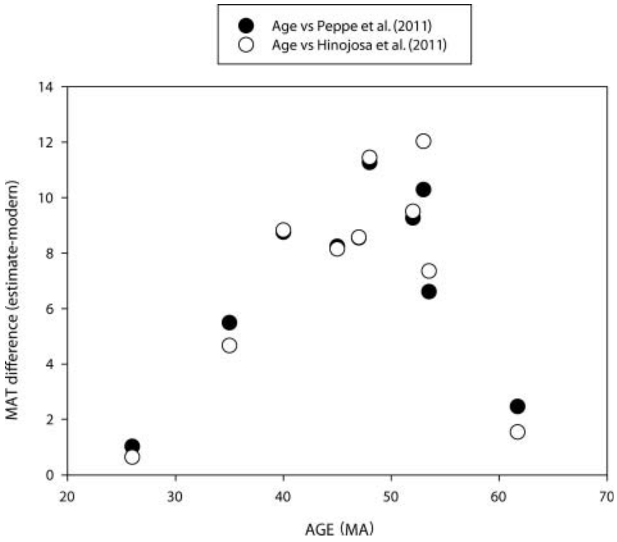

Figure 4. Physiognomical analysis. Difference between calculated Paleocene to Oligocene mean annual temperature (MAT) and modern MAT for southern South America.

## 4. Discussion

### 4.1. *Microfloristic associations of Patagonia*

Patagonian paleofloristics support the major stages of vegetation turnover defined previously for the Paleocene–Late Miocene interval (Barrera & Palazzesi 2007). These stages represent distinctive floristic assemblages, both in composition and structure, and are discussed below.

### 4.2. *Paleocene*

The Paleocene in northern Patagonia [Danian, Salamanca (first Atlantic transgression) and Bororó formations, in Figs. 2 and 3, samples 2–3] is characterized by vegetation composed by Araucariaceae, Cunionaceae, Podocarpaceae and Proteaceae that represented Southern Gondwanic lineages (palynofloras 1–3, Figs. 3–4). There is also the presence of Olacaceae [*Anacolosa* (*Anacolosidites* sp.)], Arecaceae [*Nypa* (*Spinozonocolpites* sp.)], Ulmaceae (*Ulmoideipites* sp.), Pandanaceae [*Pandanus* (*Pandaniidites* sp.)] and Symplocaceae [*Symplocos* (*Senipites* sp.)]. Regional climate is interpreted as warm and humid, with mangrove communities, humid forests, '*Araucaria*' woodland and sclerophilous forest. The dominant climate would have been the 'Cfa' type (subtropical humid) of Köppen's classification (Petriella & Archangelsky 1975). *Classopollis* (Cheirolepidiaceae) is also present (up to 50%) in the Paleocene of Patagonia (Petriella 1972; Archangelsky 1973; Petriella & Archangelsky 1975; Archangelsky & Zamaloa 1986).

In the Cerro Bororó Formation at Las Plumas (Figs. 2 and 3, sample 1), Volkheimer et al. (2007) reported proteacean pollen, indicative of subhumid to semiarid lowland. The sample analyzed was taken from a freshwater paleoenvironment with hydrophile forms (Chlorococcales, Salviniaceae, Zygnemataceae). A subtropical community of Arecaceae (palms) was also present, including *Monogemmites gemmatus* (Couper) Krutzsch. According to Jacobs (2004), palms are the first angiosperms associated with brackish settings replacing the ecological role of the Mesozoic conifer family Cheirolepidiaceae (Volkheimer et al. 2007). The Ericaceae (*Ericipites scabratus* Harris and *Ericipites microtectatum* Archangelsky & Zamaloa) integrated the subtropical subhumid to semiarid lowland community mainly composed of Proteaceae (Volkheimer et al. 2007).

