Poleward Migration of Early Angiosperm Flora

Angiosperms only displaced the relict Jurassic-type flora at high latitudes in Late Cretaceous time.

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Cretaceous floras record one of the major events in the biological history of the earth: the transformation from a world dominated by typically Jurassic-type ferns, seed ferns, and gymnosperms early in the period to a later Cretaceous landscape in which flowering plants of near-modern type were characteristic and world-wide in their distribution. This change in vegetation raises many problems for consideration, one of which pertains to the geographic center of origin of the group. The widely divergent opinions regarding this problem are evident in viewpoints which have favored temperate Holarctica (*1*), the Southern Hemisphere (*2*), Antarctica (*3*), the ancient tropical belt (*4*), and Southeast Asia (*5*) as the general area of early angiosperm evolution. I recently reexamined these ideas while preparing a review paper on the evolution of flowering plants in which attention was directed chiefly to the origin and evolution of present-day distribution patterns. As an outcome of this analysis, additional evidence was uncovered which strengthens the view that flowering plants evolved in tropical regions during pre-Cretaceous time. To avoid any possible confusion, it must be emphasized that this ancient tropical belt—which appears to reflect the normal climate of most of geologic time—was quite extensive. To judge from the paleoclimatic implications of fossil plants, the belt extended at least to latitudes 45°N and 45°S from the Permian into the Cretaceous, the interval during which angiosperms appear to have been evolving prior to their first occurrence in abundance (*4*).

The evidence supporting the belief that flowering plants originated in this broad tropical belt during pre-Cretaceous time is provided by the spatial relations of the earliest floras that contain angiosperms. The spatial relations seem to show that flowering plants first entered the lowland record within the tropical belt at lower middle latitudes at the beginning of the Early Cretaceous, that they reached high latitudes late in the epoch, and that with few exceptions they became dominant there only in Late Cretaceous time. In this article, the evidence which appears to demonstrate this relation is summarized first, and then its implications are outlined.

Early Cretaceous Sequences

In order to present concisely and clearly only the significant data which bear on the problem, the floras have been grouped according to the five major regions where they occur in sufficient number to warrant consideration. For each area a diagram has been prepared in which the floras are plotted according to latitude, age, and angiosperm content (Figs. 1–5). The curve in each figure represents an approximate time line that largely separates floras with no angiosperms (below) from those with them (above). The percentage of angiosperms shown for each flora is not precise because some of the floras need taxonomic revision and others are based on an inadequate number of samples. However, the critical point is not the exact percentage but the relative abundance—whether they are rare (less than 10 percent), moderately common (10 to 30 percent), common (30 to 60 percent), abundant (60 to 80 percent), or predominant (over 80 percent).

With respect to the age assignment of the floras shown in the figures, those marked with an asterisk occur in sections that interfinger with the marine Cretaceous rocks which have been zoned chiefly on the basis of ammonites. Thus, they afford a relatively sound basis for determining the essential contemporaneity of sedimentary units and their contained fossils in widely separated parts of the world; current research on marine Cretaceous microfossils (foraminifera, discoasterids) has largely substantiated and further refined the correlations made on the basis of the megafaunas. A number of the remaining floras (marked by a dagger in the figures) are reasonably well fixed in time on the basis of their occurrence in stratigraphic sections which are dated either by vertebrate or by marine faunas.

North American region (Fig. 1). The oldest floras containing angiosperms are the Patuxent of Maryland-Virginia and the Lower Horsetown of California. Floras of generally similar age at higher latitudes, such as the Kootenai of Montana, Alberta, and the British Columbia, the Nikanassin of Alberta and British Columbia, and the Tantalus from Yukon Territory, Canada, are not now known to contain flowering plants. Angiosperms do not appear in Canada until Aptian time, when they make up only 1 to 2 percent of the Lower Blairmore and Gething floras. At the same time, however, the angiosperm content of floras at lower latitudes had increased, as shown by the Funson (45 percent) of Wyoming; even the older Arundel of Maryland has 25 percent angiosperms. A predominant Jurassic aspect was maintained by the floras at higher latitudes well into the Albian stage, as illustrated by the Kennicott flora of south-central Alaska and by the Corwin flora from the arctic seacoast of Alaska, neither of which is now known to contain flowering plants. By contrast, floras of similar age at middle latitudes—for instance the Upper Blairmore (40 percent) and Cheyenne (50 percent)—have a prominent angiosperm content.

