

IMPACT OF THE EOCENE ON THE EVOLUTION OF *PINUS* L.¹

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ABSTRACT

Pinus evolved in middle latitudes of the Northern Hemisphere in the middle Mesozoic. By the late Cretaceous pines had spread east and west throughout Laurasia, attaining high diversity in eastern Asia, the eastern United States, and western Europe, but having little representation at high northern latitudes. Changing climates in the early Tertiary established warm and humid tropical/subtropical conditions in a broad zone to 70°N throughout middle latitudes. Pines and their relatives disappeared from many middle-latitude areas during this time and were replaced by diverse angiosperm taxa of the boreotropical flora, which were adapted to the equable, tropical climate. The effect of this climate change and spread of boreotropical flora was to displace pines from their former habitats. A hypothesis is defended that pines shifted, during the three warm periods of the Eocene, into three major refugial areas in the Northern Hemisphere: high latitudes, low latitudes, and upland regions of middle latitudes, especially in western North America. Some of these refugial areas (e.g., Mexico/Central America) underwent active volcanism and mountain-building in the Eocene and became secondary centers of pine diversity. Many phylogenetic patterns within *Pinus* can be traced to this fragmentation, isolation, and evolution in Eocene refugia. Subsections *Oocarpae* and *Sabinianae* appear to have originated from refugia in Mexico and Central America. Older subsections such as *Sylvestres*, *Ponderosae*, *Contortae*, and *Strobi* were distributed over several refugia; subsections *Leiophyllae*, *Australes*, and *Cembroides* evolved in southern refugia in North America; and *Canarienses* evolved in southern refugia along the Tethys seaway in Eurasia. Following the cooling and drying of the climate at the end of the Eocene, many angiosperm taxa of the boreotropical flora became extinct and pines recolonized middle latitudes, a zone they have occupied to the present. Migration out of refugia provided additional opportunities for hybridization and introgression, as formerly isolated lineages expanded and met.

The past two decades have seen an explosion of information on the paleohistory of the Earth. Evidence on plate tectonics has clarified the position of continents in different ages, continental geomorphology, and the dynamics of inland seaways and changing coastlines. Physical and biological evidence has been used to infer paleoclimates with finer resolution in time and space. New fossil discoveries have added to the record of past vegetation, and new diagnostics for identifying taxa have led to systematic revisions of many fossil floras. The widespread use of radioisotope dating has added precision to determining the ages of fossil floras.

This information, together with phylogenetic analyses of extant taxa, has contributed new insights and a revised understanding of evolution for many plant groups. In pines (family Pinaceae, genus *Pinus* L.), major syntheses have focused on two time periods in the history of the genus. Studies on the Mesozoic history of the pine family, and especially *Pinus*, have significantly changed our

understanding of the origin of the genus (Miller, 1976, 1977, 1982, 1988; Robison, 1977; Blackwell, 1984; Stockey & Ueda, 1986; Stockey & Nishida, 1986). Similarly, studies on the Quaternary history of pines have led to new interpretations about the impact of recent paleohistoric events on the genetic structure and evolutionary relationships of extant species (Critchfield, 1984, 1985).

The broad-scale events that influenced the evolution of the genus between its origins in Mesozoic (Table 1) and its present diversity remain obscure. How did important secondary centers of pine diversity in Mexico, western North America, and eastern Asia originate? How do these areas relate to the primary centers of origin for the genus? What events triggered the diversifications of taxa within the genus, and how have historical events influenced current and fossil distribution? Although there have been important contributions to understanding regional biogeography and evolution of pines in the Tertiary (Eguiluz Piedra, 1985, 1988; Axelrod, 1986; Lauria, 1991), the impact of Pa-

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TABLE 1. Approximate ages and durations of geological eras from the Mesozoic to present.

Era	Period	Epoch	Duration (millions of years)	Millions of years ago
Cenozoic	Quaternary	Holocene	Approximately the last 10,000 years	
		Pleistocene	2.4	2.5
	Tertiary	Neogene	Pliocene	4.5
				7
		Miocene	19	26
	Paleogene	Oligocene	12	34 ¹
		Eocene	16	54
		Paleocene	11	65
Mesozoic	Cretaceous		71	136
	Jurassic		54	190
	Triassic		35	225

¹ The Oligocene–Eocene boundary is accepted to be 34 Ma, coinciding with the terminal Eocene event. Authors publishing before the middle 1970s and some current ones accept the boundary as 38 Ma.

leogene (Paleocene through Oligocene) events, especially the Eocene, on the evolution of the genus as a whole has not been analyzed. In this paper, I attempt to synthesize recent information on plate tectonics, climate, fossils, and biogeography of pines and other dominant plant groups as they affected pine evolution. From this synthesis, I argue that the Eocene was one of the most important phases in pine evolution.

SYSTEMATICS AND CURRENT
BIOGEOGRAPHY OF *PINUS*

The genus *Pinus* is one of the most widely distributed genera of trees in the Northern Hemisphere. Pines occur predominantly at middle latitudes (30°–55°N), but important centers of pine species also exist at high (> 55°N) and low latitudes (< 30°N) (Figs. 1, 2; Critchfield & Little, 1966). Pines are abundantly represented in North America, Central America, Europe, and Asia, with some taxa extending into northern Africa. Within their range, pines occur in diverse habitats, extend from sea level to 3,700 m, and dominate natural vegetation in many regions. They are absent from hot, wet, tropical environments, where they are poor competitors with other taxa (Mirov, 1967; Bond,

1989). At tropical latitudes, pines occur only in uplands or semi-arid regions.

Pinus contains more species than any other genus of conifers, although *Podocarpus* may rival it. Pines have been recognized since Classical times, and more than 40 classification systems have been proposed (Critchfield & Little, 1966; Mirov, 1967; Little & Critchfield, 1969; Price, 1989; Millar & Kinloch, 1991). The most widely accepted is the system of Little & Critchfield (1969), which built upon and modified the classification of Shaw (1914, 1924). Little & Critchfield (1969) divided *Pinus* into 3 subgenera, 5 sections, 15 subsections, and 94 species (Fig. 3). They updated the classification by incorporating new types of information based on genetic data, especially from contemporary studies on hybridization and biochemical variation. Thus, their classification implicitly suggests phylogenetic relationships and common origins of species and groups of species. Since the time of Little and Critchfield's classification, several new species have been described, especially from species-rich and as yet still incompletely known regions such as Mexico. In this paper, I accept Little and Critchfield's authority for species, and cite authors of taxonomic names only for those taxa outside of their system. I also accept most aspects of their

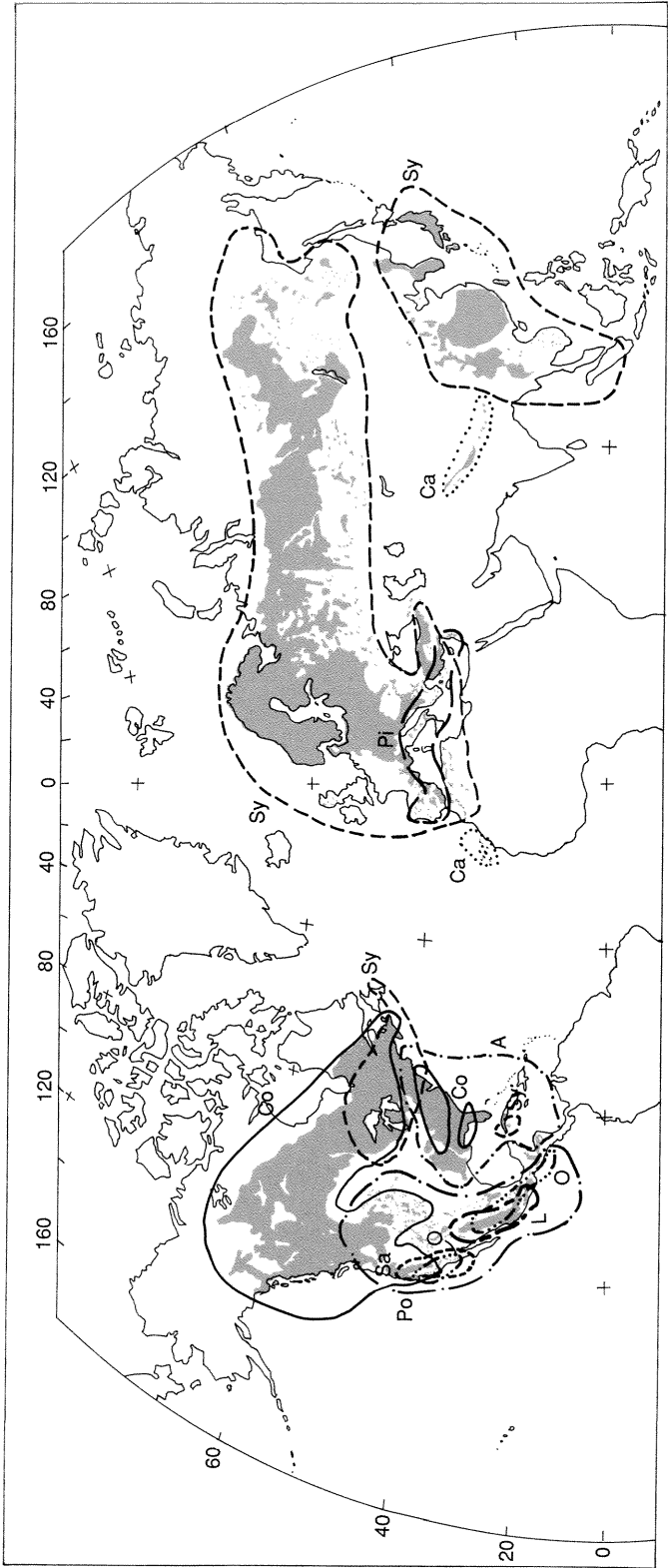


FIGURE 1. Distribution of *Pinus* subgenus *Pinus*, showing general locations of subsections within the subgenus. A = *Australes*, Ca = *Canarienses*, Co = *Contortae*, L = *Leicophyllae*, O = *Oocarpae*, Pi = *Pineae*, Po = *Ponderosae*, Sa = *Sabinianae*, Sy = *Sylvestres*.

