Revista Chilena de Historia Natural
*64:* 413-446, 1991

# Historical development of temperate vegetation in the Americas

## Historia de la vegetación templada en Norte y Sudamérica

DANIEL I. AXELROD[1], MARY T. KALIN ARROYO[2] and
PETER H. RAVEN[3]

[1] Department of Botany, University of California, Davis, CA 95616, USA;
[2] Departamento de Biología, Universidad de Chile, Casilla 653, Santiago, Chile;
[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, USA

## ABSTRACT

North American and South American temperate forests developed independently. These initially different forests, continue to be distinct, not only because of their different histories resulting in their domination by different woody plants, but because of the distinctive climatic regimes under which they presently occur.

In North America, modern vegetation types, though much richer in taxa, first appeared in the Paleocene-Eocene, when the region north of Colorado supported rich deciduous hardwood forest and lowland conifers. Cold-loving conifers were associated with deciduous hardwoods in lowlands farther north. Pure montane conifer forest and mixed conifer-hardwood forests were present in upland areas in Nevada-Idaho in the Middle and Late Eocene. The first appearence of nearly pure montane conifer forest in the north (e.g. Alaska Range) was in the Miocene. Essentially pure conifer forests in lowland areas in the Arctic region appear in the Pliocene, although similar forest is reported from Iceland earlier (9-7 m.y.a.). Conifer parkland (semi-taiga) was spreading over the lowlands of northern Alaska by the close of the Miocene. Taiga spread widely only in the Pliocene and subsequently.

In the Southern Hemisphere, the geological history of Gondwanaland is consistent with the occurrence of widespread austral forests across Antarctica, Australia and southern South America. Connections between these areas were eventually severed with the opening of Drake's Passage between the Antarctic Peninsula and southern South America in the late Oligocene. Angiosperms first appear in the Cretaceous, with modern forest types present by the Middle Eocene, fairly contemporaneously with the appearence of modern forests in North America. Mixed with subtropical elements, the South American forests reached their greatest extent in the Early and Middle Miocene, and then moved northward as the climate deteriorated. Antarctica was occupied, starting at least 83 m.y.a., with a mixed forest of *Nothofagus,* Podocarpaceae and Araucariaceae. Myrtaceae, Proteaceae and Lauraceae, families typical of the southern forests today occurred there becoming increasingly depauperate in the Neogene.

The more diverse, biologically-richer temperate forests that occurred around the Northern Hemisphere and on the fragments of Gondwanaland until the Middle Miocene, have persisted, respectively, in areas of greatest equability: eastern Asia in the north, and Southeast Asia-northeastern Australasia (including New Caledonia) in the south. Just as there are fossil plants in North America now confined to eastern Asia, there are some taxa now restricted to Australasia that occurred in the temperate forests of South America prior to the Middle Miocene. The relative degree of Neogene extinction in North American and South American temperate forests is a theme requiring attention. Important clues to independent forest development and earlier richness will be found in disjunct lands that lie in areas of greater equability. Hypotheses on the ecological dynamics of these forest must consider the tendency for greater dominance by gymnosperms with their given life-history traits in North American forests, versus angiosperms in South America.

We hypothesize that: (1) The origin and abundance of the deciduous habit in the Northern Hemisphere, is linked with the restriction of seaways, widespread vulcanism, and development of more continental, cooler climates from the Middle Paleocene onward, rather than the postulated impact of a bolide at the close of the Cretaceous; and (2) The mixtures of temperate and subtropical elements that characterize many Tertiary sites reflect greater climatic equability at that time, which allowed many taxa to extend far outside what we have come to regard as their "normal" areas of distribution.

**Key words:** Antarctic forests, boreal forests, deciduous vs. evergreen habit, Gondwanaland, mixed paleofloras, temperate forests, plate tectonics.

## RESUMEN

Las floras templadas de Norte y Sudamérica se desarrollaron en forma independiente. Estas floras, inicialmente distintas, continúan siéndolo, no sólo debido a sus diversas historias que tuvieron como resultado el dominio de diferentes especies leñosas, sino debido también a los regímenes climáticos distintivos bajo los cuales se presentan actualmente.

En Norteamérica, los tipos vegetacionales modernos aparecieron por primera vez en la transición Paleoceno-Eoceno, cuando la región al norte de Colorado presentaba bosques ricos en especies arbóreas deciduas y coníferas de tierras bajas. Coníferas con requerimientos de frío estuvieron asociadas a especies arbóreas leñosas en tierras bajas más hacia el norte.

(Received 30 August 1990.)

Los bosques montanos puros de coníferas y los bosques mezclados de coníferas y especies arbóreas estuvieron presentes en tierras altas en Nevada-Idaho en el Eoceno medio y tardío. El primer surgimiento de bosques montanos puros de coníferas ocurrió en el norte (ejemplo Alaska Range) en el Mioceno. Los bosques de coníferas esencialmente puros de tierras bajas en la región ártica aparecieron en el Plioceno; no obstante, un bosque similar más antiguo se ha descrito para Islandia (9-7 m.a.A.P.). A finales del Mioceno se dispersó un bosque ralo y abierto de coníferas (semi-taiga) sobre las tierras bajas del norte de Alaska. La taiga se expandió ampliamente sólo durante el Plioceno y períodos posteriores.

En el hemisferio sur la historia geológica de Gondwana es consistente con la presencia de bosques australes ampliamente distribuidos en Antártica, Australia y Sudamérica austral. Las conexiones entre estas áreas fueron eventualmente destruidas con la apertura del Paso de Drake entre la Península Antártica y Sudamérica austral durante el Oligoceno tardío. Durante el Cretácico aparecieron por primera vez angiospermas y durante el Eoceno medio aparecieron por primera vez los tipos forestales modernos, contemporáneamente con la aparición de los bosques modernos en Norteamérica. Los bosques sudamericanos, mezclados con elementos subtropicales, alcanzaron su máxima distribución en el Mioceno temprano y medio, desplazándose luego hacia el norte cuando el clima se deterioró. La Antártica fue ocupada, comenzando desde los 83 m.a.A.P. por una flora mixta de *Nothofagus*, Podocarpaceae, Araucariaceae y Myrtaceae. Proteaceae y Lauraceae, familias típicas de los actuales bosques australes, también se presentaron allí. Dichos bosques se tornaron progresivamente depauperados durante el Neogeno.

Los bosques templados más diversos y biológicamente más ricos que se presentaron en el Hemisferio Norte y en los fragmentos de Gondwana hasta mediados del Mioceno, persistieron respectivamente en áreas de mayor equitabilidad: en el norte de Asia occidental, y en el sur desde Asia suroccidental hasta Australia noroccidental (incluyendo Nueva Caledonia). Así como se han encontrado fósiles en Norteamérica de plantas actualmente restringidas a Asia occidental, existen algunos taxa restringidos actualmente a Australasia, que se presentaron en los bosques templados de Sudamérica, antes del Mioceno medio. El grado relativo de extinciones en el Neogeno en los bosques templados de Norte y Sudamérica es un tema que requiere atención. Claves importantes para el desarrollo independiente temprano de los bosques y su riqueza podrían encontrarse en las áreas disyuntas que se encuentran en regiones de mayor equitabilidad. Las hipótesis sobre la dinámica ecológica de los bosques templados de Norte y Sudamérica deberían considerar la mayor dominancia de gimnospermas en los bosques de Norteamérica en comparación con los de Sudamérica y diferencias en las características de historia de vida de los grupos de plantas dominantes.

Nosotros predecimos que: (1) El origen y abundancia del hábito deciduo en el Hemisferio Norte está ligado con la restricción de corrientes marinas, vulcanismo, y desarrollo de climas más continentales y fríos a partir del Paleoceno medio, y no debido al impacto de meteoritos a finales del Cretácico como se había postulado anteriormente; y (2) La mezcla de bosques templados y subtropicales que caracterizaron muchas regiones terciarias, reflejan un clima de mayor equitabilidad en el momento, lo que permitió a muchos taxa extenderse más allá de lo que actualmente consideramos su área "normal" de distribución.

**Palabras claves:** Bosques antárticos, bosques boreales, hábito deciduo vs. siempreverde, Gondwana, paleofloras de mezcla, bosques templados, tectónica de placas.

## INTRODUCTION

The flora and vegetation of cold temperate and temperate regions of North and South America differ greatly in their composition, physiognomy, and general aspect. Judging from the fossil record, these differences extend back into the Middle Cretaceous, well over 100 million years ago. In other words, the temperate forests of North and South America are not only very different in their floristic composition now, but they have been very different since distinctive assemblages of seed plants –gymnosperms, and then angiosperms– first evolved into the zones of cooler climate flanking the tropics. Whatever structural and functional similarities may be discerned between these forests must be viewed against a background of completely separate historical development and taxonomic dissimilarity. In this paper, we shall review the development of the temperate forests of North and South America during the Cretaceous and Tertiary. We shall not consider the extensive changes that have occurred in both areas during Quaternary time, the past two million years, a topic partly covered by Villagrán (this volume).

To set the background for understanding the divergent histories of forests in the North and South America, we recall first the role plate tectonics has had in the history of climate and vegetation.

## ROLE OF PLATE TECTONICS

Plate movements have not greatly affected the latitudinal positions of North and South America since the Jurassic (Smith *et al.* 1981, Smith 1981, Krutzsch 1989). The appearance of broad areas of temperate forests of modern aspect, therefore, did not originate because the continents drifted into zones of cooler climate, but rather because the world climate gradually changed. The principal changes have been opening the Atlantic basin by ocean-floor spreading from the mid-Atlantic ridge, which rafted the Americas to the west (commencing ca. 125 million years ago); the separation of Africa-South America and of Europe-North America later in the Cretaceous; and severing the link of South America (southern Chile-Argentina) with Antarctica-Australia in the Upper Oligocene (ca. 29 m.y.a.; Fig. 1).

Plate movements and accompanying tectonism have had a guiding role in climatic change (Savin 1977), and in the history of life (Hallum 1981) As lands are isolated by ocean-floor spreading and seaways spread onto continents more moderate climates become widespread, as in the Middle Cretaceous (ca. 100 m.y.a). Active plate movements may build mountains and plateaus. These modify older climates and, as new climates appear at higher elevations, new opportunities are provided for the evolution of plants and animals. With uplift, more extreme climates develop in the lee of mountains or plateaus, where drier and/or colder climates appear that also provide possibilities for new sorts of adaptations by diverse biota. At times of isolated lands and broad marine embayments, more heat is transported into higher latitudes and tropical regions become cooler, although still tropical. This is shown by ocean temperatures reconstructed from oxygen isotope evidence (Shackleton 1979, 1984). The data suggest that from the Maastrichtian of the Late Cretaceous (73-65 m.y.a.) into the Miocene (perhaps 15 m.y.a.), surface waters in the low latitude Pacific Ocean were near 18-20°C, rising to 28°C only in the later Neogene, several million years before present. Furthermore, deep waters that reflect high latitude surface temperatures had a temperature of about 10°C in the Maastrichtian-Lower Paleocene (approximately 73-50 m.y.a.), decreasing to about 8°C during the Late Eocene (42-38 m.y.a.), and to 3-4°C in the Oligocene, which began 36 million years ago.

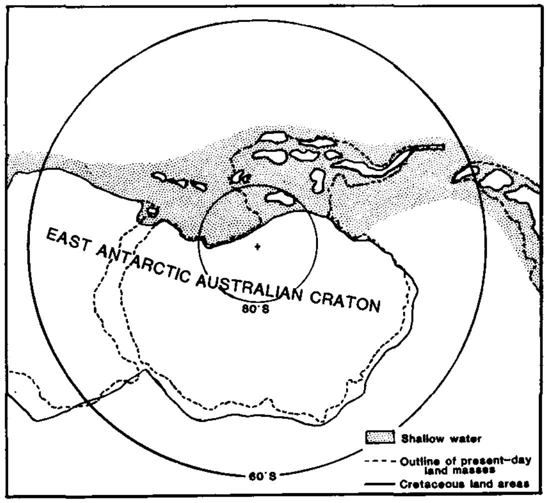

*Fig. 1:* Late Cretaceous-Eocene paleogeography (Zinsmeister 1982). An essentially continous land between South America-Antarctica-Australia provided a route for the interchange of biota.

Paleografía del Cretácico-Eoceno (Zinsmeister 1982). Un territorio prácticamente continuo se extendió entre Sudamérica, Antártica y Australia proporcionando una vía para el intercambio de biota.

The reassembly of the fragments of Gondwanaland shows that during the later Mesozoic they were centered in tropical latitudes. This is the area that still harbors the greatest concentration of angiosperm families and also has, in more isolated areas (New Caledonia, northeastern Australia, Madagascar, Fiji), some of the most ancient families and genera of angiosperms (Axelrod 1952, 1970, Raven & Axelrod 1974). The present climatic requirements of these ancient taxa, as well as the cycads, tree ferns, araucarias, and podocarps associated with them, shows that they are confined chiefly to areas of ample precipitation and high equability. Such areas have a mean annual temperature near 14°C and a low mean annual range of temperature (Bailey 1960, 1964, Axelrod 1965, Fig. 9; 1979, Fig. 10; 1991b). The ideal (theoretical) rating is *M* (= moderation) 100, and is approached by stations such as Quito, Ecuador, with *M* 94. The most extreme stations have ratings less than *M* 20, as in eastern Siberia. It is the highly equable climates (> *M* 60) that support the more ancient (archaic, or "primitive") groups, such as the magnolioids, hamamelids, and annonoids, as well as the surviving members of the more primitive angiosperm orders. Inasmuch as the pre-Cretaceous radiation of angiosperms evidently occurred in equable tropical uplands, in relatively open areas, with some seasonal drought (Axelrod 1952, 1970, Stebbins 1974), they must have entered mesic lowland regions at a later date, an inference supported by the known fossil record.

As the Americas separated from the larger land area of Gondwanaland of the Jurassic and earlier times, the Atlantic Ocean rapidly widened and seaways commenced to flood the continents, reaching maximum extent during the Late Albian to Cenomanian (about 100-95 m.y.a.). These changes resulted in a more equable global climate (i.e., a lower range of temperature) and a more nearly aseasonal condition. It was this that may have been the principal factor that enabled angiosperms rapidly to invade lowland regions away from their tropical center (Axelrod 1970) where they had presumably originated much earlier (cf. Cornet 1986, 1991)

## NORTH TEMPERATE VEGETATION

The fossil record for North America is rich. Selected localities referred to in this paper are shown in Figs. 2, 3.

### *The Cretaceous (144-65 m.y.a.)*

The earliest angiosperms first appeared in the record in low-middle latitudes (ca. 35°N) in the Early Cretaceous (124 m.y.a.) of eastern North America. Then they shifted northward, gradually entering polar latitudes in the Late Albian age (ca. 100 m.y.a.), more than 20 millions years later (Axelrod 1959). The lower and Middle Albian age (113-105 m.y.a.) Alaskan floras are dominated by ferns, ginkophytes, and *Podozamites* species. Among the taxa are *Baiera, Cladophlebis, Coniopteris, Czerkanowskia, Ginkgo, Nilssonia,* and *Sagenopteris,* which range up into the Middle Albian age (ca. 105 m.y.a.). The first angiosperms appear at high latitudes near the close of the Upper Albian age (ca. 98 m.y. a.), if not in the earliest Cenomanian age (i.e., 1-2 million years later), associated with pteridophytes, ginkophytes, conifers, and the last cycadophytes (Smiler 1969a, 1969b, 1972). Evidence from the Kuk River area, on the Arctic Slope of Alaska, indicates that angiosperms may have appeared there even later, in the Late Cenomanian-Turonian transition (ca. 91 m.y.a., Smiley 1966). This megafossil record that indicates the later occurrence of angiosperms in Arctic regions is supported by the microfossil record (Stanley 1966, Brenner 1976). Furthermore, as reviewed by Spicer *et al.* (1987), a plot of the distribution of diverse taxa from the Cenomanian into the Paleocene (i.e., from ca. 98-50 m.y.a.) shows that the derived taxa are found in the north. This applies to such divergent alliances as Magnolian-like, Platanoid, Trochodendralean, Juglandoid, and Fagoid as well. In general, vegetation was characterized by low diversity, especially at the family level, with few genera and species.

During the succeeding Cenomanian age (98-91 m.y.a.), dicotyledons were wholly dominant over lowland areas. These were chiefly members of now extinct groups, though in leaf form some resemble the leaves of modern general, such as *Platanus, Vitis, Magnolia, Betula,* and others. Associated with these early angiosperms, which apparently were largely deciduous, were diverse conifers of genera such as *Metasequoia, Sequoia,* and *Pinus,* which had now largely replaced the older Jurassic and Lower Cretaceous conifers.