These relations show that, in general, angiosperms entered lowland areas at higher latitudes in rocks of successively younger age and only displaced the relict Jurassic vegetation there during the Late Cretaceous.

Northeast Asian region (Fig. 2). Angiosperms have not yet been described from the numerous floras of Neocomian age that are known in northeastern Asia.

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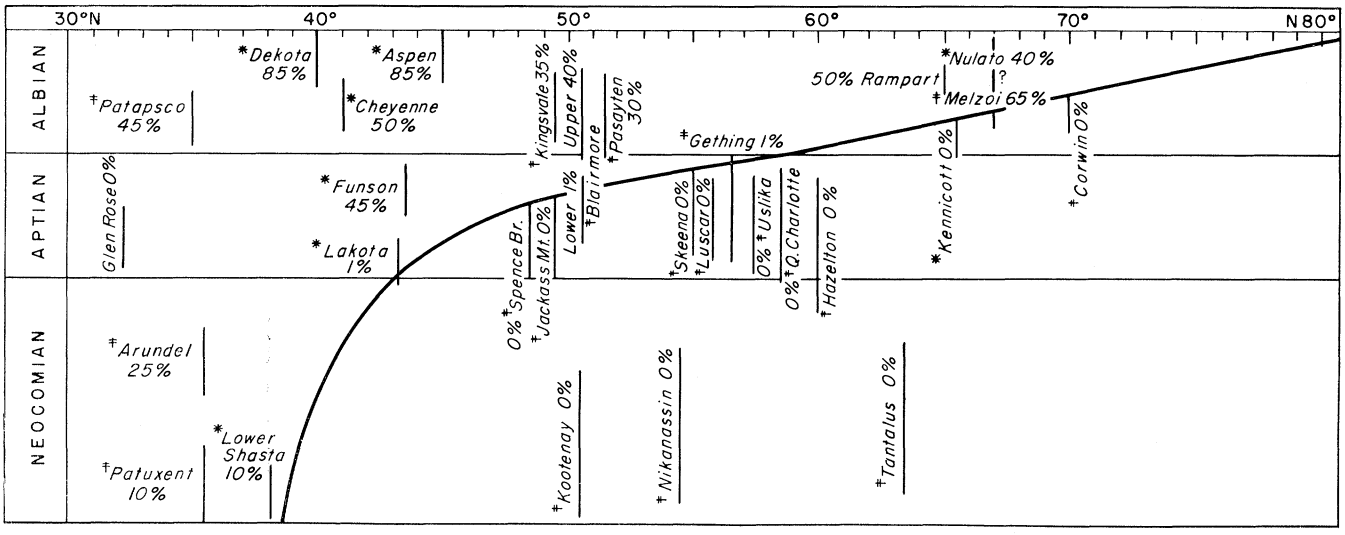


Fig. 1. North American region. Time-space relations of Early Cretaceous floras and the percentage of angiosperms they contain.

They first appear in the Aptian of Ussuriland (Suchan). By Albian time they made up nearly 45 percent of the Upper Keisho flora of Korea, but at higher latitudes in Siberia, Albian floras contain few members of the alliance. As in Alaska and Greenland, the delayed appearance of angiosperms in the lowland floras of northeast Asia is reflected in the fact that even the mid-Cretaceous (Cenomanian-Turonian) floras of the region rarely contain more than 40 percent angiosperms. Thus, the Yezo flora of Hokkaido has approximately 40 percent flowering plants; the Gyliakian of northern Sakhalin, 30 percent; and the Pekuleni of Anadyrland, 20 percent.

Although the evidence is less complete than for North America, it suggests that angiosperms gradually invaded higher latitudes from more southerly areas during the Early Cretaceous, and that northern Siberia was a refuge for remnants of the Jurassic flora well into the Late Cretaceous, a view expressed earlier by Vakhrameev (*6*).

West European region (Fig. 3). The general time-space relations of the more important Early Cretaceous floras show that angiosperms were represented in Portugal during the Neocomian. However, contemporaneous floras to northward, such as the Wealden of England, France, Belgium, and adjacent areas, do not contain them, nor are they represented in the floras from Spitzbergen, Franz Josef Land, the King Karl Island in the Arctic Ocean. During Aptian time the floras of Portugal contained 25 percent angiosperms, but angiosperms are less abundant in the Greensand of England, where they are represented only by wood, which probably was carried into the lowland basin from bordering highlands. To the northward, the Aptian floras of Klin, U.S.S.R., and Pattorfik, Greenland, do not contain angiosperms.

