



Changes of the palynobiotas in the Mesozoic and Cenozoic of Patagonia: a review

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This study describes the compositional changes of Mesozoic–Cenozoic palynologic assemblages in Patagonia, the succession of phytogeographic scenarios and some evolutionary key events. The Triassic ‘Ipswich Microflora’, characterized by bisaccate pollen and high frequencies of trilete spores, represents the warm–temperate province of south-western Gondwana (*Dicroidium* Flora), followed in time, in Patagonia, near the Triassic/Jurassic boundary, by the ‘*Classopollis* Microflora’, indicating warm and (seasonal) arid conditions. Araucariaceans and podocarpaceans grew on Jurassic uplands. The exclusively Early Cretaceous taxa *Cyclusphaera* and *Balmeiopsis* (Coniferae) appeared in the Valanginian. The oldest angiospermous pollen types of Argentina appear in the Barremian–Aptian of southern Patagonia. During the Maastrichtian, the Nothofagaceae and Myrtaceae are incoming. In the Palaeocene, a vegetation dominated by tropical elements would have developed in Patagonia. Increasing *Nothofagidites* frequency in northern Patagonia during the Middle to Late Eocene indicates climatic change from warm to temperate. Of three Early to Middle Miocene phytogeographic provinces (Neotropical–Transitional and Austral), the Transitional one was replaced during the Late Miocene–Pliocene by the xerophytic Proto Espinal/Steppe with a shrubby–herbaceous vegetation. The Pleistocene and Holocene times were characterized by frequent latitudinal and altitudinal changes in the vegetation distribution, as a response to recurrent climatic oscillations, fluctuations of sea level and ice extent, and changing patterns of atmospheric circulation. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 380–396.

ADDITIONAL KEYWORDS: Cheirolepidiaceae – Cretaceous – early angiosperms – evolution – Jurassic – palaeopalynology – palaeophytogeography – scenarios.

El presente trabajo describe los cambios composicionales en las asociaciones palinológicas del Mesozoico-Cenozoico en Patagonia, la sucesión de escenarios fitogeográficos y algunos eventos evolutivos. Durante el Triásico, la ‘Microflora Ipswich’, caracterizada por la presencia de polen bisacado y alta frecuencia de esporas triletas, representa la provincia templado cálida del ‘Sudoeste de Gondwana’ (Flora de *Dicroidium*), seguida en el tiempo en Patagonia, cercano al límite T/J, por la ‘Microflora de *Classopollis*’, indicativa de condiciones cálidas y áridas (estacionales). Las araucariáceas y podocarpáceas habrían ocupado las tierras altas. Los taxa exclusivos del Cretácico Temprano, *Cyclusphaera* y *Balmeiopsis* (Coniferae) aparecen en el Valanginiano. Los tipos de polen de angiospermas de Argentina más antiguos aparecen en el Barremiano-Aptiano, del sur de Patagonia. Durante el Maastrichtiano las Nothofagaceae y Myrtaceae ingresan en Patagonia. En el Palaeoceno una vegetación dominada por elementos tropicales se habría desarrollado en Patagonia. El aumento de la frecuencia de *Nothofagidites* en el Norte de Patagonia indica un cambio climático de cálido a templado durante el Eoceno Medio a Tardío. De las tres Provincias Fitogeográficas del Mioceno Temprano (Neotropical-Transicional y Austral) la Transicional fue reemplazada durante el Mioceno Tardío-Plioceno por la provincia xerofítica ProtoEspinal/Estepa con una vegetación

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arbustiva y herbácea. El Pleistoceno-Holoceno está caracterizado por frecuentes cambios latitudinales y altitudinales en la distribución de la vegetación, en respuesta a las recurrentes oscilaciones climáticas, fluctuaciones del nivel del mar, extensión de los hielos y cambios en los patrones de circulación atmosférica.

PALABRAS CLAVE: Cheirolepidiaceae – Cretácico – Jurásico – Angiospermas primitivas – evolución – Cenozoico – palaeopalínología – palaeofitogeografía – escenarios.

INTRODUCTION

The aim of this paper is to describe the changes in plant communities, palaeoclimates and palaeophytogeographic provinces in Patagonia from the Jurassic to the present. The plant communities and depositional environments are seen as non-linear systems that are unique and highly changing in any given time. External factors influencing plant communities include: climate, sea level changes, tectonics, soil development and even planetary forcing. Internal processes of forest dynamics include competition among existing species and interactions between existing species and potential invading species (Bennett & Willis, 1995). From many points of view, Patagonia is a rather unique region, not only in the Southern Hemisphere, but also at the global level (Rabassa, 2008a). The geologic evolution during the Mesozoic involves rifting, extension and magmatism (passive margins form new oceanic crusts). The palaeogeography is characterized by a Gondwanic margin which is active (where subduction occurs) towards the Pacific Ocean.

A mosaic of Palaeozoic cratons (old and stable part of the continents) and Mesozoic rift basins related to the opening of the South Atlantic Ocean are backed by a very massive mountain range, the Patagonian Andes, of highly complex lithologic, structural and geomorphologic distinctiveness and history. With a long history behind it, Patagonia became what it is today, during the Late Miocene, when it reached its present latitudinal position, becoming separated from the Antarctic Peninsula as the Drake Passage was opened by the eastward push of the Scotia Plate (Rabassa, 2008b). 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 Palaeogene (Barreda & Palazzesi, 2007). Important contributions to the understanding of the history of southern South American forests are those of Menéndez (1971), Volkheimer (1971), Romero (1978, 1986, 1993), Axelrod, Kalin-Arroyo & Raven (1991), Hinojosa & Villagrán (1997), Villagrán & Hinojosa (1997), Palazzesi, Barreda & Prieto (2003), Prámparo *et al.* (2007),

Barreda *et al.* (2007), Artabe, Morel & Ganuza (2007) and Ottone (2009), among others. Menéndez (1971) showed that the maximum southwards advance of the tropical flora in Patagonia took place during the Palaeocene and Early Eocene and that the northwards retreat of the warm floristic elements and the parallel advance of the cool-temperate elements of the flora began in the Late Eocene. Volkheimer (1971) showed, using statistical studies of the proportion of entire margined leaves in Eocene dicotyledonous floras in northern Patagonia, that the climate was subtropical with permanent moisture ('Virginian climate: Cfa-type' as classified by Köppen, (1948). The mean temperature of the warmest month was above 22 °C and that of the coolest month between 13 and 10 °C. Precipitation, distributed during the whole year, exceeded 1000 mm/year. The principal climatic indicators which Volkheimer (1971) studied are the Eocene fossil floras of Laguna del Hunco (Chubut), Río Pichileufú (Río Negro) and Lota-Coronel (Chile).

Efforts to understand the transition from Mesozoic terrestrial ecosystems, dominated by ferns, conifers, cycads and bennettitales, to Late Cretaceous and Tertiary ecosystems dominated by flowering plants have revived research into the origins and diversification of angiosperms. Fossil pollen grains remain the earliest evidence for the overwhelming majority of archaic angiosperm families (from Macphail, Partridge & Truswell, 1999).

MESOZOIC: TRIASSIC

During the Triassic (between 251 and 199.6 Ma, Ogg, Ogg & Gradstein, 2008), Patagonia was part of the phytogeographic province of south-western Gondwana, with a warm-temperate climate, in which continental environments were dominant, these palaeocommunities were characterized by the *Dicrodium* flora (Artabe, Morel & Spalletti, 2003). Dolby & Balme (1976) recognized the Onslow flora (Euroamerican affinities with many dry indicators) and the Ipswich flora (Gondwanaland affinities with many moist indicators). From a palynological point of view, the Argentine Triassic deposits were included into the Ipswich Microflora of Dolby & Balme

(1976), characterized by the abundance of bisaccate pollen (*Alisporites* and *Falcisporites*), monosulcate pollen (*Cycadopites*) and trilete spores (*Osmundacidites*, *Dictyophyllidites*, *Neoraistrickia*, among others). These floras were probably latitudinally controlled, the Onslow flora representing forest at 30–35°S and the Ipswich flora, with a higher latitude plant association (Traverse, 2007).