Crabtree (1987) provides an excellent summary of the sequence of change in vegetation and taxa in the northern Rocky Mountain region, from Wyoming into British Columbia, during the Albian age (113-98 m.y.a.) and subsequently; more than 20 individual floras have been described from this region. During a period of about 3 million years, from the Middle to Late Albian (ca. 100 m.y.a.), angiosperms displaced ancient gymnosperms as the dominant vegetation over the lowland region, although gymnosperms were still abundant in the uplands. The Middle Albian age (ca. 105 m.y.a.) flora is allied to the floras of lower latitudes, with the similarity largely at the generic level. Platanophylls and Sapindophylls are prominent. Some alliances, such as the Cinnamonophylls and

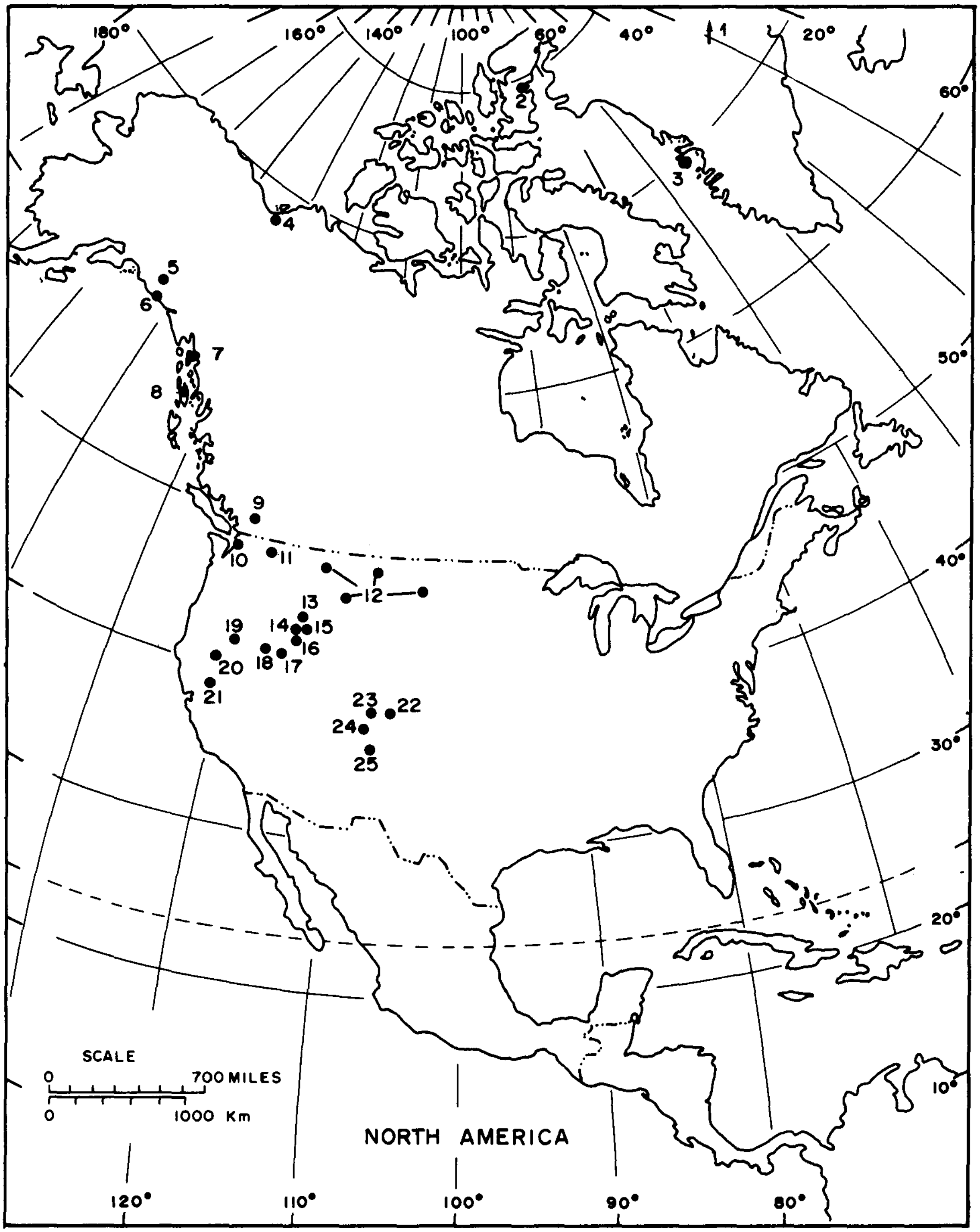

*Fig. 2:* Selected Paleogene floras in North America referred to. 1. East Greenland, 2. Ellesmere Island, 3. Disko Island, 4. MacKenzie (Yukon), 5. Kushtaka, 6. Angoon, 7. Kootznahoo, 8. Kupreanof, 9. Princeton, 10. Puget, 11. Republic, 12. Fort Union, 13., 14. Thunder Mountain, 15. Germer, 16. Haiwee, 17. Copper Basin, 18. Bull Run, 19. Lo Cedarville, 20. Susanville, 21. Chalk Bluffs, 22. Denver, 23. Florissant, 24. Creede, 25. Ratón.

Floras fósiles paleogenas de Norteamérica seleccionadas. 1. East Greenland, 2. Ellesmere Island, 3. Disko Island, 4. MacKenzie (Yukón), 5. Kushtaka, 6. Angoon, 7. Kootznahoo, 8. Kupreanof, 9. Princeton, 10. Puget, 11. Republic, 12. Fort Union, 13, 14. Thunder Mountain, 15. Germer, 16. Haiwee, 17. Copper Basin, 18. Bull Run, 19. Lo Cedarville, 20. Susanville, 21. Chalk Bluffs, 22. Denver, 23. Florissant, 24. Creede, 25. Ratón.

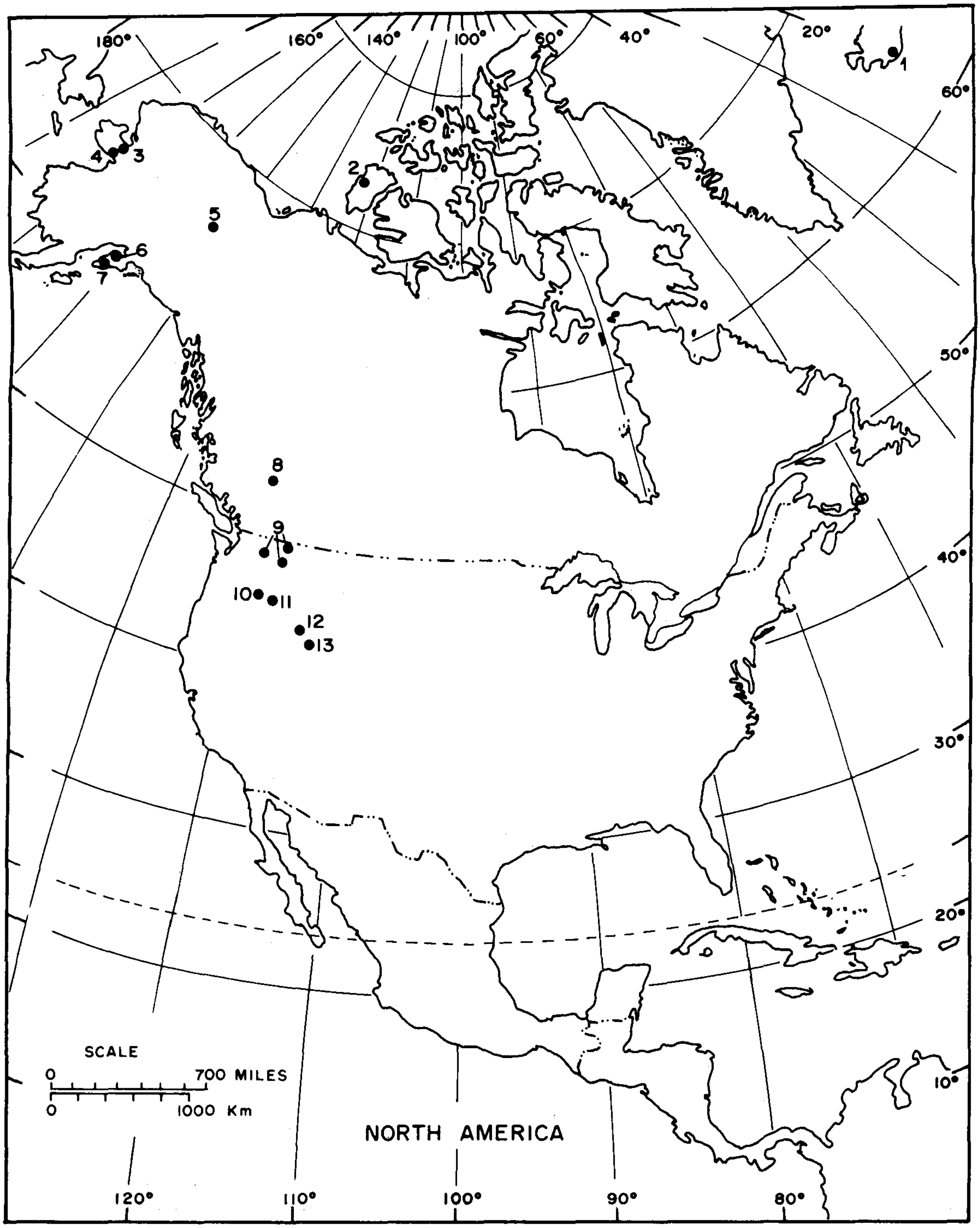

*Fig. 3:* Neogene fossil floras in North America referred to. 1. Iceland, 2. Banks Island (Beaufort), 3. Lava Camp Mine, 4. Kivalina, 5. Circle, 6. Seldova, 7. Homer, 8. Red Lake, 9. Latah Grande Coulee, 10. Mascall, 11. Blue Mountains, 12. Thorn Creek, 13. Trapper Creek.

Floras fósiles neogenas de Norteamérica. 1. Iceland, 2. Banks Island (Beaufort), 3. Lava Camp Mine, 4. Kivalina, 5. Circle, 6. Seldova, 7. Homer, 8. Red Lake, 9. Latah Grande Coulee, 10. Mascall, 11. Blue Mountains, 12. Thorn Creek, 13. Trapper Creek.

Pentalobophylls appear earlier as dominants in this region than elsewhere, suggesting that the regional flora constituted a rather distinct subprovince. Early members of some recent higher taxonomic categories existed by the Middle Albian age, and they increased rapidly so that by the Campanian age (83-73 m.y.a.), numerous modern families and some genera were represented in a very diverse flora (Crabtree 1987).

The Early Cretaceous (pre-Cenomanian age; before 98 m y.a.) floras of high latitudes indicate the existence of a mild, temperate climate. The abundance of deciduous hardwoods with serrate leaves reflects seasonality, as shown also by fossil woods with regular growth rings (Creber & Chaloner 1984). This was the result of the tilt of the Earth's axis that imparts a long period of darkness in winter and light in summer. The absense of much biological degradation of plant material (especially leaves) also implies cool, moist climate (Spicer & Parrish 1986). The general thermal conditions suggest a mean annual temperature near 10-12°C, and a very low range of mean annual temperature (January-July, probably near 6-8°C, as implied by the large reptile (dinosaurs, alligators) fauna that occurs with the plant fossils. These animals may have hibernated during the long, dark period or migrated seasonally into the area. The suggested temperatures imply that the temperature fell below freezing for scarcely 0.5% of the hours of the year (43 hrs.). Others have suggested a greater range of temperature (i.e., 25-30°C), but this means that 20-25% of the hours of the year (1,752-2,190 hrs, or fully 2.4-3.1 mos) would have had temperatures below freezing. Such conditions would not favor large animal migration north of, or to, the Arctic Circle (where they occurred), and doubtfully would have allowed hibernation there.

In their review of the Arctic Cretaceous floras, Sveshnikova & Budantsev (1969) note that floras attained maximum floristic differentiation in the Late Cretaceous (i.e., 85-65 m.y.a.). Floras in the east sector (northeast Canada, Greenland) exhibit a strong influence from warm temperature-subtropical floras of eastern North America. In the west sector (eastern Siberia-northwest North America), boreal (cooler) elements dominate. Similar relationships were present during the Tertiary and have persisted to the present day.

### *The Paleocene (65-55 m.y.a.)*

By Paleocene time (Fig. 2), floras from the far north, as in northwest Greenland (Koch 1963), include conifers and angiosperms. The latter have an "older" aspect and chiefly appear to represent extinct members of the modern alliances to which they have been referred. Among the conifers are *Ginkgo* and *Metasequoia.* Of the dicotyledons, taxa referred to modern genera such as *Carpinus, Cercidiphyllum, Corylopsis, Credneria, Juglans, Magnolia, Platanus, Rhododendron, Quercus,* and *Vitis* mostly need further study, as do species referred to fossil genera such as *Dictylophyllum, Lauraeceaephyllum,* and the enigmatic *Macclintockia.*

Whereas some of the fossil members of these genera have the aspect of ancient plants not fully stabilized in terms of modern genera, the rich Paleocene flora of the Great Plains and Rocky Mountains, distributed from the Canada-United States border to New Mexico (Brown 1962) has a decidedly modern aspect. Among the genera represented are many gymnosperms —*Fokienia, Glyptostrobus, Metasequoia, Taxodium, Thuja,* and *Zamia*— and diverse angiosperms, including *Acer, Bauhinia, Betula, Carya, Castanea, Cercidiphyllum, Cinnamomum, Cissus, Cornus, Corylus, Eucommia, Ficus, Fraxinus, Magnolia, Menispermum, Nyssa, Persea, Platanus, Prunus, Pterocarya, Rhamnus, Robinia, Quercus, Sabal, Sapindus, Sassafras, Viburnum, Zelkova,* and *Zizyphus.* Brown (1962) pointed out that there is a floristic-climatic difference from south to north, for the remains of breadfruit (*Artocarpus*), *Cinnamomum, Menispermum,* and other evergreens, notably palms, are generally limited to areas south of central Wyoming. On the other hand, *Ginkgo,* together with *Acer, Betula, Corylus, Vi-*

*burnum,* and other genera that occur in temperate forests today are found in areas north of the Colorado-Wyoming boundary. In general, leaves with toothed margins far outnumber those with entire margins, implying a generally temperate climate. The flora was certainly mesophytic in a warm temperate to mild temperate environment that was cooler northward. This is apparent from the Paleocene flora of western Alberta (Bell 1949). Notably absent are the abundant palms and broadleaved evergreens that are so abundant in the Ratón and Denver floras of Colorado-New Mexico, as well as the poor representation of entire-margined species that occur to the south, such as fossils referred to *Cinnamomum, Ficus, Magnolia,* and *Persea.* The Alberta flora also includes some ancient conifers that evidently are not in the Paleocene to the south notably *Androvettia, Cryptometites,* and *Elatocladus.*

To the north, in the Yukon Territory, Rouse & Srivastava (1972) note that there is a marked floristic change across the Cretaceous-Paleocene boundary (65 m.y.a.) in the Bonnet Plume Formation. In addition, there is an marked influx of conifers, including *Cedrus, Glyptostrobus, Picea, Pinus, Metasequoia,* and *Taxodium.* Associated angiosperms include taxa referred to *Alnus, Betula, Corylus, Fraxinus, Myrica,* and *Ulmus.* Several genera of pollen taxa –*Aquilapollenites, Beaupreadites, Cranwellia,* and *Mancicorpus*– that occur here are generally taken as indicators of the disappearance of warm temperate conditions. The change that we have just described is paralled by that which occurs across the Lance-Fort Union transition in Montana, the Dakotas, and Wyoming.

In eastern north Greenland, at a paleolatitude of 77-79°N, the Thyra 0 flora, of Late Paleocene-Early Eocene age, has recently been studied (Boyd 1990). This diverse flora records mild temperate climatic conditions with little frost, as judged from the relationships of the taxa present; among them were *Ginkgo, Fokienia, Metasequoia, Platanus,* and *Cercidiphyllum.* The leaf physiognomy of the taxa present at this locality, on the other hand, indicates cool temperate conditions. These features were probably related to the high latitudes and seasonal darkness at this very high latitude.

In general, Paleocene floras show a gradation to a moist, milder temperate climate extending northward from the Gulf region, where the climate was tropical –as illustrated by the small Midway Flora of Texas (Berry 1916). The floias also indicate a trend from relatively modern taxa to more ancient ones (relicts) in the north, paralleling the Middle Cretaceous shift to more ancient, relict taxa northward. Vegetation shows a change from broadleaved rainforest in the Gulf area, to rich warm-temperate broadleaved evergreen forest with few deciduous hardwoods (Ratôn, Denver, and allied floras), to mesic dominantly deciduous forest north of Colorado, to mixed deciduous-coniferous forests in the north with a few montane conifers. The record has not yet provided evidence of pure montane conifer forest, although it may be inferred for areas where the mountains were high enough to support a cool temperate climate. There is no record of taiga or tundra at this early time.

### *The Eocene (55-38 m.y.a.)*

In the far north, floras from Spitzbergen (Schloemer-Jager 1958), Ellesmere Island (Manum 1962, Christie & Rouse 1976), northern Canada (Norris 1982, Staplin 1976, Rouse & Srivastava 1972), and eastern Greenland (Koch 1963, Manum 1962) provide records of rich deciduous hardwood-conifer forests. Among the conifers are species of *Abies, Glyptostrobus, Larix, Metasequoia, Picea, Pinus,* and *Taxodium.* Angiosperms include species of *Alnus, Betula, Carya, Castanea, Cercidiphyllum, Fagus, Liriodendron, Nyssa, Platanus, Populus, Pterocarya, Quercus, Ulmus,* and *Zelkova.* In this general region, situated for the most part above 60°N, the mixed hardwood-conifer forest, dominated by hardwoods, most probably gave way to montane conifer forest at elevations somewhat above 500 m. The character of the lowland forest indicates cool temperate climate, with ample rain in the warm season. Owing to the lower elevation of the continents, to margin seaways, as well as to the absence of a polar ice cap, temperatures were more moderate than those in related montane forests. In general aspect, the broadleaved deciduous hardwood-conifer forest of the Eocene at higher latitudes resembled the forests that now occur around the Great Lakes, extending into the northern and central Appalachians at middle elevations, where *Abies, Picea, Pinus,* and *Tsuga* mix with deciduous hardwoods. Comparable relationsships are also present in Japan (Ito 1961, Ito *et al.* 1966) and also in the mountains of Sichuan and Hubei provinces of south-central China (Wang 1961).