The Kome flora of Greenland, with 10 percent angiosperms, was once considered to be the oldest Cretaceous flora containing flowering plants. This led Seward, Berry, and others to champion the idea that flowering plants had their origin in high northern latitudes from which they gradually spread southward during the Cretaceous. More recent evidence indicates that the Kome is relatively high in the Early Cretaceous, and that it may be as young as Albian (7). Such an assignment is wholly consistent with the time-space relations of angiosperms in the well-dated Albian floras of Alaska and northeastern Siberia discussed above, and on this basis the Kome is here assigned an Albian age (Fig. 3). Such an assignment is consistent with the persistence of a dominant (55 to 60 percent) Jurassic-type element into the Late Cretaceous (Turonian, Campanian) Atane and Patoot floras of Greenland. By contrast, floras of similar and of even greater age (Cenomanian, Albian) at lower latitudes in Europe and North America are preponderantly angiospermous.

These relations support the thesis that angiosperms were migrating northward during the Cretaceous, and that they only displaced the older Jurassic-type vegetation at high latitudes during the Late Cretaceous.

Australia–New Zealand region. (Fig. 4). Angiosperms are not now known in floras of Neocomian age in the Australia–New Zealand region. They first appear in Australia in the Styx River and Winton floras of transitional Aptian-Albian age. The evidence in New Zealand, as revealed chiefly by recent pollen studies, shows that flowering plants entered the record there only in Albian time. The small flora from Kaipara, New Zealand, associated with ammonites of Turonian age, indicates that a Jurassic-type floral element was dominant well into mid-Cretaceous time in the lowlands of the region, much as it was in northern Alaska, Greenland, and Siberia.

The data are still incomplete, it is true, but the results to date agree with those indicated for the other regions discussed above.

South American region (Fig. 5). At the present time only a few floras are known from South America, yet they are sufficiently significant to warrant comment. The Lago San Martin flora, which has strong Jurassic affinities and was assigned to the Neocomian with considerable reservation by Halle, is now known, on the basis of associated ammonites, to overlap the Aptian-Albian boundary. The older floras of the region, apparently Neocomian, do not contain flowering plants. The data thus show that angiosperms did not invade the lowlands of southern Patagonia (latitude 45°S) until late in the Early Cretaceous (Albian), when they were also appearing in New Zealand at a comparable latitude.

This evidence leads to the inference that Jurassic-type vegetation persisted at high southern latitudes well into the Late Cretaceous, much as it did in the Northern Hemisphere.

