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The evolution of Patagonian climate and vegetation from the Mesozoic to the present

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In this review, Patagonian phytogeographical patterns are analysed from a global and evolutionary perspective that takes into account aspects from the geology, climatology and plant evolution. The biomes contained within the different climatic belts are inferred through time for the southwestern Gondwana supercontinent on the basis of palaeogeographical reconstructions, climate-sensitive rocks and plant distribution. Some current plant components of Patagonia can be traced back to early Mesozoic times, to the Triassic and Jurassic mesophytic floras. The main features of the Cretaceous and Palaeogene Patagonian floras are described and compared with other Gondwanic areas that shared, at the time, more plant components than they do today. The Neogene floras are analysed in relation to the rise of the Andes and the global climatic cooling, which differentiated the Andean and the Extra-Andean regions, and ended in the modern cool-temperate Andean forest and the arid steppe. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 409–422.

ADDITIONAL KEYWORDS: biome evolution – climatic change – Gondwana – palaeobotany – palaeoclimate – palaeogeography.

En esta revisión se analizan, desde una perspectiva evolutiva y a una escala global, los patrones fitogeográficos de Patagonia tomando en cuenta la evolución vegetal y aspectos geológicos y climáticos. Se infieren los biomas del pasado en relación con las franjas climáticas para el sector sudoccidental de Gondwana, basados en la distribución de plantas, rocas climato-sensitivas y reconstrucciones palaeogeográficas. Algunos componentes de la vegetación actual de Patagonia pueden retrotraerse hasta el Mesozoico Temprano, en las floras mesofíticas del Triásico y Jurásico. Se describen los caracteres generales de las floras del Cretácico y Paleógeno, se comparan con las de otras áreas de Gondwana y se verifica que compartían mayor cantidad de componentes vegetales que las actuales. Las floras del Neógeno son analizadas en relación con el levantamiento de los Andes y el enfriamiento climático global, que diferenciaron la región andina de la extra-andina y que culminó en la formación del Bosque Andino templado-frío y la Estepa árida.

PALABRAS CLAVE: evolución de biomas – cambio climático – Gondwana – palaeobotánica – palaeoclima – palaeogeografía.

INTRODUCTION

The emergence, diversification and decline of fossil plant groups and, in general, the palaeofloristic turnover and evolution of floras are the keys to understanding the evolution of past climates and environments. The aim of this article is to explain, from a geological–evolutionary perspective, the current phytogeographical pattern in Patagonia. For this purpose, the evolution of floras in this area is

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considered through the analysis of Mesozoic, Palaeogene and Neogene plant records. More specifically, past Patagonian biomes and their relationship with palaeoclimate are inferred on the basis of past floristic assemblages.

It is important to note that current seemingly uniform floras are the result of complex histories, involving the development of different lineages through space and time – measured in tens of millions of years. Past phytogeographical distributions are related to independent evolution of floral assemblages characterizing the major regions of the Earth.

From a phytogeographical point of view, the largest biological partitioning is the realm that includes both spatial and temporal ranges, and differs in plant composition at the level of orders and families (Wnuk, 1996). The floristic realms, differentiated in floras, can be divided into biomes characterizing diverse climates and substrate conditions (DiMichele, Gastaldo & Pfefferkorn, 2005). Ten or eleven biomes are identified in the modern world (Walter, 1985; Fine & Ree, 2006).

Broad-scale patterns of Mesozoic climates and biomes have been described on the basis of various lines of sedimentological and palaeobotanical evidence, because of the strong relationship with climate shown by the global distributional patterns of modern vegetation (e.g. Ziegler *et al.*, 1996, 2003; Scotese, Boucot & McKerrow, 1999; Rees, Ziegler & Valdes, 2000; Rees, 2002; Willis & McElwain, 2002). The synergistic analysis of the physical environment (geology) and the resident flora (palaeobotany) allows us to increase our understanding of the evolution of the biota.

In this contribution, a brief reference is given to the great Permian–Triassic extinction, because of the first appearance of plant groups that now grow in Patagonia, which occurred in the Mesozoic. The main features of Patagonian floras are described throughout the Mesozoic and the Palaeogene in comparison with other areas of Gondwana. The Neogene floras are analysed in relation to the rise of the Andes. As mentioned above, the main objective of this contribution is the joint analysis of palaeofloras and lithological indicators, in order to infer the palaeoclimatic zones and biomes of Patagonia – as a part of southwestern Gondwana – and their evolution through time.

THE TRIASSIC AND THE SPREADING OF MESOPHYTIC FLORAS

The biotic crisis that marked the beginning of the development of the Triassic fossil floras is included among the five largest mass extinctions of the Phanerozoic (Anderson, Anderson & Cleal, 2007). The Permian–Triassic extinction and the turnover from palaeophytic to mesophytic floras are two of the most striking examples of the direct influence of the physical environment on plant communities. The Pangea coalescence, the unequal distribution of land masses and seas, the spreading of continental climates (megamonsoonal conditions) and global warming determined the expansion of xeromorphic (drought-tolerant) plant groups, which became dominant during the whole Mesozoic (Spalletti, Artabe & Morel, 2003). In the Extratropical regions of Gondwana, the turnover from palaeophytic elements to mesophytic ones was abrupt, and the *Glossopteris* Flora was replaced by the *Dicroidium* Flora, which remained until the end of the Late Triassic. In the Extratropical Gondwana areas, two continental mass extinctions are recognized, one during the Middle Permian (260 Ma) and the other in the Late Permian (251 Ma) (Retallack *et al.*, 2006). The Permian–Triassic biodiversity crisis was classified as first category because it was associated with the collapse of Palaeozoic ecosystems with a great replacement event. This biodiversity crisis was characterized by the simultaneous occurrence of new adaptive types in several plant lineages, which were dissimilar from those found among their Palaeozoic ancestors.