The Middle to Late Eocene Kushtaka flora from the Gulf of Alaska region (60°N) presents a floristic anomaly. The florules represent outer tropical rainforest vegetation, as judged from plants identified as members of the Annonaceae, Dipterocarpaceae, Icacinaceae, Menispermaceae, Myristicaceae, and Myrtaceae (Wolfe 1977). In terms of the global symmetry of vegetation-climate, the flora contrasts markedly with respect to floras of western Europe and Greenland that were then at a lower latitude (35°N) and include temperate taxa. In addition, the Eocene floras of northern Japan-Kamchatka are temperate, not tropical. These occurrences of temperate Eocene forests in coastal areas at latitudes lower than the Kushtaka support evidence that the latter was on a tectonic block that has been displaced many kilometers northward (Jones *et al.* 1972, 1977, Packer & Stone 1974, Coney *et al.* 1980, Cowan 1982, Jones & Silberling 1982, Plumley *et al.* 1982, Helwig & Emmett 1983, Saleeby 1983, Bruns 1983). This is indicated also by the Eocene marine microfossil fauna, which also suggests a considerable degree of latitudinal displacement (Keller *et al.* 1984). Furthermore, the estimated paleotemperature of the Kushtaka flora, with a mean annual temperature of 10-20°C (average 15°C) and a range of 10-15°C (average 10°C), indicates on the order of 4% of the hours (350 hrs) of the year would have had temperatures below freezing, hence prohibiting the existence of the Indomalaysian taxa that occur as fossils at this latitude.

The mixed deciduous hardwood-conifer forests of higher latitudes extended south into the northern Rocky Mountains, as shown by the Princeton and allied floras of British Columbia (e.g., Penhallow 1908, Berry 1926, Arnold 1955, Piel 1971). Among the genera recorded are species of *Acer, Aesculus, Alnus, Betula, Carya, Castanea, Crataegus, Fagus, Fraxinus, Juglans, Liquidambar, Nyssa, Prunus, Pterocaya, Sassafras, Ulmus,* and diverse conifers, notably *Abies, Cedrus, Glyptostrobus, Metasequoia, Picea, Pinus, Pseudotsuga,* and *Taxodium.* Similar forests ranged southward, as shown by the Republic flora of northeastern Washington (Wolfe & Wehr 1987), the Salmon flora of east-central Idaho (Brown 1937), and the Copper Basin flora of northeastern Nevada (Axelrod 1966a). Of these, the Republic flora has a few broadleaved evergreens, indicating a somewhat lower elevation and warmer climate.

In the Middle Eocene (47-43 m.y.a.), the central to northern Rocky Mountains were a site of extensive vulcanism (Lipman *et al.* 1972). Preserved in lake beds associated with the ashflows and welded tuffs are several floras wholly dominated by montane conifers. These assemblages are much like the present montane conifer forests that now occur above the mixed conifer-hardwood forest zone, although they were much more diverse in composition. Occupying elevations near 1,250-1,500 m (north to south) for the most part, these fossil floras, dated in the range of 46-35 m.y.a., occur in northeastern Nevada (Upper Bull Run flora) and Idaho (Haiwee, Thunder Mountain floras). Two of them record the transition from hardwood-conifer forests that lived in slightly warmer conditions. This is shown by the Bull Run sequence. The lower three florules show that the deciduous hardwoods (*Acer, Quercus, Ulmus, Zelkova*) gradually decrease as conifers increase at higher levels. The upper six florules, distributed through about 1,000 m of continuous section, are wholly dominated by pure montane conifer forest species belonging to the genera *Abies, Chamaecyparis, Larix, Picea, Pinus,* and *Thuja.*

A large flora from Coal Creek, east-central Idaho, is wholly dominated by montane conifers (85% of the specimens), and has few deciduous hardwoods, notably *Acer, Betula, Cornus, Crataegus, Sassafras, Sorbus,* and *Viburnum*, as well as several broadleaved evergreens that have not yet been identified. Pure montane conifer forest no doubt occupied slightly higher levels in the area, where it was composed of most of the Coal Creek taxa, notably *Abies, Chamaecyparis, Larix, Picea, Pinus, Pseudotsuga, Sequoia, Sequoiadendron,* and *Thuja.* Associated forest-floor shrubs in the montane conifer forests belonged to genera including *Alnus, Arctostaphylos, Comptonia, Mahonia, Prunus, Ribes,* and *Vaccinium.* Deciduous hardwoods were absent from these montane conifer forest, apart from an occasional leaf of *Alnus, Betula,* or *Populus.*

An essentially contemporaneous flora from the Germer Member, Challis Volcanics, situated 90 km southeast of the Thunder Mountain flora and at a somewhat lower elevation (ca. 600 m), represents a deciduous hardwood-conifer forest (Edelman 1975). Hardwoods dominate and include *Aesculus, Alnus, Betula, Carya, Cercidiphyllum, Eucommia, Juglans,* and *Ostrya.* Among the conifers are *Metasequoia* (most abundant), *Pseudolarix* and *Sequoia* (frequent), and *Abies, Chamaecyparis, Picea, Pinus,* and *Tsuga* (uncommon to rare). Radiometrically dated at 47-46 m.y.a., this flora clearly demonstrates that the Eocene forests of the Arctic extended southward along cooler mountainous uplands at this early date. It was later, with the cooling cycle of Oligocene-Miocene times, that this mixed conifer-hardwood forest zone shifted to lower levels at middle elevations in western North America. By mid-Eocene time, vegetation east and west of the continental divide was developing in different ways. This was the result of the building up of a broad, relatively high topographic barrier by vulcanism that ranged from northern Nevada into Canada (Lipman *et al.* 1972). Mid-Eocene floras to the east reflect drier climate as seen in the Green River flora of Colorado-Utah, with its subtropical forest/scrub and oak-pinyon woodland (MacGinitie 1953). By contrast, at lower elevations to the west, broadleaved evergreen forest was represented by the Comstock flora of western Oregon (Sanborn 1935), the Susanville flora of eastern California (University of California Palentology Museum), and floras from the Puget group, Washington (U.S. National Museum of Natural History). At moderate elevations inland, temperate rainforest (Chalk Bluffs, flora, MacGinitie 1941) and temperate deciduous hardwood forest with a few broadleaved evergreens (Lower Cedarville flora, University of California Paleontology Museum) were present.

In response to the trend to cooler, drier climate, and also to the building up to the broad volcanic upland of mid-Eocene age in the northern and central Rocky Mountains, areas it is lee show evidence of spreading drier climate. This is especially apparent from floras in the Ruby and Beaverhead basins, south-western Montana (Becker 1961, 1969). Taxa of drier environments are present, notably small-leaved species of *Amelanchier, Celtis, Cercocarpus, Mahonia, Philadelphus, Ribes,* and *Sapindus.* The Florissant flora, Colorado, also has members of this group (MacGinitie 1953), notably a scrub oak (*Quercus*), *Mahonia, Rhus, Vaquelinia,* and several legumes with small leaflets, notably *Prosopis.* These probably occupied drier sites on the andesite tuffs and breccias that rimmed the lake in which the flora was preserved. The Florissant flora also has species of *Abies, Chamaecyparis, Picea, Pinus,* and *Sequoia,* associated with a rich mixed hardwood forest at the borders of a sclerophyllous woodland. Similar relations are shown by the Late Oligocene (27 m.y.a.) Creede flora of southwestern Colorado, where a mixed conifer forest of *Abies, Picea, Pinus,* and *Pseudotsuga* is recorded in ecotone with sclerophyll woodland (Axelrod 1987). At higher levels (ca. 900 m), pure montane conifer forest probably was present.

Summarizing, by Middle Eocene time (47-46 m.y.a.), vegetation zones representing broadleaved deciduous forest, mixed deciduous-conifer forest, and pure montane conifer forest were present from the central United States northward into the Arctic. These were arranged with respect to elevation, with montane conifer forests largely above 1200 m elevation in Nevada-Idaho (Axelrod 1968), decreasing northward to an elevation near 300 m in the Arctic, where they are inferred to have been above mixed conifer-hardwood forest recorded there. Existence in the north was favored by mild temperatures resulting from more uniformly distributed global temperature with cooler tropical and warmer polar zones. Drier climate was spreading in the lee of the volcanic cordilleran axis by the Middle Eocene, when zones of drought-deciduous and sclerophyll vegetation are recorded. Since then, the differences in temperate vegetation east and west of the continental divide have increased, with more mesic forests and woodland in the west.

### *The Neogene (25-2 m.y.a.)*

During the mid-Tertiary (Fig. 3), major physical events directly influenced the flora and vegetation. Australia was rafted farther north, away from Antarctica; early glaciation developed on Antarctica; and Drakes Passage between Antarctica and the southern tip of South America opened (during the Middle Oligocene, ca. 27 m.y.a.). Cold water now flowed north into equatorial latitudes and strengthened high pressure systems, so that drier climates spread more widely. Sea level was lowered significantly at about 27 m.y.a., the Mississippi embayment in North America retreated rapidly, and major volcanic activity is recorded in western North America. Exotic taxa were now being reduced in numbers in response to colder winters and drier summer climate. The uplift to mountains favored the general spread of cold-temperate conifer forests and their species. In addition, in the lee of these topographic barriers drier vegetation types, including conifer woodland and grassland, commenced to spread.

During the Miocene (25-5 m.y.a.), conifer-hardwood forests were present at moderate elevations over the western United States. Examples are provided by the Blue Mountains flora of eastern Oregon (in Chaney & Axelrod 1959) and by the Trapper Creek (Axelrod 1964) and Thorn Creek (Smith 1941) floras of southern Idaho, with the latter two largely dominated by conifers (*Abies, Chamaecyparis, Picea,* and *Pinus*), mixed with some deciduous hardwoods (*Acer, Betula, Quercus, Ulmus,* and *Zelkova*). These were situated above the rich mixed hardwood lowland conifer (*Metasequoia, Taxodium*) forests at elevations generally below 600 m, where species of *Ailanthus, Betula, Cedrela, Diospyros, Fagus, Hamamelis, Ilex, Pterocarya, Quercus* (broadleaved), *Sassafras, Ulmus,* and *Zelkova* are recorded, with a few broadleaved evergreens, including species of *Magnolia, Persea,* and *Phoebe* (in Chaney & Axelrod 1959). This mixed hardwood forest ranged north to Alaska, as seen in the Seldova Point and allied floras (Wolfe & Tanai 1980).

This is evident from floras in sediments interbedded with dated basalts (13-12 m.y.a.) in south-central British Columbia (Matthews & Rouse 1963). The megafossil flora has species similar to those in the Miocene of Oregon and Alaska. Together with pollen, the species include *Abies, Picea, Pinus, Pseudotsuga,* and *Tsuga,* as well as Cupressaceae and Taxodiaceae (pollen genera not identified). Diverse angiosperms are also present, notably *Alnus, Carya, Corylus, Ilex, Juglans, Liquidambar, Pterocarya, Quercus, Salix, Tilia,* and *Ulmus/Zelkova.* Of special interest is the dominant coniferous pollen (80-90%), as compared with angiosperm pollen. This indicates a cooler, more upland environment not far removed from montane conifer forest and grading to lower elevation at the Red Lake site, which is situated farther east and includes dominant angiosperm pollen (63%).

The Neogene plant record at high latitudes is poorly known, except for that in Alaska (Wolfe 1966, 1987b, Wolfe & Tanai 1980, Wolfe *et al.* 1966). The Early to Middle Miocene floras include numerous woody dicotyledons, belonging to genera such as *Alnus, Betula, Carpinus, Carya, Cercidiphyllum, Cocculus, Corylus, Liquidambar, Nyssa, Platanus* and *Tilia. Metasequoia* is common in these floras, but remains of upland conifers that represent cold temperate climate are rarely encountered in lowland areas. However, a flora from the Wrangell Mountains has a number of conifers –*Abies, Picea, Pinus, Thuya, Tsuga*– together with exotic genera including *Fagus, Pterocarya,* and *Ulmus.* The abundant conifers imply a higher elevation, as compared with the mixed deciduous hardwood-conifer forest of the Cook Inlet region. This suggests that conifer forests were present at higher elevations throughout the higher latitudes. This may be inferred from the Paleocene records of floras at high latitudes, as well as from the Miocene record from Iceland, where a mixed deciduous forest included *Abies, Picea,* and *Sequoia,* associated with species of *Acer, Betula, Carya, Comptonia, Fagus,* and *Sassafras,* all now absent from the region (Heer 1868, Schwarzbach & Pflug 1957, Pflug 1959, Manum 1962, Ahmatev *et al.* 1978).

Conifer forests are not recorded in the far north until the Late Miocene and Pliocene. This raises the question as to whether their taxa were derived from Eocene-Oligocene species at middle latitudes that spread northward with cooling climate and the uplift of mountainous tracts during the Miocene and later. Only the discovery of more numerous floras in the far north can certainly provide the answer to this question. Nonetheless, current evidence suggests that conifer forests spread northward and down in elevation following the Eocene as a cooler climate developed. Such a sequence is well represented in the later Neogene of both Alaska and Iceland.

By the Late Miocene in Alaska, the Homer and allied floras have relatively few exotic broadleaved hardwoods, but still include *Carya* and *Ulmus;* those hardwoods that remain are not common either as megafossils or in the pollen record. Shrubs such as *Rhododendron, Spiraea,* and *Vaccinium* are locally abundant. Pollen of *Picea* and *Tsuga* is present at most localities. The shift from a rich to a poor forest with scarcely any deciduous hardwoods heralds the spread of colder climate, although floras to the south –in Washington, Oregon, and Idaho– still have the aspect of older Miocene floras like that from Seldova Point in Alaska. They are of mild temperate aspect, as indicated by members of the families Aceraceae, Fagaceae, Juglandaceae, and Ulmaceae. The shift in composition from the Middle to the Late Miocene evidently disrupted a continuous forest that ranged across Beringia to northern Japan, where some of the same species are recorded in the Middle Miocene (Wolfe & Leopold 1967), although those forests include more numerous broadleaved evergreens (Tanai *et al.* 1963).

The major floristic changes in Alaska, as documented by the differences between the Middle and Late Miocene floras, occurred at ca. 15 m.y.a. (between the Seldova Point and Homer floras) and ca. 7-6 m.y.a. (between the Homer and Clam Gulch floras). These correspond closely with comparable floristic changes that occurred in the floras of Nevada-California-Oregon-Washington Axelrod 1987, 1992).

Pollen floras from the Holmatindur Tuff, eastern Iceland (65°N), come from sediments between dated basalt flows; they provide evidence of rapid cooling in the Late Miocene (Mudie & Helgason 1983). The lowest sample consists of a rich palynoflora that includes *Larix, Picea, Pinus, Sequoia,* and *Taxodium,* together with deciduous hardwoods that include *Carpinus/Ostrya, Carya, Fagus, Juglans, Nyssa, Quercus,* and *Ulmus.* The overlying sample has a similar flora, but a slightly higher percentage of *Picea* and *Pinus,* and a lower percentage of *Fagus.* Higher samples contain palynofloras dominated by *Picea,* with a strong representation of cold-tolerant shrubs, including *Betula* sect. *Nanae* and *Alnus viridis.* The data suggest a floral sequence from a temperate *Taxodium*-hardwood forest, to cool temperate deciduous hardwood-conifer forest, to microthermal spruce forest, and finally to a subarctic *Alnus* woodland. The sequence indicates major climatic cooling during the dated time, 10.3-9.5 m.y.a. The cooling predates the earliest Iceland tillites (6-4.8 m.y.a.), and evidently corresponds in time to the oldest Alaskan tillites (Denton & Armstrong 1969).

The Late Miocene Beaufort Formation on Banks Islands, Arctic Canada (73°N), has well-preserved cones of *Picea (banksii), Pinus banksiana,* and *P. strobus,* as well as megafossil remains of *Larix, Metasequoia, Pseudolarix, Alnus,* and *Juglans cf. cinerea* fruits. In addition, there is pollen of *Tsuga cf. canadensis, Carya, Corylus,* and others. A pollen profile indicates that the area was covered initially with mixed deciduous hardwood forest with abundant conifers, such as *Pinus* (dominant) and *Picea.* This was followed by increased *Larix* and *Picea,* and the rapid decrease and disappearance of pollen from deciduous trees (Hills, 1971).

A small Late Tertiary flora near Circle, Alaska, from old terrace deposits of the Yukon River, includes 9 cones of *Picea* and 3 of *Larix.* Pollen is represented by *Abies, Larix, Picea, Pinus,* and *Tsuga,* as well as these genera of shrubs: *Alnus, Betula, Diervillea,* and *Salix,* and species of Caprifoliaceae, Caryophyllaceae, Ericaceae, and Poaceae (Yeend *et al.* 1989). Most of this assemblage is not found in the immediate region today. The principal exotics are *Diervillea,* now in British Columbia, and *Pterocarya,* possibly reworked from older rocks, which is a native of Asia. The conifers are chiefly in more distant areas where the summers are warmer. These include *Tsuga* (now in Alaskan Coast Ranges), *Pinus (banksiana)* (800 kilometers east) *P. contorta* (500 kilometers south), *Abies (lasiocarpa)* (350 kilometers south), and *Larix (laricina)* (150 kilometers east and 200 kilometers west) (data from Little 1971). The assemblage represents a rich interior conifer forest, and suggests that tundra was at higher levels in the area. Its age is not known precisely, but it appears to be transitional Mio-Pliocene, or about 5-6 m.y.a.

During the Pliocene, the Cook Inlet region, Alaska, supported *Picea* and *Tsuga,* and a few exotics as megafossils, including *Glyptostrobus* and *Rhus,* as well as rare pollen of *Pterocarya* and *Ulmus,* which may have been reworked from older rocks (Wolfe & Leopold 1967). In transitional Mio-Pliocene rocks of the Alaska Range is a record of montane conifer forest including *Abies, Larix, Picea, Pinus,* and *Tsuga,* and with *Populus* and *Salix* associated in lake border and riparian sites. Thus, even at this late date, pure conifer forest was not yet of wide occurrence over the lowlands of the Arctic.