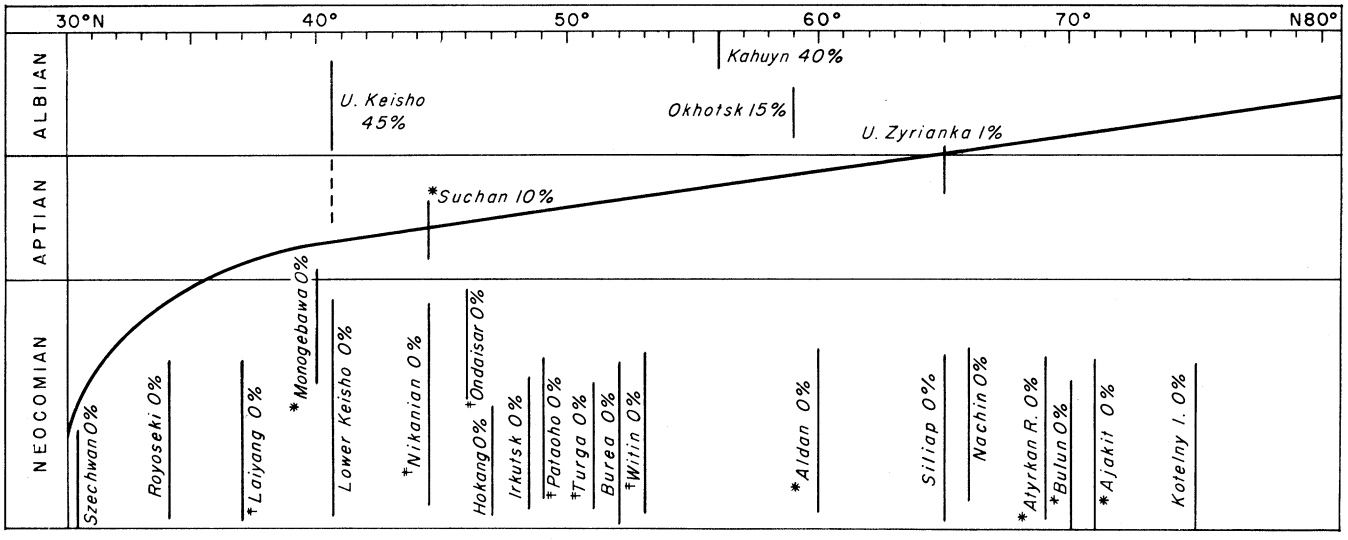
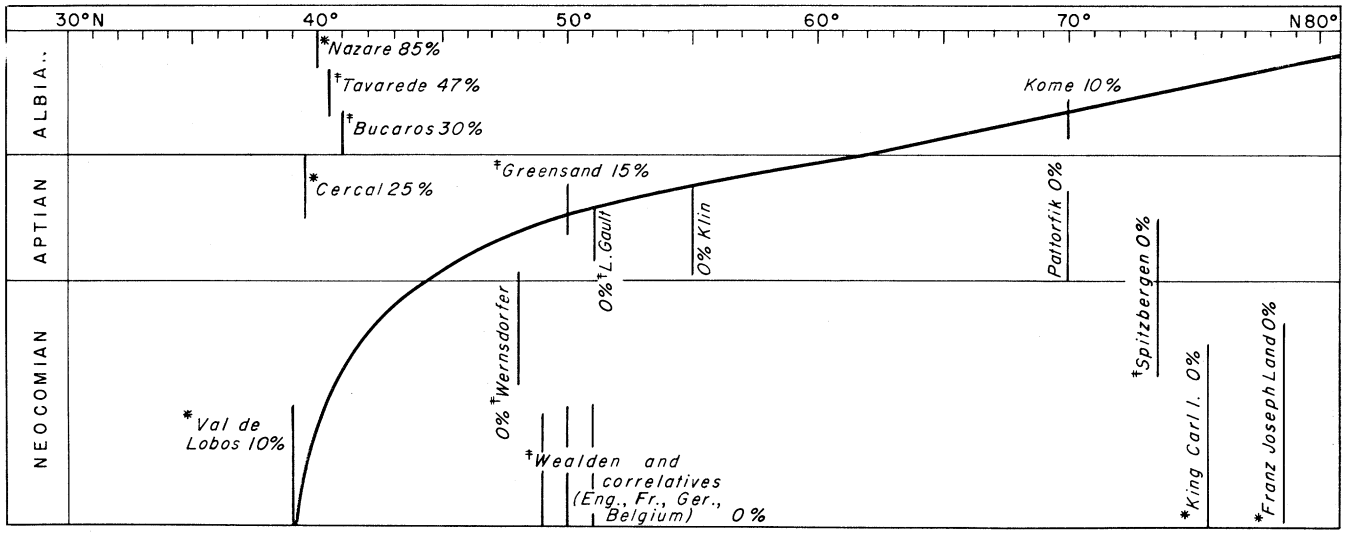


Fig. 2. Northeast Asian region. Time-space relations of Early Cretaceous floras and the percentage of angiosperms they contain.