The Genus *PINUS* Little and Critchfield

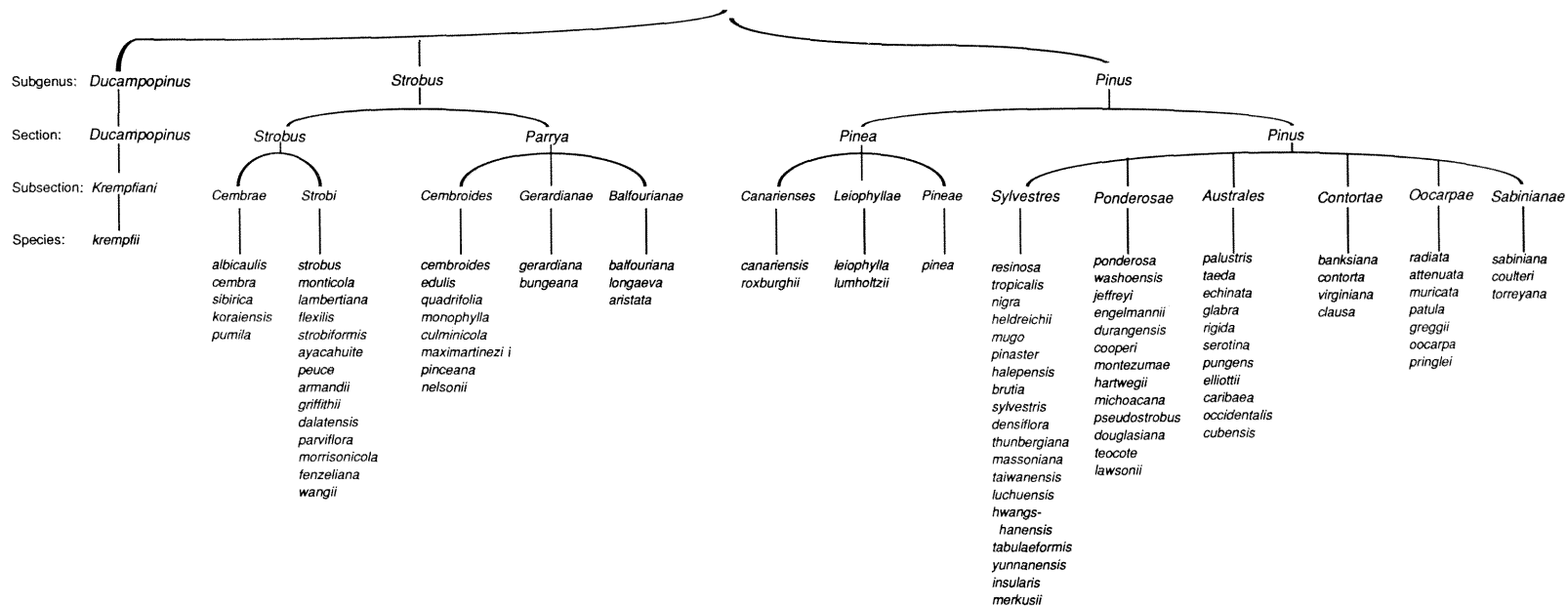


FIGURE 3. Taxonomy of the genus *Pinus* according to Little & Critchfield (1969), showing the species classified into subgenera, sections, and subsections.

classification as the best presently available hypothesis of phylogenetic relationships among the groups of extant taxa.

MESOZOIC BIOGEOGRAPHY

ORIGIN OF PINES

The prevailing hypothesis until the mid-1970s on the origin of the genus relied on the contemporary interpretation of Mesozoic fossil flora and the prevailing theories of the origin of cool temperate vegetation (Chaney, 1940; Mirov, 1967; Mirov & Hasbrouck, 1976). Fossil pines had been described from Triassic, Jurassic, and abundant Cretaceous locales, with pines especially abundant and diverse at high northern paleolatitudes. Mirov's widely cited interpretation dated the genus to the late Paleozoic or earliest Mesozoic, with its origin centered in a far-northern circumpolar continent known as Beringia. According to Mirov, the subsequent evolution of pines unfolded in a steady and progressive migration southward during the Mesozoic and Tertiary, culminating in a final southward thrust toward the equator during the Pleistocene.

This interpretation was cast into doubt by systematic revisions of Mesozoic coniferous fossils. Alvin, Creber, Miller, Stockey, and others compared internal anatomy of fossil and extant pinaceous cones and found four diagnostic traits that characterize *Pinus* (summarized in Miller, 1976). When previously described fossils were reanalyzed, many that were originally ascribed to *Pinus* were reclassified in the extinct pinaceous genera *Pityostrobus* and *Pseudoaraucaria*. This applied to all the known pinaceous remains from the Triassic and Jurassic, and many from the Cretaceous. In particular, all of the high-latitude macrofossils, primarily in the collections of Heer, 1868–1883, originally treated as *Pinus* were reclassified, in some cases, even as angiosperms.

The revisions, combined with new fossil discoveries in the last two decades, result in a Cretaceous fossil record of about 25 species of pines from eight Northern Hemisphere regions (Table 2; Fig. 4). About half are known from petrified cones whose internal anatomy has been confirmed as *Pinus*. Others are needle, wood, or pollen fossils, generally accepted to be *Pinus*. Of special note is the distribution of these fossil pines. Although a geographic bias may be expected due to proximity of fossil locations to active paleobotanists, fossil pines occur at middle and a few high latitudes, widely spread east and west, with apparent centers in the northeastern United States, Japan, and western Europe.

The earliest known pine, *P. belgica*, from the early Cretaceous (about 130 Ma) was found in Belgium. Pollen of an early Cretaceous pine was also found in amber deposits from Alaska (Langenheim et al., 1960). All other pine fossils are known from middle to late Cretaceous deposits.

The taxonomic diversity of fossil pines in the Cretaceous record is broad; two major subgenera and five subsections are represented. The origin of the genus is thought to be early-middle Mesozoic, although probably not the Paleozoic as suggested by Mirov (Miller, 1976; Eguluz Piedra, 1985; Axelrod, 1986; Millar & Kinloch, 1991). A major change from Mirov's thinking concerns the location of the center of origin of the genus and the paths of subsequent radiation. At the beginning of the Mesozoic, there was one land mass, Pangaea (Smith et al., 1981). By the early Jurassic, a northern supercontinent, Laurasia, separated and began to drift from a southern continent, Gondwanaland. Although there may have been more land above sea in northern latitudes than at present (Wolfe, 1985) little evidence exists for a circumpolar continent, Beringia, that would have supported the origin of pines (Hickey et al., 1983; Eguluz Piedra, 1985; Wolfe, 1985).

Most importantly, no fossil evidence exists for a high-latitude Mesozoic center of origin for pines. Mesozoic pine fossils occur between 31°N and 50°N latitude, with only two records from higher latitudes (Table 2). Similarly, fossils of six species of *Pseudoaraucaria* and over 20 species of *Pityostrobus*, genera considered most closely related to *Pinus* and most likely to have been the ancestral gene pool to *Pinus*, also occurred exclusively at middle latitudes, concentrated in eastern North America and western Europe (Miller, 1976, 1988). Hence, a circumpolar origin for *Pinus* is unsupported, and pine origins in middle latitudes are more likely. The regions of the northeastern United States and western Europe, which would have been contiguous in the early and middle Mesozoic (Smith et al., 1981), are the current candidates for the center of origin of the genus (Miller, 1976; Eguluz Piedra, 1985; Axelrod, 1986; Millar & Kinloch, 1991). Alternatively, the diversity of Cretaceous pines and *Pityostrobus* in Japan suggests that pines might have evolved in eastern Asia.

DISTRIBUTION OF PINES AND CLIMATE OF THE LATE CRETACEOUS

To understand the impact of the early Tertiary on pines, it is important to stress the Late Cretaceous distribution of pines and the prevailing cli-

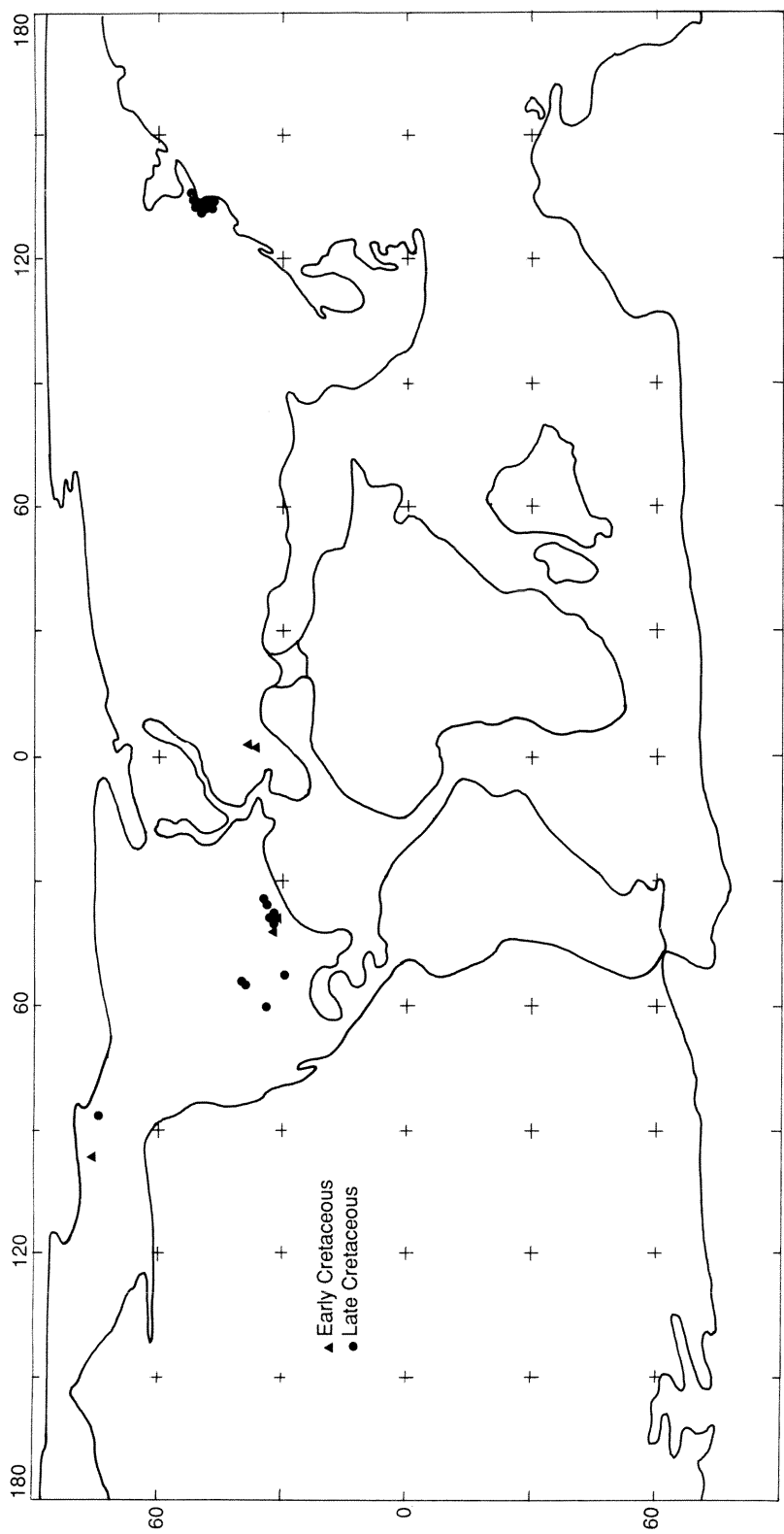


FIGURE 4. Distribution of pine fossils from Cretaceous deposits, mapped by estimated paleocoordinates on map of the late Cretaceous world. Base map © Cambridge University Press 1981, taken from Smith, Hurley & Briden, *Phanerozoic paleocontinental world maps*.