A Pliocene flora from Lava Camp Mine, on the Seward Peninsula in the Bering Strait region (65°N), provides a record of rich conifer forest (Hopkins *et al.* 1971). Megafossils include species identified as *Picea glauca, P. mariana, P. sitchensis, Pinus monticola,* and *Tsuga heterophylla,* as well as seeds of *Symphoricarpos, Vaccinium,* and Cyperaceae (*Carex, Cyperus*). Associated pollen includes species of *Alnus, Betula, Corylus, Salix,* and *Symphoricarpos,* as well as several ericads, *Epilobium,* and *Oenothera.* Approximately ten species of conifers are represented by needles, cones, or pollen. Some of these are now found on the order of 850 kilometers or more to the south. This is not a taiga community, but represents vegetation near the northern border of the Coast coniferous forest.

The evidence indicates that a rich Coastal conifer forest dominated by *Picea* and *Pinus,* but including *Abies, Larix* or *Pseudotsuga,* and *Tsuga,* as well as members of the families Cupressaceae and/or Taxodiaceae, extended from the Cook Inlet area to the Arctic Circle during the Pliocene (5-2 m.y.a.). The authors note that *Glyptostrobus, Diervilla,* and *Ulmus* were present in the Cook Inlet region, but have not been recorded farther north. *Pterocarya* was present as a rare tree in the Cook Inlet and Nome regions in the Pliocene. Pollen of *Tilia* is rare in the Pliocene floras of the Cook Inlet region and in the Nome area, and the location and abundance of the trees that shed this pollen is unknown.

The large insect fauna associated with the plant megafossils at the Lava Camp Mine locality includes a number of extinct species. In discussing the affinities of this fauna, Hopkins *et al.* (1971, p. 119) stated: "It seems clear that a similar assemblage of living insects and mites could not be collected on the modern tundra of the Seward Peninsula, nor in the boreal woodland of present-day interior Alaska. A comparable assemblage of insects probably could be collected in southern British Columbia or northern Washington."

That the northern limit of the Coast conifer forest was nearer the Arctic Circle in the Pliocene is suggested by a Pliocene pollen flora from Kivalina, 100 km north of the Lava Camp Mine assemblage dominated by megafossils. The Kivalina assemblage is dominates by *Pinus, Tsuga,* and *Betula,* and lacks *Abies, Chamaecyparis, Larix, Tsuga,* and *Corylus.* It more nearly resembles the vegetation of the Yukon Territory, northwest Canada, than it does the Lava Camp Mine flora.

Summarizing, the differences in vegetation east and west of the continental divide that existed in the Paleogene were accentuated in the Neogene (i.e., after 25 m.y.a.). As forests and woodlands retreated in response to drier, cooler climates, grasslands east and west of the divide were being segregated into seral communities in local open areas, probably by the Middle Paleogene (ca. 45 m.y.a.). Differences between the grass communities east and west increased as drier climates spread, especially during the past 15 million years as forests retreated. This is inferred from the rapid increase in hypsodont equids (15 contemporaneous species) in the Late Middle Miocene (ca. 12 m.y.a., MacFadden & Hulbert 1988). With the rise of the cordilleran axis and the building of the Cascade-Sierran barrier, especially following during the past 7-6 million years, grasslands spread more widely in the lee of these barriers and developed into distinct floras (Leopold & Denton 1987). Increasingly drier climate during the Late Miocene and Pliocene (i.e., the last 7-5 million years) on the High Plains and northward into Alberta resulted in rapid ("explosive") speciation of grasses and herbs (Elias 1942). Generally similar relations are inferred for the much smaller grasslands (a quarter of the size of the Great Plains) west of the continental divide, as on the Snake River Plain, and the coastal valleys of California and Oregon, where they assumed dominance in the Pleistocene. The spread of drier, colder climate in the lee of the Alaska Ranges, which are relatively young, favored the taiga and (later) tundra vegetation, especially in the Wisconsin glacial and later (reviewed by several authors in Hopkins *et al.* 1982).

As taxa were eliminated from the temperate forests of North America under the influence of a cooler, drier, and less equable climate, they were also being eliminated even more rigorously from western Eurasia. In Chile and Japan, where the climate remained more equable and there was ready access to mountainous areas to the south, many more elements of the north temperate forest survived. The modern flora of China, which is about the same size as the United States, consists of about 30,000 species of angiosperms, at least 50% more than are found in the United States and Canada combined; and the modern flora of Europe consists of only about 11,000 species. The survival of archaic, temperate forest plants and animals in eastern Asia, where they persist in conditions of greater equability than have been maintained elsewhere parallels the survival of south temperate forest elements in Southeast Asia, northern Australia, New Caledonia, and to some extent, New Zealand and Chile (Arroyo *et al.* 1991).

## SOUTHERN TEMPERATE VEGETATION

As compared with the record in the Northern Hemisphere, fewer fossil floras dominated by angiosperms are presently known from south temperate regions (Figs. 4, 5); in addition, their precise (radiometric) ages have mostly not yet been established and there are many difficulties with identifications. For these reasons, an analysis of the development of vegetation in South America cannot be as complete as that for temperate North America.

The general background history of the region has been reviewed by Plumstead (1962), commencing with the earliest land plants (Devonian; 408-360 m.y.a.) and continuing up to the Tertiary. As

*Fig. 4:* Selected fossil floras referred to in South America. Paleogene: 1. Coronel Lota, 2. Río Pichileufú, 3. Río Turbio, 4. Fuenes, 5. Laguna d'Hunco, 6. Loreto; Neogene: 1. Cuenca, 8. Loja, 9. Pisllypampa, 10. Potosí.

Floras fósiles de Sudamérica seleccionadas. Paleogeno: 1. Coronel Lota, 2. Río Pichileufú, 3. Río Turbio, 4. Fuentes, 5. Laguna d'Hunco, 6. Loreto; Neogeno: 1. Cuencia, 8. Loja, 9. Pisllypampa, 10. Potosí.

she noted, the similarity of the pre-Cretaceous floras of South America, Africa, Australia, India, and Antarctica indicates that the southern continents were joined into the earliest Cretaceous, following which floristic links between the continents, as judged from the fossil record, became less common. In this connection, Raven & Axelrod (1974) pointed out that the distributions of numerous conifer and angiosperm families common to the southern lands demand connections in the

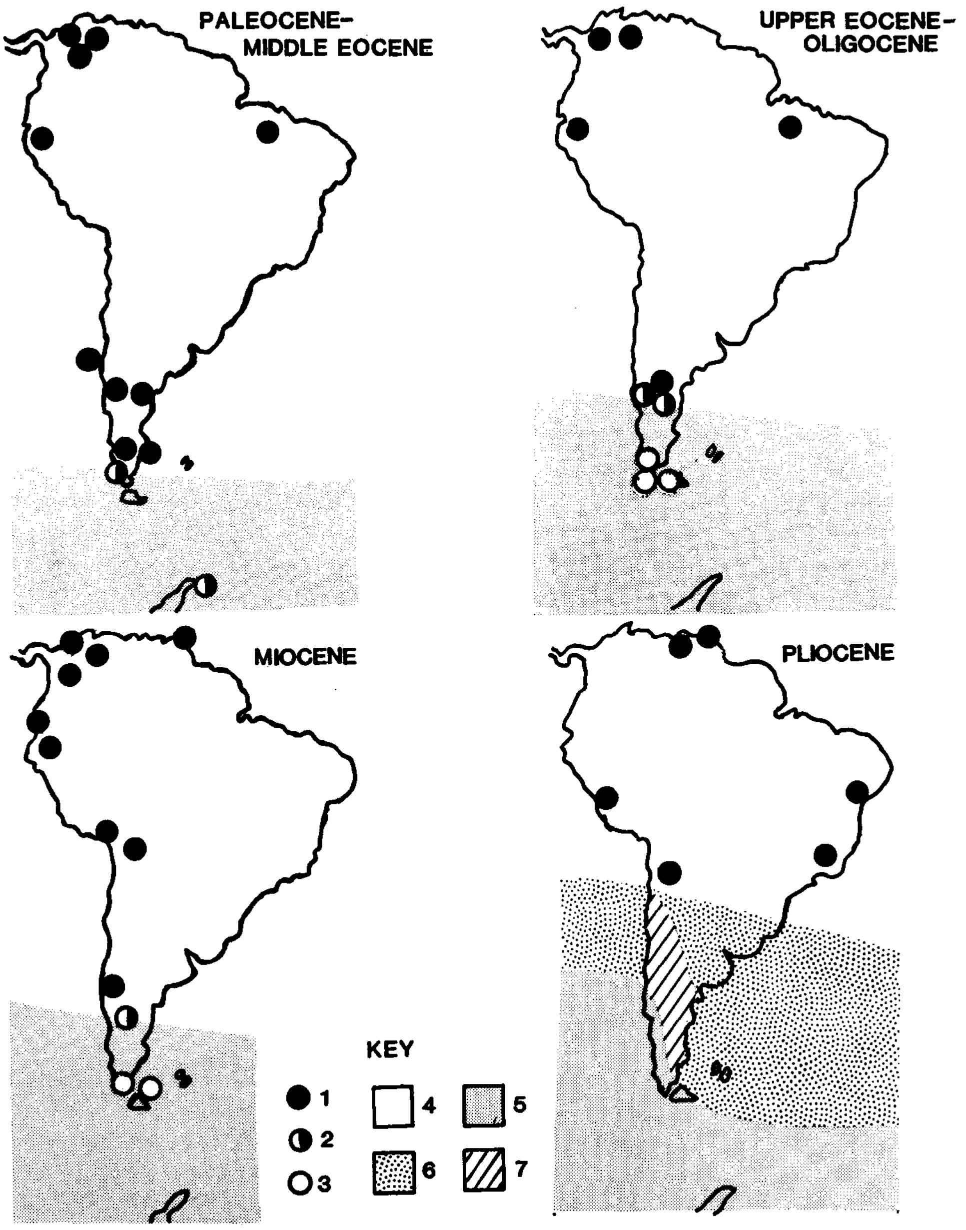

*Fig. 5:* Distribution of floras in South America during the Tertiary. 1. floras from tropical to subtropical climates; 2. floras representing mixtures of temperate and warm climates; 3. floras representing temperate and cool-temperate climates; 4. warm climate floras; 5. austral and cool-temperate floras; 6. temperate floras; 7. arid and semi-arid floras (from Menéndez 1971).

Distribución de floras en Sudamérica durante el Terciario. 1. floras de climas tropicales a subtropicales; 2. floras que representan mezclas de climas templados y cálidos; 3. floras de clima templado o templado-frío; 4. floras de clima cálido; 5. floras australes o de clima templado frío; 6. floras templadas; 7. floras de clima árido y semiárido (tomado de Menéndez 1971).

Late Cretaceous (i.e. 100-65 m.y.a.). Links between New Zealand-New Caledonia and Australia-Antarctica mostly date from 80-60 m.y.a., while those between southern South America and southeastern Australia-Tasmania were finally interrupted with the opening of the Drake Passage between South America and Antarctica about 29 million years ago, in the Late Oligocene.

The vegetation history of southern South America has been reviewed comprehensively by Menéndez (1971) and Romero (1986). The present discussion is drawn partly from those studies, in which extensive bibliographical references are included.

## *The Cretaceous (144-65 m.y.a.)*

The Early Cretaceous palynology of Argentina (Archangelsky 1980, Archangelsky *et al.* 1984) shows a generally similar flora throughout the area, with ferns and gymnosperms dominant and angiosperms appearing only late in the sequence. The vegetation was dominated by conifers, with the family Cheirolepidaceae (*Classopollis*) conspicuous, along with Podocarpaceae (*Callialasporites, Microcachrydites*) and Araucariaceae. Angiosperm polen appears only as a rare element in the Aptian (119-113 m.y.a.). At present, Albian (113-97.5 m.y.a.) strata have not yielded floras. By the Maastrichtian (73-65 m.y.a.), the pollen reveals a diversified angiosperm and conifer flora that has continued to exist in the area to the present time.

Angiosperms are first recorded in the Albian of Antarctica and gradually increased during the remainder of the Cretaceous. By Campanian and later times, recognizable alliances of gymnosperms and angiosperms (Araucariaceae, Podocarpaceae, Casuarinaceae, *Nothofagus*, Myrtaceae, Proteaceae *-Macadamia*-type, *Xylomelium*, Sapindaceae) are not only on Antarctica, but on the adjoining southern continents (Dettman 1989, Figs. 3, 6; Askin 1989, Dettman & Thomson 1987). The perennial herb *Gunnera* appears in the record even earlier, in the Turonian, was widespread in both hemispheres in the later Cretaceous and Paleogene, and then became progressively restricted to the Southern Hemisphere as global climates deteriorated (Jarzen & Dettmann 1989). The paleogeographic distribution of *Nothofagus* has been reviewed recently by Dettmann *et al.* (1990). The distribution of the forests that occurred in Antarctica and neighboring lands by the Campanian suggests that Antarctica may have been a center for the origin and dispersal of much of the perhumid, evergreen rainforests that are now disjunct in Chile, Australia-Tasmania, and southern Africa (Dettmann 1989). This view was supported earlier by Darwin, Hooker, and others, at a time when these lands were considered to have been permanently separated by long stretches of open ocean, thus requiring long distance dispersal to account for the disjuncts. Seward (1941, pp. 41-44) was one of the first to accept the likelihood that continental displacement, as visualized by Wegener, provided a means for reassembling the now-disjunct fossil and modern forests of austral lands.

The problem of the existence of evergreen rainforests in polar latitudes may be explained by photoperiodic ecotypes that made all their annual growth during the long light period, with cambial activity concentrated in rapid growth of wood during the polar summer (Chaloner & Creber 1989). However, this also requires a highly equable (M 65-70) perhumid climate with an annual range of temperature of 5-7°C, and hence a nearly frostless environment (Axelrod 1966b, Fig. 2; 1979, Fig. 10).

Reference to the disjunct occurrence of evergreen rainforest taxa of southern South America brings up the occurrence of *Lactoris*, the only genus of Lactoridaceae, now confined to the mesic, equable uplands of the Juan Fernández Islands. Its primitive features indicate that *Lactoris* is a relict, ancient angiosperm. *Lactoris* pollen is now known from Upper Cretaceous (Turonian-Campanian, 88-84 m.y.a.) sediments off the southwest coast of Africa (Zavada & Benson 1987). This implies a former distribution across temperate western Gondwanaland, with the Juan Fernández population the only surviving relicts.

Among the earliest angiosperm leaves from southern South America are a few specimens from the Barquero formation of Patagonia. They are associated with a fossil flora dominated by more than 100 species of gymnosperms and pteridophytes. The large, lobate, craspedodromous and dentate leaves have ramified tertiary veins and random fourth-order veinlets. In general aspect, they are much like those of the Potomac Group, ranging in age from the areas, especially those from Zone 1 of the Potomac Group, ranging in age from the Barremian through the Aptian age (ca. 125-115 m.y.a.; Romero & Archangelsky 1986). Because of the links that were present at the time, it is to be expected that the Cretaceous paleofloras of southern South America, when better known, will resemble the contemporary ones of New Zealand, Australia, and Antarctica, and that the earlier ones will exhibit similarities with the contemporary floras of India and Africa also.

Oxygen-isotope studies of marine megafossils of Santonian-Campanian age (85-70 m.y.a.), James Ross Island, and from the Maastrichtian (70-65 m.y.a.) of Vega Island, Antarctica (Pirrie & Marshall 1990), indicate cool temperate climate during the Late Cretaceous, with cooling between the Santonian-Campanian and the Maastrichtian (70-65 m.y.a.). A generally similar temperature decline in the high Arctic is supported by the morphology of fossil leaves (Parrish & Spicer 1988). Fossil woods from James Ross Island suggest unstressed but seasonal conditions during the Campanian (Francis 1986). Large leaves (> notophyll) from the Late Cretaceous of King George Island (Zastawniak 1990), indicate a perhumid climate with little temperature change. By contrast, Late Maastrichtian-Paleocene woods show a marked change in growth patterns, implying slower tree growth as a result of important climatic cooling. These data are consistent with evidence for Early Eocene (ca. 50 m.y.a.) glaciation on King George Island (Birkenmajer & Zastawniak 1989). We suggest that it probably was the general trend to lowered temperature that modernized the ancestral (Cretaceous) evergreen forests. Particularly interesting in this connection is the evidence for alternating glacial-interglacial climates on King George Island, with cool (glacial) periods in the Early Eocene and Late Oligocene. With continued climatic fluctuation, species of the fossil forests became increasingly modernized, as seen in the gradual reduction of their leaf sizes and also in the geographic restriction of the larger-leaved evergreen taxa (see Birkenmajer & Zastawniak 1989).

### *The Tertiary (65-2 m.y.a.)*

As reviewed by Menéndez (1971) and Romero (1986), two major vegetation zones were present in southern South America during much of the Tertiary (Fig. 6). Cool temperate forests were in the south, extending to Antarctica and, especially earlier, with links to Australia, whereas subtropical to tropical forests ranged from near 40°S into equatorial regions. The maximum southern advance of subtropical (or warm temperate) elements seems to have occurred in the Middle Eocene (i.e., about 40 to 45 m.y.a.), following which elements associated with warmer climate retreated and cool temperate forests, dominated by *Nothofagus* and austral gymnosperms, spread some 10° northward. Only late in the period is there clear evidence of the existence of drier climates on the eastern side of the southern Andes in Argentina-Chile.