Typical assemblages in this interval are composed of *Rousea patagonica* Archangelsky, *Syndemicolpites petriellai* Archangelsky, *Rhoipites baculatus* Archangelsky, *R. minusculus* Archangelsky, *Restioniidites pascualii* Archangelsky, *Polyporina romeroi* Archangelsky and *Ulmoideipites patagonicus* Archangelsky (= *Verrustephanoporites simplex* Leidelmeyer) among others.

Sparse palynological information are available from the Late Paleocene of Argentina. Only the Late Paleocene from La Sara core in Tierra del Fuego has been studied, yielding 50% *Nothofagus* (Menéndez and Caccavari de Filice 1974, 1975).

Physiognomic analysis by Iglesias et al. (2007) in the Palacio de Los Loros megaflora (61.7 ± 0.2 Ma, Danian–Selandian age) report 57.6% of species with toothed margins that would indicate a MAT of 12.3–13 °C; i.e. 1.5–2.5 °C warmer than today (Figure 4). Iglesias et al. (2007) reported an annual precipitation of over 1000 mm, indicating a lack of Andean rain shadow at this time. Paleocene–Eocene climates in this region were humid and subtropical on both sides of the proto-Andes.

This Paleocene flora has been recognized previously and named the Gondwanic Paleoflora (Hinojosa 2005), or Neotropical (Romero 1986). The Gondwanic Paleoflora (Group I, Figs. 2–3) was characterized by dominant Australasian, Neotropical and Pantropical phytogeographical elements. The climate was warm and very humid. Paleoenvironmental reconstructions based on Patagonian Paleocene floras allowed us to infer the presence of mangroves (with *Nypa* palms and *Pandanus*), swamp woodlands, mossy forests and sclerophyllous forests (Petriella & Archangelsky 1975).

Huber and Sloan's (1999) simulation of the Paleocene–Eocene Thermal Maximum (PETM) climate conditions suggests that surface winds for January were dominated by mid–high latitude easterlies centered on 50 to 60 °S and a weak westerly wind belt around 30 °S. The presence of mid–high latitude easterlies is not the result of an expansion of the tropical easterlies so much as an expansion of the polar easterlies. This wind scenario, characterized by relatively strong easterlies over Patagonia and a weakened wind system over the Pacific Ocean, likely generated air mass advection from the Atlantic inducing convection and increased precipitation over land.

A generalized unconformity between the Upper Paleocene and Lower Eocene (in part) developed in the Patagonian Platform (Malumián 1999).

### 4.3. *Early Eocene*

In the Early Eocene, samples 4–9 (Group II, Figs 3–4) are represented by Gondwanic taxa, such as *Proteacidites symphyonemoides* (Proteaceae), with tropical-subtropical taxa, for example *Periporopollenites demarcates* (?Trimenaceae). Other important taxa are represented by *Rhoipites sphaerica*, *Plicatopollis wodehousi* (Juglandaceae), megathermal taxa such as palms (i.e. *Longapertites patagonicus*) and *Triatriopollenites bertelsii*, a member of the Myricaceae, a cosmopolitan family, distributed today in tropical and subtropical areas of South America. Melendi et al. (2003) recorded microfloras without *Nothofagidites* of Early Eocene age in the Huitrera Formation at Pampa de Jones (Figs. 2 and 3 samples 4 to 6) while the ?Middle to Late Eocene (samples 7 to 9) at Confluencia are dominated by *Nothofagidites* ('*brassii*' and '*fusca*' types) underscoring the rapid transition of the Subtropical Gondwanic Paleoflora to the Mixed Paleoflora. The early Eocene age of Pampa de Jones has been recently confirmed by radiometric dating (Wilf et al. 2010). In contrast, a Middle Eocene age for the Confluencia area is still in dispute, as preliminary radiometric dating also suggests Early Eocene (Wilf et al. 2010). The localities are near each other, indicating that the between-site differences in *Nothofagus* abundances are due to rapid climate and/or landscape changes (Wilf et al. 2010).