JURASSIC

The palaeogeography of the Early Jurassic is characterized by eustatic (global sea level) rise which induced regional flooding (Cisternas, 1979; Chong & Hillbrandt, 1985) beyond the boundaries of the Triassic troughs and led to the development of a linear marine belt fringing the continental slab in northern and central Chile (Cecioni, 1970; Riccardi, 1983). Most of the studied microfloras from the Jurassic (199.6–145.5 Ma) came from the Neuquén Basin (north-western Patagonia). The Neuquén Basin is located at the southern end of the more extensive Chilean Basin. Most of the Jurassic and Cretaceous microfloras are characterized by the predominance of the genus *Classopollis* (Pflug) Pocock and Jansonius, a common feature with contemporary microfloras of other parts of the world (Volkheimer & Pöthe de Baldis, 1976). Microfloral similarities indicate close Gondwanic relations between Australia and South America, especially in the Liassic (Quattrocchio, Sarjeant & Volkheimer, 1996). The Upper Sinemurian–Lower Toarcian (approximately 189.6–180 Ma) is characterized by the presence of *Classopollis classoides* and the absence of the *Callialasporites* ‘complex’. *Microcachrydites antarcticus* is registered since the Lower Bajocian. Significant increase in abundance of *Microcachrydites antarcticus* and a corresponding decline of the *Callialasporites* ‘complex’ (*C. dampieri*, *C. trilobatus* and *C. microvelatus*) were registered in the Tithonian (150.8–145.5 Ma). A similar situation was observed in the Tithonian of Australia (Helby, Morgan & Partridge, 1987) (Quattrocchio *et al.*, 1996).

Comparison with palaeomagnetic data (Volkheimer *et al.*, 2008) shows that the Neuquén Basin shifted from the highest palaeolatitudes (50°S), by the end of the Triassic to the end of the Sinemurian. During the Pliensbachian–Toarcian (189.6–175.6 Ma) it moved northward, reaching the lowermost palaeolatitudes (25°S) and, subsequently (Middle to Late Jurassic), the area moved again and eventually attained a position similar to its present-day position (30°S) (Iglesia Llanos, Riccardi & Singer, 2006). These movements are reflected by the Jurassic palynofloras. The high frequency of the pollen genus *Classopollis* (cheirolepidiacean gymnosperms) is of special palaeoclimatic importance in the Jurassic of Argentina, as it is

indicative of seasonal aridity or semi-arid conditions during large intervals of this period. During the shift of the South American continent to the northernmost position, the arrival of an important group of Araucariaceae in the Toarcian, represented by *Callialasporites* spp., could indicate climate amelioration as reflected by increased humidity (Volkheimer *et al.*, 2008). Using modern analogues, the Middle Jurassic communities of the Neuquén Basin and the rest of Patagonia are partly represented today in the Argentine–Chilean Patagonian Forest and the Planalto of southern Brazil (Quattrocchio *et al.*, 2001) (Fig. 1).

The Tithonian is regionally transgressive above deposits of different ages and it is transitionally related with the overlying Neocomian, taking into account sedimentologic, faunistic and floristic viewpoints. The coastal vegetation characteristic of the Tithonian inhabited swamps located at the external margins of deltas. This vegetation comprised principally several species of Cheirolepidiaceae (conifers), producing *Classopollis simplex*, *C. cf. classoides*, *C. torosus* and *C. itunensis*. During the regressive phases (shorelines shift in a seaward direction), the local elements were dominating the swamps with ferns and, in lower proportions, the Caytoniales. Araucariaceans (*Araucariacites* and *Callialasporites*) and podocarpaceans (*Podocarpidites*, *Microcachrydites* and *Trisaccites*) were instead growing in more distant and relatively elevated areas. The regressive events are characterized by the diversification of acritarchs and a low diversity of dinocysts. The transgressive events are dominated by the organic walled palaeomicroplankton, while local elements were diminishing. Especially, the dinocysts are more abundant and diverse in the upper part of the middle to high Tithonian (the Picún Leufú Formation), such as *Dichadogonyaulax culmula* var. *curtospina*, *Aptea notialis* and *Hystrichosphaerina neuquina*.

The Tithonian–Berriasian (150.8–140.2 Ma) microfloras are very similar and correspond to the *Equisetosporites–Trisaccites* Assemblage (Volkheimer & Pöthe de Baldis, 1976). In Cañadón Asfalto Basin (Jurassic), Volkheimer, Quattrocchio & Cabaleri (2001) presented a preliminary palynologic study of the Cañadón Asfalto Formation at the Cañadón Lahuincó locality and published a complete study in Volkheimer *et al.* 2008. The algal assemblage of this formation is of special interest, composed of planktonic (*Botryococcus*) and non-planktonic green algae (the *Spirogyra*-like spores of the genus *Ovoidites*), both indicative of freshwater conditions. High percentages of *Classopollis* spp., representing the thermophilic Cheirolepidiaceae, indicate warm climatic conditions and well-drained soils around the lakes. Elevated hinterlands were characterized by Araucariaceae, represented by several species of