In southern South America, the oldest Tertiary deposit includes the small Funes flora of Danian age (65-70 m.y.a.; Berry 1937a, Romero 1978). Taking into account the results of palynological and paleoxylogical studies (Petriella 1972, Archangelsky 1976a, b), a paleoenvironmental analysis of this flora was made by Petriella & Archangelsky (1975). This analysis indicates that in the area of the Golfo de San Jorge (46°S), vegetation similar to that now found in southern Brazil, some 2,000 km and 20° of latitude to the north, occurred at that time. Represented are mangrove communities, swamp forest, tropical rainforest, and montane rain forest, all implying the existence of a humid subtropical forest. The presence of crocodiles indicates that minimum winter temperatures (i.e., in July) were not less than 10°C (cf. Axelrod 1984); such conditions now occur some 1,500 km to the north (Volkheimer 1971).

Of interest is the occurrence in this flora of a few plant genera that provide

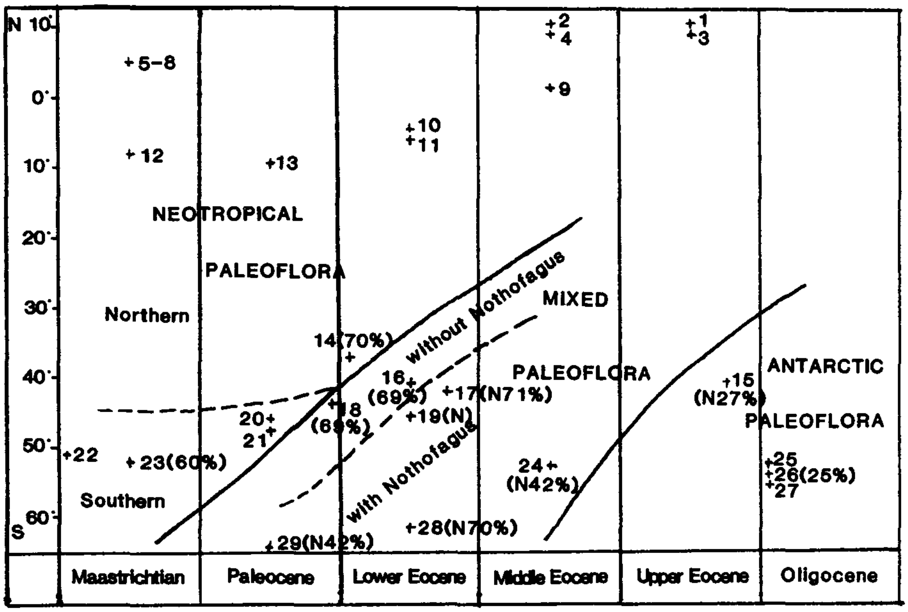

*Fig. 6:* Shifting areas of the Neotropical and Antarctic Paleofloras during the Tertiary (from Romero 1986).

Areas derivadas de paleofloras neotropicales y antárticas durante el Terciario (de Romero 1986).

links to Australasia, including *Dracrycarpus, Dicranocarpus* and *Gunnera,* as well as *Tricolpites fillii,* which is a pollen fossil that resembles *Beauprea* (Proteaceae), recorded in New Zealand in the Cretaceous (see Fig. 1). Other elements that link New Zealand and South America are *Anacolosa* and *Nypa,* although they are not as common as in Australasia. Indications of genera that appear in the record in South America for the first time, evidently reaching New Zealand during the Eocene and Oligocene, are provided by pollen similar to that of *Banksia* and *Weinmannia.*

Of evolutionary interest is fossil palm wood (*Palmoxylon patagonicum* Romero), from the Danian age of Chubut Province, Argentina (Romero 1968). The author concludes that since the wood has characteristics intermediate between those of the subfamilies Sabaloideae, Cocoideae, and Bactrioideae, now represented in Chile and Argentina, that this fossil may belong to an ancestral stock from which these groups subsequently differentiated.

The Paleocene flora of Laguna del Hunco, northwest Patagonia, dated at 59 million years old (Archangelsky 1974), includes some 25 species (Berry 1925); the names applied to these taxa by Berry are doubtless much in need of revision. More than two-thirds of them, however, have leaves with entire margins, indicating that the forest at the sites was a marginal tropical rainforest, perhaps consisting mainly of present-day Neotropical genera and their relatives. Endemics of the present Australian region, including *Gymnostoma* (Casuarinaceae), also occurred in this flora (Freguelli 1943). Somewhat surprisingly, *Nothofagus* has not yet been found in this flora.

Petrified wood from the vicinity of Chile Chico, XI Región of Chile, located directly east of these Argentine localities, has been reported from the Paleocene (Nishida *et al.* 1990). The three samples resemble the wood of *Kageneckia* or *Quillaja* (dominant elements in the mediterranean-type vegetation of central Chile today), Proteaceae, and Lauraceae, respectively, and clearly reflect a warm-temperate to subtropical climate at that time. Notably, the genus *Quillaja* and other matorral elements are today disjunct to southern Brazil (Arroyo *et al.* 1991).

The flora from Lota and Coronel in Chile (37°S), from the Early Eocene (ca. 55-50 m.y.a.), was described by Berry (1922) as including well over 100 species; he compared it with modern species from the Amazon Basin. Certainly the aspect of the flora suggests that the climate was wet, lacked freezing temperatures, and was considerably warmer than at present, which agrees with a lack of mountain barriers at the time, and the presence of a very equable climate. This fossil assemblage is poorly described, and would repay additional study.

Berry (1938) described another Early Eocene flora from Río Pichileufú, Argentina. He considered that many of the species were the same as those at Lota and Coronel, Chile, which agrees with the lack of mountain barriers at that time. Berry interpreted this rich flora as including tropical and temperate elements; its variability suggest that it represents an ecotonal climate. The absence of *Nothofagus* here implies that the Paleocene-Early Eocene climate was warmer than that of the later Eocene in these regions.

Middle Eocene Patagonian fossil floras occur in the Río Turbio formation (Hunicken 1966). The flora contains a mixture of Neotropical and Antarctic genera, among which are species of *Acmopyle, Allophyllus, Cissus, Cupania, Drimys, Mespilodaphne, Myrica, Nectandra, Nothofagus, Notophoebe, Ocotea, Persea, Phoebe, Rhamnidium, Styrax,* and *Zizyphus.* Although these determinations should be examined critically, the leaves suggest that these plants constituted a moist, warm-temperate forest in which elements that currently occur farther north were mixed with others that are characteristic of South American temperate forest today. The leaves are of intermediate size (notophyll, microphyll), and many are serrate.

On Antarctica (Fig. 7) during the Campanian age to Paleocene (83-55 m.y.a.), the development of the regional vegetation has been traced by several authors (Baldoni & Barreda 1987, Dettmann & Thomson

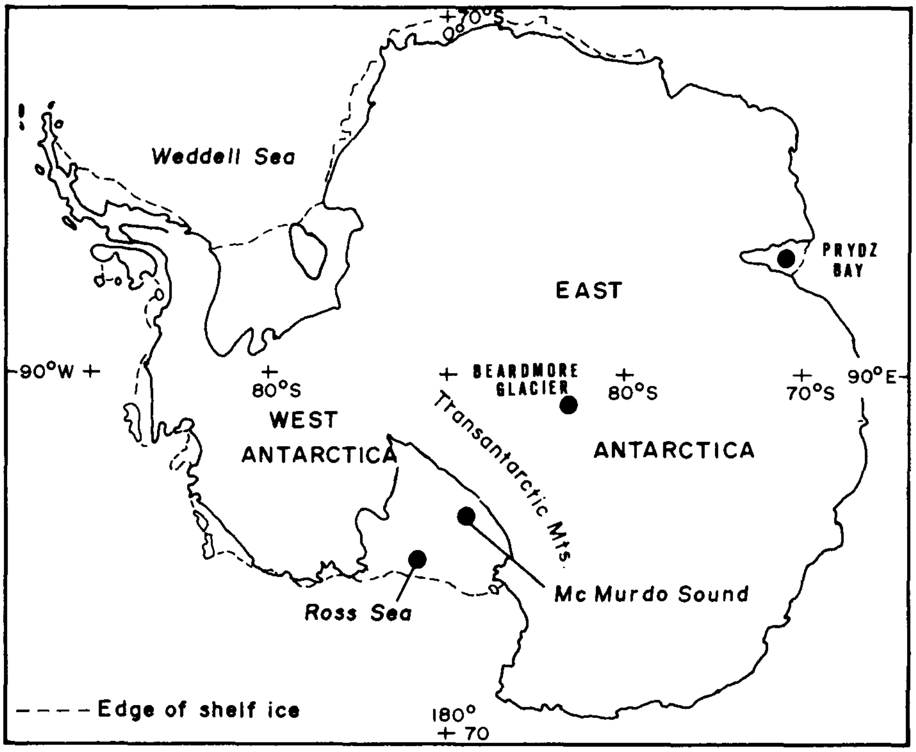

*Fig. 7:* Fossil floras on Antarctica.
Floras fósiles de la Antártica.

1987, Romero 1987). The pollen of podocarps is abundant and diverse (Askin 1988a). Araucarian pollen is also represented, moss and fern spores are common, and all three groups of *Nothofagidites (Nothofagus* pollen-*brassii, fusca, menziesii* types) are recorded. Other angiosperm pollen can be referred to diverse families, notably Proteaceae, Loranthaceae, Myrtaceae, and Casuarinaceae, and to the orders Ericales and Liliales, although the modern generic affinities have not been established. These fossils represent members of lowland forest and moist fluvial-lacustrine-swamp areas mixed with some palynomorphs probably transported from upland communities. The dominant podocarp vegetation suggests a cool temperate, moist climate such as that now in southern Chile, with its podocarps and araucariads growing with *Nothofagus.* The distinctive pollen of *Phyllocladites,* common on Seymour Island, may be that of the modern genus *Dacrydium,* which occurs in western Tasmanian rainforests.

Compressions of ferns, *Nothofagus,* and podocarp foliage in the upper Cross Valley Formation represent a cool temperate rainforest (Case 1988). Wood from the Cross Valley and Sobral formations have uniform growth rings indicating a "stable" forest environment (Francis 1986). From the Campanian and Maastrichtian ages (83-65 m.y.a.), there is an increased diversity of angiosperms, with approximately 100 pollen and spore taxa represented. The pollen sequence provides no evidence of a major extinction event at the Cretaceous-Tertiary boundary in this region (Askin 1988b).

In their review of the *Nothofagus* species described by Dusén, Romero & Dibbern (1985) point out that the Seymour Island fossils from the Cross Valley Formation can be compared with four living South American species, all deciduous and including the *fusca* and *menziesii* pollen types.

Of special interest is the finding of a polydolopoid marsupial (*Eurydolops seymourensis*) from the Late Eocene La Meseta Formation of Seymour Island (Case *et al.* 1988), (Fig. 8). It apparently had a South American ancestry near *Polydolops thomai* or *P. rothi,* similar to that suggested by the contemporaneous La Meseta species *Antarctodolops dailyi.* This suggests a Paleocene age for the origin of the Seymour Island polydolopids, with a likely time of dispersal from South America about 60-55 million years ago. Isolation apparently accounts for the Seymour taxa being differently specialized from each other, as well as from their South American allies; they differ remarkably from the trends exhibited by the South American polydolopids during the Paleocene and Eocene (Case *et al.* 1988). These authors further point out that the land area in southern South America-Antarctica, New Zealand, and Australia was covered with a relatively dense *Nothofagus*-dominated forest (see Fig. 1). The arboreal marsupials would have been at a selective advantage in such forests. Polydolopoids

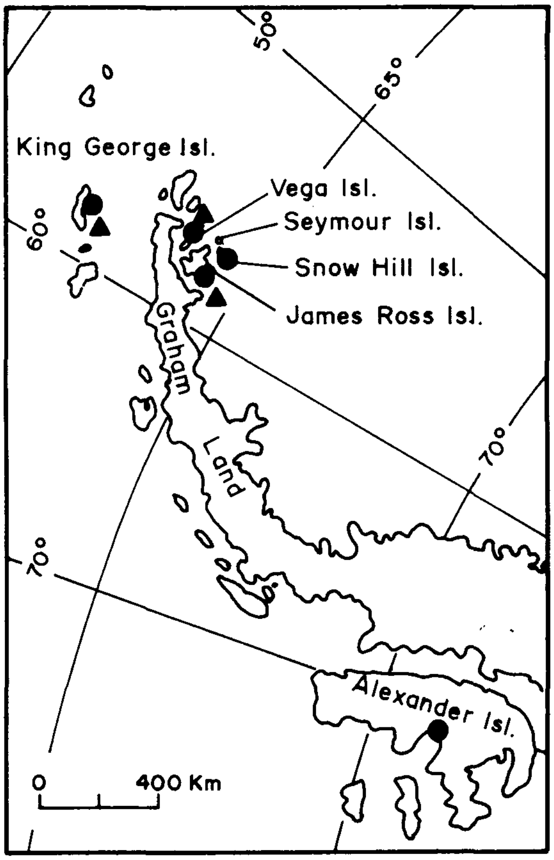

*Fig. 8:* Fossil floras on the Antarctic Peninsula.
Floras fósiles de la Península Antártica.

possibly filled the rodent or primate adaptive niches in South America and the Antarctic Peninsula prior to the introduction of these groups to South America. Probable microbiotheriid marsupial remains have also been found in Antarctica in Paleogene time (Carlini *et al.* 1990).

Other lines of evidence are not in agreement with the hypothesis that Antarctica at this time was covered with temperate *Nothofagus* forest, however. The recent discovery of a tardigrade edentate, a placental mammal, from the Paleogene of Antarctica rather suggests the existence of warm-temperate environments (Carlini *et al.* 1990). Such mammals were apparently relictual in northern Antarctica at the time, but may have been widespread there earlier.

The occurrence in the La Meseta Formation of a fossil beak of a two-meter tall canivorous bird in the Late Eocene (40 m.y.a.) of Seymour Island is significant for both biogeographical and ecological reasons (Woodburne *et al.* 1987). It is allied to other predaceous (flightless) birds of the phororhacoid group known also in South America in the Tertiary. The occurrence of such a bird on Seymour Island indicates that its ancestors made use of the land connection that existed before the opening of the Drake Passage some 10 million years later. The bird would have inhabited relatively open country, and its occurrence suggests that such a community may have been widespread in greater West Antarctica, presumably in large gaps in the *Nothofagus*-dominated forest.

From the Dufayel Island Group, situated in a western arm of Admiralty Bay, King George Island, numerous plant remains that are diverse, but poorly preserved, were reported by Birkenmajer & Zatawniak (1986). The beds are dated radiometrically as transitional Paleocene-Eocene (57-51 m.y.a.) on the basis of associated lavas above and below the flora. The plant assemblage is dominated by *Nothofagus,* Myrtaceae, and various taxa that resemble Lauraceae. Leaves are of nothophyll size, implying a cool temperate rainforest environment much like that of southern Chile today. No remains of gymnosperms were recorded. The assemblage resembles the contemporary deciduous forest of *Nothofagus obliqua* and *N. procera* that is associated with evergreen, laurophyllous taxa (Hueck 1966). These thrive under a mean annual temperature of 11-12°C, in a highly equable climate (*M* 65+), one with a very low mean annual range of temperature (7-8°C), and represent a warmth (*W*) of 12.5-13°C, with 138-153 days warmer.

A rich pollen flora from Ezcurra Inlet is close to the Dufaley Island locality (Stuchlik 1981). Also of Eocene age, it includes a rich fern flora with taxa assigned to Schizaeaceae, Hymenophyllaceae, Gleicheniaceae, Cyatheaceae, and Salviniaceae. Angiosperms include *Nothofagus* and Rhammaceae. The absence of conifers is noteworthy (also see Barton 1963). In any event, the assemblage indicates a humid, cool temperate forest environment.

Megafossil plants have been described from the Mount Wawel Formation, Upper Oligocene (25 m.y.a.), Admiralty Bay, King George Island, in the South Shetland Islands (Zastawniak *et al.* 1985). Numerous impressions of *Nothofagus* represent several species, and Podocarpaceae are represented by shoot fragments and numerous seeds. Dicotyledonous remains also include leaves resembling those of *Cochlospermum* and Rhamnaceae, and indicate a diverse temperate forest in West Antarctica at the close of the Oligocene. Small leaves (notophyll and microphyll) dominate the flora and compare well with those that are frequent in recent Australian-New Zealand cool temperate rainforests.

From McMurdo Sound, Antarctica (see Fig. 7), McIntyre & Wilson (1966) note that the microfloras in erratic boulders of Eocene age are dominated by *Nothofagus,* representing all three major groups. Also recorded are *Araucaria, Dacrydium, Phyllocladus, Podocarpus* and Myrtaceae, as well Proteaceae. *Nothofagus* comprises some 80% of the pollen, with gymnosperms 5-10% and angiosperms other than *Nothofagus* the remainder. The flora compares with that in the cool temperate forests of New Zealand, and indicates ample rainfall.

From glacial marine sediments in Prydz Bay-West Ice Shelf, East Antarctica, Kemp (1972) records abundant pollen of *Nothofagus,* as well as that of several species of Proteaceae, Myrtaceae, *Microcachrys,* Podocarpaceae, and several families of ferns. Noteworthy is the presence of all three groups of *Nothofagus.* The bulk of the evidence indicates that the assemblage was derived from eroded Eocene sedimentary rocks and that the flora represents a rich *Nothofagus* forest filled with ferns and associated gymnosperms and angiosperms, in an area now under ice.