Amidst the major environmental changes that occurred during the Permian–Triassic, we cannot fail to mention the passage from a Cold House to a Warm House (Green House). According to Scotese *et al.* (1999), the Earth has fluctuated between Cold House conditions – in which both polar regions were covered by permanent ice and the global mean temperature was *c.* 12–14 °C – and Warm House conditions – in which there was no permanent ice in the polar caps and global mean temperatures reached 18–22 °C. Equatorial temperatures may have reached 30 °C and, at the poles, it may have been as warm as 14 °C.

By the late Palaeozoic, the planet was emerging from a Cold House period. The Permian climatic subdivision was similar to that of the present day (Fig. 1A), and ten biomes have been recognized within it: Tropical Everwet, Tropical Seasonal Dry (summerwet), Desert, Subtropical Seasonal Dry (winterwet), Warm Temperate, Cool Temperate, Mid-Latitude Desert, Cold Temperate, Tundra and Glacial (Rees *et al.*, 1999; Scotese *et al.*, 1999). By contrast, the Mesozoic Era was characterized by particularly warm climates, with less climatic differentiation, and five main biomes were recognized for the Triassic: Tropical Seasonal Dry (summerwet), Desert, Subtropical Seasonal Dry (winterwet), Warm Temperate and Cool Temperate. Five climate zones/biomes have not been recognized for this period: Glacial, Tundra, Cold Temperate, Steppe (Arid Cold Temperate) and Tropical

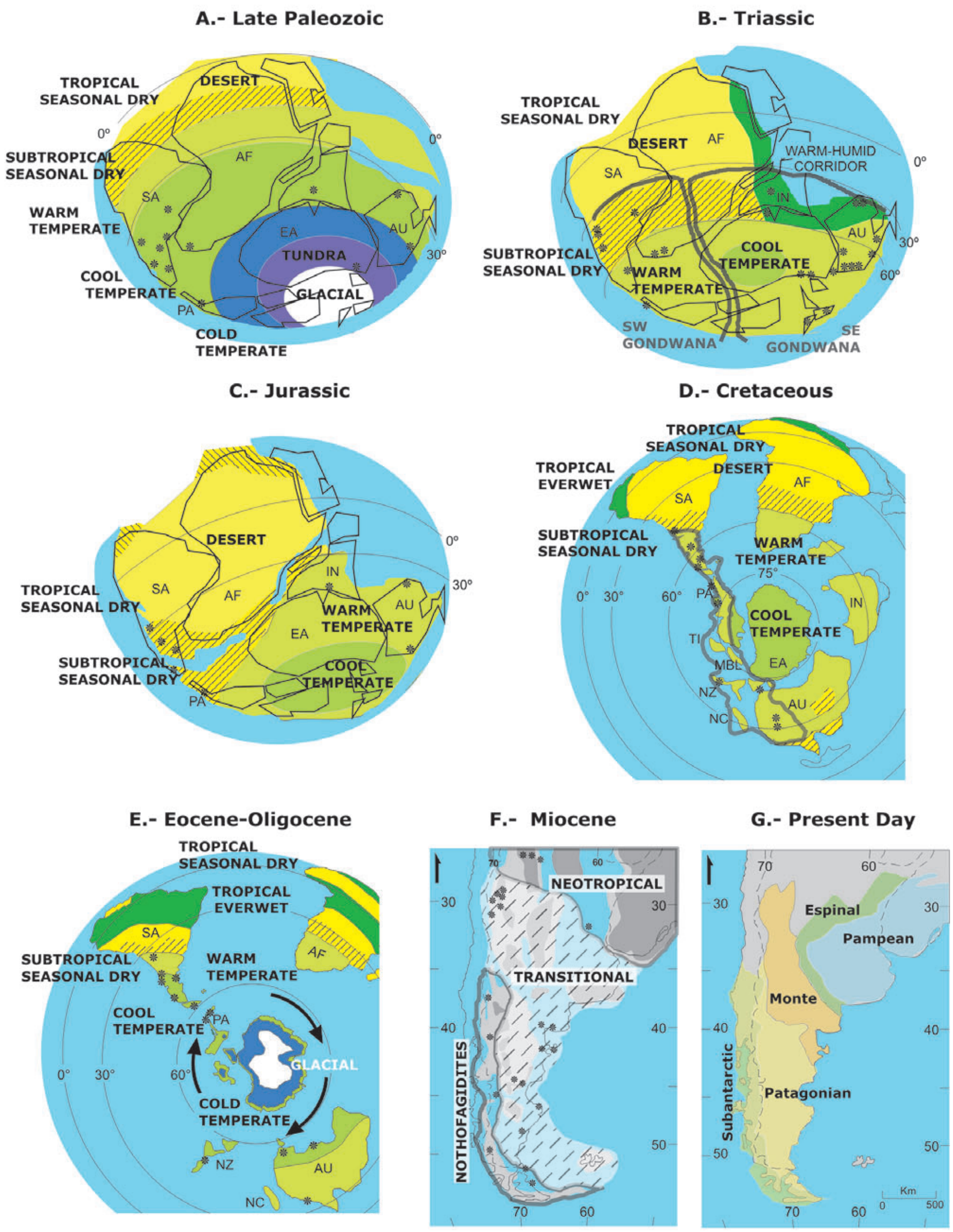

Figure 1. Geographical, climatologic and biome evolution for Gondwana and southern South America. A, Permian Gondwanic reconstruction (based on Wnuk, 1996; Ziegler *et al*., 1996, 2003). B, Triassic Gondwanic reconstruction (modified from Artabe *et al*., 2003; Spalletti *et al*., 2003). C, Late Jurassic Gondwanic reconstruction (modified from Artabe *et al*., 2003; Macdonald *et al*., 2003; Spalletti *et al*., 2003). D, Mid-Cretaceous South Polar reconstruction (based on Smith, Smith & Funnell, 1994; Wilford & Brown, 1994). E, Latest Eocene–early Oligocene South Polar reconstruction (based on Wilford & Brown, 1994; Bohaty & Zachos, 2003; Somoza, 2007; Liu *et al*., 2009). F, Early Miocene reconstruction of southern South America with phytogeographical provinces and the Miocene greatest marine ingression (light blue in online version, light grey in print), and the border of South American Continental Shelf; grey, mainly highlands (based on Uliana & Biddle, 1988; Barreda *et al*., 2007). G, Present-day phytogeographical provinces (based on Cabrera, 1976); note that Sub-Antarctic Biome = Sub-Antarctic Province and Steppe Biome = Patagonian, Monte, Espinal and Pampean Provinces. AF, Africa; AU, Australia; EA, East Antarctica; IN, India; MBL, Marye Bird Land; NC, New Caledonia; NZ, New Zealand; PA, Antarctic Peninsula; SA, South America; TI, Thurston Island. Stars indicate plant fossil records.