These palynological assemblages agree with the Subtropical Gondwanic Paleoflora of Hinojosa (2005), characterized by the mixture of Neotropical, Pantropical and Australasian taxa with a low proportion of Antarctic elements.

Our physiognomic analysis shows MATs of 9–12 °C higher than today, similar to that obtained by Zachos et al. (2001) (Figure 4). The Early Eocene was a globally warm period (Huber & Caballero 2011; Lunt et al. 2011). In Patagonia, leaf floras yield estimated MATs of around 14–18 °C (Wilf et al. 2005; Hinojosa et al. 2011) and mean annual precipitation of > 2000 mm (Wilf et al. 2009). No significant ice accumulation existed at high latitudes in either hemisphere (Compagnucci 2011).

The climate throughout Patagonia was humid and subtropical; as the humid easterlies (Atlantic monsoon) extended so far south as to dominate continental Patagonia (Campagnucci 2011).

### 4.4. *Middle Eocene–Oligocene*

The Middle Eocene and Oligocene palynofloral group, 10–32 (Group III, Figs. 2–3) has been recognized as the 'Mixed Paleoflora' (*sensu* Romero 1978), with the exception of sample 12 (Sloggett Formation). The Middle Eocene–Early Oligocene interval was characterized by the invasion of *Nothofagus* forests. There was a progressive replacement of megathermal communities by meso- and microthermal rainforest (Barreda & Palazzesi 2007, Fig. 3.2).

The Río Turbio Formation (Middle Eocene) in western Patagonia (in Figs. 2 and 3, samples 10 and 11) is characterized by abundant Gymnospermae, Nothofagaceae, Myrtaceae, Proteaceae and spores (Archangelsky 1972; Romero 1977; Romero & Zamaloa 1985). Characteristic species include *Peninsulapollis gillii* (Cookson) Dettmann & Jarzen, Proteaceae and *Striatricolporites gamerroi* Archangelsky. The Río Turbio microfloras exhibit a significant difference marked by the abundance of *Nothofagidites* (Nothofagaceae) but with the presence of tropical to subtropical taxa like *Ilexpollenites clifdenenseis* (*Ilex*, Aquifoliaceae). *Ilex* is dispersed mainly in America and Eurasia, but also in Oceania and Africa. South America is considered one of the main areas of diversification of *Ilex* and it is mostly found in areas with tropical or subtropical climates, mainly in northeastern Argentina, southeastern Brazil and eastern Paraguay.

The palynological assemblage recovered from the basal pelitic section of the San Julián Formation, (?Late Eocene–Oligocene), in Cabo Curioso area, Santa Cruz Province (in Figs. 2 and 3, samples 17–27), is composed of continental palynomorphs that reflect a forest dominated by Nothofagaceae, Myrtaceae, Podocarpaceae and Palmae, developed under a temperate to warm-temperate and humid climate (Nañez et al. 2009). This assemblage reflects also the ‘Mixed Paleoflora’ of Romero 1978. The assemblage includes *Proteacidites subscabratus* Couper (Proteaceae) (Middle to Late Oligocene), *Graminidites* sp. (Poaceae), *Chenopodipollis chenopodiaceoides* (Martin) Truswell, (Chenopodiaceae) and *Baumannipollis variaperturatus* Barreda (Malvaceae).

The Sloggett Formation (in Figs. 2 and 3, sample 12), in Bahía Sloggett, Isla Grande de Tierra del Fuego (Olivero et al. 1998), probably is Late Eocene in age, and is excluded from the suggested distribution of the ‘Mixed Flora’, due to the presence of beech, podocarpacean and proteacean pollen, fern and fungal spores and freshwater algae, indicating temperate to cold/temperate and humid conditions. Species here considered are *Foveotriletes palaequetrus* (Late Eocene–Early Miocene) and *Pseudowinteropollis couperi* (Late Eocene–Pleistocene). Menéndez and Caccavari de Filice (1975) also described a palynoflora dominated by *Nothofagidites* for the Late Eocene/Oligocene of Isla Grande de Tierra del Fuego.