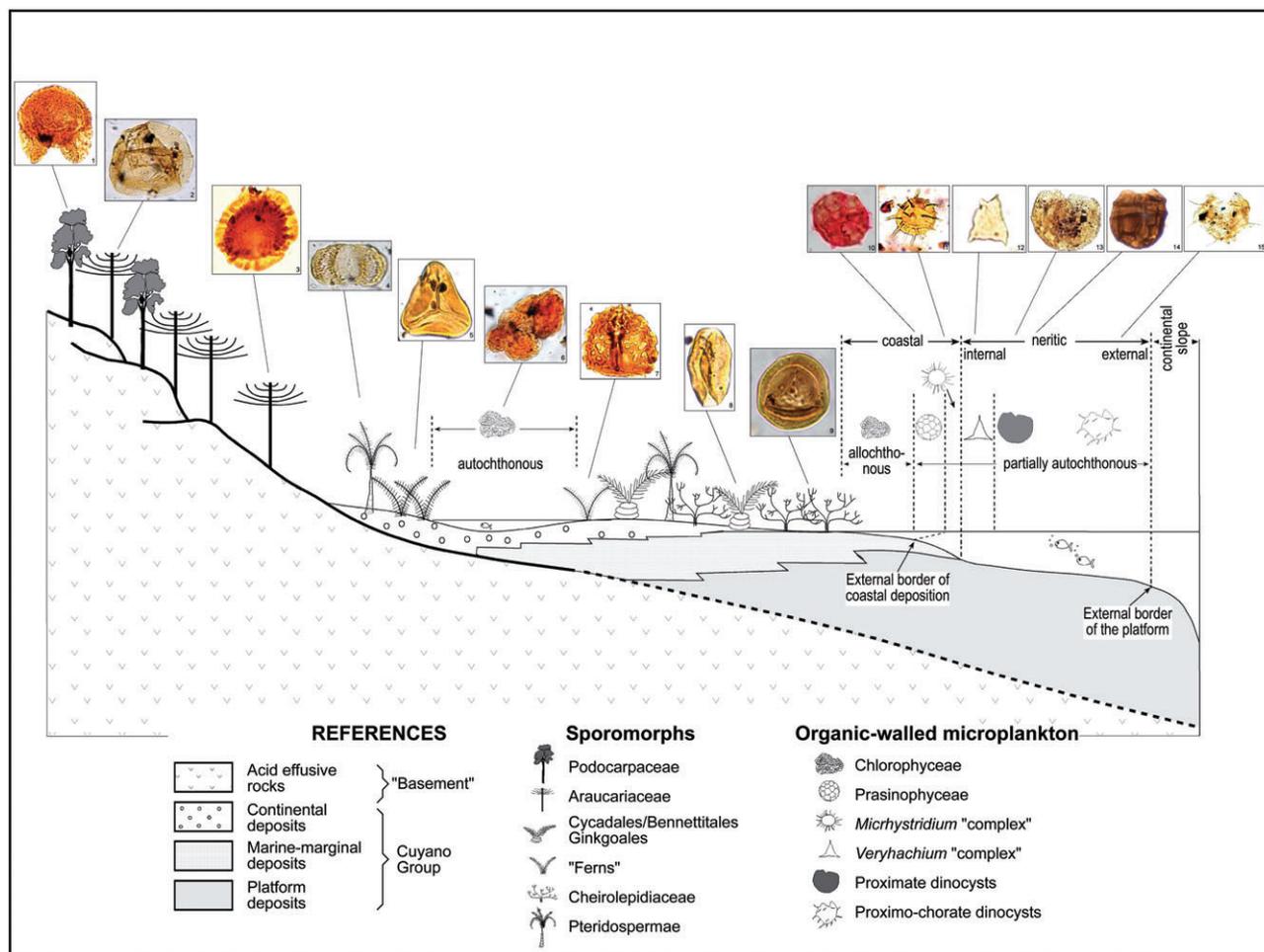


Figure 1. Reconstruction of the palaeoenvironments corresponding to the Los Molles Formation, Cuyo Group, Neuquén Basin (modified from Martínez *et al.*, 2008 and Volkheimer *et al.*, 2011).

the genera *Callialasporites* and *Araucariacites*, and Podocarpaceae, represented by *Podocarpidites* and *Phrixipollenites* (Fig. 2).

Summarizing, one of the main palynological stories of the Jurassic is that of conifer pollen (*Classopollis*, *Callialasporites*, *Podocarpidites*, *Microcachryditites*, *Trisaccites*, among others), which never before had been so common and so diverse.

CRETACEOUS

The palaeogeographic evolution of southern South America during the Cretaceous (145.5–65.5 Ma) when angiosperms appeared, is conditioned by two main events: (1) an active western continental margin, with permanent subduction of the Pacific tectonic plates and the development of a magmatic arch; and (2) the separation of Africa and South America from each other and the expansion of the ocean floor in the southern Atlantic Ocean. During the Early Creta-

ceous (145.5–99.6 Ma) the vegetation was dominated by conifers. The family Cheirolepidiaceae (*Classopollis*) is conspicuous and it is also associated with Podocarpaceae and Araucariaceae and, within Araucariaceae, with the genera *Cyclusphaera* and *Balmeiopsis* in particular. For the Hauterivian–Barremian and parts of the Aptian a *Cyclusphaera psilata* subprovince is established (Volkheimer, 1980) within the southern Gondwana province (Brenner, 1976). By the high percentages of *Classopollis* and the common presence of bisaccates, trisaccates and cosmopolite trilete spores such as *Gleicheniidites*, *Trilobosporites*, *Densoisporites* and *Pilosporites*, this palynofloristic subprovince differs from the tropical province of northern Gondwana. *Cyclusphaera psilata* Volkheimer and Sepúlveda is the pollen of the araucariacean *Alkastrobos peltatus* (Del Fueyo & Archangelsky, 2005) and *Balmeiopsis limbatus* (Balme) Archangelsky is the pollen of the araucariacean *Brachyphyllum irregulare* (Archangelsky) (see bibliography in Del

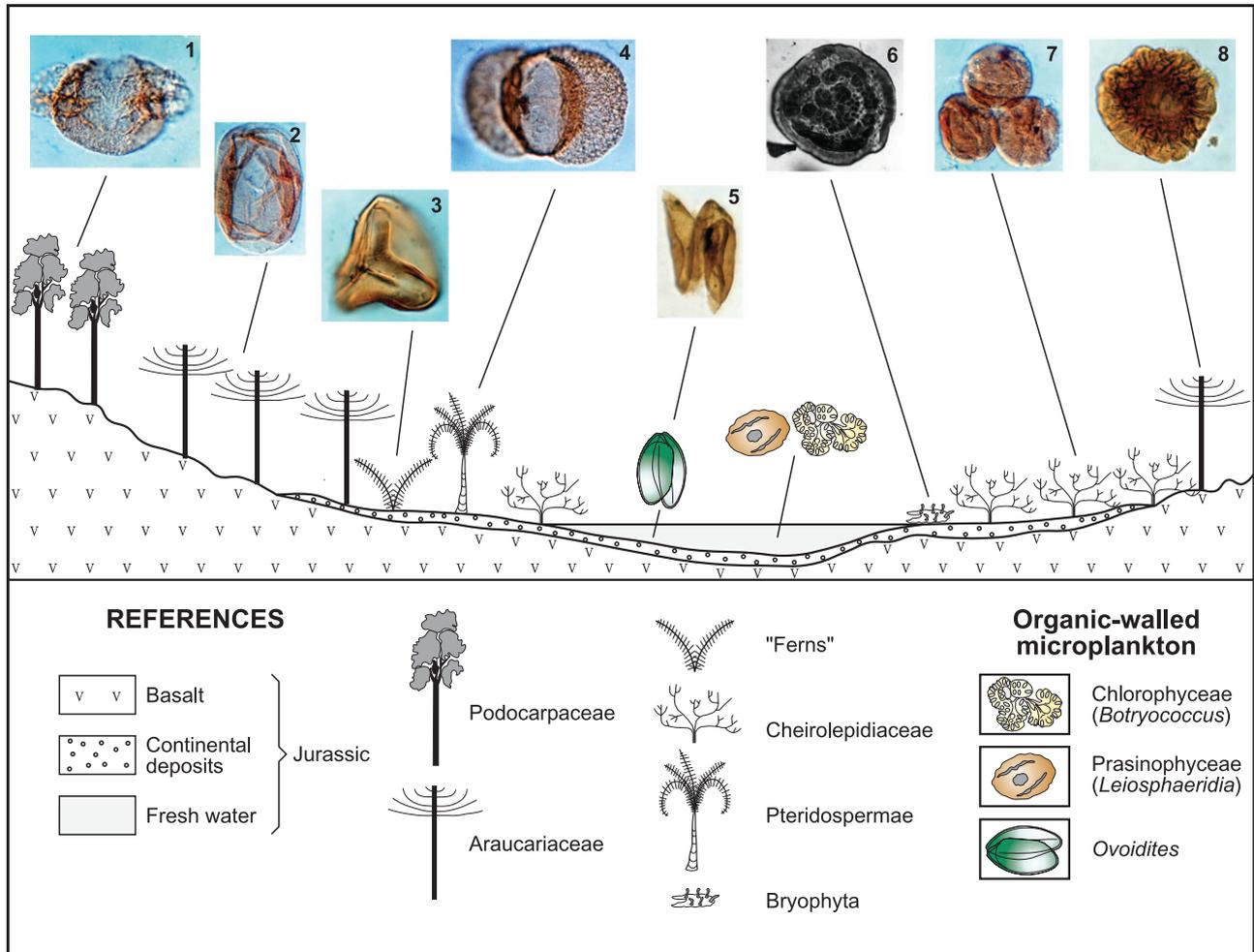


Figure 2. Depositional environmental model and cross-section of the Middle Jurassic palynobiota at Cañadón Lahuincó locality, middle Río Chubut, showing the sequence from planktonic protocists and hydrophilous zygnetacean algae to a hygrophilous community of Bryophyta, a thermophilic community of cheirolepidiacean conifers, a lowland araucariacean community represented by *Callialasporites* spp., forests of *Araucaria* at somewhat higher areas, which could be represented by the very frequent *Araucaciacites* pollen grains and a Podocarpaceae community, which is thought to have grown on elevated areas.