Everwet (Scotese *et al*., 1999; Sellwood & Valdes, 2006). In southeast Australia and Antarctica, the Early Triassic warming was responsible for the replacement of the Permian Cold Temperate climate by the Cool Temperate one, as is evident from the changed composition of both the vegetation and the palaeosols (Retallack, 1999; Retallack & Krull, 1999; Chumakov & Zharkov, 2003).

The disappearance of several climatic belts in the earliest Mesozoic caused a greater floristic uniformity in the Triassic. Thus, the four Palaeozoic floristic realms – Euro-American (= Atlantic), Cathaysian, Angarian and Gondwanic – were reduced to two in the Triassic: Laurasic and Gondwanic (Artabe, Morel & Spalletti, 2003).

The Triassic Gondwanic Realm, distinguished by the presence of the *Dicroidium* Flora, expanded into Australasia, India, South America, South Africa and Antarctica. It is characterized by Corystospermales (extinct primitive Gondwanic gymnosperms) and typical endemic genera. Endemism also occurs in cosmopolitan genera with species restricted to Gondwana.

The Gondwanic Realm can be subdivided into two second-range units: the Tropical and Extratropical Areas (Artabe *et al*., 2003). The Extratropical Area shows differences in the phytogeographical distribution of many groups and can be divided into two provinces. The Southwest Gondwana Province corresponds to where southern America and southern Africa are today, and the Southeast Gondwana Province corresponds to where Antarctica and Australasia are today. The Southwest Gondwana Province developed (from 30°S) covering two climatic belts – Subtropical Seasonal Dry and Warm Temperate – and the Southeast Gondwana Province was mostly governed by the Warm Temperate climatic belt (Fig. 1B).

The Argentine Triassic System has one of the best records of sedimentary exposure and biota in the world. It is identified in several – mostly continental – sedimentary basins. The most important outcrops are located towards the west-central region of Argentina and Chile, and in Patagonia (Deseado and North Patagonian Massifs). These basins are narrow and elongated depressions, markedly asymmetric half-grabens as a result of extensional tectonism (Spalletti, 2001; Spalletti & Franzese, 2007). Floras with moderate taxonomic biodiversity were preserved in them. Thus, the Argentine Triassic flora, included in the Southwest Gondwana Province (Extratropical Area), comprises 86 genera and 238 species. The filicopsids represent the most diverse fern group (42 species). Among the gymnosperms, 61 genera and 176 species are identified, and the Corystospermales, Peltaspermales, Cycadales and Ginkgoales are the dominant groups.

The plant fossil records of different stratigraphic units from Argentina allow us to recognize three floristic events, which seem to be quite related to abiotic changes (Morel, Artabe & Spalletti, 2003; Spalletti *et al*., 2003). These events are characterized by: (1) the appearance of mesophytic elements and the coexistence of Palaeozoic and Mesozoic groups; (2) a higher diversification of the *Dicroidium* Flora; and (3) the decline of the *Dicroidium* Flora and its replacement by forms with more Jurassic affinity.

Artabe, Morel & Ganuza (2007) proposed a model that takes into account the evolution of the Triassic floras in southwestern Gondwana. This model proposes two successive extinction pulses – each followed by two successive biotic turnovers. The observed biodiversity shows a maximum in the early Late Triassic, when the first extinction pulse took place, affecting 57% of the floras. The latest Triassic floras show a marked decrease in the biodiversity of Corystospermales, Peltaspermales, Cycadales, Ginkgoales and Gnetales. The study of Triassic palaeocommunities suggests that the decline in Corystospermales triggered a permanent reorganization of the ecosystems. Mixed forests of Corystospermales and conifers, which characterize the Middle Triassic, were replaced – during the latest Triassic – by a mixed forest of Ginkgoales, Coniferales and *Linguifolium* (an extinct gymnosperm). During the latest Triassic, some Corystospermales were still the only tree stratum of sclerophyllous forests. The second extinction pulse, attributed to the latest Triassic, reached 67% of the taxa and caused the disappearance of all the Corystospermales, Peltaspermales and other typical Triassic forms. In the Jurassic, almost the whole of the *Dicroidium* Flora was replaced, only some pteridophytes – such as Gleicheniaceae, Dipteridaceae and Osmundaceae – survived, and several conifers became differentiated in the latest Triassic (Artabe *et al*., 2007).

The presence of Araucariaceae (a typically Gondwanic conifer family) in the mixed Middle Triassic *in situ* forest – discovered by Charles Darwin in 1835 – in Mendoza Province, Argentina, should be emphasized. The structure of the vegetation, the growth ring analyses and sediments suggest that the Darwin forest developed in seasonal dry conditions (Brea, Artabe & Spalletti, 2008a, 2009).

Another important Patagonian conifer family, the Cupressaceae (today represented by three genera – *Austrocedrus*, *Fitzroya* and *Pilgerodendron* – restricted to the Andean Patagonian forests), has its earliest record in the Triassic (Bodnar & Artabe, 2007).