Palynological evidence from drilling in the Ross Sea by Glomar Challenger suggests that vegetation persisted in that area into the Late Oligocene (Kemp & Barrett 1975). The sample occurs with a dated (26 m.y.a.) glauconitic sandstone. The assemblage is dominated by *Nothofagus* of all three groups, and includes Podocarpaceae (*Dacrydium, Microcachrys*) and pollen assigned to angiosperm families including Proteaceae and Myrtaceae, as well as several families of ferns. Taken as a whole, the forest here was apparently less diverse than that from the older Seymour Island deposits, indicating a somewhat cooler climate. The authors suggest that forests in the area may have been confined chiefly to the coastal zone, and to slopes above the valley glaciers that debouched into Ross Sea. The *Nothofagus* flora was still essentially continuous at sea level from the Palmer Peninsula to Ross Sea, a distance of some 4,700 kilometers, at the close of the Oligocene (Mildenhall 1989), then linking the biotas of southern Chile with those of southeastern Australia/Tasmania. Similar vegetation persisted in this area until the Middle Miocene (ca. 14 m.y.a.) although its diversity seems to have decreased progressively as the continental glaciers expanded (Brady & Martin 1979). Fig. 9 illustrates the development of the ice sheet on Antarctica during the past 20 million years (Ciesielski *et al.* 1982).

Following the lead of Romero (1980) and Romero & Aguirre (1982) on the comparative architecture of *Nothofagus* leaves, Tanai (1986) reviewed the fossil species of the genus and compared them with the living ones. He divides the extant species into five groups, as follows:

Group 1. Five species, South America.
Group 2. Two species in South America, one in Tasmania.
Group 3. Three species on South America.
Group 4. Seven species in New Zealand, Australia, Tasmania.
Group 5. Species of New Caledonia and New Guinea.

These groups appear to be of fundamental significance. *Nothofagus* apparently originated in the far south in the Middle Cretaceous, migrating northward as the climate became cooler during the Tertiary; it apparently reached its maximum extent during the Miocene. Considering the wide distribution of presently Australian-New Zealand-New Guinea gymnosperms in South America during the Early Tertiary, it is noteworthy that only a single contemporary group of the genus, group 2, links these two regions. The much richer representation of fundamentally austral groups in Australasia than in South America at present, together with the earlier occurrence of additional groups, now restricted to the Old World, in South America (Raven and Axelrod 1974), implies much extinction in South America.

In northwestern Patagonia, at the general latitude of Puerto Montt, are several florules of Late Miocene age (8-5 m.y.a.) that have yielded some 45 species, many with Antarctic affinities (Berry 1928). These florules are dominated by genera such as *Araucaria* and *Nothofagus* as well as by leaves resembling Proteaceae. The percentage of species with non-entire leaf margins has increased from that found in older floras to fully 70%; these florules apparently represent a cool temperate rain forest. As judged from the small size of the leaves represented (microphyll, nanophyll), this forest seems to reflect major cooling following the Middle Eocene. A continuation of this trend is shown by a number of small floras in southernmost Chile and Argentina (reviewed by Romero 1986). These show few species with entire

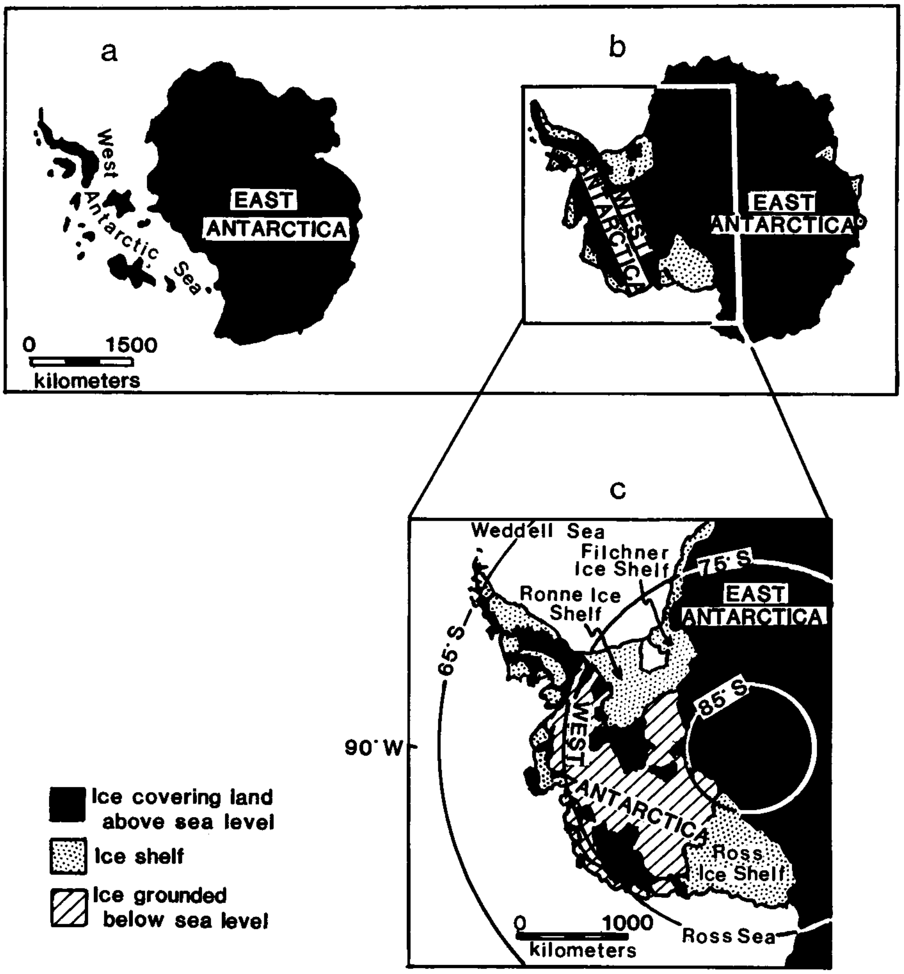

*Fig. 9:* Stages in the history of West Antarctica since the Oligo-Miocene. a. Antarctica archipelago prior to late Miocene; b. showing ice sheets since late Miocene; c. present West Antarctica showing exent of ice shelves and ice sheet grounded below sea level (from Ciesielski *et al.* 1982).

Estados en la historia de Antártica occidental desde el Oligoceno-Mioceno. a. antes del Mioceno tardío. b. extensión de los casquetes de hielo desde el Mioceno tardío. c. situación actual indicando la extensión de los casquetes de hielo por debajo del nivel del mar (tomado de Ciesielski *et al.* 1982).

leaf margins and an increase in the number of smaller leaves, chiefly nanophylls and a few microphylls.

Miocene floras are well known to the north —outside of our area of general interest— where they have been elevated in the Andes to 2,000-3,000 meters above sea level. The elevation of the Andes resulted in the development of drier climates along the west coast of South America, and also southward on the east side of the Andes, resulting in the formation of the pampas and allied scrub formations, such as the monte. The uplift occurred in several phases, as outlined by Van der Hammen (1961), of which those of the Miocene and Pliocene-Pleistocene account for most of the present relief (Van der Hammen 1961, Arroyo *et al.* 1988). The Andes provided an important corridor for northward migration of southern genera such as *Weinmannia* and the north-south migration of temperate elements such as *Escallonia* (Arroyo *et al.* 1988). Although the identifications should be reviewed, such genera have been recorded in Miocene deposits in Bolivia, intermixed with tropical elements (Berry 1917, 1939). At present, however, they are largely absent on the western flanks of the Andes at similar latitudes, presumably because of the Late Tertiary development of the Atacama Desert. Noteworthy is the fact that no cool-temperate tree genus of North America has reached the temperate forests of southern South America by this route, despite the elevation of the Isthmus of Panama several million years ago.

In his review of the paleogeography and paleoclimatology of South America, Romero (1986) synthesized available data that show the general trend of paleoenvironment. His graph, reproduced here as Fig. 6, illustrates the environmental change. A Neotropical paleoflora reached southward to near 45°S in the Maastrichtian-Paleocene (73-55 m.y.a.), with a southern phase represented by numerous (60%) entire-margined leaves. This paleoflora was replaced in the Early to Middle Eocene (55-45 m.y.a.) by mixed forest in which *Notofagus* and its associates are mingled with those of the "tropical" vegetation. From the Middle Eocene into the Oligocene, the southern province was dominated by the Antarctic Paleoflora, with *Nothofagus* making up to 25-27% of the floras. Similar relationships have been analyzed among the present-day floras of other Southern Hemisphere areas, as for example along the western side of the South Island of New Zealand (Haase 1990); they help greatly to illuminate past conditions.

There is little fossil evidence from southern South America that documents the floristic changes that resulted in the formation of present-day communities over the past 25 million years, since the close of the Oligocene. These changes, however, may be inferred from geologic evidence (e.g., Ramos 1989) and floristic information provided by floras from the Andes to the north, in Ecuador, Perú, Bolivia, and northern Chile. The floras, largely described and reviewed by Berry (1938), and in need of revision, include the following:

*Loja, Ecuador.* A large flora now at an elevation of 2.135 meters in temperate climate. It represents a wet, tropical lowland flora of Amazonian character. Miocene age. Considerable uplift has clearly occurred since the flora was deposited.

*Zorritos, Perú.* A rich flora from the present coastal desert area of Perú. The leaves are of tropical rainforest plants, indicating that the Andes had not been sufficiently elevated by the Middle Miocene (ca. 12 m.y.a.) to intercept rains from the Amazon Basin to the east, and that the Humboldt Current was not sufficiently effective by that time to give the present coastal region a dry climate.

*Potosí, Bolivia.* The flora comes from the high altiplano at an elevaton of 4,100 meters; it consists of plants now found at much lower elevations. It is a dry thorn bush or thorn scrub community that includes many small leaves and leaflets. The revision of this flora, and the accurate identification of the elements in it, would be of great interest in tracing the evolution of the plant communities of South America.

*Psillypampa, Bolivia.* This flora is from the Sierra de Cochabamba at an elevation of 3,600 meters. The leaves represented indicate a diverse, wet tropical forest like that now found in the yungas of Bolivia below 1,500 m elevation.

Considering that the ages of these latter floras need to be determined more accurately using radiometric dating whenever possible, they nonetheless document floras wholly different from those that occurred on Antarctica (and presumably southern South America) at the same time. All now occur at elevations much higher than those at which they were deposited, indicating the uplift of the Andes in Late Cenozoic time –initially during the later Miocene and Pliocene, and especially during the Pleistocene. At these times, the dry climate that now covers the eastern side of the southern Andes and supports the Patagonian desert, pampas, and monte developed from forerunners in the bordering Tertiary vegetation (Fig. 5). To the north, the matorral and vegetation of the Atacama Desert and bordering semidesert spread from small, isolated areas to form the present vegetation. Likewise, the vegetation of the high altiplano is clearly of comparatively recent origin (Arroyo *et al.* 1988).

As these modern vegetation types spread, there were increased opportunities for accelerating the interchange of plants and some animals between comparable communities in North and South America (Raven 1963, Raven & Axelrod 1974). Such interchange had been occurring between dryland species in local pockets of semiarid vegetation in the tropics since at least the Eocene, but it was greatly accelerated during the past 15 million years, and especially during Quaternary time (the past two million years), accounting for some of the detailed similarities between the dryland –but not, by and large, the temperate forest communities of North and South America.

The floristic changes and the accompanying (inferred) climatic modifications that we have reviewed are paralleled by changes in the South American mammalian faunas (Pascual 1984). Pascual notes that there were contemporaneous changes in global marine temperature, sea level variations, and diastrophic events. The marked cooling following the Early Middle Miocene is reflected in the Patagonian Friasian (ca. 16-12 m.y.a.) mammals, the age of which is charted with radiometric dates by Marshall *et al.* (1977) and is centered at 15-14 million years ago. This was the commencement of a major cycle of aridity, cooler climate, and more varied environmental subdivision. Most of the Early Miocene Santa Cruzian taxa related to subtropical woodlands became extinct or disappeared from Patagonia. The commencement of the Friasian Land Mammal Age correspond to a diastrophic phase that resulted in the rise of the Patagonian Andean Cordillera leading to the initial steps of Patagonian desertification. Very probably there is also a correlation with the onset of major continental glaciation on Antarctica. It is indeed significant that this was the first time (15-14 m.y.a.) major floristic changes occurred in the Great Basin of the western United States. At the time, there was a very rapid disappearance of broadleaved deciduous hardwoods that previously were co-dominants of the forests there (Axelrod 1985, p. 102; 1991a).

## PROBLEMS FOR CONSIDERATION

### 1. *Origin of evergreen and deciduous habits in temperate forests*

In the far south, land areas were basically under insular climates following the Early Cretaceous (Krutzsch 1989): in other words, for 125 million years or more. These climates, like those that now prevail in southern Chile and New Zealand are characterized by highly equable conditions, with a range of mean annual temperature of generally less than 10°C. Similar conditions are found also in the high mountains of the tropics, as in New Guinea, Kenya, and the eastern Himalayas. Genera of these austral evergreen forests were derived chiefly from evergreen ancestral taxa that deployed there from more tropical regions during the Cretaceous.

By contrast, in north temperate regions the broadleaved angiosperms are chiefly deciduous. They originated from ancestral groups (e.g., *Acer, Betula, Carya, Diospyros, Magnolia*), as they spread northward and encountered more continental climates, owing to the larger land masses there. It is noteworthy that in southwestern North America, North Africa, and southwest Asia, woods from the Jurassic and Early Cretaceous show either prominent or faint growth rings (Creber & Chaloner 1985, Table 1, Fig. 2). All of these regions are centered in the present deserts, which developed recently. This record shows that a seasonally dry climate existed in these areas during the Mesozoic. The deciduous habit can be related to seasonally drier climate, which may have influenced the early development of this habit on the northern margins of the tropics (Axelrod 1966b). In this regard, it is recalled that even a slight period of drought–say two weeks– in the superhumid inner tropics, will bring many forest trees into a severe wilting state, and their leaves may fall. A moderately longer period of drought on its borders would have a similar effect on the broadleaved trees ancestral to the present deciduous genera. Actually, much of the so-called rainforest region does have a dry season of slight to moderate length. In some areas, it is in the winter season, in others in the summer (see precipitation data in Wernstedt 1972). Inasmuch as most deciduous genera have their roots in tropical families, and a number of them also have evergreen species (as in *Acer, Alnus,* and *Magnolia*) in the tropical and warm temperate regions today, gradual adaptation to drought on the drier margins of the wet tropics probably accounts for the deciduous habit. It was, in essence, a preadaptation to the developing colder winters and longer dark winter period that angiosperms encountered as they migrated northward.

In the south, the forests are predominantly evergreen, as mentioned above, but with some widespread species of *Nothofagus* deciduous. The first evidence of deciduousness in southernmost South America is from the Eocene, far removed from regions of seasonal darkness (Romero 1988). Clearly, the origin of the deciduous habit in South America is related to the appearance of cool, seasonal climates, and not to winter darkness. Northern-hemisphere, trees are adapted to the periodical occurence of freezing temperatures, whereas southern-hemisphere ones are not (e.g. Read & Hill 1989). The deciduous habit in *Nothofagus* may have originated under cool climate on Antarctica. In this regard, a current detailed study suggests that deciduousness is primitive in *Nothofagus*, and that the evergreen habit has arisen more than once (Hill & Read, 1991).

Another view (Wolfe 1987a), considers that the terminal Cretaceous event (the "impact winter") resulted in widespread selection for plants of deciduous habit and diversification of deciduous taxa in the Northern Hemisphere. There is no evidence that the bolide impact affected Southern Hemisphere vegetation (see Askin 1986b). In the north, the duration of the light-intercepting bolide impact must have been brief, perhaps a few to several months, according to Wolfe's estimate. That such a brief period of semi-darkness could have affected the genetic makeup of so many divergent families of plants seems unlikely. Seeds in the ground would have been unaffected by the darkness or semidarkness —they were already under such conditions. The fossil record shows that the deciduous habit had already developed in the Cretaceous. That deciduous taxa rapidly rose to dominance in the Paleocene at middle and higher latitudes seems consistent with the restriction of seaways at this time (see Krutzsch 1989), widespread vulcanism, and the development of more continental, cooler climates (see Axelrod 1981, Hallam 1984, Crowley & North 1988, Officer *et al.* 1987, Officer & Drake 1985). Since broadleaved evergreens were less adapted to such conditions than deciduous hardwoods, they became less prominent in the vegetation over temperate latitudes and soon disappeared from the forest there.

### 2. *What accounts for the mixed paleofloras?*

Romero (1986) reviewed the problem of mixed paleofloras in the austral portion of South America, where members of the Neotropical Paleoflora mingled with those of the Antarctic Paleoflora in an intermediate zone (Fig. 6). Among the explanations previously offered are the following:

Dusén (1899) explained the mixing of species on the basis of topography, with those of the Antarctic Paleoflora occupying higher, cooler terrains than those of the Tropical Paleoflora in the lowlands. In the Appalachian region, the mingling of temperate deciduous hardwoods with broadleaved evergreen (Brown 1944) was also explained by transport form distant montane sites in the Eocene Appalachian Range.

Romero (1988) suggested that these mixtures were the remains of an Eocene stable phytogeographic unit, and that the species had ecologic-climatic requirements unlike those of present-day plant formations. Kemp (1978) also found that in the Australian region, there is a mixture of pollen representing tropical-subtropical taxa with those of cool temperate rainforest communities. This suggested that the Early Tertiary vegetation is not represented by a modern forest, and that the Eocene forest had a climate unlike any at present.