Fueyo & Archangelsky, 2010). There is no record of *Cyclusphaera* and *Balmeiopsis* in the Late Cretaceous; they seem to be characteristic of Early Cretaceous sediments all over Patagonia (Archangelsky, 1980; Archangelsky *et al.*, 1994). Aptian (125–112 Ma) mega- and microfossils that are recovered from the Baqueró Group in Santa Cruz Province are especially abundant. These assemblages include fungi, bryophytes, lycopods, sphenophytes, Filicales, Caytoniales, Cycadales, Bennettittales, Ginkgoales, Coniferales and a few angiosperms (Archangelsky, Del Fueyo & Villar de Seoane, 2003). The oldest angiosperm pollen of Argentina has been reported from Patagonia (Springhill Formation, Austral Basin) (Archangelsky & Archangelsky, 2002, 2004; Quattrocchio *et al.*, 2006), in the formations of the Baqueró

Group, Baqueró Basin (Andreis, 2002), in the Anfitatro de Ticó and Punta del Barco, Deseado Massif, Santa Cruz Province (Archangelsky & Gamero, 1967; Archangelsky & Taylor, 1993; Llorens, 2003) from sediments of Barremian to early Aptian age. They mainly correspond to two pollen types: the form genus *Asteropollis* Hedlund and Norris and *Clavati-pollenites* Couper. Both types show a demonstrated affinity with the family Chloranthaceae and have a wide distribution in Cretaceous sediments worldwide (from Prámparo *et al.*, 2007). The association of early angiosperm pollen with marine dinoflagellates and with freshwater phytoplankton suggests that the parent plants flourished near aquatic sites in lowland and coastal environments, a scenario largely consistent with lowland and coastal hypotheses for

the dispersal of flowering plants proposed by different authors (Llorens, 2003; Quattrocchio *et al.*, 2006). The foliar morphotype (nymphaeaphyll morphological type) is found in some members of extant angiosperms of usually herbaceous habit. By analogy this is likely to have been the original habitat of the primitive angiosperm fossil leaf from the Aptian of Santa Cruz Province (Passalia *et al.*, 2003). Based on the taxonomic composition of the floras, including the temporal distribution and relative abundance of angiosperms, three major stages of angiosperm evolution can be recognized in the Cretaceous of southernmost South America: Stage I, or the Late Barremian–Aptian phase, is characterized by the appearance of the first angiosperms within gymnosperm-fern dominated floras; Stage II or the latest Aptian–earliest Albian phase, includes the first definitive occurrences of eudicots among gymnosperm-fern dominated floras; Stage III, or the Middle Albian–Coniacian phase, is clearly characterized by a progressive angiosperm diversification, as indicated by several leaf and pollen morphotypes, and their increasing participation in plant communities to the end of this phase (Archangelsky *et al.*, 2009). Sedimentary accumulation during the Late Cretaceous was characterized by a trend towards enlargement of depositional sites and an increase in the amount of marine influence (Uliana & Biddle, 1988). The Late Cretaceous flooding of the Argentine margin during a period of tectonic quiescence, when the continental interior was devoid of large topographic barriers, produced a spectacular increase in the size of the areas under marine influence (e.g. Malumián, Nullo & Ramos, 1983; Salfity *et al.*, 1985). The Nothofagaceae and Myrtaceae appeared during the Maastrichtian (70.6–65.5 Ma) and this occurred in association with the destruction of the coastal environments by the marine transgression. After the Maastrichtian, the world flora changed considerably. Many modern families had differentiated and the old groups (Normapolles, Aquilapollenites, elatereous pollen) had become relicts or extinct (Romero, 1993). The lower Lefipán Formation at Barranca de los Perros, Chubut Province, is Maastrichtian in age, calibrated by invertebrates. The Lefipán flora is considered marginally Weddellian as it contains some endemic Weddellian Province species, but does not reflect the ‘typically Weddellian’ forest vegetation. The fern and angiosperm-rich Lefipán palynoflora probably represents shrubby angiosperm-fernland vegetation, with patchy wooded areas growing in warm temperate (to subtropical?) climate conditions. Within the Patagonian region, the Lefipán palynoflora is similar to that of the Maastrichtian El Cain locality (Río Negro province), the Coli Toro Formation in the Río Negro province and Paso del Sapo Forma-

tion in Chubut province, none of which contain *Nothofagidites* pollen (from Baldoni & Askin, 1993). During the Late Cretaceous and Palaeogene, at southern high latitudes, a cool temperate biogeographical province extended, across Antarctica (mainly Western Antarctica) to New Zealand and south-eastern Australia. This Weddellian Province (Zinsmeister, 1979, 1982) included shallow marine faunas, as well as terrestrial biotas (Case, 1988, 1989; Askin, 1989; Baldoni & Askin, 1993). The Weddellian vegetation was characterized by a podocarpaceous conifer/Proteaceae/*Nothofagus* forest (and especially *Lagarostrobos/Phyllocladidites mawsonii* pollen), which dominated the floras during the Campanian through the Palaeocene. *Nothofagus* was more abundant in the Eocene (Baldoni & Askin, 1993). The presence of locally abundant cycads and palms suggests a warm and relatively humid climate towards the end of the Cretaceous (Ottone, 2009). Warm vegetation was present in northern and central Patagonia at that time, as indicated in particular by the taphoflora (Volkheimer, 1971; Romero, 1978).

Summarizing, the Early Cretaceous is a continuation of the Jurassic trends in which conifers dominated. The primitive angiosperms came from sediments of Barremian to Early Aptian age. The parent plants flourished near aquatic sites in lowlands and coastal environments. During the Albian–Coniacian a progressive angiosperm diversification was produced. In the Maastrichtian, the Nothofagaceae and Myrtaceae families appeared.

CENOZOIC PALAEOGENE

During the Palaeocene (65.5–55.8 Ma) (Danian; the Salamanca and Bororó formations), a vegetation dominated by tropical elements would have developed in Patagonia. The first testimonies of the Atlantic marine ingression correspond to the Salamanca Formation (Archangelsky, 1973). The plant microfossil assemblages from southern South America reveals distinct differences in Palaeogene times. Palaeophysiographical reconstruction based on fossil palynoflora on palaeobotanical data show that all taxa in the Danian could be accommodated within an altitudinal range from sea level to 1200–2500 m. The Palaeocene vegetation in south-eastern Chubut was composed by several communities: mangrove, swamp woodland, tropical rainforest, mossy forest, ‘*Araucaria*’ woodland and sclerophilous forest (or savanna). The dominant climate would have been the ‘Cfa’ type (subtropical humid) of Köppen’s classification (Petriella & Archangelsky, 1975). *Classopollis* is present (up to 50%) in Palaeocene levels of Patagonia. This genus is not recorded from the Late Palaeocene upwards. The absence of this genus in the Late Cretaceous sedi-



Figure 3. Danian phytogeographic provinces in Argentina (from Quattrocchio & Volkheimer, 2000).