The distribution pattern of different groups of Triassic plants allows us to make some palaeoclimatic considerations (Artabe *et al*., 2003). To begin with, the Dipteridaceae are restricted to continental basins in west-central Argentina and northern Patagonia. The great Dipteridaceae biodiversity in this area would support the theory of the development of Subtropical Seasonal Dry climates (megamonsoonal) at middle palaeolatitudes (40–50°S). However, the fossil floras with Marattiales – recorded at high palaeolatitudes (higher than 60°S) in Patagonia (El Tranquilo Basin) – were probably controlled by the Warm Temperate climate, with uniform rains throughout the year. Furthermore, in southwestern Gondwana, there was a uniform high biodiversity of Corystospermales, Cycadales and Ginkgoales, but, in South America, the highest biodiversity of Ginkgoales was recognized only at high palaeolatitudes in the Warm Temperate belt.

As stated above, according to the group distribution, the Southwest Gondwana Province covered two climatic belts. Therefore, Patagonia and southernmost Africa are assigned to the Warm Temperate Biome. These inferences are consistent with global palaeoclimatic reconstructions (Parrish, 1993; Scotese *et al*., 1999).

THE JURASSIC AND THE FLORISTIC UNIFORMITY

The Triassic/Jurassic extinction at 201 Ma is among the largest mass extinctions of Phanerozoic times (Anderson *et al*., 2007). A volcanic cause is inferred for this biotic mass extinction based on carbon isotopic studies and large flood basalt eruptions (Whiteside *et al*., 2010), although other authors provide gradual extinction patterns as an explanation (Niklas, Tiffney & Knoll, 1983; Ash, 1986; Edwards, 1993).

In Argentina, a floristic turnover is verified by the disappearance of pteridosperms, such as Peltaspermales and Corystospermales. Of the early Jurassic flora, only 28 Triassic species survived, and 66 species (27 genera) appeared for the first time (Artabe *et al*., 2005; Spalletti *et al*., 2007; Escapa *et al*., 2008).

Five main biomes have been identified in the early Jurassic (Rees *et al*., 2000): Tropical Seasonal Dry (summerwet), Desert, Subtropical Seasonal Dry (winterwet), Warm Temperate and Cool Temperate. There is no geological evidence of Tropical Everwet, Tundra or Glacial Biomes for the Jurassic. The equatorial regions were markedly drier than they are today, with a large continental interior. A general symmetry of climate zones about the palaeoequator is seen throughout the Jurassic. Taking into account the combined floral and lithological data, the Jurassic world is interpreted as essentially one in which low latitudes had Tropical Seasonal Dry climates (summerwet). Poleward, both hemispheres hosted: Desert, Subtropical Seasonal Dry (winterwet), Warm Temperate and Cool Temperate Biomes. Rees *et al*. (2000) stated that the highest latitudes of both hemispheres were characterized by a relatively low diversity of species and the dominance of Ginkgoales and macrophyllus conifers, as well as ferns. Closer to the equator – in lower latitudes, where the climate was warmer – biomes were richer in Cycadales, Bennettitales and microphyllus conifers.

Most plant localities in southern Gondwana belong to the Warm Temperate Biome. The floras in Argentina and the Antarctic Peninsula are the exception, and have been assigned to the Subtropical Seasonal Dry Biome (Fig. 1C). The presence of diverse Dipteridaceae ferns indicates Subtropical Seasonal Dry climates in the early Jurassic in Argentina. The analyses of Jurassic wood from southwestern Gondwana also support the Subtropical Seasonal Dry Biome (Cantrill, 1995; Rees *et al*., 2000; Philippe *et al*., 2004). The vegetational differences across southern Gondwana are also consistent with the distributional patterns of lithological indicators, such as coals (which are common in Australia) and aeolian sandstones (preserved in southern Africa and South America). There is no direct geological evidence of a Cool Temperate Biome in Gondwana similar to that interpreted from findings in high-latitude sites in Eurasia. However, because of the otherwise symmetrical arrangement of biomes about the equator, it is reasonable to attribute such a biome to areas distant from maritime influence, in the interior of southern Gondwana (Fig. 1C).

Jurassic floras are clearly distinguished by the extinction of major groups that were dominant during the Triassic, such as Corystospermales and Peltaspermales.

The Jurassic sedimentary basins are associated with intense volcanism and plutonism, as a result of the subduction in the western margin of Patagonia (Macdonald *et al*., 2003; Spalletti & Franzese, 2007). Jurassic marine ingressions occurred mostly from the Pacific and began to influence the climate and the characteristics of the palaeocommunities in southwestern Gondwana.

The Argentine early Jurassic floras, in particular, consisted of 94 taxa, and were dominated by ferns, Bennettitales and Coniferales. In addition to low biodiversity, the early Jurassic floras were characterized by a spatial uniformity. The palaeocommunities show a similar floristic composition from the Mendoza Province (35°S palaeolatitude) to the Antarctic Peninsula (75°S palaeolatitude), indicating that these floras belonged to a single floristic unit (Quattrocchio, Martínez & Volkheimer, 2007). Furthermore, the Gondwanic floras, in general, have many taxa in common with the Lower Jurassic floras of the Northern Hemisphere (Del Fueyo *et al*., 2007).

A marked decline of Ginkgoales, which were so abundant during the Triassic, is also evident (Del Fueyo *et al.*, 2007; Quattrocchio *et al.*, 2007). This also correlates with the assignment of the Argentine floras to the Subtropical Seasonal Dry Biome and the absence of the Warm Temperate Biome in Patagonia and the Antarctic Peninsula.