Another explanation calls on an equable climate, one in which conditions are neither too cool for tropical plants nor too warm for temperate ones (Axelrod 1984). Climates with a low range of temperate are closer in elevation. Under a theoretical climate with no annual range of temperature (A = 0), tropical and polar climates are only 8°C apart, or 1,464 meters in elevation assuming a normal terrestrial lapse rate. Under a regime of 10°C mean annual range of temperature, polar and temperate climates are separated by 18°C, or 3,294 meters. Owing to the absence of high mountains and plateaus, seaways on the continents, and no ice cover, global climates were much more equable than at present. On this basis, the mixtures of warm-and cool-adapted taxa were in broad ecotones characterized by a low range of temperature in which species regularly intermingled near sites of deposition. The overlapping nature of species distributions along altitudinal gradients is a common feature of present-day North Island forest of New Zealand (e.g., Elder 1965, Druitt *et al.* 1990), with a markedly equable climate. Woody vegetation types in the mediterranean-type climate zone of central Chile, with a fairly equable climate, seem to be less discrete than analogous communities in California, which has a comparatively continental climate compared with that in Chile. Moreover, in southern South America at the present time, deciduous species such as *Nothofagus obliqua* grow along side evergreen taxa such as the taxonomically isolated and seemingly relictual *Aextoxicon punctatum.* Detailed studies of the altitudinal ranges of contemporary woody species in Chile, as compared with California and the Pacific Northwest, might shed additional light on the development of this hypothesis.

Equable climate enabled taxa to extend far outside their "normal" ranges of distribution as we know them today (Axelrod 1984). This applies to cycads in South Africa and Australia that enter wholly temperate regions; species of *Araucaria* are distributed from tropical up into cold temperate climates; and palms in New Zealand occur in cool temperate regions. In these examples, distribution is governed by a moist climate of high equability (temperateness), chiefly with a rating of *M* 60-70. These relations also clarify the problem of the mixtures of taxa representing the Antarctic and Neotropical Paleofloras. As pointed out earlier (Axelrod 1984, pp. 114-115), a number of basically tropical genera that range south in eastern Australia to 20-30°S, occur in New Zealand at much higher latitudes, chiefly 35-42°S. Among these genera are *Alectryon, Beilschmeidia, Corynocarpus, Dysoxylum, Elatostema, Freycinetia, Geniostoma, Litsea, Macropiper, Peperomia, Schefflera, Tecomanthe,* and *Vitex.* Most of them range southward into the northern half of South Island. In New Zealand, they are in proximity to, and often associated with, *Agathis, Nothofagus, Podocarpus,* and their usual associates –plants of Antarctic affinities. We suggest therefore that the mixtures of genera representing the two major paleofloras in the Southern Hemisphere was not an unusual relationship, but normal and expectable under the widespread, more equable Tertiary climate.

### 3. *Did the Antarctic Ice Sheet disappear during the Pliocene?*

Recently, a deposit with numerous unaltered leaves of *Nothofagus* was collected from the Transantarctic Mountains, at a site within 400 km of the South Pole (Peterson 1991, Raymond, 1991). The deposit has been considered to be about 3 m.y., or middle Pliocene (see Fig. 9). This raises the question as to whether the Antarctic ice sheet melted during (or before) the Pliocene, or whether the deposit is older than now considered by the collectors. However it is possible that the deposit is young and the leaves are from trees that lived on slopes above valley glaciers, much as illustrated for the Franz Joseph Glacier in southern New Zealand today (Seward, 1941 - frontispiece).

## ACKNOWLEDGMENTS

We acknowledge support from the U.S. National Science Foundation to PR and DA, as well as from FONDECYT Grant No. 88-11-77 to MTKA. Critical comments from William A. Clements and Edgardo Romero are gratefully acknowledged.

## LITERATURE CITED

AHMATEV MA, GM BRATISHEVA, RE GITERMAN, LA GODUBEVA & AI MOISEEVA (1978) Late Cenozoic stratigraphy and flora of Iceland. Academy of Sciences of the USSR Transactions 316. (in Russian).

ARCHANGELSKY S (1974) Notas paleonontólgicas: Sobre la edad de la tafoflora de la Laguna del Hunco, Provincia de Chubut. Ameghiniana 11: 413-417.

ARCHANGELSKY S (1976a) Palinología del Paleoceno de Chubut. II. Diagramas polínicos. Ameghiniana 13: 43-55.

ARCHANGELSKY S (1976b) Palinología del Paleoceno de Chubut. III. Análisis numérico II. Introducción y matrices de similitud. Ameghiniana 13: 169-184.

ARCHANGELSKY S (1980) Palynology of the Lower Cretaceous in Argentina. IV Interntional Palynological Conference, Lucknow (1976-77) 2: 425-428.

ARCHANGELSKY S, AM BALDONI, JC GAMERRO & J SEILER (1984) Palinología estratigráfica del Cretácico de Argentina Austral. III. Distribución de las especies y conclusiones. Ameghiniana 21: 15-33.

ARNOLD CA (1955) Tertiary conifers from the Princeton coal field of British Columbia. Contributions from the University of Michigan Museum of Paleontology 12: 245-258.

ARROYO MTK, F SQUEO, J ARMESTO & C VILLAGRAN (1988) Effects of aridity on plant diversity in the northern Chilean Andes: results of a natural experiment. Annals of the Missouri Botanical Garden 75: 55-78.

ARROYO MTK, J ARMESTO, F SQUEO & J GUTIERREZ (1991) Global change: The flora and vegetation of Chile. In: Mooney H, Fuentes E, Kronberg B (F Fuenzalida (eds.). Northern and Southern Hemisphere Responses to Global Change (accepted). Academic Press, New York.

ASKIN RA (1988a) Campanian to Paleocene palynological succession on Seymour and adjacent islands, northeastern Antarctic Peninsula. Memoirs of the Geological Society of America 169: 131-153.

ASKIN RA (1988b) The palynological record across the Cretaceous-Tertiary transition on Seymour Island, Antarctica. Memoirs of the Geological Society of America 169: 155-162.

ASKIN RA (1989) Endemism and heterochroneity in the Late Cretaceous (Campanian) to Paleocene palynofloras of Seymour Island, Antarctica: Implications for origins, dispersal, and paleoclimates of southern floras. In: Crame JA (ed.). Origins and Evolution of the Antarctic Biota: 107-119. Geological Society of London Special Publication Number 47.

AXELROD DI (1952) A theory of angiosperm evolution. Evolution 6: 29-60.

AXELROD DI (1959) Poleward migration of early angiosperm flora. Science 130: 203-207.

AXELROD DI (1964) The Miocene Trapper Creek flora of southern Idaho. University of California Publications in Geological Sciences 51.

AXELROD DI (1965) A method for determining the altitudes of Tertiary floras. Palaeobotanist 14: 144-171.

AXELROD DI (1966a) The Eocene Copper Basin flora of northeastern Nevada. University of California Publications in Geological Sciences 59.

AXELROD DI (1966b) Origin of deciduous and evergreen habits in temperate forests. Evolution 20: 1-15.

AXELROD DI (1968) Tertiary floras and topographic history of the Snake River Basin, Idaho. Bulletin of the Geological Society of America 79: 713-734.

AXELROD DI (1970) Mesozoic paleogeography and early angiosperm evolution. Botanical Review (Lancaster) 36: 277-319.

AXELROD DI (1979) Desert vegetation, its age and origin. In: Goodin JR & DK Northington (eds). Arid Land Plant Resources: 1-72. International Center for Arid and Semi-arid Land Studies, Texas Tech University, Lubbock, Texas.

AXELROD DI (1981) Role of volcanism in climate and evolution. Special Papers of the Geological Society of America 185.

AXELROD DI (1984) An interpretation of Cretaceous and Tertiary biota in polar regions. Palaeogeography, Palaeoclimatology, Palaeoecology 45: 105-147.

AXELROD DI (1985) Miocene floras from the Middlegate basin, west-central Nevada. University of California Publications in Geological Sciences 129.

AXELROD DI (1987) The Late Oligocene Creede flora, Colorado. University of California Publications in Geological Sciences 130.

AXELROD FI (1991) The Miocene Buffalo Canyon flora, western Nevada. University of California Publications in Geological Sciences 135.

AXELROD DI (1992) What is an equable climate? Paleogeography, Paleoclimatology, Paleoecology: in press.

BAILEY HP (1960) A method of determining the warmth and temperateness of climate. Geografisker Annaler 52: 1-16.

BAILEY HP (1964) Toward a unified concept of the temperate climate. The Geographical Review 54: 516-545.

BALDONI AM & V BARREDA (1987) Estudio palinológico de las Formaciones López de Bertodano y Sobral, Isla Vicecomodoro Marambio, Antártida. Actas V Reunião de Paleobotánicos e Palinólogos.

BARTON CM (1963) Significance of Tertiary fossil floras of King George Island, South Shetland Islands. Antarctic Geology, SCAR Proceedings, XI. Palaentology: 603-608.

BECKER HF (1961) Oligocene plants from the upper Ruby River basin, southwestern Montana. Memoirs of the Geological Society of America 82.

BECKER HF (1969) Fossil plants of the Tertiary Beaverhead basins in southwestern Montana. Palaeontographica B, 127.

BELL WA (1949) Uppermost Cretaceous and Paleocene floras of western Alberta. Canada Department of Mines and Resources, Geological Survey Bulletin 13.

BERRY EW (1917) Fossil plants from Bolivia and their bearing on the age of uplift of the eastern Andes. Proceedings of the United States National Museum 53: 103-164.

BERRY EW (1919) Miocene fossil plants from northern Perú. U.S. Nat. Mus. Proc. 55: 279-254.

BERRY EW (1922) The flora of the Concepción-Arauco coal measures of Chile. Johns Hopkins University Studies in Geology 4: 73-142.

BERRY EW (1925) A Miocene flora from Patagonia. Johns Hopkins University Studies in Geology 6: 183-252.

BERRY EW (1926) Tertiary floras from British Columbia. Canada Department of Mines, Geological Survey Bulletin 42: 91-116.

BERRY EW (1928) Tertiary fossil plants from the Argentine Republic. U.S. Nat. Mus. Proc. 73 (art. 22): 1-27.

BERRY EW (1937) A Paleocene flora from Patagonia. Johns Hopkins University Studies in Geology 12: 22-50.

BERRY EW (1938) Tertiary flora from the Río Pichileufú, Argentina. Special Papers of the Geological Society of America 12.

BERRY EW (1939) The fossil flora of Potosí, Bolivia. Johns Hopkins, University Studies in Geology 13: 9-72.

BIRKENMAJER K & E ZASTAWNIAK (1986) Plant remains of the Dufayel Island group (Early Tertiary?), King George Island, South Shetland Islands (West Antarctica). Acta Palaeobotanica 26: 33-54.

BIRKENMAJER K & E ZASTAWNIAK (1989) Late Cretaceous-early Tertiary floras of King George Island, West Antarctica: Their stratigraphic distribution and paleoclimatic significance. In: Crame JA (ed.). Origins and Evolution of the Antarctic Biota: 227-239. Geological Society of London Special Publication Number 47.

BOYD A (1990) The Thyra 0 Flora: Toward and understanding of the climate and vegetation during the Early Tertiary in the high Arctic. Review of Palaeobotany and Palynology 62: 189-203.

BRADY H & H MARTIN (1979) Ross Sea region in the Middle Miocene: A glimpse into the past. Science 203: 437-438.

BRENNER JG (1976) Middle Cretaceous floral provinces and early migrations of angiosperms. In: Beck CB (ed.). Origin and Early Evolution of Angiosperms: 23-47. Columbia University Press, New York.

BROWN RW (1937) Additions to some fossil floras of the western United States. U.S. Geol. Surv. Prof. Paper 186: 163-206.

BROWN RW (1944) Temperate species in the Eocene flora of the southeastern United States. Journal of the Washington Academy of Sciences 34: 349-351.

BROWN RW (1962) Paleocene flora of the Rocky Mountains and Great Plains. United States Geological Survey Professional Paper 375.

BRUNS TR (1983) Model for the origin of the Yakutat block, and acreeting terrane in the northern Gulf of Alaska. Geology 11: 718-721.

CARLINI AA, R PASCUAL, MA REGUERO, GH SCILLATO-YANE, EP TONNI & SF VIZCAINO (1990) The first Paleogene land placental mammal from Antarctica: its paleoclimatic and paleobiogeographical bearings. Abstracts of the Fourth International Congress of Systematic and Evolutionary Biology, University of Maryland, College Park, Maryland (pages unumbered).

CASE JA (1988) Paleogene floras from Seymour Island, Antarctic Peninsula. Memoirs of the Geological Society of America 169: 523-530.

CASE JA, MO WOODBURNE & DS CHANEY (1988) A new genus of polydolopod marsupial from Antarctica. Memoirs of the Geological Society of America 169: 505-521.

CHALONER WG & GT CREBER (1989) The phenomenon of tree growth in Antarctica: A review. In: Crame JA (ed.), Origins and Evolution of the Antarctic Biota: 85-88. Geological Society of London Special Publication Number 47.

CHANEY RW & DI AXELROD (1959) Miocene floras of the Colombia Plateau. Part 1. RW Chaney, Composition and Interpretation, pp. 1-134. Part II. RW Chaney and DI Axelrod, Systematic Considerations, pp. 139-229. Carnegie Inst. Wash. Pub. 617.

CHRISTIE RL & GE ROUSE (1976) Eocene beds at Lake Hazen, northern Ellesmere Island. Geological Survey of Canada, Report of Activities, Part C, Paper 76-1C: 153-156.

CIESIELSKI PR, MT LEDBETTER & BD ELWOOD (1982) The development of Antarctic glaciation and the Neogene paleoenvironment of the Maurice Ewing Bank. Marine Geology 46: 1-51.

CONEY PJ, DL JONES & JHW MONGER (1980) Cordilleran suspect terranes. Nature 288: 329-333.

CORNET B (1986) The leaf venation and reproductive structures of a Late Triassic angiosperm, *Sanmiguelia lewisii.* Evolutionary Theory 7: 231-309.

CORNET B (1991) Late Triassic dicot-leaf from the western margin of the tropical Newark Supergroup rift zone, USA (manuscript).

COWAN DS (1982) Geological evidence for a post-40 m.y. B.P. large-scale displacement of part of southeastern Alaska. Geology 10: 309-313.

CRABTREE DR (1987) Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. Annals of the Missouri Botanical Garden 74: 707-747.

CREBER GT & WG CHALONER (1984) Climatic indications from growth rings in fossil woods. In: Benchley PJ (ed.). Fossils and Climate: 49-74. John Wiley & Sons, New York.

CREBER GT & WG CHALONER (1985) Tree growth in the Mesozoic and Early Tertiary and the reconstruction of paleoclimates. Palaeogeography, Palaeoclimatology, Palaeoecology 52: 35-60.

CROWLEY TJ & GR NORTH (1988) Abrupt climate change and extinction events in earth history. Science 240: 996-1002.

DENTON GH & RL ARMSTRONG (1969) Miocene-Pliocene glaciation in Alaska. American Journal os Science 267: 1121-1132.

DETTMAN ME (1989) Antarctica: Cretaceous cradle of austral temperate rainforests? In: Crame JA (ed.). Origins and Evolution of the Antarctic Biota: 89-105. Geological Society of London Special Publication Number 47.

DETTMAN ME, DT POCKNALL, EJ ROMERO & MDC ZAMALOA (1990) *Nothofagidites* Erdtman ex Potonie, 1960; a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* Bl. (Southern Beech). New Zealand Geological Survey Paleontological Bulletin 60.

DETTMAN ME & MRA THOMSON (1987) Cretaceous palynomorphs from the James Ross Island area, Antarctica –a pilot study. British Antarctic Survey Bulletin 77: 13-60.

DRUITT DG, NJ ENRICHT & J OGDEN (1990) Altitudinal zonation in the mountain forests of Mt. Hauhungatahi, North Island, New Zealand. Journal of Biogeography 17: 205-220.

DUSEN P (1899) Uber die tertiare Flora des Seymour Insel. Wissenschaftliche Ergegnisse schwedisch Sudpolar-Expedition 1901-1903, 3: 1-27.

EDELMAN DW (1975) The Eocene Germer Basin flora of south-central Idaho. MS Thesis, University of Idaho, Moscow.

ELDER NL (1965) Vegetation of the Ruahine Range: an introduction. New Zealand Journal of Botany 3: 13-66.

ELIAS MK (1942) Tertiary prairie grasses and other herbs from the High Plains. Special Papers of the Geological Society of America 41.

FLORIN R (1963) The distribution of conifer and taxad genera in time and space. Acta Horti Bergiani 20: 122-312.

FRANCIS JE (1986) Growth rings in Cretaceous and Tertiary wood from Antarctica and their paleoclimatic implications. Palaeontology 29: 665-684.

FRENGUELLI J (1943) Restos de *Casuarina* en el Mioceno en El Mirador, Patagonia Central. Revista del Museo de La Plata, Sección Palaeontológica 8: 349-354.

HAASE P (1990) Environmental and floristic gradients in Westland, New Zealand, and the discontinuous distribution of *Nothofagus*. New Zealand Journal of Botany 28: 25-40.

HALLAM T (1984) Asteroids and extinction –no cause for concern. New Scientist 104 (1429): 30-33.

HALLUM A (1981) Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the Early Mesozoic. In: Nelson G & DE Rosen (eds.). Vicariance Biogeography: 303-330. Columbia University Press, New York.

HEER O (1868) Flora fossilis arctica I. Die Fossil Flora der Polarlaender enthaltend die in Nordgronland, auf der Melville-Insel, in Banksland, am Mackenzie, in Island und in Spitzbergen entdecken fossilen Pflanzen. Zuerich.

HELWIG J & P EMMETT (1983) Structure of the Early Tertiary Orca group in Prince William Sound and some implications for the tectonic history of southern Alaska. Abstracts of the Programs, Geological Society of America 15(5): 386.

HILLS LV (1971) Climatic interpretation of the Beaufort flora, Banks Island, Arctic Canada. American Journal of Botany 58: 469-470 (abstract).

HILL RS & J READ (1991) A revised infrageneric classification of *Nothofagus* (Fagaceae). Botanical Journal of the Linnean Society 105: 37-72.