ments of Patagonia is difficult to explain, considering that it is one of the dominant elements in the Early Cretaceous palaeofloristic assemblages. Probably, the ecological conditions produced the temporal retraction of the Cheirolepidiaceae to drier mountain areas. This type of environment is recorded in the Early Palaeocene of the San Jorge Gulf, where it allowed the development of the last representatives of the family (Archangelsky & Romero, 1974). Based on the palynological record at the genus or species level and at the palaeocommunity level, two major palaeophytogeographic provinces could be recognized during the Danian in Argentina: the Ulmaceae Phytogeoprovince in the north and the Phytogeoprovince of *Nothofagidites* in the south. A subprovince with triprojectate (which

possess apertures borne in three arms that project from a central body) pollen (*Mtchedlishvilia*) could be distinguished in central north-western Argentina. Warm and humid climatic conditions are inferred for the Ulmaceae Phytogeoprovince and more temperate conditions for the Phytogeoprovince of *Nothofagidites* (Quattrocchio & Volkheimer, 2000; Fig. 3). There was a general retraction of the genus *Nothofagidites* during the Early Palaeocene and an increase during the Late Palaeocene (Thanetian; the Río Chico Formation), and a great expansion during the Eocene (the Río Turbio Formation), probably related to the generation of new habitats originated attributable to the first movements of lifting of the Andean Ridge (Romero, 1973). The characteristic floras from the

Eocene (55.8–33.9 Ma) are summarized by Romero (1993), who distinguished two microfloral provinces: Neotropical and Mixed. According to Hinojosa & Villagrán (1997), the ‘Palaeoflora Mixta’ is characterized by cool–temperate (e.g. *Nothofagus*, *Laurelia*, *Lomatia*), subtropical (e.g. *Annona*, *Nectandra*, *Ocotea*) and endemic (e.g. *Schinopsis*, *Schinus*) taxa. These mixed floras, with elements that are now distributed in different climatic zones, have been interpreted as changes in the climatic tolerance of their components or by atmospheric thermal stability. Studies in foliar physiognomy demonstrate that these floras would have grown under subtropical climatic conditions with relatively warm temperature and high annual precipitation, low seasonal variability and a climatic regime without modern equivalents (Hinojosa & Villagrán, 2005). The Río Turbio Formation (late Middle Eocene) in western Patagonia bears mostly Gymnospermae, Nothofagaceae, Myrtaceae, Proteaceae and spores with few species of angiosperms (Archangelsky, 1972; Romero, 1977; Romero & Zamaloa, 1985). Hinojosa & Villagrán (2005) classified this taphoflora as Mixed Palaeofloras. In the Palaeogene Huitrera Formation of north-western Patagonia, Melendi, Scafati & Volkheimer (2003) recorded microfloras without *Nothofagidites* of Early Eocene age, and others dominated by *Nothofagidites* (‘brassii’ and ‘fusca’ groups) of Middle to Late Eocene age. These authors recognized a ‘mixed flora’ for the Middle to Late Eocene. Tropical elements were recognized for the Early Eocene, which were later replaced by a ‘mixed’ forest with both Neotropical and Antarctic elements occupying most of the emerged lands (Palazzesi *et al.*, 2003). The taxacean (or cephalotaxacean) stem *Taxaceoxylon katuatenkum* in the Early to Middle Eocene Koluel–Kaike Formation of south-western Chubut indicates the presence of a subtropical forest in this area of Patagonia during the Early to Middle Eocene (Brea, Bellosi & Krause, 2009).

The palynological assemblage recovered from the basal, fine-grained sedimentary section of the San Julián Formation (?Late Eocene–Oligocene), in the Cabo Curioso area, Santa Cruz province (Austral Basin), 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, Quattrocchio & Ruiz, 2009). This palynologic assemblage also reflects the ‘Mixed Palaeoflora’ of Romero (1978). Some of the palaeocommunities of the ‘basal fine-grained sedimentary section’ are similar to those of the Valdivian District of the Subantarctic Province and Dominion (Cabrera, 1976), whose flora, adapted to a cool–temperate climate, is very different from that of the other dominions of the Argentine territory (Fig. 4). The assem-

blages of the ‘basal fine-grained sedimentary section’ differ from the Valdivians by containing podocarpaceans related with modern forms restricted to Tasmania and New Zealand (*Phyllocladidites*, *Dacrycarpites*, *Microcachryidites*, etc.), as mentioned for other Palaeogene assemblages of Patagonia (e.g. Romero, 1977; Báez, del Zamaloa & Romero, 1990). They contain *Nothofagidites* of the *brassii* type, which is not present in the modern Valdivian forest, and some representatives of megathermal families of angiosperms. The coexistence of elements indicating temperate to warm–temperate climate, together with others of cool–temperate climate, is consistent with a relationship with the so-called ‘Mixed Palaeoflora’, characteristic for southern South America during the Palaeogene (Romero, 1978). These relatively warm conditions would have prevailed even in southern Patagonia, up to the early Middle Miocene, allowing the development of taxa whose modern distribution is tropical (Palazzesi *et al.*, 2003). Hence, the traditional Cenozoic plant evolution scheme has changed where the ‘Palaeoflora Mixta’ was replaced following the Late Eocene by a cool–temperate forest south of 40°S (Palazzesi *et al.*, 2003). The Slogget Formation, in Bahía Slogget, Isla Grande de Tierra del Fuego (Olivero *et al.*, 1998), probably Late Eocene in age, is excluded from the suggested distribution of the ‘mixed flora’, because of the presence of beech, podocarpacean and proteacean pollen, fern and fungal spores and freshwater algae, of temperate to cool–temperate and humid conditions (Fig. 5). In the Oligocene (33.9–23.03 Ma), a community dominated by Myrtaceae, Palmae and Araucariaceae trees with Podocarpaceae and Nothofagaceae is recognized in the San Julián Formation at Playa Mina, Santa Cruz province (Barreda, 1997). However, the presence of small amounts of Anacardiaceae, Malvaceae, Symplocaceae, Ephedraceae, Poaceae, Asteraceae and Chenopodiaceae suggests the development of local open vegetation. The spore–pollen 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, 2000). Similar palynologic assemblages are recognized in the lower part of the Centinela Formation (Oligocene–Miocene boundary) in south-western Santa Cruz province (Guerstein, Guler & Casadío, 2004). Analysis of the Palaeogene sporomorphs of the Río Foyel section (Foyel Group, Ñirihuau Basin, north-western Patagonia, Argentina) allows the characterization of the palaeofloristic and palaeoclimatic scenario of the studied section during the Late Eocene(?)–Oligocene. It reflects a regional forest dominated by Nothofagaceae, Myrtaceae, Podocarpaceae and Palmae, developed under temperate to warm temperate and humid climate. In the Río