In the middle Jurassic (180 Ma), the magmatic activity began to intensify in Patagonia and in several Gondwanic areas, and huge volcanic areas developed (Spalletti & Franzese, 2007), affecting the distribution and features of plant communities. Thus, the floras from Patagonia began to diverge from those of Laurasia. The forest landscape included conifer trees, such as the Araucariaceae, Cheirolepidiaceae, Podocarpaceae and some Taxodiaceae, which occupied broad upland regions (Quattrocchio *et al.*, 2007). In open areas, small trees of Cycadales and Bennettitales, together with pteridosperms, developed. Pteridophytes were less diverse and were represented mainly by ferns (Osmundaceae, Gleicheniaceae) and Equisetaceae (Del Fueyo *et al.*, 2007). The decline in the diversity of the Dipteridaceae indicates that drier wet seasons and less humid conditions prevailed during the early Jurassic (Cantrill, 1995). Some authors have linked this variation to the migration south of the southern edge Desert Biome (Scotese, 2001; Escapa *et al.*, 2008).

It is important to note that the Araucariaceae formed *in situ* forests in Patagonia (such as the Monumento Bosques Petrificados and Cerro Madre e Hija Petrified Forests), with trunks that reached extraordinary dimensions. The fossil forms found – assigned to *Araucaria mirabilis* – were related to the Section *Bunya* (today restricted to Australia). The two extant species from South America are assigned to the Section *Araucaria* (*Araucaria angustifolia*, restricted to the Tropical Everwet Biome, and *Araucaria araucana*, restricted to the Cool Temperate Biome).

THE EARLY CRETACEOUS AND THE LAST MESOPHYTIC FLORAS

Like the rest of the Mesozoic Era, the Cretaceous is characterized by a large Hot House climatic period. However, a short Cold House period developed between the end of the Jurassic and the beginning of the Cretaceous, although this period did not generate large ice caps or extensive glacier development (Scotese *et al.*, 1999).

During the Early Cretaceous, the South Atlantic and Indian basins began to open, thus generating ocean crusts and splitting the Gondwanic continents. As a result, the Pangean monsoonal circulation breakdown ended the palaeoclimatic history that had been dominant for the previous 250 million years (Parrish & Doyle, 1984). This is why it is inferred that, for the Early Cretaceous, the palaeofloras were restricted by a new zonal circulation in both hemispheres, more humid conditions developed and palaeoprecipitations increased in tropical areas. In addition, further extensions of Cold Temperate climates were verified in high latitudes. Thus, two biomes that did not exist in the Jurassic can be recognized in the Cretaceous: Cold Temperate and Tropical Everwet can be added to the five pre-existing ones – Tropical Seasonal Dry (summerwet), Desert, Subtropical Seasonal Dry (winterwet), Warm Temperate and Cool Temperate (Fig. 1D).

The assumption that, during the Cretaceous, the entire Patagonian region was in a Warm Temperate climatic zone (Scotese *et al.*, 1999) is partly supported by the presence of thermophilic plant groups (Cyatheaceae, Cycadales and Cheirolepidiaceae), the high CO_2 pressure interpreted from cuticle analyses (Passalía, 2009) and the amount of kaolinite. The Cretaceous floras show some considerable increase in floristic diversity with regard to the Subtropical Seasonal Dry palaeofloras of the early and middle Jurassic.

The Patagonian floras were limited to the north by drier conditions, which are shown by some palyno- and macrofloras from the Subtropical Seasonal Dry Biome. To the south, the Patagonian floras still shared strong similarities with those from the Antarctic Peninsula. Therefore, both could be included in the same Warm Temperate belt. The Cold Temperate Biome could have spread even at higher latitudes, and the South Pole was on the far edge of East Antarctica (Scotese *et al.*, 1999). In fact, Patagonia, the Antarctic Peninsula, West Antarctica (which, at the time, included Thurston Island, Marye Bird Land, New Zealand, New Caledonia and other smaller islands), Tasmania and Australia could all have belonged to the Warm Temperate climatic zone (Fig. 1D). They had the striking floristic similarity that can be consistently traced among them up to the early Palaeogene, and has later been seen as disjunctive distributions.

In Patagonia, there are several Cretaceous outcrops preserving fossil plants, which can be differentiated into: (1) those with mainly continental sediments that were located in highlands; and (2) those related to littoral environments, developed mainly in marine basins.

The volcanic character of the continental environments in Patagonia coincides with the greater activity of the volcanic arc that is related to the Pacific subduction. The intense ash fall influenced the composition of plant communities and printed a peculiar character in the adaptation of plants to these particular Cretaceous environments (Archangelsky *et al*., 1995).

From the palaeofloristic point of view, there is a diversification of the Araucariaceae, Podocarpaceae and Taxodiaceae families, with taxa that are linked to Australasian forms (Llorens & Del Fueyo, 2003). The Cheirolepidiaceae had a high participation in the palaeocommunities, and the thermophilic characters of this family indicate warm climates. The Ginkgoales regained a great representation in the Patagonian floras with a family that is completely extinct – the Karkeniaceae – which formed patches of monotypic forests in the central and eastern Santa Cruz Province. Ferns were very diverse, and some groups – such as Schizaceae, Gleicheniaceae, Pteridaceae and the oldest Patagonian record of Lophosoriaceae – are still present in the modern Andean Patagonian forests (Archangelsky *et al*., 2003). There are extensive records of Lycopodiaceae, Selaginellaceae, Isoetaceae and aquatic ferns, such as Salviniaceae and Marsileaceae (Villar de Seoane & Archangelsky, 2008).

It is important to indicate that the first Patagonian records of the early angiosperms are verified in the Early Cretaceous. These early angiosperms, however, remained as subordinate elements in the floras until they began to dominate ecosystems in the Late Cretaceous (Archangelsky & Archangelsky, 2002; Quattrocchio *et al*., 2006; Archangelsky *et al*., 2009). Few angiosperm extinct taxa are recorded, mostly inhabiting disturbed and flooded environments.

The Bennettitales and Cycadales reached high diversity and abundance in the Early Cretaceous, but diminished at the beginning of the Late Cretaceous, when the Bennettitales became extinct. In other worldwide Cretaceous biomes, the Bennettitales lasted until the end of the Late Cretaceous.