TABLE 2. Distribution and affinities of fossil pines from Cretaceous deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

Identification	Affinity	Location	Latitude/longitude		Age (Ma)	Reference
			Current	Paleo		
<i>P. belgica</i>	<i>Sylvestres</i>	Belgium, Wealden	50°N 4°E	39°N 5°E	130	Alvin (1960)
<i>Pinus</i> pollen	genus	Alaska, Kuk River	70°N 160°W	80°N 100°W	Early	Langenheim et al. (1960)
<i>Pinus</i> pollen	genus	Maryland	39°N 79°W	32°N 41°W	Late Early	Brenner (1963)
<i>Pinus</i> pollen	genus	Delaware	39°N 75°W	31°N 39°W	Late Early	Groot et al. (1961)
<i>P. wohlgenuthi</i>	subg. <i>Pinus</i>	France	48°N 4°E	35°N 18°E	Late Early	Alvin (1960)
<i>P. ponderosoides</i>	<i>Ponderosae</i> / <i>Australes</i>	Mississippi, Prentiss Co.	34°N 88°W	31°N 52°W	Early Late	Blackwell (1984)
<i>Pinus</i> pollen	<i>Sylvestres</i>	Minnesota	44°N 95°W	40°N 55°W	Early Late	Pierce (1957)
<i>P. clementsii</i>	<i>Sylvestres</i>	Minnesota	44°N 95°W	40°N 55°W	Late	Chaney (1954)
<i>Pinus</i> sp.	<i>Sylvestres</i>	Delaware	39°N 75°W	32°N 40°W	Late	Penny (1947)
<i>P. triphylla</i>	<i>Sylvestres</i> / <i>Leiophyllae</i>	Massachusetts	41°N 71°W	33°N 35°W	Late	Robison (1977)
		New York, Staten Island	41°N 74°W	34°N 37°W	Late	Hollick & Jeffrey (1909)
		Japan, Hokkaido	42°N 142°E	48°N 135°E	Late	Stockey & Nishida (1986)
<i>P. tetraphylla</i>	<i>Sylvestres</i>	Japan, Hokkaido	42°N 142°E	48°N 135°E	Late	Stockey & Nishida (1986)
<i>P. bifoliata</i>	<i>Sylvestres</i>	Japan, Hokkaido	43°N 142°E	49°N 135°E	Late	Stockey & Nishida (1986)
<i>P. pseudotetraphylla</i>	<i>Sylvestres</i>	Japan, Hokkaido	43°N 142°E	49°N 135°E	Late	Stockey & Nishida (1986)
<i>P. flabellifolia</i>	<i>Canarienses</i>	Japan, Hokkaido	43°N 142°E	49°N 135°E	Late	Ogura (1932), Stockey & Nishida (1986)
<i>P. quenstedti</i>	<i>Ponderosae</i>	Kansas	38°N 99°W	34°N 61°W	Late	Lesquereux (1883)
<i>P. quinquefolia</i>	<i>Ponderosae</i>	Massachusetts	41°N 71°W	33°N 35°W	Late	Penny (1947), Robison (1977)
		New York, Staten Island	41°N 74°W	34°N 37°W	Late	Hollick & Jeffrey (1909)
		Japan, Hokkaido	42°N 142°E	48°N 135°E	Late	Stockey & Nishida (1986)
<i>P. pachydermata</i>	subg. <i>Pinus</i>	Japan, Hokkaido	42°N 142°E	48°N 135°E	Late	Ueda & Nishida (1982)
<i>P. pseudostrobifolia</i>	<i>Ponderosae</i>	Japan, Hokkaido	43°N 142°E	49°N 135°E	Late	Ogura (1932), Stockey & Nishida (1986)
<i>P. pseudoflabellifolia</i>	subg. <i>Pinus</i>	Japan, Hokkaido	44°N 142°E	50°N 136°E	Late	Ueda & Nishida (1982)
<i>P. harborensis</i>	<i>Ponderosae</i>	Japan, Hokkaido	44°N 142°E	50°N 136°E	Late	Stockey & Nishida (1986)
<i>P. hokkaidoensis</i>	<i>Ponderosae</i> / <i>Leiophyllae</i>	Japan, Hokkaido	44°N 142°E	50°N 136°E	Late	Stockey & Ueda (1986)
<i>P. cliffwoodensis</i>	<i>Australes</i> / <i>Ponderosae</i>	New Jersey, Magothy	40°N 74°W	32°N 38°W	Late	Miller & Malinky (1986)

TABLE 2. Continued.

Identification	Affinity	Location	Latitude/longitude		Age (Ma)	Reference
			Current	Paleo		
<i>Pinus</i> sp.	subg. <i>Strobus</i>	New York, Staten Island	41°N 74°W	34°N 37°W	Late	Jeffrey (1908)
<i>P. magnothensis</i>	<i>Strobi</i>	Delaware	39°N 75°W	31°N 38°W	Late	Penny (1947)
<i>P. yezoensis</i>	subg. <i>Strobus</i>	Japan, Hokkaido	43°N 142°E	49°N 135°E	Late	Stopes & Kershaw (1910)
<i>Pinus</i> pollen	genus	Alaska, Colville River	70°N 151°W	75°N 88°W	Late	Frederiksen et al. (1988)

mate at the end of the Mesozoic. By the Late Cretaceous, pines had reached eastern and western edges of Laurasia and occurred at middle latitudes in many locations between these extremes (Table 2; Fig. 4). The widespread distribution of pines in Laurasia by this time indicates that wherever within middle latitudes they originated, their main route of migration was east and west, and not predominately southward, as Mirov suggested. Migration from eastern North America to western Europe was not impeded until late in the Mesozoic, by which time Laurasia had begun to split into North America and Europe. Laurasia severed first in the south and last in the north. High-latitude connections in the North Atlantic became increasingly reduced toward the end of the Mesozoic, and low seas may have covered the land (Ziegler et al., 1983; Tiffney, 1985a; Parrish, 1987). This region would have provided only minor corridors for pine migration. Evidence also exists for land connections at high latitudes in the Bering Sea region between Siberia and Alaska being used as corridors for temperate-adapted flora.

Within the new continents, continuing east-west migration in the late Cretaceous must have been hindered by seaways that extended the full north-south length of the continents (Kurten, 1966; Tiffney, 1985a). These seaways divided the continents into separate phytogeographic provinces, creating greater floristic affinities between eastern North America and western Europe, and western North America and eastern Asia, than between the east-west parts of each continent (Wolfe, 1975; Tiffney, 1985a).

The Late Cretaceous was a time of climatic quiescence and equability (Parrish, 1987; Upchurch & Wolfe, 1987; McGowran, 1990). Sea levels were high, and tectonic activity low, creating stable global climates. Although the breakup of Pangaea had commenced, paleocontinents were still relatively undispersed, resulting in average temperatures in the middle and high latitudes about 10°–20°C warmer than the present (Savin, 1977; Shackleton & Boersma, 1981; Parrish, 1987; Upchurch & Wolfe, 1987). Evidence on rainfall in the Cretaceous inferred from foliar physiognomy of angiosperms indicates that rainfall patterns were zonal. The Northern Hemisphere had a humid region around the paleoequator, a dry zone at low-middle latitudes, and a zone of higher rainfall above 45°N (Parrish, 1987). In general, however, latitudinal gradients were shallower, and changes in temperature with latitude were about 1/2–1/3 of present gradients (Parrish, 1987; Upchurch & Wolfe, 1987). Temperature and rainfall appear to have

been stable annually, with little seasonality at latitudes below 45°N (Upchurch & Wolfe, 1987). At higher latitudes, day lengths and precipitation apparently varied seasonally. The major cordillera of the Northern Hemisphere were not developed, or existed only at low elevations. Volcanic activity was minor, so there were few orographic effects on climate and little regional diversity in climate.

EARLY TERTIARY BIOGEOGRAPHY

CHANGING CLIMATES

Major changes in climate and vegetation characterized the early Tertiary (Wolfe, 1990). Although these events have long been discussed by paleobotanists interested in angiosperm evolution (Wolfe, 1975; Tiffney, 1985a, b; Friis et al., 1987), their impact on conifer evolution has not been analyzed. In general, average temperatures rose and rainfall increased in the early Tertiary. The trends toward increasing temperature and humidity started in the early Paleocene and continued into the Eocene, reaching maxima in the early Eocene, about 52 Ma. By this time, average temperatures had increased 5°–7°C above the Late Cretaceous (Savin, 1977), and tropical/subtropical conditions apparently extended at many middle and high latitudes to 70°–80°N (Wolfe, 1985; McGowran, 1990). High temperatures and humidity, however, did not persist stably throughout the Eocene. Although the late Paleocene/early Eocene (54–52 Ma) was the warmest and wettest period, there were at least two other warm periods, from about 46 to 42 Ma, and about 36 to 34 Ma, separated by cooler intervals that were approximately equal in duration to the warm periods (Fig. 6; Wolfe, 1978, 1985; McGowran, 1990). Average annual temperatures may have fluctuated as much as 7°–10°C between warm and cool periods of the Eocene (Wolfe, 1978). Several causes for these climatic developments have been suggested, including major tectonic events, changes in sea level, and submarine volcanism resulting in accumulation of atmospheric carbon dioxide and greenhouse heating (Wolfe, 1978; Parrish, 1987; McGowran, 1990; Kerr, 1991). Alternatively, large amounts of carbon dioxide may have been produced as a result of ocean-atmosphere interactions following a major extraterrestrial impact at the Cretaceous/Tertiary boundary (O'Keefe & Ahrens, 1989), which led to greenhouse warming (Wolfe, 1990).

Although latitudinal gradation was not great, the pattern in the Eocene differed from both the Cretaceous and the later Tertiary and Quaternary: in general, many low-latitude locations were relatively warm and seasonally dry, middle latitudes were

warm and wet, and high latitudes were cool and dry (Parrish, 1987; Wolfe, 1978). Truly arid zones apparently did not exist; there is no evidence for Paleogene arid deserts or tundra (Axelrod, 1979).

Although these general trends in temperature and humidity existed throughout a broad latitudinal zone worldwide, there was geographic heterogeneity in the intensity of conditions. The warm humid zone was widest in North America and western Europe, and narrower in central and eastern Asia (Chaney, 1940; Parrish, 1987; Hsu, 1983). In general, continental elevations were low throughout the Paleogene, and upland areas apparently existed primarily in one middle-latitude region of western North America and in Antarctica (Axelrod, 1966; Wolfe, 1985, 1987; Wolfe & Wehr, 1987; Wing, 1987). In the upland area of western North America, the climate was anomalously temperate compared to other middle-latitude areas. Volcanism and mountain-building in this area during the Eocene also created heterogeneity in local climates and habitats.

THE ANGIOSPERM BOREOTROPICAL FLORA

The changes in climate during the early Tertiary drastically affected global floristics (Friis et al., 1987; Wolfe, 1975, 1978, 1985). Diverse tropical and subtropical angiosperm floras appeared with increasing geographic representation during the Paleocene and the warm intervals of the Eocene throughout broad zones at middle latitudes in both Northern and Southern Hemispheres. Originally identified from the London Clay formations of England (Reid & Chandler, 1933), similar angiosperm floras have been described from many deposits elsewhere, including western and eastern North America (from the Pacific Coast to Nebraska and Texas; Vermont, Alabama), western and eastern Europe (including England, France, Belgium, Germany, Bulgaria, Ukraine, and Russia), northern Egypt, China, and Japan (Mai, 1970; Graham, 1972; Wolfe, 1975, 1985; Tiffney, 1985a, b). Subtropical assemblages occurred north as far as 70° in Alaska, and at other high-latitude locations in Canada, Greenland, and Siberia (Wolfe, 1977, 1985). In North America, the average zone extended from 30°N to 50°N (Wolfe, 1985). The origin and major radiation of many angiosperm taxa is documented in these diverse floras.