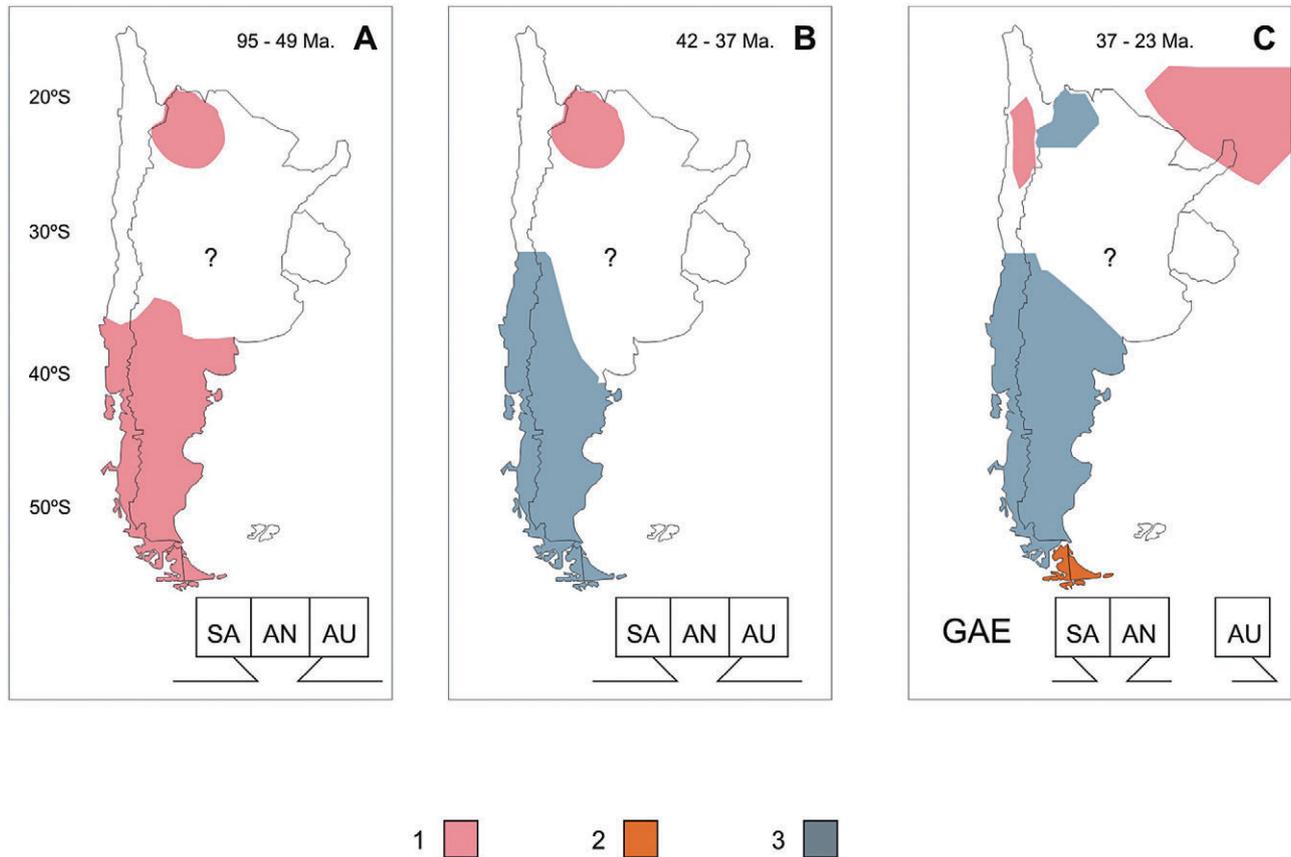


Figure 4. Modern Valdivian forest (A); *Nothofagus* forests and *Sphagnum* mires (B), forest–steppe ecotone (C) and steppe (D) from Isla Grande de Tierra del Fuego.

Foyel Formation (Ñirihuau Basin, western Río Negro province), a first marine ingression came from the Pacific Ocean early in the Oligocene (Asensio *et al.*, 2010) and a second one during the Late Oligocene and Early Miocene from the Atlantic Ocean. The marine dinocyst assemblage was dominated by *Tuberculodinium vancampoe* and a group of protoperidinoïd species also identified in the ‘Patagonian’ sequences of the San Jorge Gulf Basin and Mazarredo Sub-basin: *Lejeunecysta communis*, *L. globosa*, *Selenopemphix* sp. and *Operculodinium centrocarpum* (Barreda *et al.*, 2003).

Summarizing (Fig. 6), warm and humid climatic conditions are inferred for central and northern Patagonia during the Palaeocene and Early Eocene. The characteristic floras from the Late Eocene correspond to the ‘Palaeoflora Mixta’, with the exception of the Fuegian Archipelago, where temperate to cool families dominated. The ‘Palaeoflora Mixta’ has grown under subtropical climatic conditions, with relatively warm temperatures and high annual precipitations, with low seasonal variability and a climatic regime without modern equivalents. These floras continued during the Oligocene until the early Middle Miocene.

NEOGENE

The Early–Middle Miocene (23.03–11.61 Ma) floras were assembled in three well-supported Palaeophytogeographic Provinces: the Neotropical, northern Argentina, characterized nowadays as the Chaco Domain (e.g. Apocinaceae, Aquifoliaceae, Cactaceae, Fabaceae, Sapotaceae, Moraceae, Anacardiaceae, Ulmaceae, Amaranthaceae), the *Nothofagidites* Province, to the south-western tips, dominated by elements of the austral forest (e.g. Nothofagaceae, Podocarpaceae, Araucariaceae, Misodendraceae, Menianthaceae, Rosaceae, Cunoniaceae); and the Transitional, in central and south-eastern Argentina (Patagonia specially), defined by a mixed flora with Neotropical and Austral components. By the Late Miocene–Pliocene, the area previously occupied by the Transitional Province was replaced by the ProtoEspinal/Steppe (earliest Espinal/Steppe) Province characterized by a xerophytic shrubby–herbaceous vegetation (e.g. Chenopodiaceae, Ephe-draceae, Convolvulaceae, Anacardiaceae, Fabaceae, Asteraceae, Ulmaceae, Celtoideae (Barreda *et al.*, 2007). Several forcing factors controlled the vegeta-