The Late Eocene (?)–Oligocene Río Foyel section (Foyel Group, Ñirihuau Basin, northwestern Patagonia, Argentina) (in Figs. 2 and 3 samples 13 to 15) reflects a forest dominated by Nothofagaceae, Myrtaceae, Podocarpaceae and Palmae, developed under a temperate to warm temperate and humid climate (Quattrocchio et al. 2012). In the Río Foyel Formation (Ñirihuau Basin, western Río Negro Province), an initial marine ingression came from the Pacific Ocean during the Early Oligocene and a second one during the Late Oligocene and Early Miocene from the Atlantic Ocean (Asensio et al. 2010).

Near the Eocene/Oligocene boundary, there is a sharp climatic cooling (Zachos et al. 2001) related to the formation of Antarctic ice (Kennett et al. 1975) and to the appearance of a circumpolar current around Antarctica as a result of the opening of the Drake Passage (Zubakov & Borzenkova 1990).

From the Late Oligocene to the Early Miocene, the Northern Patagonian Massif (NPHP), with its 100,000 km$^2$ area and 1200 m altitude, may have been the most important topographic feature remaining to interact with the monsoon (if present), as suggested by floral data (Aragón 2011).

### 4.5. Late Oligocene–Early Miocene

By the Late Oligocene–Early Miocene, warm climates allowed the dispersal of some neotropical elements southward (palms, *Cupania*, *Alchornea*, Rubiaceae, Combretaceae), adding megathermal elements to the local Gondwanic floras.

The appearance of some Neotropical families (Symplocaceae, Euphorbiaceae *Alchornea*) in the Upper section of the Río Leona Formation (sample 31, Figs. 2 and 3) might indicate the beginning of the Late Oligocene global warming event (Barreda et al. 2009). The rise of xerophytic and halophytic shrubby-herbaceous elements (Convolvulaceae, Asteraceae, Poaceae, Chenopodiaceae, Ephedraceae) during the Late Oligocene and their subsequent increase in abundance during the Early Miocene began to give a modern appearance to plant communities (Barreda & Palazzesi 2007). During the Early Miocene, distinctive elements of the Chaco Domain increased (Anacardiaceae *Schinus*, Fabaceae *Caesalpinia* and *Anadenanthera*, Combretaceae, *Combretum*), and some of them may have grown in gallery forests.

By the Late Oligocene–Early Miocene, the proto-Andes underwent a major period of erosion. This paleogeographical interval is characterized by transgressions reflecting of global eustatic changes (Malumián 1999; Malumián et al. 2008). Volcanism changed from a single belt to widespread activity, extending from the Atlantic Ocean to the Pacific coast (Aragón et al. 2011). The NPHP became the new topographic barrier between the Atlantic and Pacific oceans, and probably between Patagonia and the rest of South America (Aragón et al. 2011).

In the Late Oligocene, a community dominated by Myrtaceae, Palmae and Araucariaceae trees with Podocarpaceae and Nothofagaceae is recognized in the San Julián Formation at Playa La Mina (in Figs. 2

and 3, sample 28), Santa Cruz Province (Barreda 1997). However, the presence of small amounts of Anacardiaceae (*Striatricolporites gamerroi* Archangelsky), Asteraceae (*Tubulifloridites* sp.), Chenopodiaceae (*Chenopodipollis* sp.), Ephedraceae (*Equisetosporites claricristatus* (Shakmundes) Barreda, Malvaceae (*Baumannipollis variaperturatus* Barreda), Symplocaceae (*Senipites patagonica* Barreda) and Poaceae (*Graminidites* sp.) suggests the development of local open vegetation. The palynological assemblage suggests warm and humid conditions. These conditions are also inferred for the Late Oligocene in the southern part of San Jorge Gulf, Santa Cruz Province (Barreda & Palamarczuk 2000b). Similar assemblages are recognized in the lower part of the Centinela Formation (Oligocene–Miocene boundary) in southwestern Santa Cruz Province (Guerstein et al. 2004). Hence, the traditional Cenozoic vegetational floristic scheme where the 'Paleoflora Mixta' was replaced since the Late Eocene by a cold temperate forest South of 40° latitude (Romero 1986), needs to be modified (Palazzesi et al. 2003; Quattrocchio 2006).