HOPKINS DM, JV MATTHEWS, JA WOLFE & ML SILBERMAN (1971) A Pliocene flora and insect fauna from the Bering Strait region. Palaeogeography, Palaeoclimatology, Palaeoecology 9: 211-231.

HOPKINS DM, JV MATTHEWS Jr, CE SCHWEGER & SP YOUNG (1982) Palaeoecology of Beringia. Academic Press, New York.

HUECK K (1966) Die Walder Sudamerikas. VEB G. Fischer Verlag, Jena.

HUNICKEN M (1966) Flora terciaria de los estratos de Río Turbio, Santa Cruz. Universidad Nacional de Córdoba, Facultad de Ciencias Exactas, Físicas y Naturales, Serie Ciencias Naturales 27: 139-262.

ITO K (1961) Tatwaki's iconography of the vegetation of the natural forest of Japan. VIII. Vegetation of the forests in the vicinity of Lake Shikotsu, Pref. Iburi, Hokkaido. 208 pp.

ITO K, M TOHYAMO & Y YOKOMIZO (1966) Tatewaki's Iconography of the vegetation of the natural forest of Japan. X. Forest vegetation of Oku-Nikko, Pref. Tochigi in central Honshu. Research Bulletins of the College of Experiment Forests, Faculty of Agriculture, Hokkaido University 24(2): 291-498.

JARZEN DM & ME DETTMANN (1989) Taxonomic revision of *Tricolpites reticulatus* Cookson ex Couper, 1953 with notes on the biogeography of *Gunnera* L. Pollen et Spores 31: 97-112.

JONES DL, WP IRWIN & AT OVENSHINE (1972) Southeastern Alaska –a displaced continental fragment? United States Geological Survey Professional Paper 800B: B211-B217.

JONES DL & NJ SILBERLING (1982) Mesozoic stratigraphy –the key to tectonic analysis of southern and central Alaska. In: Leviton AE *et al.* (eds.). Frontiers of Geological Exploration of Western North America: 139-153. California Academy of Sciences Press, San Francisco.

JONES DL, NJ SILBERLING & J HILLHOUSE (1977) Wrangelia –a displaced terrain in northwestern North America. Canadian Journal of Earth Sciences 14: 2565-2577.

KELLER R, R VON HUENE, K McDOUGALL & TR BURNS (1984) Palaeoclimatic evidence for Cenozoic migration of Alaskan terranes. Tectonics 3: 473-495.

KEM EM (1972) Reworked palynomorphs from the west ice shelf area, East Antarctica, and their possible geological and palaeoclimatological significance. Marine Geology 13: 145-157.

KEM EM (1978) Tertiary climatic evolution and vegetational history in the southeast Indian Ocean region. Palaeogeography, Palaeoclimatology, Palaeoecology 24: 169-208.

KEM EM & PJ BARRET (1975) Antarctic glaciation and Early Tertiary vegetation. Nature 258: 507-508.

KOCH BE (1963) Fossil plants from the lower Paleocene of the Agatdalen (Amgmartussut) area, central Nugssuaq Peninsula, northwestern Greenland. Meddelungen Gronland 172.

KRUTZSCH W (1989) Paleogeography and historical phytogeography (paleochorology) in the Neophyticum. Plant Systematics and Evolution 162: 5-61.

LEOPOLD EB & MF DENTON (1987) Comparative age of grassland and steppe east and west of the northern Rocky Mountains. Annals of the Missouri Botanical Garden 74: 841-867.

LIPMAN PW, HJ PROTSKA & RL CHRISTIANSEN (1972) Cenozoic volcanism and plate tectonic evolution of the western United States. I. Early and Middle Cenozoic. Royal Society of London, Philosophical Transactions, series A, 271: 217-248.

LITTLE EL, Jr. (1971) Atlas of United States Trees. Vol. 1. Conifers and Important Hardwoods. United

States Department of Agriculture, Forest Service Miscellaneous Publication 1146.

MACFADDEN BJ & RC HURLBERT Jr. (1988) Explosive speciation at the base of the adaptive radiation of Miocene grazing horses. Nature 336: 466-468.

MACGINITIE HD (1941) A Middle Eocene flora from the central Sierra Nevada. Publications of the Carnegie Institution of Washington 534.

MACGINITIE HD (1953) Fossil plants of the Florissant beds, Colorado. Publications of the Carnegie Institution of Washington 599.

MANUM S (1962) Studies in the Tertiary flora of Spitzbergen, with notes on Tertiary floras of Ellesmere Islands, Greenland and Iceland. Norsk Polarinstitut Skriftung 125.

MARSHALL LG, R PASCUAL, G CURTIS & RE DRAKE (1977) South American geochronology: Radiometric time scale for Middle to Late Tertiary mammalian-bearing horizons in Patagonia. Science 195: 1325-1327.

MATTHEWS WH & GE ROUSE (1963) Late Tertiary volcanic rocks and plant-bearing deposits in British Columbia. Bulletin of the Geological Society of America 74: 55-60.

MCINTYRE & GH WILSON (1966) Preliminary palynology of some Antarctic Tertiary erratics. New Zealand Journal of Botany 4: 315-321.

MENENDEZ CA (1971) Floras terciarias de la Argentina. Ameghiniana 8: 209-212.

MILDENHALL, DC (1989) Terrestrial palynology. In: Barrett PJ (ed.). Antarctic Cenozoic History from the CIROS-1 Drillhole, McMurdo Sound: 119-127. Department of Scientific and Industrial Research Bulletin 245.

MUDIE PJ & J HELGASON (1983) Palynological evidence for Miocene climatic cooling in eastern Iceland about 9.8. Myr ago. Nature 303: 689-692.

NISHIDA M, T OHSAWA & H NISHIDA (1990) Anatomy and affinities of the petrified plants from the Tertiary of Chile (VI). Botanical Magazine Tokyo 103: 255-268.

NORRIS G (1982) Spore-pollen evidence for Early Oligocene high latitude cool climatic episode in northern Canada. Nature 297: 387-389.

OFFICER CB & CL DRAKE (1985) Terminal Cretaceous environmental events. Science 227: 1161-1167.

OFFICER CB, A HALLUM, CL DRAKE & JD DEVINE (1987) Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions. Nature 326: 143-149.

PACKER DR & DB STONE (1974) Paleomagnetism of Jurassic rocks from southern Alaska and the tectonic implications. Canadian Journal of Earth Sciences 11: 976-997.

PARRISH JT & RA SPICER (1988) Late Cretaceous terrestrial vegetation: A near-polar temperature curve. Geology 16: 22-25.

PASCUAL R (1984) Late Tertiary mammals of southern South America as indicators of climatic detioration. In: Rabassa J (ed.). Quaternary of South America and Antarctic Peninsula, Vol. 2: 1-30. A.A. Balkema, Rotterdam.

PENHALLOW DP (1908) Report on Tertiary plants of British Columbia collected by Lawrence M. Lambe in 1906. Canadian Department of Mines, Geological Survey Branch, Number 1013.

PETERSON C (1991) Leafing through Antarctica's balmy past. New Scientist 129 (No. 1755): 20.

PETRIELLA BTP (1972) Estudio de maderas petrificadas del Terciario Inferior del área central de Chubut (Cerro Bororo). Revista del Museo de La Plata, nueva serie, 6: 159-254, pls. 1-9.

PETRIELLA BTP & S ARCHANGELSKY (1975) Vegetación y ambientes en el Paleoceno de Chubut. Actas I Congreso Argentino de Palaeontología y Biostratigrafía 2: 257-270.

PFLUG HD (1959) Beitraege zur Klimageschichte Islands. VIII. Sporebilder aus Island und ihre stratigraphische Deutung. Neues Jarbuch der Geologie und Palaontologie Abhandlung 107: 141-172.

PIEL KM (1971) Palynology of Oligocene sediments from central British Columbia. Canadian Journal of Botany 49: 1885-1920.

PIRRIE D & JD MARSHALL (1990) High-paleolatitude Late Cretaceous paleotemperatures: New data from James Ross Island, Antarctica. Geology 18: 31-34.

PLUMLEY PW, RS COE, T BYRE, MR REID & RC MOORE (1982) Paleomagnetism of volcanic rocks of the Kodiak Islands indicates northward latitudinal displacement. Nature 300: 50-52.

PLUMSTEAD EP (1962) Trans-antarctic Expedition, 1955-1958. Scientific Reports No. 9, Geology. 2. Fossil floras of with an appendix on Antarctic fossil wood by R Krausel. Trans-Antarctic Expedition Committee, London.

RAMOS VA (1989) The birth of Southern South America. American Scientict 77: 444-450.

RAVEN PH (1963) Amphitropical relationships in the floras of North and South America. Quarterly Review of Biology 38: 151-177.

RAVEN PH & DI AXELROD (1974) Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden 61: 539-673.

RAYMOND C (1991) Discovery of leaves in Antarctica sparks debate over whether region had a near-temperate climate. Chronicle of Higher Education, March 10.

READ J & RS HILL (1989) The response of some Australian temperate rain forest tree species to freezing temperatures and its biogeographical significance. Journal of Biogeography 16: 21-27.

ROMERO EJ (1968) *Palmoxylon patagonicum* n. sp. del Terciario inferior de la Provincia de Chubut, Argentina. Ameghiniana 5: 417-431.

ROMERO EJ (1978) Paleoecología y palaeofitogeografía de las tafofloras del Cenofítico de Argentina y áreas vecinas. Ameghiniana 15: 209-227.

ROMERO EJ (1980) Arquitectura foliar de las especies sudamericanas de *Nothofagus* Bl. Boletín de la Sociedad Argentina de Botánica 19: 289-308.

ROMERO EJ (1986) Paleogene phytogeography and climatology of South America. Annals of the Missouri Botanical Garden 73: 449-461.

ROMERO EJ (1987) El género *Nothofagus* en Antártida. VII Simposio Argentino de Paleobotánica y Palinología Actas, pp. 181-185, Buenos Aires.

ROMERO EJ (1988) Momentos importantes en la evolución de *Nothofagus* Bl. Memorias de la Academia Nacional de Ciencias 5: 15-23. Buenos Aires.

ROMERO EJ & AC AGUIRRE (1982) Arquitectura foliar de las especias de *Nothofagus* (Fagaceae) de Nueva Guinea y Nueva Caledonia. Boletín de la Sociedad Argentina de Botánica 21: 213-241.

ROMERO EJ & S ARCHANGELSKY (1986) Early Cretaceous angiosperm leaves from southern South America. Science 234: 1580-1582.

ROMERO EJ & MC DIBBERN (1985) A review of the species described as *Fagus* and *Nothofagus* by Dusen. Palaeontographica B, 197: 123-137.

ROUSE GE & SK SRIVASTAVA (1972) Palynological zonation of Cretaceous and Early Tertiary rocks of the Bonnet Plume Formation, northeastern Yukon, Canada. Canadian Journal of Earth Science 9: 1163-1179.

SALEEBY JB (1983) Accretionary tectonics of the North American Cordillera. Annual Review of Earth and Planetary Science 15: 45-73.

SANBORN EI (1935) The Comstock flora of west central Oregon. Publications of the Carnegie Institution of Washington 465: 1-28.

SAVIN SM (1977) The history of the Earth's surface temperature during the past 100 million years. Annual Review of Earth and Planetary Science 5: 319-355.

SCHLOEMER-JAGER A (1958) Altertiäre Pflanzen aus Flözen der Brogger Halbinsel Spitzbergens. Palaeontographica B, 104: 39-103.

SCHWARZBACH M & HD PFLUG (1957) Das Klima des jungeren Tertiars in Island. Neues Jahrbuch der Geologie und Palaeontologie, Abhandlung 104: 279-298.

SEWARD AC (1941) Plant Life Through the Ages: A Geological and Botanical Perspective. Reprinted Edition. Cambridge University Press.

SHACKLETON NJ (1979) Evolution of the Earth's climate during the Tertiary era. In: Gautier D (ed.). Evolution of Planetary Atmospheres and Climatology of the Earth: 49-58. Centre Nationale d'Etudes Spatiale, Toulouse.

SMILEY DJ (1966) Cretaceous floras from Kuk River area, Alaska: Stratigraphic and climatic implications. Bulletin of the Geological Society of America 77: 1-14.

SMILEY DJ (1969a) Cretaceous floras of Chandler-Colville region, Alaska: Stratigraphy and preliminary floristics. Bulletin of the American Association of Petroleum Geologists 53: 482-502.

SMILEY DJ (1969b) Floral zones and correlation of Cretaceous Kukpowruk and Corwin formations, northwestern Alaska. Bulletin of the American Association of Petroleum Geologists 53: 2079-2093.

SMILEY DJ (1972) Plant megafossil sequences, north slope Cretaceous. Geoscience and Man 4: 91-99.

SMITH AG (1981) Phanerozoic equal-area maps. Geologischen Rundschau 70: 91-127.

SMITH AG, AM HURLEY & JC BRIDEN (1981) Phanerozoic Paleocontinental World Maps. Cambridge University Press.

SMITH HV (1941) A Miocene flora from Thorn Creek, Idaho. American Midland Naturalist 25: 473-522.

SPICER RA & JT PARRISH (1986) Paleobotanical evidence for cool north polar climates in Middle Cretaceous (Albian-Cenomanian) time. Geology 14: 703-706.

SPICER RA, JA WOLFE & DJ NICHOLS (1987) Cretaceous-Tertiary floras and Arctic origins. Paleobiology 13: 73-83.

STANLEY EA (1966) Cretaceous pollen and spore assemblages from northern Alaska. Review of Paleobotany and Palynology 1: 229-234.

STAPLIN FC, ed. (1976) Tertiary biostratigraphy, MacKenzie Delta region, Canada. Bulletin of Canadian Petroleum Geology 24: 117-136.

STEBBINS GL (1974) Flowering Plants: Evolution Above the Species Level. Belknap Press of Harvard University Press, Cambridge, Mass.

STUCHIK L (1981) Tertiary pollen spectra from the Ezcurra Inlet Group of Admiralty Bay, King George Island (South Shetland Island, Antarctica). Studia Geologica Polonica 72: 109-132.

SVESHNIKOVA IN & LY BUDANTSEV (1969) Florulae fossiles arcticae I. Nauka Filia Leningradensis, Komarov Botanical Institute, Leningrad.

TANAI T (1986) Phytogeographic and phylogenetic history of the genus *Nothofagus* Bl. (Fagaceae) in the Southern Hemisphere. Journal of the Faculty of Sciences of Hokkaido University, Ser. IV, 21: 505-582.

TANAI T, N SUZUKI & H MATSUO (1963) Tertiary floras of Japan: Miocene floras. Geological Survey of Japan, 80th Anniversary Commemoration Volume.

TAYLOR TN & EL TAYLOR (1989) Antarctic Paleobiology. Springer-Verlag.

VAN DER HAMMEN T (1961) Late Cretaceous and Tertiary stratigraphy and tectogenesis of the Columbian Andes. Geologie en Mijnbouw 40: 181-188.

VOLKHEIMER W (1971) Aspectos paleoclimáticos del Terciario Argentino. Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Sección Paleontológica 1: 241-264.

YEEND W, TA AGER & JT KLINE (1989) Stratigraphy and palynology of an upper Tertiary terrace deposit of the ancestral Yukon River near Circle, Alaska. United States Geological Survey Bulletin 1903: 62-67.

WANG CW (1961) The Forests of China with a Survey of Grassland and Desert Vegetation. Maria Moors Cabot Foundation Publication 5. Harvard University, Cambridge, Mass.

WERNSTEDT FL (1972) World Climatic Data. Climatic Data Press, Lemont, Pennsylvania.

WOLFE JA (1966) Tertiary plants from the Cook Inlet region, Alaska. United States Geological Survey Professional Paper 398-B.

WOLFE JA (1977) Paleogene floras from the Gulf of Alaska region. United States Geological Survey Professional Paper 977.

WOLFE JA (1987a) Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous event. Paleobiology 13: 215-226.

WOLFE JA (1987b) Alaskan Cretaceous-Tertiary floras and Arctic origins. Paleobiology 13: 73-83.

WOLFE JA, DM HOPKINS & EB LEOPOLD (1966) Tertiary stratigraphy and paleobotany of the Cook Inlet region, Alaska. United States Geological Survey Professional Paper 398-A.

WOLFE JA & EB LEOPOLD (1967) Neogene and Early Quaternary vegetation of northwestern North America and northeastern Asia. In: Hopkins D (ed.). The Bering Land Bridge: 193-206. Stanford University Press, Stanford, California.

WOLFE JA & T TANAI (1980) The Miocene Seldovia Point flora from the Kenai Group, Alaska. United States Geological Survey Professional Paper 1105.

WOLFE JA & W WEHR (1987) Middle Eocene dicotyledonous plants from Republic, northeastern Washington. United States Geological Survey Bulletin 1597.

WOODBURNE MO, JA CASE & D CHANEY (1987) New fossil vertebrates from Seymour Island, Antarctic Peninsula. Antarctic Journal of the United States 22(5): 4-5.

ZASTAWNIAK E (1990) Late Cretaceous leaf flora of

King George Island, West Antarctica. Proceedings of the Symposium "Paleofloristic and Paleoclimatic Changes in the Cretaceous and Tertiary", 1989. Prague.

ZASTAWNIAK E, R WRONA, A GAZDICK & K BIRKENMAJER (1985) Plant remains from the top part of the Point Hennequin Group (Upper Oligocene), King George Island (South Shetland Islands, Antarctica). Studia Geologica Polonica 81: 143-164.

ZAVADA MS & JM BENSON (1990) First fossil evidence for the primitive angiosperm Lactoridaceae. American Journal of Botany 74: 1590-1594.

ZINSMEISTER WS (1982) Late Cretaceous-Early Tertiary molluscan biogeography of southern circum-Pacific. Journal of Paleontology 56: 84-102.