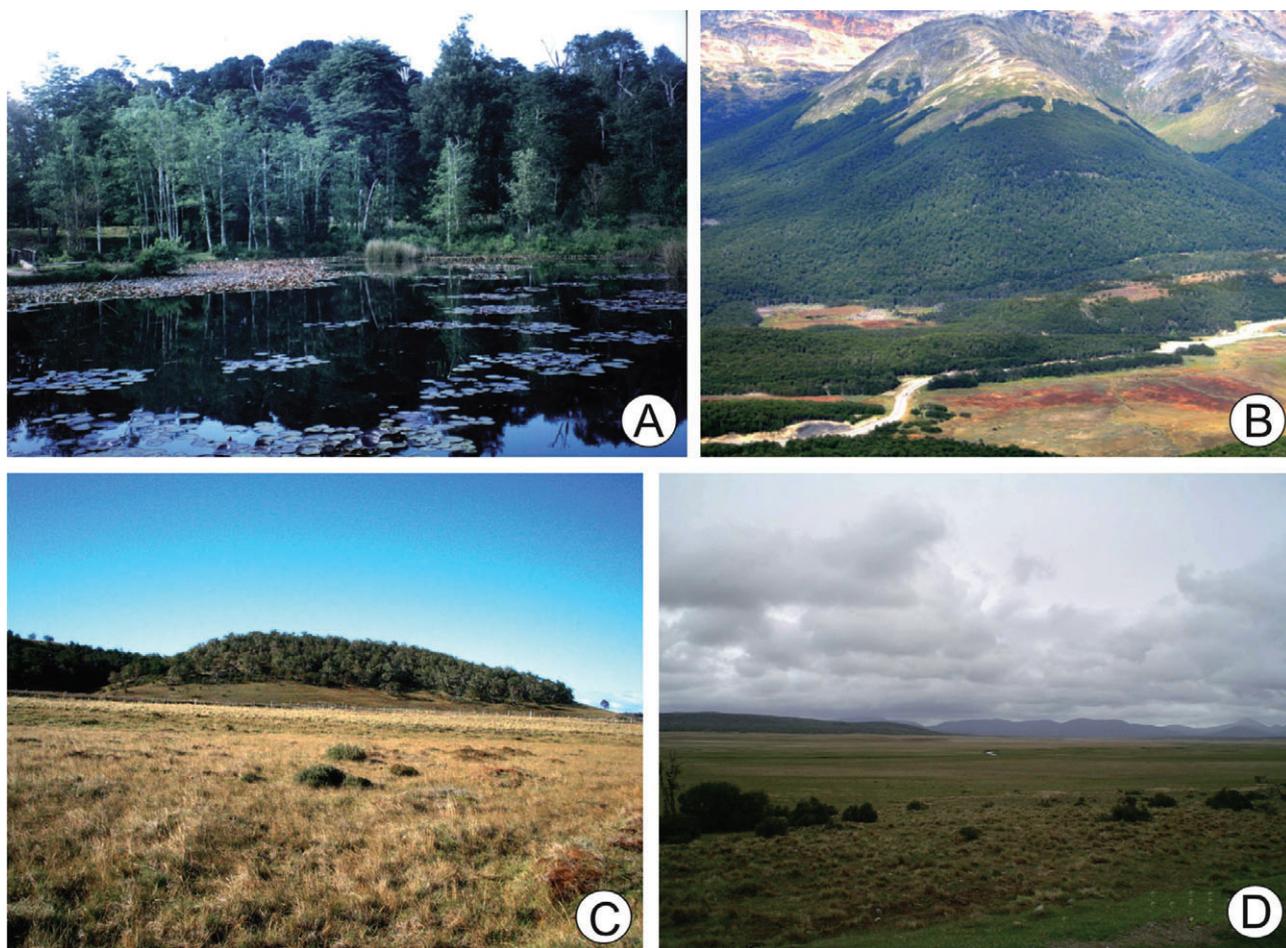


Figure 5. Evolution of Late Cretaceous and Palaeogene floras in Southern South America, after Hinojosa & Villagrán (1997) (modified from Quattrocchio, 2006). Palaeofloras: 1. Tropical; 2. Antarctica; 3. 'Mixta'. SA, South America; AN, Antarctica; A, Australia; GAE, glaciation in East Antarctica.

tion changes during the Miocene and the Pliocene. Continental drift and the changes of oceanic and atmospheric circulation, sea level changes and related changes of continental climate conditions, Andean uplift, volcanism and the gradually changing size of the Antarctic ice cap are responsible for the growing of aridity and decreasing of global temperature during the Neogene.

QUATERNARY

The Pleistocene and Holocene times were characterized by frequent latitudinal and altitudinal changes in the vegetation distribution, as a response to recurrent climatic oscillations, fluctuations of sea level and ice extent and changing patterns of atmospheric circulation. Palynological records from the Early and Middle Pleistocene are, however, scarce and discontinuous and this makes the recognition of the boundaries between palaeophytogeographic provinces

difficult. Only one pollen fossil record is available for the Middle Pleistocene, which comes from a location at 50°S (the Cañadón El Mosquito site) in the Patagonian semi-desertic area of the upper Río Santa Cruz valley (Schäbitz & Schellmann, 1999). The record probably belongs to an interglacial period (c. 430 ka B.P.; i.e. MIS 11) and suggests that the palaeovegetation was dominated by a dense forest of mainly *Podocarpus* accompanied by lesser amounts of *Nothofagus*, *N. obliqua*-type and Cupressaceae, developed under more humid and warmer climate than today (Mancini *et al.*, 2008). In the eastern Fuegian Archipelago, the landscape was during the Middle–Late Pleistocene, probably MIS 4 or even perhaps reaching up to MIS 6 (39 560 to > 58 000 years B.P.), dominated by steppe/tundra environments. This landscape reflects drier and colder conditions than today (Bujalesky *et al.*, 1997), probably corresponding to a stadial period. In extra-Andean Patagonia, at the Magallanes maar core (52°S), the vegetation pattern

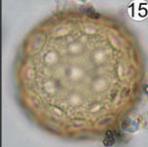
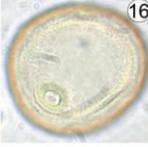
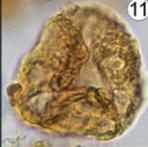
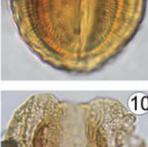
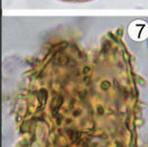
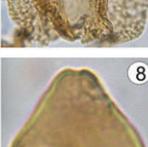
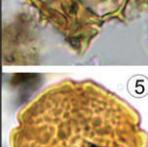
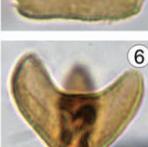
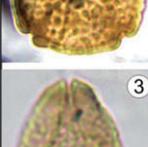
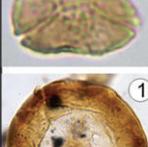
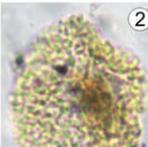
Eonothem Eon	Erathem Era	System Period	Series Epoch	Stage Age	Age Ma	Palynofloristic changes	
Phanerozoic	Cenozoic	Quaternary	Holocene		0.0117	 	
			Pleistocene	Upper		0.126	
				"Ionian"		0.781	
				Calabrian		1.806	
		Gelasian			2.588		
		Pliocene	Piacenzian		3.600		
			Zanclean		5.332		
		Neogene	Miocene	Messinian		7.246	
				Tortonian		11.608	
				Serravallian		13.82	
				Langhian		15.97	
			Burdigalian		20.43		
			Aquitanian		23.03		
			Oligocene	Chattian		28.4 ± 0.1	
				Rupelian		33.9 ± 0.1	
		Eocene		Priabonian		37.2 ± 0.1	
	Bartonian				40.4 ± 0.2		
	Paleocene	Lutetian		48.6 ± 0.2			
		Ypresian		55.8 ± 0.2			
		Thanetian		58.7 ± 0.2			
		Selandian		~ 61.1			
		Danian		65.5 ± 0.3			
		Maastrichtian		70.6 ± 0.6			
	Mesozoic	Cretaceous	Upper	Campanian		83.5 ± 0.7	
				Santonian		85.8 ± 0.7	
				Coniacian		~ 88.6	
				Turonian		93.6 ± 0.8	
				Cenomanian		99.6 ± 0.9	
			Lower	Albian		112.0 ± 1.0	
				Aptian		125.0 ± 1.0	
				Barremian		130.0 ± 1.5	
				Hauterivian		~ 133.9	
Valanginian					140.2 ± 3.0		
Berriasian		145.5 ± 4.0					

Figure 6. Subdivisions of the global geologic record (International Commission on Stratigraphy chart, 2009) with selected pollen grains recognized in Patagonia. 1. *Cyclusphaera psilata*. 2. Primitive angiosperm (*Retiacolpites* sp.). 3. Myrtaceae (*Myrtaceidites verrucosus*). 4. Nothofagaceae. 5. Ulmaceae (*Verrustephanoporites simplex*). 6. *Mtchedlishvilia saltenia*. 7. Palmae (*Spinizonocolpites* sp.). 8. Proteaceae. 9. Podocarpaceae (*Phyllocladidites mawsonii*). 10. Podocarpaceae (*Podocarpidites marwickii*). 11. Podocarpaceae (*Trisaccites* sp.). 12. Asteraceae. 13. Anacardiaceae (*Schinus* sp.). 14. Ephedraceae (*Ephedra* sp.). 15. Chenopodiaceae. 16. Poaceae.