Plant communities in these Paleogene floras were adapted to warm, humid, and equable conditions. These taxa were similar to those found in modern rainforest vegetation of Malaysia and other extant tropical rainforest regions and show comparable adaptations. Common genera include *Engelhard-*

tia, *Ficus*, *Pterocarya*, *Nypa*, *Platycarya*, *Wetherellia*, *Alangium*, and *Nyssa*. A few gymnosperms such as *Glyptostrobus*, *Taxodium*, and occasionally *Sequoia* occurred in these floras, but they, too, were apparently adapted to warm, humid conditions.

Recognizing their northern locations and their adaptations to warm, humid conditions, Wolfe (1975, 1977) referred to these widespread angiosperm assemblages as the "boreotropical flora." While this assemblage in no way suggests an organic, indivisible unit, it does imply that similarly adapted individual taxa migrated east and west rapidly and unimpeded, at middle latitudes throughout North America and Eurasia in the early Tertiary. The boreotropical flora reached its greatest development in the warm periods of the Eocene. During cool intervals, its latitudinal extent shrank.

EOCENE PINES

The early Tertiary radiation of many angiosperm lineages and the migration of angiosperm boreotropical taxa east and west at middle latitudes has many parallels with the late Mesozoic radiation and migration patterns of pines. Boreotropical floras occur in the same locations worldwide during the early Tertiary as pines did in the late Mesozoic. With very few exceptions, pines are not found in boreotropical fossil floras. This prompts the question, where did the pines go?

The Tertiary record of pines begins in the Eocene; no pines are known from the Paleocene. Pines of the earliest Eocene occur primarily in high (65°–80°N) and low (2°N) latitude deposits in North America and Eurasia (Table 3; Fig. 5). High-latitude locations include central Alaska (Wahrhaftig et al., 1969; Dickinson et al., 1987; Fredericksen et al., 1988), Ellsmere Island, Greenland, Iceland, and Spitsbergen (Manum, 1962; Schweitzer, 1974). Low-latitude pines occurred in Borneo (Muller, 1966) and from one low-middle latitude location of the late early Eocene, near San Diego, California (Axelrod, 1986). Pines in these deposits were associated with other pinaceous conifers and with cool temperate angiosperms such as *Betula*, *Alnus*, and *Ulmus*. Ages of these fossils correspond to the first warm humid period of the Eocene (Fig. 6).

Fossil pines from the middle Eocene continue to be represented at high and low latitudes, but appeared for the first time in the Tertiary in middle-high latitude locations in North America and Eurasia. Most of the known fossils from the cool period of the earlier middle Eocene are in western North America, from British Columbia (Miller, 1973; Stockey, 1983, 1984), Washington (Wolfe &

Wehr, 1987), Idaho (Axelrod, 1986), and Colorado (Wodehouse, 1933; MacGinitie, 1953) (Table 3; Fig. 5). Western North America in general contains some of the richest plant-bearing deposits from the Eocene in the world, and dozens of fossil floras have been described. Only a few of these contain pines and other temperate taxa, and these are all concentrated in northern Idaho, central Wyoming, north to central Idaho, and British Columbia. This is the region that has been identified as an upland area with average elevations of 1,200–1,500 m (Axelrod, 1965; Axelrod & Raven, 1985; Wolfe, 1987). Pine deposits in some of these areas are associated with active volcanos and high elevations (e.g., Bull Run, Thunder Mountain, Axelrod, 1965, 1986; Creede, 2,500 m, Wolfe & Schorn, 1989).

The warm humid period of the middle Eocene is represented by few pine fossils (Table 3). Pine was present at high latitudes in the Mackenzie Delta of Alaska (80°N, Norris, 1982), at low-middle latitudes in Borneo (2°N, Muller, 1966) and southern Alabama (36°N, Gray, 1960), and also at a few middle latitudes in Nevada (50°N, Axelrod, 1966, 1968), within the upland plateau of western North America.

Pine fossils from the subsequent cool period of the later Eocene occurred at middle latitudes in Washington (Miller, 1974), Nevada (Axelrod, 1966, 1968), Colorado (Leopold & MacGinitie, 1972; Axelrod, 1986), New Mexico (Leopold & MacGinitie, 1972), and Japan (Huzioka & Takahashi, 1970; Tanai, 1970, interpreted by Wolfe, 1985 to be early-late Eocene), Fushun, China (Hsu, 1983), as well as a continuing presence in Borneo (Muller, 1966) and at high latitudes (Norris, 1982) (Table 3).

The latest Eocene marks the final widespread period of tropical conditions at middle latitudes in the Paleogene (Fig. 6). Pine fossils from the late Eocene occur primarily at high latitudes in western Siberia (Dorofeev, 1963), Alaska (Norris, 1982), British Columbia (Hopkins et al., 1972), at low latitudes in Borneo (Muller, 1966), and along the Tethys seaway in southeastern Europe (Chiguriaeva, 1952). Pines from the southeast coast of China, in the provinces of Jiang-su, Zhejiang, and Fujian (Hsu, 1983), may also be from this period (Table 3).

THE TERMINAL EOCENE EVENT AND PINE EXPANSIONS

The end of the Eocene was marked by the most profound climatic event of the Tertiary (Burchardt, 1978; Wolfe, 1978; Parrish, 1987; McGowan,

TABLE 3. Distribution and affinities of fossil pines from Eocene deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

Identification	Affinity	Location	Latitude/longitude		Age (Ma)	Reference
			Current	Paleo		
<i>Pinus</i> pollen	genus	Alaska, Nenana	64°N 148°W	77°N 128°W	54	Wahrhaftig et al. (1969)
<i>Pinus</i> pollen	genus	Alaska, Colville	70°N 151°W	80°N 127°W	Early	Frederiksen et al. (1988)
<i>Pinus</i> ? pollen (bisaccate grains)	genus	Alaska, Death Valley	65°N 162°W	80°N 143°W	Early	Dickinson et al. (1987)
<i>Pinus</i> pollen	genus	Canada, Ellsmere Island	77°N 84°W	75°N 18°W	Early	Manum (1962)
<i>Pinus</i> pollen	genus	Greenland	70°N 52°W	60°N 8°W	Early	Manum (1962)
<i>Pinus</i> pollen	genus	Iceland	65°N 21°W	50°N 8°E	Early	Manum (1962)
<i>Pinus</i> pollen	genus	Spitsbergen	79°N 14°E	70°N 20°E	Early	Manum (1962), Schweitzer (1974)
<i>Pinus</i> pollen	genus	North Dakota, Dunn	47°N 103°W	56°N 70°W	Early	Leopold & MacGinite (1972)
<i>Pinus</i> pollen	genus	Northwestern Borneo	2°N 110°E	2°N 110°E	Late Early	Muller (1966)
<i>P. delmarensis</i>	subg. <i>Strobus</i>	Southern California	33°N 117°W	42°N 92°W	47–48	Axelrod (1986)
<i>Pinus</i> pollen	<i>Cembroides</i>	Southern California	33°N 117°W	41°N 92°W	47–48	Axelrod & Raven (1985)
<i>Pinus</i> pollen	<i>Ponderosae</i>	Southern California	33°N 117°W	41°N 92°W	47–48	Axelrod & Raven (1985)
<i>Pinus</i> pollen	genus	Northeastern China, Fushun	42°N 124°E	45°N 118°E	Mid and Late	Sung & Liu (1976), Hsu (1983)
<i>P. ballii</i>	<i>Cembroides</i>	Colorado, Green River	41°N 109°W	50°N 80°W	47	Wodehouse (1933), Brown (1934)
<i>P. driftwoodensis</i>	<i>Sylvestres</i> / <i>Ponderosae</i> / <i>Australes</i>	British Columbia, Smithers	55°N 127°W	66°N 97°W	46–47	Stockey (1983)
<i>P. arnoldii</i>	<i>Sylvestres</i>	British Columbia, Princeton	50°N 120°W	61°N 90°W	46–47	Miller (1973), Stockey (1984)
<i>P. similkameensis</i>	subg. <i>Strobus</i>	British Columbia, Princeton	50°N 120°W	61°N 90°W	46–47	Miller (1973)
<i>P. princetonensis</i>	<i>Sylvestres</i>	British Columbia, Princeton	50°N 120°W	61°N 90°W	46–47	Stockey (1984)
<i>P. andersonii</i>	<i>Ponderosae</i>	British Columbia, Princeton	50°N 120°W	61°N 90°W	46–47	Stockey (1984)
<i>Pinus</i> pollen	genus	Washington, Republic	49°N 118°W	60°N 87°W	46–47	Wolfe & Wehr (1987)
<i>P. balfouroides</i>	<i>Balfourianae</i>	Idaho, Thunder Mountain	45°N 114°W	55°N 84°W	46–47	Brown (1937), Axelrod (1986)

TABLE 3. Continued.

Identification	Affinity	Location	Latitude/longitude		Age (Ma)	Reference
			Current	Paleo		
<i>Pinus</i> pollen	genus	Canada, MacKenzie Delta	69°N 134°W	80°N 80°W	Mid-Late	Norris (1982)
<i>Pinus</i> pollen	genus	Alabama, Claiborne Bluffs	31°N 88°W	36°N 62°W	Middle	Gray (1960)
<i>P. wheeleri</i>	<i>Strobi</i>	Nevada, Elko	41°N 116°W	50°N 90°W	42	Axelrod (1968)
<i>P. crossii</i>	<i>Balfourianae</i>	Nevada, Copper Basin	42°N 115°W	51°N 89°W	40–44	Axelrod (1966)
<i>P. wolfei</i>	<i>Sylvestres</i> / <i>Contortae</i>	Washington, Little Falls	47°N 123°W	60°N 93°W	Early Late	Miller (1974)
<i>P. alvordensis</i>	<i>Contortae</i>	Nevada, Bull Run	41°N 117°W	50°N 91°W	38	Axelrod (1968)
<i>Pinus</i> pollen	genus	New Mexico, Bernalillo	35°N 107°W	44°N 80°W	38	Leopold & MacGinite (1972)
<i>Pinus</i> sp.	genus	Southwestern Japan, Ube	34°N 130°E	40°N 130°E	Early Late	Huzioka & Takahashi (1970)
<i>Pinus</i> sp.	genus	Japan, Kushiro	43°N 144°W	50°N 135°E	Early Late	Tanai (1972)
<i>Pinus</i> pollen	genus	Colorado, Chaffee	39°N 105°W	49°N 76°W	36–37	Leopold & MacGinite (1972)
<i>Pinus</i> pollen	genus	British Columbia, Parsnip River	55°N 122°W	66°N 90°W	35	Hopkins et al. (1972)
<i>Pinus</i> sp.	genus	Siberia, Tavda River	58°N 65°E	52°N 58°E	Late	Dorofeev (1963)
<i>Pinus</i> sp.	genus	Siberia, Ob River	57°N 85°E	54°N 75°E	Late	Dorofeev (1963)
<i>Pinus</i> sp.	genus	Siberia, Tym River	60°N 82°E	55°N 73°E	Late	Dorofeev (1963)
<i>P. spinosa</i>	<i>Sylvestres</i> / <i>Ponderosae</i>	Siberia, Irtysh River	57°N 75°E	52°N 67°E	Late	Dorofeev (1963)
<i>Pinus</i> pollen	genus	Ukraine, River Don	47°N 40°E	35°N 38°E	Late	Chiguriaeva (1952)
<i>P. sturgisii</i>	<i>Strobi</i>	Colorado, Florrissant	39°N 105°W	48°N 76°W	34–35	MacGinite (1953), Axelrod (1986)
<i>P. florissantii</i>	<i>Strobi</i>	Colorado, Florrissant	39°N 105°W	48°N 76°W	34–35	MacGinite (1953), Axelrod (1986)
<i>P. wheeleri</i>	<i>Strobi</i>	Colorado, Florrissant	39°N 105°W	48°N 76°W	34–35	MacGinite (1953), Axelrod (1986)
<i>Pinus</i> pollen	genus	Southeastern China	25–35°N 120°E	28–34°N 118°E	Late	Hsu (1983)