The Río Leona Formation (in Figs. 2 and 3, samples 29 to 31), southwestern Santa Cruz Province (Barreda et al. 2009), is assigned to the early Late Oligocene based on the presence of key species of the M-M palynological zone of Barreda and Palamarczuk (2000b). It is characterized by *Margocolporites tenuireticulatus* Barreda, *Diporites aspis* Pocknall & Mildenhall, *Mutisiapollis telleriae* Barreda & Palamarczuk (Asteraceae), *Striasyncolpites laxus* Mildenhall & Pocknall (Menyanthaceae) and *Psilatricolporites quenua* Barreda et al. (Rosaceae).

The presence of Antarctic palynomorphs (Nothofagaceae, Podocarpaceae, Proteaceae) in the lower and middle sections of the Río Leona Formation is consistent with the cooling trend recognized globally during the Late Eocene and Early Oligocene, and recognized by our leaf margin analysis (Figure 4).

The appearance of some Neotropical families (Symplocaceae (*Senipites* sp.), Euphorbiaceae *Alchornea* [*Ranunculacidites operculatus* (van der Hammen & Wijmstra)] Jaramillo & Dilcher) in the Upper section might indicate the beginning of the Late Oligocene warming event. Records of Asteraceae (*Mutisiapollis telleriae* Barreda & Palamarczuk), Menyanthaceae (*Striasyncolpites laxus* Mildenhall & Pocknall) and Rosaceae (*Psilatricolporites tenua* Barreda, Palazzesi & Marenssi) are the oldest records in Patagonia to date, and provide significant information on the early divergence and radiation times of these major angiosperm families (Barreda et al. 2009).

The deposition of the Río Leona Formation predates the 'Patagonian Sea', a significant transgressive event that flooded wide regions of southern South America during the Late Oligocene-Early Miocene (Legarreta & Uliana 1994).

The Loreto Formation (Late Eocene–Oligocene) in its type locality, near Punta Arenas, Chile (Fasola 1969, Figs. 2 and 3, sample 16) is characterized by *Proteacidites* cf. *P. symphyonemoides* Cookson (range, Oligocene–Miocene). *Proteacidites* cf. *P. subscabratus* Couper (Middle to Late Oligocene) and *Beaupreaidites elegansiformis* Cookson (Oligocene to Miocene?). The paleoflora was characterized by gymnosperms (e.g. *Phyllocladidites mawsonii* Cookson, *Dacridium* aff. *cupressinum* Soland ex Forst), angiosperms (Myrtaceae, Nothofagaceae and Proteaceae) and Pteridophyta.

### 4.6. *Early–Middle Miocene*

The Early–Middle Miocene (samples 33–37, Group IV, Figs 2 and 3) corresponds to the Transitional Paleophytogeoprovince of Barreda et al. (2007) of central and southeastern Argentina, defined by a mixed of Neotropical and Austral components. Late Miocene vegetation was similar to the present vegetation, with the steppe expanded across extra-Andean Patagonia and the forest restricted to western areas where rainfall was still abundant (Barreda & Palazzesi 2007). The Middle–Late Miocene was characterized by the final demise of megathermal elements in Patagonia, coupled with an increasing diversity and abundance of xerophytic taxa, including Asteraceae, Chenopodiaceae, and Convolvulaceae *Cressa*/*Wilsonia* (Barreda & Palazzesi 2007).