reflects a grass steppe under colder and more humid conditions than today during the MIS 3 interstadial (31 560 to > 51 700 years B.P.; Corbella, Borrromei & Quattrocchio, 2000). Likewise, the fossil pollen record from western Patagonia at the Bajada de Rahue sequence (39°S) indicates the development of steppe–scrub vegetation that suggest precipitation and temperature similar to the modern one during the MIS 3 interstadial (27 900–32 600 years B.P.) (Markgraf *et al.*, 1986). After the Last Glacial Maximum (LGM; c. 24 cal. ka B.P.; Rabassa, 2008c) the palynological data indicate variations in temperature and precipitation under global increasing temperature trend (McCulloch *et al.*, 2000; Pendall *et al.*, 2001). The pollen records from east of the Andes in Patagonia and from southern Tierra del Fuego show, with only minor local differences, a postglacial vegetation dominated by steppe/shrub/heath communities. The palaeoenvironments were drier and colder than present day conditions to the point of reduction of *Nothofagus* forest in the Andean areas. These climate conditions throughout the higher southern latitudes suggest that the southern limit of the westerly storm tracks was positioned equator-wards, and/or was substantially weaker than today (McCulloch & Davies, 2001; Markgraf & Huber, 2010). During the final Late Glacial period (after 12 800 cal. yr B.P.), the *Nothofagus* forest expanded gradually into the landscape from glacial refuges or niches located in the western regions. During the Early Holocene (11 500–8000 cal. yr B.P.), a *Nothofagus* forest more open than today spread regionally through the southern Andean Patagonia (Mancini *et al.*, 2008) and southern Tierra del Fuego (Borrromei & Quattrocchio, 2008) under conditions warmer and drier than today in an environmental setting subject to high fire incidence (Whitlock, Moreno & Bartlein, 2007) as a result of highly variable westerly precipitation regimes (Markgraf & Huber, 2010). In southern extra-Andean Patagonia, the pollen record from Laguna Potrok Aike (51°S) indicates that the grass steppe was replaced by shrub steppe, suggesting low available moisture in the steppe (Wille *et al.*, 2007). Also, the spread of grass steppe vegetation in the central–north Fuegian region indicates drier conditions (Heusser, 2003). Meanwhile, in northern extra-Andean Patagonia (40–50°S), the pollen data show the development of grass steppe and Patagonian shrubs vegetation (Mancini *et al.*, 2008). The sedimentological and pollen data from the Lago Cardiel record (49°S) also show high lake levels and steppe herbs and scrub vegetation (Markgraf *et al.*, 2003), all as a signal of higher moisture conditions. This climate pattern probably reflects a highly variable position and/or intensity of the westerly winds focused from 46 to 49°S (Markgraf *et al.*, 2003; Villa-Martínez & Moreno, 2007) or the

weakening and southward shift of westerlies' storm tracks, probably south of 54°S, along with increased advection of humid Atlantic Ocean air masses to the eastern Andean slopes of central Patagonia (Villa-Martínez & Moreno, 2007; Whitlock *et al.*, 2007). During the Middle Holocene (8000–4000 cal. yr B.P.) the vegetation scenario from the northern and southern Andean Patagonian region and southern extreme of extra-Andean Patagonia (51°S) reflect wetter conditions with the development of *Nothofagus* forest–steppe ecotone and grass steppe vegetation (Mancini *et al.*, 2008). Also, in southern Tierra del Fuego and western Isla de los Estados, the pollen record indicates more humid and colder conditions than during the Early Holocene, with the development of open forests and *Nothofagus* forest/*Empetrum* heath communities, respectively (Borrromei & Quattrocchio, 2008; Ponce *et al.*, 2010). Meanwhile, in extra-Andean Patagonia and central–north-eastern Tierra del Fuego, grass–shrub and grass steppes developed, respectively, under semi-arid conditions (Heusser, 2003; Mancini *et al.*, 2008). This palaeoclimate evidence points both to a northward latitudinal change and to the strengthening of the westerlies on the Andean region, leading to low moisture conditions east of the Andes in the area affected by the rain-shadow effect of the Andean Cordillera (Mancini *et al.*, 2008; Borrromei *et al.*, 2010). The strengthening of the Southern Hemisphere Westerly Winds (SWWW) by approximately 8000 cal. yr B.P. correlates, within dating uncertainties, with the commencement of neoglacial advances as early as 8.5 ± 0.7 and 6.2 ± 0.8 ka in central Patagonia (46°S) (Moreno *et al.*, 2010; Ponce *et al.*, 2010). The Late Holocene (the last 4000 years) has been characterized as a cooler, wetter period, with renewed glacial activity in the Central Patagonian Andes during the so-called 'Neoglaciations' (Mercer, 1976; Moreno *et al.*, 2009). Maximum precipitation levels are recorded in all pollen records from Andean Patagonia (Moreno *et al.*, 2009; Tonello, Mancini & Seppä, 2009) and the Fuegian Archipelago (Heusser, 2003; Borrromei *et al.*, 2010), including western Isla de los Estados (Ponce *et al.*, 2010). In the Andean Patagonia and Fuegian region, the vegetation was dominated by closed *Nothofagus* forests with a net eastward shift of the forest–steppe ecotone, whereas the Subantarctic Evergreen Forest expanded in western Isla de los Estados. This intensification of the westerlies may have been associated with a steepening of the pole-to-equator temperature gradient, caused by a cooling trend in the Southern Ocean and Antarctica (Divine *et al.*, 2010). In extra-Andean Patagonia, arid–semi-arid conditions prevailed, with development of the Patagonian–Monte shrub steppe vegetation. During the last 2000 years, the palaeodata document multi-

century variability, apparently reflecting drier conditions during the Medieval Warm Period (MWP) and cooler, moister conditions during the Little Ice Age (LIA) (Mauquoy *et al.*, 2004; Moy *et al.*, 2008; Fey *et al.*, 2009; Moreno *et al.*, 2009; Borronei *et al.*, 2010; Waldmann *et al.*, 2010).

Summarizing, the distribution of vegetation during the Pleistocene and Holocene has changed extensively and repeatedly both latitudinally and/or altitudinally, which were recombined markedly in different proportions from those found today in response to atmospheric circulation patterns, climate oscillations, ice extent and sea level fluctuations. Pollen records suggest a transitional stage towards the present plant distribution during the last 4000 years south of 34°S (Barreda *et al.*, 2007).

FINAL REMARKS

The changing palaeobiological scenarios in Patagonia, during Mesozoic and Cenozoic times, as reflected by the palynobiota, are intimately related to the tectonic and climatic history of the supercontinent Pangaea during the last 250 Ma and to the elevation of the Andean Cordillera during the Cenozoic. Compagnucci (2011), discussing the atmospheric circulation over Patagonia since the Jurassic to the Quaternary, mentions that Patagonia was localized mostly within the palaeolatitudes influenced by the wind system of the westerlies during the last 250 Ma. That explains the low frequency of climatic changes. During most of the Mesozoic, the continental mass (as Pangaea was fractured and dismembered) remained far from the poles, thus resulting in large periods of warm climate, without polar ice caps. High concentrations of greenhouse gases (mainly CO₂) during most of the Mesozoic have been an additional factor for global warming and an important controlling factor for the distribution of the biota. This explains the relative palaeofloristic uniformity with three principal gymnospermous groups: the cheirolepidiaceans, inhabiting warm and semi-arid lowlands with well-drained soils; two main groups of araucariaceans, growing in more or less humid biotopes at different altitudes and the podocarpacean forests, covering more elevated areas. In Middle Cretaceous times, the mesophytic landscapes underwent, regionally and globally, great changes. In Patagonia, this took place in three steps of angiospermous diversification, which led finally, during the Late Cretaceous, to the predominance of the cenophytic flora, characterized by prevailing angiosperms. Finally, during the Pliocene, the 'separating wall' of the Patagonian Cordillera impeded the moisture of the westerlies to reach the extra-Andean Patagonia east of the Andes. Consequently, the forests disappeared in the plains east of the Andes and the landscape was

transformed into a bleak plateau – the present Patagonian steppe. Associated with these vegetation transformations, the atmospheric greenhouse gases progressively diminished their concentration during the Cenozoic, reaching in the Pleistocene the low levels characteristic for the Quaternary. In this context, it is important to take into account that 'climate is only half of the story in the evolution of organisms through time', as expressed by T. J. M. Schopf (1984), considering that evolution has an internal component, based in the enormous genetic variability of species, and the genomic factors, leading to the continuous production of genetic variability. He also expressed that 'the reasons why climate and evolution often have been presented as related, may be that both are customarily considered as time series, where the scale of resolution is set by the limits of stratigraphic resolution. Rarely are the inferred correlations tested to see if they are significantly different from nonsense correlations, which are ubiquitous in time series'.

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