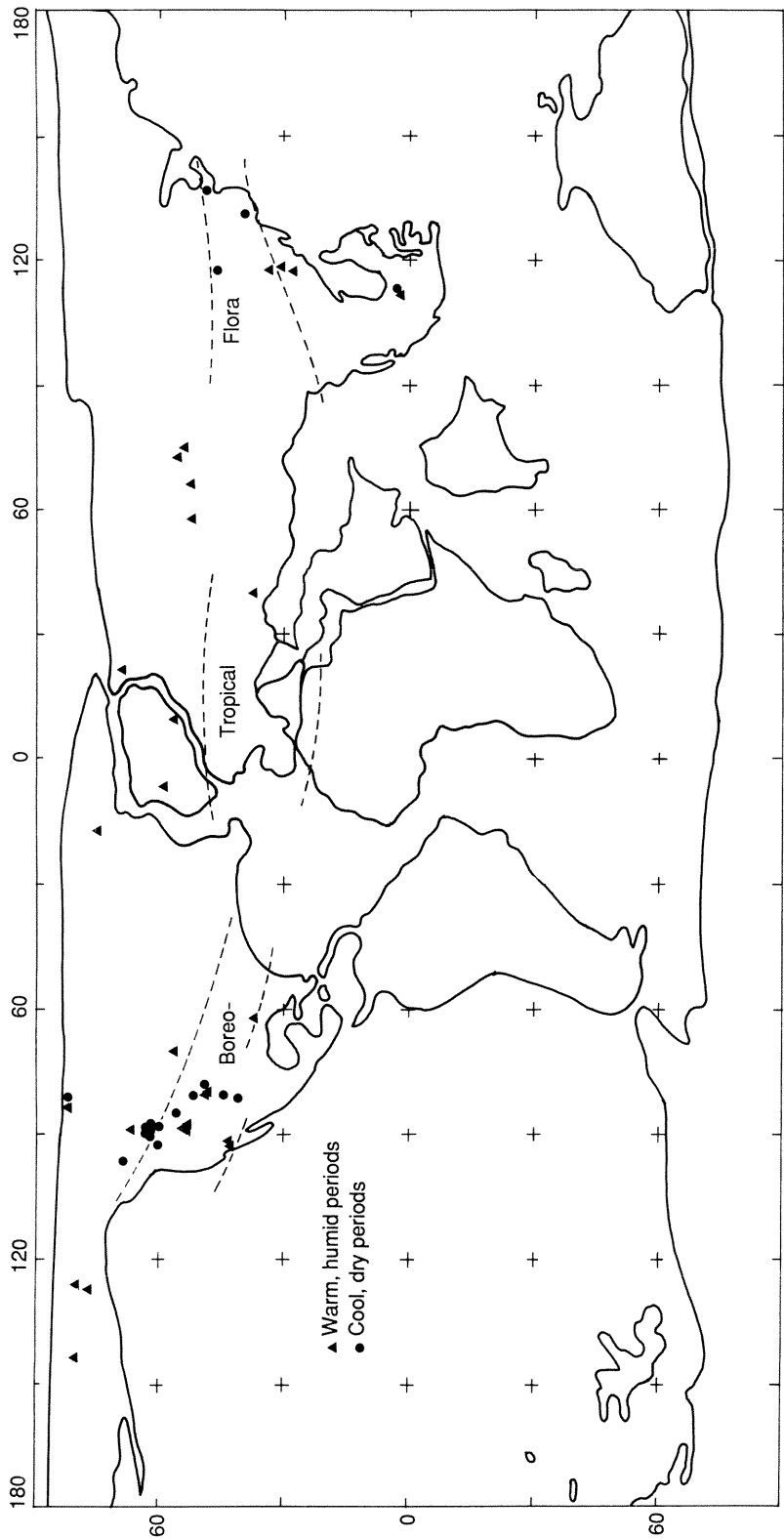


FIGURE 5. Distribution of pine fossils from Eocene deposits, mapped by estimated paleocoordinates on map of the Paleocene world. Base map © Cambridge University Press 1981, taken from Smith, Hurley & Briden, *Phanerozoic paleocontinental world maps*.

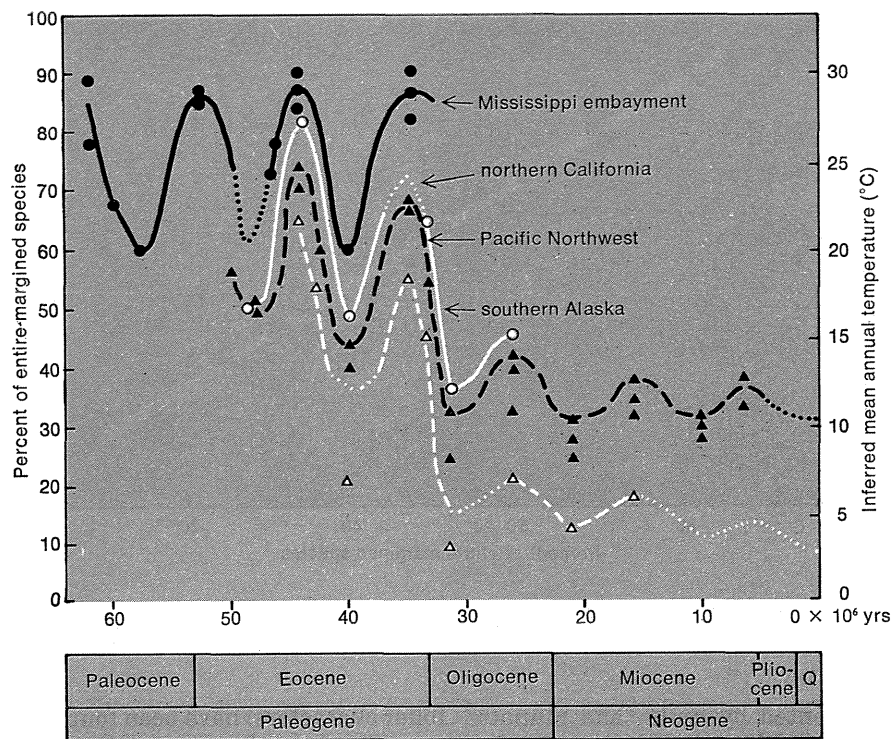


FIGURE 6. Estimated temperatures from four latitudes in North America during the Tertiary (based on percentage of entire leaves), indicating the warm and cool episodes in the Eocene and the drop in temperature at the end of the Eocene (terminal Eocene event). From Wolfe (1978). Reprinted by permission of *American Scientist*, journal of Sigma Xi, The Scientific Research Society.

1990). The fluctuations from warm to cool periods during the Eocene were minor compared to the drop in regional temperatures at the end of the Eocene. Average annual temperatures dropped approximately 10°–13°C, in some areas over only one million years (Fig. 6). The decline in average temperatures was accompanied by a large decrease in rainfall and increase in seasonality. Whereas in the Eocene the mean annual range of temperatures (seasonality) is estimated as only 3°–5°C, in the early Oligocene it is estimated as 25°C—about twice the range of the present (Wolfe, 1971). In many parts of the world, complex continental climate patterns developed, possibly for the first time, and continental ice sheets first occurred in the Oligocene (McGowran, 1990). Extensive volcanism and mountain-building in the Rocky Mountains, Himalayas, and Mexican ranges created local climatic diversity. Major tectonic events have been associated with the climatic cooling at the end of the Eocene with two schools of thought on their effect. One line of evidence suggests that changing positions of the Earth's continents and oceans had direct effects on the Earth's climate, leading to

major cooling (Barron, 1985; McGowran, 1990). Another possibility is that the formation of giant uplifted plateaus in southern Asia and the American West led to accelerated chemical weathering, a decline in atmospheric carbon dioxide, and a “greenhouse cooling” effect (Ruddiman & Kutzbach, 1989, 1991).

This terminal Eocene event (Wolfe, 1978) was marked by widespread extirpation of boreotropical angiosperm taxa from many middle latitudes worldwide, leaving only remnants in a few areas where the climate presumably remained mild. The extinctions of boreotropical floras were mirrored by great expansion of pines and other cool-adapted taxa into many middle-latitude locations. Many of the same fossil-bearing sites that contained boreotropical taxa in their late Eocene horizons were dominated by cool-temperate conifer taxa in early Oligocene horizons. In some localities, this change occurred in only one million years (Axelrod, 1965).

The existing record suggests that pines made their first Tertiary appearance at many middle-latitude locations during the Oligocene (Table 4; Fig. 7), recolonizing areas where they had occurred

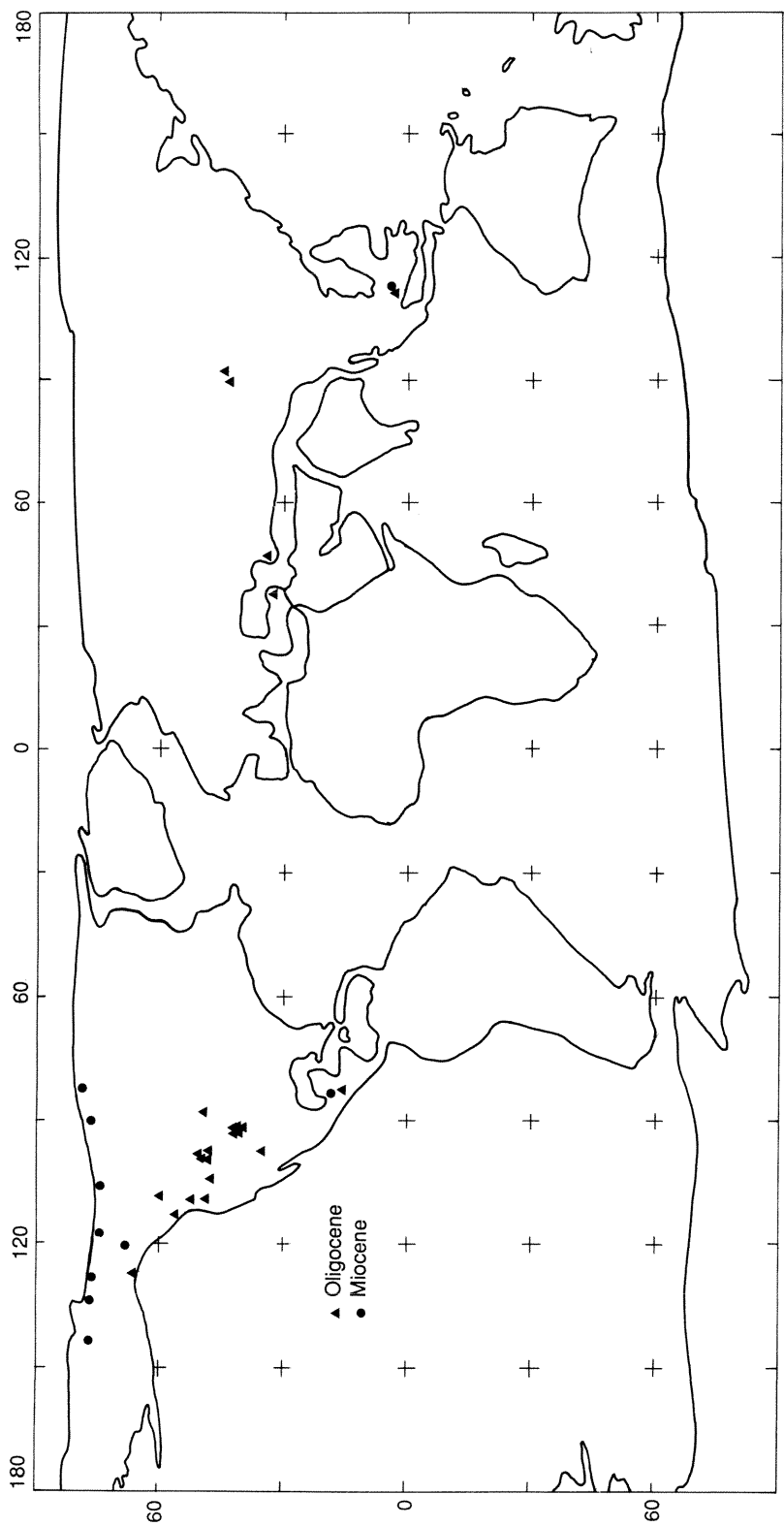


FIGURE 7. Distribution of pine fossils from Oligocene and selected Miocene deposits, mapped by estimated paleocoordinates on map of the early Miocene world. Base map © Cambridge University Press 1981, taken from Smith, Hurley & Briden, *Phanerozoic paleocontinental world maps*.