The Neogene Subtropical Paleoflora developed in central Chile (Hinojosa 2005) during the Miocene with warm elements (Neotropical, Pantropical and Australasian). The Austral Antarctic elements are reduced in abundance. The climatic conditions were relatively warmer and rainier than those of the Oligocene. This paleoflora was correlated with a global warming event (the Mid Miocene climatic optimum) (Hinojosa 2005; Hinojosa et al. 2006).

A major palaeogeographical transition in the Patagonian Andes occurred during the Miocene between ~16.5 to ~14 Ma when the Patagonian Andes were uplifted by > 1 km, increasing aridity to the east. Xeric conditions developed east of the Andes in Patagonia and west-central Argentina. The increase in abundance of shrubby and herbaceous elements, determined by a cooling and drying trend across extra-Andean Patagonia, began to give a modern appearance to the landscape during the Middle–Late Miocene. Spore/pollen assemblages are dominated by angiosperms, mainly shrubby and herbaceous taxa of the Asteraceae, Chenopodiaceae and Convolvulaceae *Cressa*/*Wilsonia*, and

Asteraceae. Anacardiaceae, Fabaceae, Malvaceae, and Poaceae are recognized as well, along with Cyperaceae, Restionaceae and Sparganiaceae/Typhaceae. Gymnosperms are mainly represented by Ephedraceae, while Podocarpaceae and Araucariaceae are scarce (Barreda & Palazzesi 2007, fig. 3.4).

The Monte León Formation (Early Miocene) in its type locality (Barreda & Palamarczuk 2000a; sample 33 in figs. 2 and 3) at the Atlantic coast in Santa Cruz Province is dominated by Araucariaceae and Podocarpaceae, while Nothofagaceae pollen is scarce and dominated by '*fusca*' type. There are some megatherm elements including Arecaceae (*Arecipites subverrucatus* (Pocknall) Mildenhall & Pocknall) and Symplocaceae (*Senipites patagonica* Barreda), and taxa typical of dry habitats including Ephedraceae (*Equisetosporites claricristatus*), Convolvulaceae (*Tricolpites trioblatus* Mildenhall & Pocknall), Chenopodiaceae (*Chenopodipollis chenopodiaceoides* (Martin) Truswell) and Asteraceae (*Mutisiapollis viteauensis* (Barreda) Barreda and *Tubulifloridites antipodica* Cookson). Aquatic herbs and hydrophytes Cyperaceae (*Cyperaceaepollis neogenicus* Krutzch, Sparganiaceae (*Sparganiaceaepollis barungensis* Harris), Restionaceae ('*Milfordia*' *argentina* Barreda) were widespread in central Patagonia and indicate the development of a hydrophytic community.

Sporomophs with stratigraphic significance are *Glencopollis ornatus* Pocknall & Mildenhall (Polygonaceae) and *Cyperaceaepollis neogenicus* Krutsch. These species were recorded in the Miocene of Argentina, Australia and New Zealand. Species indicative of the Neogene include also *Malvacipolloides comodorensis* Barreda, *Corsinipollenites atlantica* Barreda and *Tricolpites trioblatus* (Barreda & Palamarczuk 2000).