THE LATE CRETACEOUS AND THE RISE OF THE ANGIOSPERMS

The Middle and Late Cretaceous were characterized by the continuous, fast opening of the Atlantic Ocean, as well as by the Pacific subduction on the west border of South America and Antarctica. The southern monsoon breakdown in the Cretaceous also generated the increase in palaeoprecipitations in the North and in southwestern South America (Ziegler, Scotese & Barrett, 1983; Parrish, 1987). The zonal climatic model was enhanced, and temperatures began to increase at high latitudes (Parrish, 1987).

Although Patagonia was still situated in the Warm Temperate Biome during the Late Cretaceous, southern Patagonia was still very close to the Antarctic Peninsula, thus maintaining a floristic link with East Australasia via West Antarctica.

The continentalization of most Argentine basins, which was partly caused by the Patagonian Batholith emplacement that raised some areas in southern South America (Spalletti & Franzese, 2007), allowed the preservation of several continental plant records in Patagonia.

The Late Cretaceous evidenced a clear diversification of the angiosperms in most ecosystems in the world, where angiosperms were represented by herbaceous and shrub forms (Taylor & Hickey, 1996; Wing & Boucher, 1998). In Patagonia, that diversification is seen together with the presence of diverse fern groups, such as Schizaceae, Lophosoriaceae, Deenstaedtiaceae, Matoniaceae and Gleicheniaceae. In addition, the decline of the Ginkgoales and many Coniferales took place, with the simultaneous extinction of the Bennettitales and some pteridosperms (Del Fueyo *et al*., 2007; Prámparo *et al*., 2007). The West Patagonian floras have preserved more wet features than the eastern floras. Particularly, in the coastal environments of southwestern Patagonia, large entire-margin leaves of angiosperms dominated some leaf floras, suggesting relatively high temperatures and rainfall/humidity (Iglesias *et al*., 2007a). Wide areas in the Santa Cruz Province were covered by extensive monotypic forests of Podocarpaceae, with some components of Araucariaceae.

Towards the latest Cretaceous, in central and southern Patagonia, some marine ingressions triggered oceanic climates that influenced the floras. In Patagonia, the first pollen records related to the Proteaceae and Arecaceae (Palms) appeared (Archangelsky, 1973; Baldoni & Askin, 1993) during this time. Pollen records are so abundant that they define the Palmae Province.

The first *Nothofagus* records (austral beeches, the main components of the modern forests in Patagonia and New Zealand) come from the Late Cretaceous in Antarctica (Markgraf, Romero & Villagrán, 1996). In Patagonia (Río Negro Province), pollen records date back to the latest Cretaceous (Romero, 1973), although the first macrofossil records are from the Palaeocene (Iglesias *et al*., 2007b). Fossil leaves – such as those of the extant New Caledonian species – are very large, and can thus be related to warm and humid climates. The *Nothofagus* with reduced leaves, which are linked to the Cold Temperate climate, appeared in Patagonia after the middle Eocene.

Towards the end of the latest Cretaceous, the fossil floras from central Patagonia show that angiosperms reached a high richness in species, which apparently did not cross the boundary into the Palaeocene.

THE PALAEOGENE AND THE LINK BETWEEN PATAGONIAN FLORAS AND AUSTRALASIA VIA ANTARCTICA

At the beginning of the Palaeogene, the global palaeoclimatic distributions were approximately similar to those of the latest Cretaceous. The strengthening of the zonal climatic model continued and the increment in temperature in high latitudes was reinforced by the global early Palaeogene warming (Zachos *et al*., 2001). In Patagonia, there are several floras that show this climatic change.

Patagonia had a relative climatic uniformity as it was situated in the Warm Temperate belt. In the latest Cretaceous (65 Ma) and the early Palaeogene (65–57 Ma), sea levels remained high and sea ingressions fragmented the geographical continuity of the South American continent (Uliana & Biddle, 1988).

A relatively high diversity of angiosperm floras from the lower Palaeogene can be recognized in Patagonia. Although quite impoverished in comparison with those from the latest Cretaceous, their diversity is high relative to that of Northern Hemisphere analogues (Iglesias *et al*., 2007b).

Growth ring analysis of petrified forests allowed Brea *et al*. (2005) to infer that climatic growth conditions in the early Palaeogene were constant and favourable. Fossil woods from Podocarpaceae forests that extended across the centre of Patagonia (51°S palaeolatitude) suggest an evergreen habit (Brea *et al*., 2005).

The palaeotemperature and palaeoprecipitation estimations, based on the leaf margin analysis and leaf area analysis for Patagonia, yield annual mean temperatures between 12 and 15 °C and mean annual precipitations above 1100 mm (Iglesias *et al*., 2007b). The presence of Cycadales, palm trees and alligators is also consistent with warm temperatures in the early Palaeogene, and winter mean temperatures above 14 °C.

The coriaceous leaf texture of woody eudicots and marine carbonate formations in such high palaeolatitudes are also consistent with the climatic conditions mentioned above. A continuous global warming is observed in the early Palaeogene, with two thermal peaks called the thermal or climatic optima: one in the Palaeocene–Eocene (PETM, ~55 Ma) and another in the middle Eocene (EECO, ~52 Ma) – when the global average palaeotemperatures were as high as 10 °C, higher than those currently registered for South America (Zachos *et al*., 2001). In Patagonia, leaf floras yield estimated temperatures around 14–18 °C (Wilf *et al*., 2005; Hinojosa *et al*., 2010) and mean annual precipitations over 2000 mm (Wilf *et al*., 2009).

Palaeoenvironment reconstructions based on Patagonian Palaeocene floras allowed us to infer the presence of mangroves (with Palms, *Pandanus* and Rhyzophoraceae), swamp woodlands, mossy forests and sclerophyllous forests (Petriella & Archangelsky, 1975).

In Patagonia, most early Palaeogene fossil floras have humid subtropical taxa and, although they had their own features, they were closely linked with Australasia and Antarctica. Those links can still be found even in modern communities. Those subtropical fossil floras, which also show components of the Andean Patagonian forest (a mix of subtropical and sub-Antarctic taxa), were called 'Mixed Palaeoflora' by Romero (1986).