TABLE 4. Distribution and affinities of fossil pines from Oligocene deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

Identification	Affinity	Location	Latitude/longitude		Age (Ma)	Reference
			Current	Paleo		
<i>Pinus</i> pollen	genus	Oregon, Bridge Creek	44°N 118°W	47°N 105°W	31	Wolfe (1981), Mason (1927)
<i>Pinus</i> pollen	genus	Oregon, Lyons	45°N 123°W	49°N 110°W	31	Wolfe (1981)
<i>Pinus</i> pollen	genus	North Dakota, Dunn County	47°N 103°W	48°N 88°W	Early	Leopold & MacGinite (1972)
<i>Pinus</i> pollen	genus	Montana, Ruby Basin	45°N 112°W	46°N 100°W	32–36	Becker (1961), Wolfe (1977)
<i>P. crossii</i>	<i>Balfourianae</i>	New Mexico, Hillsboro	33°N 108°W	34°N 98°W	32	Axelrod & Bailey (1976)
<i>Pinus</i> pollen	genus	British Columbia, Australian Creek	56°N 126°W	60°N 110°W	Early	Piel (1971), Rouse & Matthews (1979)
<i>P. escalatensis</i>	<i>Contortae</i>	British Columbia, Escalante Island	50°N 127°W	56°N 115°W	Early–Late	Banks et al. (1981)
<i>Pinus</i> pollen	genus	Northwestern Borneo	2°N 110°E	5°N 110°E	Early–Late	Muller (1966)
<i>Pinus</i> pollen	genus	Gulf of Alaska	60°N 145°W	68°N 128°W	Late	Wolfe (1972, 1977)
<i>P. buchananii</i>	<i>Ponderosae</i>	Washington, Olympic	48°N 123°W	52°N 110°W	Late	Underwood & Miller (1980)
<i>P. avonensis</i>	<i>Ponderosae</i>	Montana, Avon	47°N 113°W	50°N 100°W	Late?	Miller (1969)
<i>P. anthrarivus</i>	<i>Strobi</i>	Idaho, Coal Creek	45°N 114°W	47°N 103°W	29	Axelrod (1986)
<i>P. balfouroides</i>	<i>Balfourianae</i>	Idaho, Coal Creek	45°N 114°W	47°N 103°W	29	Axelrod (1986)
<i>Pinus</i> pollen	genus	Montana, Beaverhead Basin	45°N 113°W	47°N 102°W	Late	Becker (1961), Leopold & MacGinite (1972)
<i>Pinus</i> pollen	genus	Colorado, Chaffee	39°N 105°W	40°N 93°W	Late	Leopold & MacGinite (1972)
<i>P. crossii</i>	<i>Balfourianae</i>	Colorado, Creede	38°N 105°W	39°N 93°W	27	Schorn & Wolfe (1989)
<i>P. riogrande</i>	<i>Ponderosae</i>	Colorado, Creede	38°N 105°W	39°N 93°W	27	Schorn & Wolfe (1989)
<i>P. sanjuanensis</i>	<i>Cembroides</i>	Colorado, Creede	38°N 105°W	39°N 93°W	27	Axelrod (1986), Schorn & Wolfe (1989)
<i>Pinus</i> sp. (cf. <i>alvordensis</i>)	<i>Contortae</i>	Colorado, Creede	38°N 105°W	39°N 93°W	27	Axelrod (1986), Schorn & Wolfe (1989)
<i>Pinus</i> pollen (1 grain)	genus	Mexico, Chiapas	16°N 92°W	14°N 83°W	Late	Langenheim et al. (1967)
<i>Pinus</i> pollen	genus	Northwestern China, Quidam	43°N 96°E	44°N 92°E	Late?	Hsu (1983)
<i>Pinus</i> pollen	genus	Northwestern China, Northwestern Gansu	42°N 95°E	43°N 90°E	Late	Sung (1958)
<i>P. prepityusa</i>	<i>Sylvestres</i>	Western Transcaucasia	42°N 42°E	35°N 40°E	Late?	Czeczott (1954)
<i>P. maikopiae</i>	<i>Sylvestres</i> / <i>Contortae</i>	Eastern Transcaucasia	40°N 50°E	35°N 45°E	Late?	Palibin (1935)

in the Mesozoic. Pines are known from Oligocene deposits that range in North America from the Gulf of Alaska (Wolfe, 1972), British Columbia (Banks et al., 1981), Washington (Underwood & Miller, 1980), Montana (Miller, 1969; Leopold & MacGinitie, 1972), Idaho (Axelrod, 1986), Oregon (Wolfe, 1981), Colorado (Leopold & MacGinitie, 1972; Schorn & Wolfe, 1989), to a single specimen from Chiapas, Mexico (Langenheim et al., 1967) (Table 4). In Asia, Oligocene deposits are in eastern and western Transcaucasia (Palibin, 1935; Czecczot, 1954), and in northwest China, in the Quidam Basin, and in the Jinguan Basin of western Gansu (Sung, 1958; Hsu, 1983). In Japan, pine was present as a minor component of a few floras (Tanai, 1972). Pine was abundant in the Oligocene strata of Borneo (Muller, 1966). Although some of the pine-bearing deposits were associated with areas of volcanism and mountain-building, others were in lowland and coastal areas where boreotropical flora had flourished in previous epochs.

The climatic deterioration of the early Oligocene was followed by an ameliorating and warming trend during the late Oligocene and into the Miocene. Rainfall, however, stayed moderately low and climatic conditions remained temperate at middle latitudes. The record indicates that pines rose in abundance throughout middle latitudes in North America (Axelrod, 1986), Europe (van der Burgh, 1973; Klaus, 1989), and Asia (Hsu, 1983) in the Miocene; the direct ancestors of many modern pine species can be traced to Miocene pines. The warm conditions of the Miocene supported expanded pine forests at high latitudes, such as Banks Island (78°–80°N, Hills et al., 1974), MacKenzie Delta (72°–85°N, Ritchie, 1984), and Wrangell Mountains, Alaska (68°N, Wolfe, 1969) (Table 5). Pine fossils in low-latitude deposits, such as Veracruz, Mexico (17°N, Graham, 1976) indicate the continued presence of pines in mountainous low latitudes, despite the fact that lowlands in these latitudes were dominated by boreotropical flora.

IMPACT OF EARLY TERTIARY CLIMATE ON PINE EVOLUTION

EOCENE PINE REFUGIA

The preceding overview of biogeography provides evidence for the hypothesis that pine distributions shifted latitudinally and that pines expanded and contracted in elevational extent several times from the late Mesozoic to the middle Tertiary. In general, the hypothesis states that pine popu-

lations (1) occurred throughout middle latitudes in the Mesozoic, (2) were fragmented and displaced to high and low latitudes and to middle-latitude uplands in the Eocene, and then (3) reappeared widely throughout middle latitudes in the Oligocene and Miocene, where they remained for the rest of the Tertiary.

The Mesozoic origin and spread of pines east and west throughout Laurasia apparently occurred under a warm temperate climate that was equable and had little latitudinal gradation. Early migration and radiation of pines was favored in the Mesozoic not only by climatic conditions, but by the absence at high-middle latitudes of competing angiosperm taxa. Although angiosperms apparently originated about the same time as the pines in the Early Cretaceous (Taylor & Hickey, 1990), their rise to dominance in middle latitudes did not occur until the late Cretaceous (Wolfe & Upchurch, 1986).

The shift in global climates toward warm humid conditions of middle latitudes in the early Tertiary appears to have favored the migration and radiation of angiosperms at the expense of pines. Although pines have broad tolerance of climatic and edaphic conditions, they do not survive or grow well in hot and humid climates (Mirov, 1967). More importantly, in these conditions they are poor competitors with angiosperms in seedling establishment, height growth, and reproduction. Conifers dominate in areas where angiosperm competition is reduced, for example, by fire, cold, or nutrient shortages (Bond, 1989).

Such a situation apparently initiated widespread extirpations of pines over the lowlands at middle latitudes. The remaining areas of suitable pine habitat acted as refugia for pines during the warm, humid periods of the Paleogene.

In general, the fossil evidence indicates three important refugial zones. The circumpolar high-latitude zone originally thought by Mirov to be the cradle of *Pinus* emerges not as a primary Mesozoic center of origin but as an important Eocene refugium. Although many Mesozoic fossils from the polar region that had been identified as pine were later discredited, credible new records, mostly pollen, confirm abundant pine at many high-latitude locations in North America and Eurasia during the warm periods of the Eocene (Table 3). Pines may have been even more widespread during the early Tertiary in polar regions than indicated by the geography of present land masses. Much of the Arctic Sea is shallow, and tectonic evidence suggests that there may have been more land above sea level in polar regions in the early Tertiary than at present (Smith et al., 1981; Wolfe, 1985). Land

connections between North America and Eurasia in the North Atlantic (Tiffney, 1985a, b) would have provided high-latitude corridors for east-west migration of pines during the Eocene (Tiffney, 1985a, b).

The major limiting condition for plant growth poleward now is light. The suggestion that the Earth may have had a lower angle of inclination in the early Tertiary (Wolfe, 1978), which would allow more light at high latitudes, has been discredited (Donn, 1982; McKenna, 1983; Barron, 1984). Alternatively, geophysical and climatic conditions of the early Tertiary may have increased availability of carbon dioxide and permitted plants to photosynthesize under light regimes that were prohibitive under conditions of lower carbon dioxide concentrations that apparently followed the end of the Eocene (Berner et al., 1983; Creber & Chaloner, 1984; Ruddiman & Kutzbach, 1989, 1991; Kerr, 1991).