The Chenque Formation (Early to Middle Miocene) crops out in the San Jorge Basin, Central Patagonia, Argentina and consists mainly of shallow-marine deposits ('Patagonian Sea'). Barreda (1996) proposed four informal palynozones (samples 34–37 in Figs. 2 and 3) for this formation in San Jorge Gulf (the studied sections are located in the southeast of Chubut province and northeast Santa Cruz Province). In Barreda & Palamarczuk (2000b), the biostratigraphic range of some taxa were modified, and are included here: lower palynozone (A), transitional palynozone (T), middle palynozone (B) and upper palynozone (C). Palynozone A is defined by the presence of *Mutisiapollis viteauensis* (Asteraceae) associated with *Haloragacidites trioratus* Couper, *Reticuloidosporites tenellis* Krutzsch, *Triorites minor* Couper among others. The transitional palynozone (T) is characterized by species present also in palynozones A, B and C. Elements only present in this palynozone are: *Foveotriletes palaequetrus* Partridge, *Rhoipites* sp. (Barreda 1996) and *Acaciapollenites myriosporites* (Cookson) Mildenhall. Palynozone B is characterized by species that are present in Palynozone T and absent in Palynozone A. The last appearance of the following taxa is recorded: *Nothofagidites flemingii* (Couper) Potonié, *Striatricolporites gamerroi* Archangelsky, *Nyssapollenites endobalteus* (McIntyre) Kemp & Harris, *Arecipites subverrucatus* (Pocknall) Mildenhall & Pocknall, and *Myrtaceidites verrucosus* Partridge and *Quintiniapollis striatulosa* Barreda among others. In Palynozone C, *Tubulifloridites antipodica* and *Baumannipollis chubutensis* appeared. There is an increase in the relative frequency of the Asteraceae and Malvaceae in this palynozone.

## 5. Conclusions

### 5.1. *A dynamic model for the evolution of Patagonian Cenozoic palynofloras*

The analysis of the available data from Patagonia supports the major stages of vegetation turnover defined for the Paleocene–Late Miocene interval. These stages represent distinctive floristic assemblages, both in composition and structure.

Detrended Correspondence Analysis (DCA) shows differences between the different formations analyzed here. They are grouped according to floristic composition (Figure 2). The cluster analysis also indicates that the samples are grouped according to their paleofloras (Figure 3). Both DCA and cluster analysis reflect a significant relationship with global climatic trends (Figure 5). In Figs 2 and 3, samples 1–3 correspond to the Danian. Following Hinojosa (2005), during the Paleocene, the Gondwanic Paleoflora (Group I, Figs. 2 and 3) of southern South America was characterized by dominant Australasian, Neotropical and Pantropical phytogeographical elements. The climate was warm and very humid. Paleoenvironmental reconstructions based on Patagonian Paleocene floras allowed us to infer the presence of mangroves (with palms and *Pandanus*), swamp woodlands, mossy forests and sclerophyllous forests (Petriella & Archangelsky 1975).

In the Early Eocene, samples 4–9 (Group II, Figs. 2 and 3) correspond to the Subtropical Gondwanic Paleoflora, with Neotropical and Pantropical taxa, with fewer Australasian and Antarctic elements. This is consistent with the suggested rich subtropical vegetation that existed over a large portion of Eocene Patagonia with the presence of megathermal families such as palms, other taxa with broader climatic requirements such as conifers, cycads, and Ginkgoales as well as the coals in east Patagonia (Compagnucci 2011).

The Middle Eocene and Oligocene samples 10–32 (Group III, Figs. 3–4) are characterized by the 'Mixed