In the Eocene floras, there are taxa that are clearly linked to Australasian floras. The *Papuacedrus* (Cupressaceae), *Agathis* (Araucariaceae), *Acmopyle* and *Dacrycarpus* genera (the last two belong to Podocarpaceae) – which show subtropical conditions with abundant rainfalls – have been recognized (Wilf *et al*., 2009). Among the angiosperms, the presence of Akaniaceae – a family now endemic in northeastern Australian and southeastern Asian tropical rainforests – is remarkable (Gandolfo *et al*., 1988). The Patagonian records of *Eucalyptus* and the Casuarinaceae are related to a significant biogeographical pattern, because these two taxa had no previous records outside the Australasian region (Zamaloa *et al*., 2006). Three tribes of Proteaceae, within the Grevilloideae Subfamily (Macadamieae, Oriteae and Embothrieae), have been identified in Patagonia (González *et al*., 2007). Among the Neotropic components, Bixaceae, Lauraceae, Myrtaceae, Pandanaceae, Cochlospermaceae, Salicaceae, Ulmaceae, Symplocaceae, Rubiaceae, Myricaceae and Olacaceae were present. Other identified families are Rosaceae, Cunoniaceae, Malvaceae, Menispermaceae, Sapindaceae, Urticaceae, Gunneraceae and Boraginaceae. As it has already been stated, the early Palaeogene *Nothofagus* species had similar leaf sizes to those species that grow in Warm Subtropical climates today (Iglesias *et al*., 2007b). The oldest records of Fabaceae (legume family) and Asteraceae appear among these floras (Brea *et al*., 2008b; Barreda *et al*., 2010). Fabaceae and Asteraceae show greater diversification in later cooler and drier periods in the Oligocene–Miocene. The oldest record for *Araucaria* (Section *Araucaria*) is also from this time period – the section that contains the two modern South American species (Panti *et al*., 2007). There is also one of the oldest records of the Bambusoideae – cane subfamily – (Frenguelli & Parodi, 1941) which are represented today in the Patagonian understorey forest.

The extremely high biodiversity reached in Patagonia during the Eocene (the highest ever recorded for fossil floras) could be related to the better climatic growth conditions due to high rainfalls, fast diversification, fast recovery rates or lesser extinction rates (Wilf *et al*., 2005, 2009).

THE OLIGOCENE–MIOCENE AND THE DIFFERENTIATION OF THE COOL TEMPERATE BIOME AND THE STEPPE BIOME IN PATAGONIA

The global increase in temperature that took place in the early Palaeogene ended in the Eocene (~50 Ma) with a long global episode of decreasing temperature. That change is related to the early opening of the Drake Passage (between South America and Antarctica) and the subsequent formation of the Tasmania Passage (between Australia and Antarctica), which activated the Circum-Antarctic Circulation, causing declining global temperatures that strongly affected Patagonia (Fig. 1E).

A major environmental change occurred because of the passage from a Warm House to a Cold House that took place in the Oligocene (34–23 Ma) and then extended into the Neogene (23 Ma to the present). In the Oligocene, large ice caps developed in Antarctica (Zachos *et al*., 2001), and all biogeographical regions migrated to lower latitudes (Fig. 1E). The ten extant biomes that have been identified in the biogeographical distribution of global vegetation in the Oligocene and Miocene are: Tropical Everwet, Tropical Seasonal Dry, Desert, Subtropical Seasonal Dry, Warm Temperate, Cool Temperate, Cold Temperate, Steppe, Tundra and Glacial.

In Patagonia, cool temperate forests – with conifers and deciduous angiosperms – developed and extended to lower latitudes. Sub-Antarctic floras dominated by diverse *Nothofagus* expanded their distribution, covering wider regions in the provinces of Tierra del Fuego and Santa Cruz (Troncoso & Romero, 1998; Malumián, 1999).

For the early Miocene (24–15 Ma), Nothofagaceae, Podocarpaceae and Araucariaceae forests are still documented in the Extra-Andean region (Fig. 1F), characterized by Gunneraceae, Caryophyllaceae, *Weinmannia* (Cunoniaceae), *Lomatia* and *Embotrium* (Proteaceae), and the *Nothofaidithes* Province is identified (Romero, 1993; Barreda & Palazzesi, 2007; Barreda *et al*., 2007). Nevertheless, a transitional zone also begins to be identified towards the Atlantic coast, with Lauraceae, palms, Rosaceae (*Acaena*), Simplocaceae, Anacardiaceae, Proteaceae, Asteraceae (Muticieae and Muticiinae), Sparganiaceae and Myrtaceae. The first expansion of herbaceous shrub elements is noticed. This expansion defines the Transition palaeophytogeographical province (Fig. 1F) – with Ephedraceae, Quenopodiaceae, Convolvulaceae and Poaceae (Barreda & Palazzesi, 2007; Barreda *et al*., 2007).

In the middle Miocene (13–15 Ma), there was a short climatic optimum with high global temperatures (Zachos *et al*., 2001) that generated a strong marine ingression over Patagonia (Fig. 1F), and caused some wet tropical elements (such as Sapindaceae-*Cupania*, Euphorbiaceae, Bombacaceae, Malpighiaceae, Cyperaceae, Sparganiaceae/Tifaceae, Restionaceae, Malvaceae and Polygonaceae) to move southwards (Barreda *et al*., 2007).

The diversity and abundance of xeric forms increased in the late Miocene (13–5 Ma) in the Extra-Andean region. These forms include Asteraceae, Chenopodiaceae, Convolvulaceae, Anacardiaceae (*Schinopsis*), Goodeniaceas, Cyperaceae, Poaceae, Fabaceae and Caesalpinoidea Mimosoideae. They define the Proto-Espinal/Steppe palaeophytogeographical province (Barreda *et al*., 2007) that was developed in areas formerly occupied by the Transition Province and that, today, correspond to the Espinal Province (Cabrera, 1976).