Low latitudes in North America and Eurasia also appear to have been refugia for pines during the warm humid periods of the Eocene. There is ample evidence that conditions in general were warmer and drier at low latitudes than at middle latitudes in the Eocene. These conditions have been documented for the southeastern United States, Central America, Taiwan (Wolfe, 1975), southern China and southeastern Asia (Guo, 1980; Hsu, 1983), and Borneo (Muller, 1966). During the Paleogene, the southern boundary of Eurasia was the Tethys seaway. Since the Indian subcontinent had not collided with Asia, the area of the present Himalayas marked the Tethys coastline in Asia. Unlike circumpolar regions, the low-latitude dry areas were disjunct and disconnected, even between the southeastern United States and Central America, and refugial populations were unlikely to have been connected by broad migration routes (Wolfe, 1975).

There is less abundant fossil evidence for pines at low latitudes than at high latitudes during the Eocene. There are few early Tertiary plant-bearing deposits in the areas of special interest, such as Mexico, Central America, and the Mediterranean, primarily due to the lack of depositional sediments (Martin & Harrell, 1957; Eguiluz Piedra, 1985). Nevertheless, Eocene pine fossils have been found at low latitudes in southeastern Asia, the southeastern and southwestern United States, and in areas of southeastern Europe that were at low latitudes during the Eocene (Table 3). In Mexico, the single specimen of pine at Chiapas (14°N) from the Oligocene (one of the earliest Tertiary plant records in Mexico), and the abundance of pines in

TABLE 5. Distribution and affinities of select high- and low-latitude fossil pines from Miocene deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

Identification	Affinity	Location	Latitude/longitude		Age (Ma)	Reference
			Current	Paleo		
<i>Pinus</i> sp.	<i>Strobi</i>	Canada, Banks Island	72°N 122°W	78°N 92°W	Early	Hills et al. (1974)
<i>Pinus</i> sp.	genus	Canada	74°N 122°W	80°N 87°W	Early	Hills et al. (1974)
<i>Pinus</i> pollen	genus	MacKenzie Delta/Alaska	70–80°N 130–150°W	72–85°N 94–122°W	Early	Ritchie (1984)
<i>Pinus</i> pollen	genus	Northwestern Borneo	2°N 110°E	5°N 110°E	Early	Muller (1966)
<i>Pinus</i> pollen	genus	Alaska, Nuwuk	70°N 160°W	78°N 142°W	22–26	Wolfe (1972), (1977)
<i>Pinus</i> pollen	genus	Alaska, Wrangell Mountains	62°N 140°W	68°N 122°W	Middle	Wolfe (1969)
<i>Pinus</i> pollen	genus	Mexico, Veracruz	17°N 94°W	17°N 85°W	Middle	Graham (1976)
<i>Pinus</i> sp.	<i>Sylvestres</i>	Spain		not available		Klaus (1989)
<i>Pinus</i> sp.	<i>Sylvestres</i>	Greece		not available		Klaus (1989)
<i>Pinus</i> sp.	<i>Sylvestres</i>	Yugoslavia		not available		Klaus (1989)
<i>Pinus</i> sp.	<i>Sylvestres</i>	Romania		not available		Klaus (1989)

Veracruz (17°N) from the Miocene suggest that pines may have been present in Mexico and Central America earlier (Table 4). Similarly, pines were present in the Oligocene and abundant in Miocene deposits from southern Europe in the region of the Tethys (Palibin, 1935; Czecczott, 1954; Klipper, 1968; van der Burgh, 1973; Klaus, 1989).

Pines were not absent from middle latitudes during the Eocene. Their presence in select fossil deposits from interior western North America testifies to the presence of mid-latitude refugia. Pines in these regions more commonly date to the cool periods of the Eocene. During these times pine populations apparently expanded, whereas during the warm humid periods they contracted into narrow refugial areas where conditions were favorable. During warm humid periods, pines in interior western North America may have been fragmented into small local refugia and, therefore, poorly represented in fossil deposits.

The interior of western North America was anomalous for the Eocene world in having upland areas and centers of volcanism. Several of the pine-bearing deposits occurred at high elevations in Eocene calderas (Thunder Mountain, Idaho; Creede, Colorado), where climates were more temperate than elsewhere at middle latitudes. This region has been documented for angiosperm flora as being one of the first areas at middle latitudes in North America where climatic conditions became temperate during the Paleogene. Widespread volcanism along the cordillera added many cubic meters to the landscape in this region, building a highland that stretched from Arizona to Canada (Leopold & MacGinitie, 1972; Wing, 1987; Wolfe, 1987; Ruddiman & Kutzbach, 1991).

Other middle-latitude areas such as eastern Asia may have supported pines during the warm humid periods of the Eocene, although only western North America is known to have had important upland regions. Although the early Tertiary fossil record of eastern Asia is not as complete as in western North America, pines have been found at a few middle-latitude locations in the Eocene. In Japan, the first Tertiary pines date to the last cool period of the Eocene and are not documented for the warm period at the end of the Eocene (Huzioka & Takahashi, 1970; Wolfe, 1985). These Eocene records may represent marginal populations of species that were centered farther north and expanded southward during the cool periods. Boreotropical angiosperms occurred throughout Asia in the warm humid periods of the Eocene, although they do not appear to have extended as far north as in North America (Chaney, 1940; Hsu, 1983).

SECONDARY CENTERS OF PINE DIVERSITY

The widespread extirpation of pine populations from middle latitudes at the end of the Mesozoic is hypothesized to have led to extinction of many pine species and to have greatly depleted genetic diversity in others. Many Cretaceous fossil pines had combinations of traits not known in extant species and represent lineages that went extinct. Of two closely related pinaceous genera of the Mesozoic, *Pseudoraucaria* fossils have not been found in rocks younger than the Late Cretaceous, and the youngest *Pityostrobus* fossils date to the early Eocene (Miller, 1976). The disappearance in these two genera of many diverse lineages closely related to *Pinus*, represents major extinctions in the pine family during the early Tertiary.

Despite this depletion of diversity in pines and taxa related to pines, the tectonic events and consequent migrations of the early Tertiary appear to have culminated in the creation of several new centers of pine diversity and the evolution of new pine lineages. This change appears to have been due in large part to increased tectonic activity. Although the period from the Mesozoic through the Paleocene had been relatively quiescent and land elevations were generally low across the continents, by the late Eocene several regions were active tectonically. In subsequent epochs, volcanism and mountain-building became increasingly important locally and globally.

The uplift of new mountain ranges and volcanic activity created environmental heterogeneity. Areas where active mountain-building coincided with Paleogene pine refugia are hypothesized to have become centers of pine radiation. Local climatic diversity was created by elevational differences, and rainshadow and other orographic effects developed. Diversity of soils evolved, with many areas having newly disturbed sites following volcanic activity. Mountain-building created new barriers to migration and gene flow, causing lineages to be fragmented and isolated. All these conditions must have favored divergence and speciation in pines. Conversely, refugial areas that did not undergo major early Tertiary mountain-building, such as the high-latitude zones, were centers from which pines migrated in the Neogene, but did not become important centers of pine speciation.

Although pines expanded and contracted from refugial areas during the fluctuating warm and cool periods of the Eocene, it was the terminal Eocene event that seemed to initiate major migrations out of refugia and to coincide with a time when pines appeared more widespread at middle latitudes. These

migrations provided further opportunities for divergence. As new environments were encountered, genetic isolation may have occurred, and possibilities for genetic drift by founder effects arose, as well as for hybridization with formerly isolated lineages.

EVOLUTION WITHIN *PINUS* IN RELATION TO EOCENE REFUGIA

By the end of the Paleogene, all subsections of *Pinus*, with the possible exception of *Cembrae*, had evolved (Axelrod, 1986; Millar & Kinloch, 1991). The events of the early Tertiary probably gave rise to at least two subsections, speciation of lineages within several subsections, and the current biogeography of many subsections and groups within several subsections.

The hypothesis that pines were concentrated into refugial regions during the Eocene explains the current bimodal distribution and pattern of diversity of pines at low and high latitudes (see Axelrod, 1986, for maps of pine subsections). In North America three subsections, *Cembroides*, *Leiophyllae*, and *Australes*, appear to have been concentrated in southern refugia during the Eocene and radiated from them subsequently (Axelrod, 1986). Subsections *Cembroides* and *Leiophyllae* seem to have been limited to western North America and Central American refugia whereas *Australes* may have had refugial areas with a broader southern distribution, including the Gulf Coast (Tables 3, 4). The current distribution of *Australes* in both the southeastern United States and in Central America/Caribbea suggests that *Australes* may have had refugia in both regions. Although not identifiable to subsection, the abundant pine fossils of the Eocene from southern Alabama (Table 3) are from a site that is within the range of several extant species of *Australes*. Small genetic distances between taxa of *Australes* versus *Leiophyllae* (Strauss & Doerksen, 1991) suggest that these subsections were in contact or did not diverge from each other until after the Mesozoic.

Four subsections in North America appear to have been fragmented by Eocene events into several refugial regions. A division into northern and southern refugia in subsection *Sylvestres* is indicated by the extant lineages of *P. resinosa* (40°–52°N) and *P. cubensis* (restricted to Cuba, 22°N). Eocene fossils with affinities to *Sylvestres* that support a northern refugium have been found in British Columbia and northern Washington (Table 3).

Subsection *Contortae* similarly seems to have been divided into northern and southern refugia:

the lineages leading to *P. contorta* and *P. banksiana* clearly had northern origins and boreal adaptations, whereas those leading to *P. clausa* and *P. virginiana* had southeastern affinities. Eocene fossils with affinities to *Contortae* have been found in northern Washington, and Oligocene fossils in British Columbia, corroborating a northern refugium (Tables 3, 4).

Subsection *Ponderosae* also may have had both northern and southern refugia. There are 10–17 species endemic or nearly endemic to Mexico and Central America, whereas wide-ranging *Pinus ponderosa* has a northern distribution and northern ecological affinities in its habitat preference and vegetation associates. Early Tertiary pines most closely allied to *Ponderosae* have been found in British Columbia (Eocene, Table 3), northern Washington, and Montana (Oligocene, Table 4). Lineages of *Ponderosae* may have been concentrated also in Rocky Mountain refugia, as suggested by Oligocene fossils from Colorado with affinities to this subsection (Table 3). A recent re-evaluation of evolutionary patterns in *Ponderosae* also indicates northern and southern division in the subsection (Lauria, 1991). *Pinus ponderosa* is considered to originate in northern latitudes, while other distinct phylads had southern origins in Mexico and Central America.

Subsection *Strobi* has northern and southern lineages in North America. Ancestral lineages of *Pinus monticola* and *P. strobus* would have migrated from northern refugia, and those of *P. strobiformis*, *P. ayacahuite*, and *P. chiapensis* (Martinez) Andresen (distinct from *P. strobus*, of which it was once classed as a variety; Andresen, 1964, 1966) would have migrated from southern refugia. Northern refugia are corroborated by Eocene fossil pines allied to subsection *Strobi* from British Columbia (Table 3). Lineages of subsection *Strobi* may also have been fragmented into middle-latitude refugia in the Rocky Mountain region, represented currently by *P. flexilis* and possibly *P. strobiformis*, and by Oligocene fossils from Idaho and Colorado (Table 4).

The small subsection *Balfourianae* is an ancient lineage (Kossack, 1989; Strauss & Doerksen, 1991; Millar & Kinloch, 1991) that appears to have been entirely concentrated in middle-latitude Rocky Mountain refugia during the early Tertiary. Present distribution of the three closely related species is in the Rocky Mountain/Great Basin/Sierra-Cascades Ranges of the western United States between 35°N and 41°N latitude. Early Tertiary fossils with probable affinities to this subsection were found in Idaho (Eocene) and Colorado (Oligocene) (Tables 3, 4).