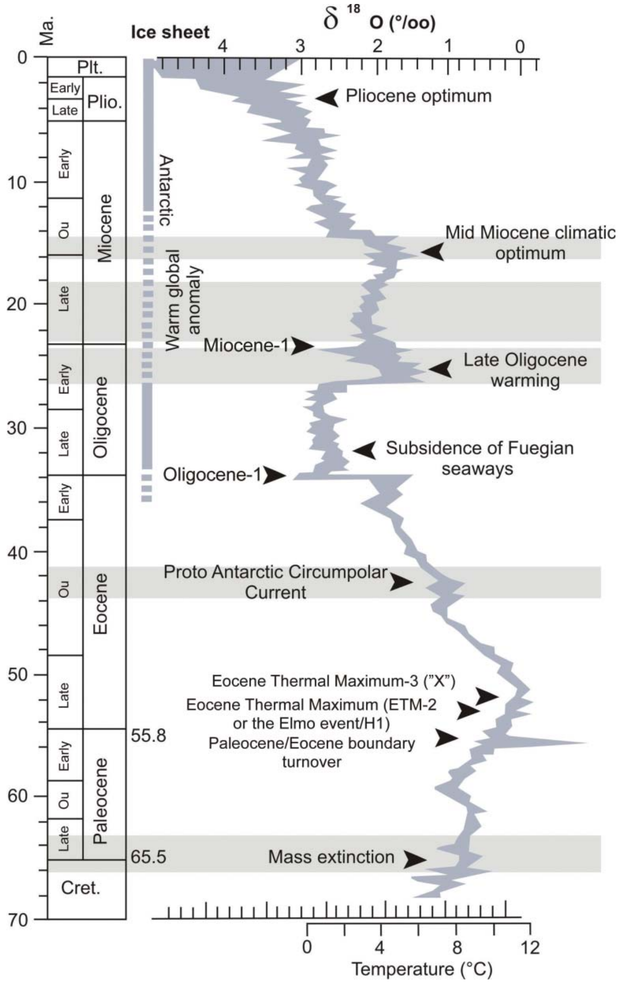

Figure 5. Relations between temperature and the most relevant events during the Cenozoic (after Zachos et al. 2001 and Malumián & Náñez 2011). P/E: Paleocene/Eocene boundary, ETM: Eocene Thermal Maximum, Oi-1 and Mi-1: oxygen isotope events.

Paleoflora' (*sensu* Romero 1978) with the exception of sample 12 (Sloggett Formation). Near the Eocene/Oligocene boundary the sharp climatic cooling has been related to the formation of Antarctic ice (Kennett et al. 1975) and to the appearance of a circumpolar current around Antarctica as a result of the opening of the Drake Passage (Zubakov & Borzenkova 1990). The presence of Antarctic palynomorphs (Nothofagaceae, Podocarpaceae, Proteaceae) in Patagonia is consistent with the cooling trend recognized globally during the Late Eocene and Early Oligocene (Barreda & Palamarczuk 2000a, 2000b).

By the Late Oligocene–Early Miocene, warm climates allowed the dispersal of neotropical elements southward (palms, *Cupania*, *Alchornea*, Rubiaceae, Combretaceae), adding megathermal elements to the local Gondwanic floras. The appearance of some Neotropical families (Symplocaceae, Euphorbiaceae *Alchornea*) in the Upper section of the Río Leona Formation (sample 31) might indicate the beginning of the Late Oligocene global warming event (Barreda et al. 2009). The rise of xerophytic and halophytic shrubby-herbaceous elements (Convolvulaceae, Asteraceae, Poaceae, Chenopodiaceae, Ephedraceae) during the Late Oligocene, and its subsequent increase in abundance during the Early Miocene began to give a modern appearance to plant communities (Barreda & Palazzesi 2007).

During the Early Miocene, distinctive elements of the Chaco Domain increased (Anacardiaceae *Schinus*, Fabaceae *Caesalpinia* and *Anadenanthera*, Combretaceae *Combretum*), and some of them may have grown in gallery forests. The Early–Middle Miocene (samples 33–37, Group IV, Figs. 2 and 3), correspond to the Transitional Paleophytogeoprovince (Barreda et al. 2007) of central and southeastern Argentina, defined by a mix of Neotropical and Austral components. Late Miocene vegetation was similar to the present vegetation, with the steppe expanded across extra-Andean Patagonia and the forest restricted to western areas where rainfall was still abundant (Barreda & Palazzesi 2007). The Middle–Late Miocene was characterized by the final demise of megathermal elements in Patagonia, coupled with an increasing diversity and abundance of xerophytic taxa, including Asteraceae, Chenopodiaceae, and Convolvulaceae *Cressa*/*Wilsonia* (Barreda & Palazzesi 2007). By this time at ~14 Ma, deposition in the eastern foreland of the Southern Patagonian Andes had essentially ceased as the result of rain shadow formation (Blisniuk et al. 2005).

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