The greatest rates in the Andean uplift and the fall in global temperature contributed to the development of extreme aridity, and climates with stronger seasonality in eastern areas, deeply differentiating the Andean and the Extra-Andean regions. The climatic change in Patagonia caused the extinction of megathermal and nonseasonal plants. The Miocene floristic composition and species' distribution are quite close to the modern flora of Patagonia, 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 temperature decrease during glacial periods in the Pliocene and Pleistocene, and the new precipitation gradient from the rain shadow of the Cordillera de los Andes, left a characteristic and definitive mark in the geography and the floras of different regions in Patagonia. Cold Temperate Andean forests were relegated to the present Antarctic domain, and the arid Steppe to the Patagonian domain (Fig. 1G).

The present semi-arid conditions were established by the end of the Pliocene and hyperaridity did not begin until the late Pliocene (Kleinert & Strecker, 2001), with *Podocarpus* dominating the glacial intervals, and *Nothofagus* doing so in the interglacial intervals (Markgraf *et al*., 1996). The floras were formed in northeast–southwest bands, primarily oriented by the Pacific winds (South Pacific anticyclone) and the Cordillera de los Andes (Fig. 1G)

CONCLUSIONS

1. The Permian–Triassic passage is characterized by the greatest mass extinction of the Phanerozoic

and a floristic turnover of palaeophytic to mesophytic floras. The global climate change occurred between the Late Permian and the early Mesozoic, involving the passage from Cold House to Warm House. The Permian climate was similar to the present, and ten biomes and four floristic realms have been identified. By contrast, the Mesozoic Era is characterized by warm climates, with fewer climatic belts. Five main biomes and two Triassic floristic realms are identified in the Triassic. The disappearance of several climatic belts caused a greater floristic homogeneity.

2. During the Triassic, the Southwest Gondwana Province covered two climatic belts: Subtropical Seasonal Dry and Warm Temperate. The Patagonian Triassic floras were assigned to the Warm Temperate Biome/climatic zone.
3. With regard to the Triassic floral evolution of southwestern Gondwana, a model with two successive extinction pulses, each followed by two successive biotic turnovers, is proposed. The first extinction pulse took place in the early Late Triassic. The second extinction pulse is identified in the latest Triassic. This second extinction pulse caused the disappearance of all the Corystospermales, Peltaspermales and other typical Triassic elements.
4. In the Jurassic, almost all the *Dicroidium* Flora was replaced, and only some ferns and conifers – which were differentiated in the latest Triassic – survived. The Jurassic Gondwana floras are clearly characterized by the extinction of Triassic-dominant major groups. The long history of Gondwanic lineages, represented by Araucariaceae, Cupressaceae and Podocarpaceae, can be traced back to early Mesozoic times. Jurassic floras are characterized by a low biodiversity and a spatial uniformity, and five main biomes are identified. The floras in Argentina and the Antarctic Peninsula belonged to the same Subtropical Seasonal Dry Biome.
5. The southern monsoon breakdown in the Cretaceous generated a zonal climatic model, which increased the palaeoprecipitations in northern and southwestern South America, and increased the temperature at higher latitudes. Two new biomes are added to the previously existing ones – Cold Temperate and Tropical Everwet – yielding a total of seven biomes in the Cretaceous. The Atlantic opening and the drifting of the continents began to generate more oceanic climates in the Gondwanic continents.
6. In the Cretaceous and early Palaeogene, the Patagonian floras were situated in a Warm Temperate Biome/climate together with the floras from the Antarctic Peninsula, West Antarctica, Tasmania and Australia.
7. The appearance of angiosperms in the Early Cretaceous Patagonian communities had an impact only beginning in the Late Cretaceous, when they became dominant in some ecosystems. Some taxa may have originated among the Patagonian warm temperate communities and may have later adapted to drier and cooler climates.
8. At the beginning of the Palaeogene, the global palaeoclimatic distribution was quite similar to that of the latest Cretaceous. A continuous global warming is observed in the early Palaeogene, with two climatic optima. The early Palaeogene Patagonian angiosperm floras show a relatively high diversity, although they seem to be quite impoverished when compared with the latest Cretaceous ones. Throughout the Palaeogene, the Patagonian floras show some increase in biodiversity, partly caused by the frost-free Warm Temperate climate with abundant rainfalls. The composition of the floras was both Neotropical and Australasian.
9. During the Oligocene and Miocene, the Circum-Antarctic Circulation by the Tasmania and Drake Passages caused the passage from Warm House to Cold House. The global climate change involved the development of large ice caps in Antarctica, and the migration of all the biogeographical regions to lower latitudes. Ten extant biomes have been identified regarding this period: Tropical Everwet, Tropical Seasonal Dry, Desert, Subtropical Seasonal Dry, Warm Temperate, Cool Temperate, Cold temperate, Steppe, Tundra and Glacial. The worsening of the global climate strongly affected Patagonia. The Warm Temperate Biome that characterized Patagonia in the early Palaeogene was replaced by the Cool Temperate Biome with *Nothofagus*-dominated forests.
10. In the Miocene, the largest rate in the Andean uplift and the decrease in the global temperatures contributed to the development of extreme aridity and stronger seasonality in eastern Patagonia, resulting in a deep differentiation of the Andean and Extra-Andean regions. In the early Miocene, some forests are still documented in the Extra-Andean region, but a transitional zone is beginning to be identified towards the Atlantic coast, with the first expansion of herbaceous shrub plants. The late Miocene shows some increase in diversity and the abundance of xeric forms in the Extra-Andean region, which defined the Proto-Espinal/Steppe Province.
11. Glacial periods with strong winds and lower global temperatures during the Pliocene and the

Pleistocene, and the new precipitation gradient from the rain shadow of the Cordillera de los Andes, pushed the Cool Temperate Andean forest to the current Antarctic domain and led to the aridization of the Extra-Andean region to the Steppe.

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