In Eurasia, sequences of conifer-bearing deposits from the early Tertiary are not as widely distributed as in North America, but evidence for pine evolution in relation to refugia exists. Three ancient subsections, *Canarienses*, *Pineae*, and *Krempfiani*, have extant species restricted to regions that were along the Tethys seaway. Fossil evidence exists for a Tethys refugial area of pines in southeast Asia, in the region where *P. krempfii* now occurs. Pine was recorded in abundance throughout early Tertiary strata and in coastal southeast China and in northwest Borneo (Tables 3, 4). Other fossil floras for southeast Asia include temperate taxa, suggesting that pines would have found favorable habitats.

In western Europe, the boreotropical angiosperm flora was recorded abundantly from 45°N to 56°N (Chaney, 1940). Although there are no fossil records from currently low latitudes in Europe, pine fossils are known from areas of southeast Europe that were along the Tethys seaway (Chiguriaeva, 1952; Mirov, 1967). Furthermore, there is indication of dry zones in the middle Eocene along the European and north African Tethys, indirectly supporting the occurrence of pines there (Parrish et al., 1982; Parrish, 1987). Fossil pines allied to *Canariensis* and *Pineae* were widespread along the Tethys seaway in western Europe during the Miocene (reviewed in Klaus, 1989), suggesting more widespread distributions for both subsections in this region in the early Tertiary.

As in North America, in Eurasia several subsections appear to have been divided by Eocene events into northern and southern refugia. In *Sylvestres*, lineages represented by extant *P. sylvestris* most likely migrated from northern refugia. Eocene pine fossils from high latitudes in western Siberia allied to *Sylvestres* corroborate a northern refugium in Eurasia. The remaining 14 extant species in *Sylvestres*, excluding *P. densiflora*, and *P. thunbergiana*, and possibly *P. yunnanensis*, represent lineages from southern refugia. Although few Eocene deposits from southern Europe are plant-bearing, abundant fossils allied to *Sylvestres* are known from Oligocene and Miocene deposits in the Tethys region (Table 5; Palibin, 1935; Czeczott, 1954; Klipper, 1968; van der Burgh, 1973; Klaus, 1989). The exceptional three species may represent lineages from middle-latitude refugia, as documented by fossil pollen of unknown affinity from the Eocene and Oligocene of Japan and northern China (Tables 3, 4). Subsection *Gerardianae* may have been divided between a southern Tethys refugium, as represented by extant *P. gerardiana*, and a middle-latitude refugium in northern China,

as represented by extant *P. bungeana*, and by early Tertiary deposits containing pine pollen in China (Tables 3, 4).

Refugia for subsection *Strobi* in Eurasia were mostly along the Tethys. Of the eight extant Eurasian species in the subsection, only *P. parviflora* seems clearly allied to lineages derived from more northerly refugia. The remaining seven modern species are all distributed along the former Tethys region. No early Tertiary fossils from Eurasia have been specifically allied with subsection *Strobi*, although Miocene fossils of the subsection testify to their presence in that region (Klipper, 1968).

The consequence of certain Eocene refugia becoming secondary centers of pine diversity is best described for Mexico and Central America. Although parts of the Mexican and Central American isthmuses were transiently under water during the Mesozoic (Kellum, 1944; Eguiluz Piedra, 1985), they were elevated during the Eocene and later Tertiary. Tectonic activity was especially great in Mexico during the late Eocene and Oligocene/Miocene. Tertiary volcanic activity significantly reshaped the Sierra Madre Occidental and created the Sierra Madre Oriental and the Transversal Neovolcanic Axis. Uplift in the early Eocene rebuilt almost the entire ranges of the Sierra Madre del Sur and Sierra Madre de Chiapas (Eguiluz Piedra, 1985).

Mexico and Central America are home to as many as 83 extant taxa of pines, including 48 species, 21 varieties, and 14 forms (Eguiluz Piedra, 1985). Within many subsections, extensive radiation and speciation are ongoing, which has been attributed to active mountain-building that began in the Eocene (Eguiluz Piedra, 1985; Axelrod, 1986; Karamangala & Nickrent, 1989; Lauria, 1991). Active radiation is evidenced by closely related species clusters, with subsections *Ponderosae* and *Cembroides* the best examples. There are 10–17 species of *Ponderosae* (Eguiluz Piedra, 1985) endemic to Mexico and Central America and 10–16 species in *Cembroides* (Zavarin, 1988). The difficulty of separating the taxa of *Cembroides*, implying close genetic relationship, has led some botanists to the conclusion that *Cembroides* is a young subsection. Phylogenies based on DNA-sequence divergence indicate, however, that section *Parrya*, including subsection *Cembroides*, is ancient (Kossack, 1989; Strauss & Doerksen, 1991). Ancestral *Cembroides* lineages would have been concentrated in Mexican/Central American refugia during the early Tertiary, and the major pulse of radiations now occurring in the subsection may have begun in the early Tertiary.

Two subsections may have originated in Mexican/Central American refugia (Axelrod, 1980, 1986). Unlike other subsections, *Oocarpae* and *Sabinianae* have no Mesozoic fossil record and are not clearly documented until the Miocene. On the basis of specialized and apparently derived morphological adaptations (Shaw, 1914, 1924; Little & Critchfield, 1969; Klaus, 1980; van der Burgh, 1984), these subsections have long been considered to have originated recently. Phylogenetic analysis of DNA divergence also confirms their relative youth, especially of *Oocarpae* (Strauss & Doerksen, 1991). Using fossil and floristic evidence, Axelrod (1980) traced the origins of the northern (California/Baja California) elements of *Oocarpae* to mainland Mexico/Central America prior to the Miocene. The northern lineages appear to have diverged by the time they reached California (Millar et al., 1988), indicating that the radiation events occurred farther south in the early Tertiary. Although the systematic coherence of the extant Latin American taxa of *Oocarpae* remains uncertain, genetic relationships of some Latin American species link *Oocarpae* with *Austroales* and *Ponderosae* (Critchfield, 1967), both of which have Mesozoic fossil records, appear to have had Mexican/Central American Paleogene refugia, and may have been ancestral to *Oocarpae*.

Subsection *Sabinianae* has a limited fossil record consisting of a single taxon allied to *P. sabiniana* and confined to southern California (Axelrod, 1986). Fossils are known only from the late Miocene through Quaternary, and Axelrod (1981) traced the origin of the extant species to Mexican species of *Ponderosae*. Genetic relationships of extant taxa link *Sabinianae* with *Ponderosae* on the basis of terpene affinities (Zavarin et al., 1967) and crossing evidence (Critchfield, 1966; Conkle & Critchfield, 1988). Together this evidence points to a Mexican/Central American origin of *Sabinianae* from early Tertiary *Ponderosae* lines.

PLEISTOCENE VERSUS EOCENE IMPACTS

In this paper I document that tectonic, climatic, and biogeographic events of the Eocene had a major impact on pine distributions and evolution. The question may arise whether the effects of the Eocene were so confounded by subsequent events of the Tertiary and especially the Quaternary as to be indecipherable. I will address only the Pleistocene, since its potential was probably the greatest.

The Pleistocene was a time of profound change unprecedented in the history of the Earth. In some

ways the Pleistocene was analogous to the Eocene. The Pleistocene was also an epoch with fluctuating climates, but the deviation from temperate climates in the Pleistocene was toward glacial conditions, whereas in the Eocene it was toward tropical episodes. The amplitude in average temperature between glacial and interglacial periods of the Pleistocene (5°–10°C, Bowen, 1979) was about the same as estimated for the cool and warm periods of the Eocene. The Pleistocene differed in lasting only 2 million years (cf. 20 million years for the Eocene), in having many more cycles (16–18, Bowen, 1979), and in having alternating periods of unequal duration with glacials longer than interglacials.

The events of the Pleistocene had enormous effects on vegetation, including pines. In northern latitudes, pine distributions were displaced by continental ice sheets (e.g., *Pinus contorta*/*P. banksiana*, Critchfield, 1985); in mountainous regions elsewhere, species migrated up or down in elevation (Miki, 1957; Van Devender & Spaulding, 1979). Along coasts and in other lowlands, pine populations shifted north and south in response to the climate cycles (e.g., *Oocarpae*, Axelrod, 1980; Millar, 1983). Concomitant to the shifts in distribution of pines were major changes in the genetic structure of species. The flux of population expansion and contraction, coupled with drastically changing selection regimes, affected the structure of genetic variation within species and allowed some species to hybridize (Critchfield, 1984, 1985; Kinloch et al., 1986; Millar, 1989).

In general, however, the Pleistocene does not appear to have completely reshuffled the genus in the way the Eocene did, and many of the Tertiary patterns and the evolutionary events that date to that period have been maintained. Notwithstanding the existence of local refugia, Pleistocene events primarily affected *Pinus* in a gradient from north to south, with the effect that species and populations shifted south then north (or down then up in elevation) following the cycle of the glacial and interglacial periods.

The impact of the Eocene, by contrast, was greatest in the latitudinal center of the genus and had the effect of dissecting the genus and concentrating pines into widely disjunct regions. Furthermore, during the early Tertiary, and unlike the Pleistocene, almost no upland regions (except in interior western North America) could offer local refuge from unfavorable climates. Whereas many pine species appear to have gone extinct in the early Tertiary, no pine extinctions in North America are attributed to the Pleistocene (Critchfield,

1984), although western Europe suffered a significant impoverishment of pine flora (Klipper, 1968). Some speciation, for example, in *Balfourianae*, *Cembroides*, and *Oocarpae*, seems to have been triggered by the Pleistocene, but no major new trends have emerged.

Insufficient time has elapsed since the close of the Pleistocene for its full impact to be felt on evolution in *Pinus*. Patterns initiated by the Pleistocene appear minor compared to the effects of the Eocene and are insufficient to erase the evolutionary impacts of the early Tertiary. Thus, many of the major evolutionary patterns of the early Tertiary can still be traced in the biogeography and relationships of extant pines.

VALIDATION OF THE HYPOTHESIS

The arguments developed in this paper result in a working hypothesis about the effect of the Eocene on pine evolution. The hypothesis is a reconstruction of pine history based on available information from the fossil record, climatic and tectonic evidence, and biogeographic record of angiosperms and conifers. Many gaps in information exist that, if filled, would corroborate or negate this hypothesis. These gaps fall into several categories. Expanded fossil records are urgently needed, especially in regions hypothesized as Eocene pine refugia that currently have meager fossil documentation. These include Paleogene records for Central America and Mexico, low latitudes along the European Tethys, and high latitudes in eastern Asia. Technologies that allow more accurate identification of fossil affinities for macro- and especially micro-fossils at intrageneric levels would help in tracking the biogeography and evolution of these groups. These technologies need to be applied to published fossil floras, with revised taxonomic lists. Certain pine lineages have especially meager fossil records, including Cretaceous records of sections *Parrya*, especially *Gerardianae* and *Balfourianae*, and Cretaceous/early Tertiary records of section *Pinea*. Accurate dating of fossils and correlation with paleoclimatic and paleogeological events will also help to track the fine scale paths of these pines. Finally, existing and emerging genetic and molecular technologies should be applied to estimate genetic distances and divergence times among subgeneric groups. Such genetic techniques will allow tests of the hypothesized times of geographic isolation.

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