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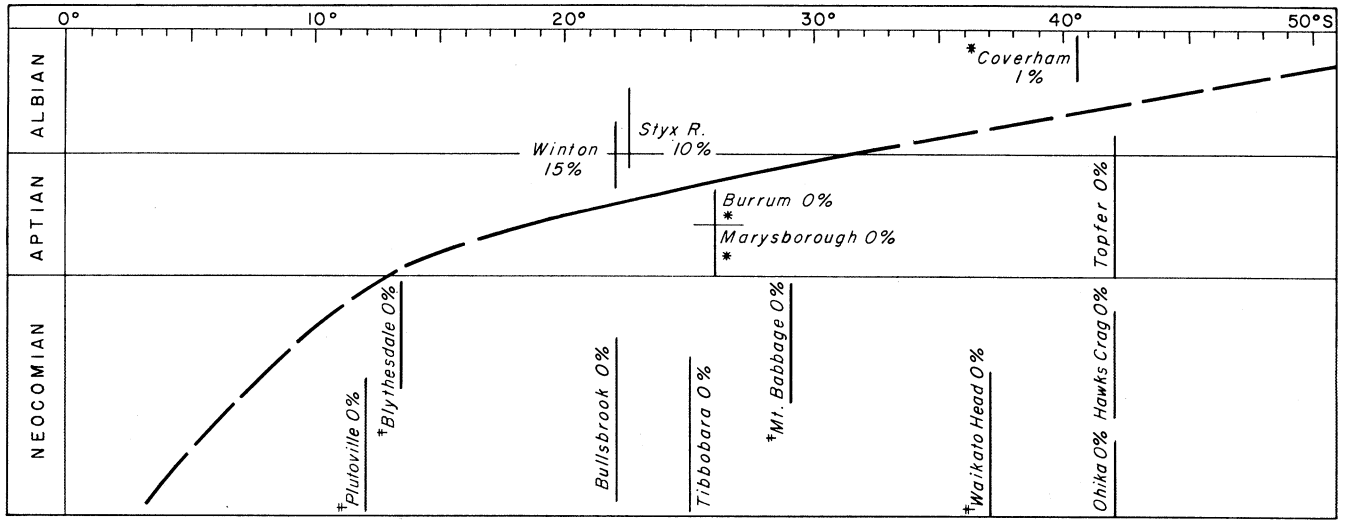

Fig. 4. Australia-New Zealand region. Time-space relations of Early Cretaceous floras and the percentage of angiosperms they contain.

Discussion

Available evidence for all regions thus indicates that angiosperms initially invaded lowland basins at generally lower latitudes and appeared in the record at higher latitudes only in the later part of the Early Cretaceous. Even by mid-Cretaceous (Cenomanian-Turonian) time, many high-latitude floras still had a prominent relict Jurassic element (more than 50 percent), whereas floras at lower latitudes were preponderantly angiospermous. This poleward migration of angiosperms during Early Cretaceous time can best be explained on the assumption that angiosperms evolved within the ancient tropical belt (latitudes 45°N to 45°S). With such a center of origin, it naturally follows that flowering plants would appear first in the record at lower latitudes and enter the lowland basins of higher latitudes at a later time. This conclusion, based on the time-space relations of angiosperms, agrees with both distributional and evolutionary evidence provided by Late Cretaceous and Cenozoic flowering plants, which also suggests that the phylum evolved within the tropical zone (*4*). The absence of angiosperms from the record there in pre-Cretaceous time seems chiefly due to the fact that they were confined to upland areas earlier in their history.

Several important factors appear to account for the fact that angiosperms did not invade the lowlands at a given latitude simultaneously during any particular stage of the Early Cretaceous.

1) If angiosperms were evolving in upland areas prior to the Cretaceous, they would have initially entered lowland basins situated near mountainous tracts. This seems to explain their early appearance at lower middle latitudes in California, Maryland, and Portugal. Conversely, lowland basins situated in nearly level regions generally remote from upland angiosperm populations were invaded at a somewhat later date. Such a relation may explain, at least in part, their apparent absence from the Neocomian floras of such tropical regions as India, northern Australia, central Africa, and Venezuela; available evidence indicates that the sedimentary basins of these regions were situated in low-lying tracts generally remote from areas of high relief.

2) An edaphic factor may account for their delayed appearance in the lowland record in some regions. Many of the Early Cretaceous basins which have yielded fossil floras were typified by conditions favorable for coal formation. These swampy lowland basins were dominated by ferns, seed ferns, and various gymnosperms which were highly adapted to such environments. By contrast, flowering plants were evolving chiefly in well-drained, upland regions and only became adapted to swampy sites secondarily. Thus, their late appearance in lowland areas in some basins, even though these basins were bordered by uplands, may have been due to the persistence of swampy sites of wide extent which they could not yet invade. Future pollen studies in such basins may reveal that flowering plants actually were present in the nearby highlands.

3) Favorable relict sites probably enabled the older Jurassic-type vegetation to persist for a somewhat longer interval in some areas, much as the Tropical-Tertiary geofloras lingered on the west coasts of the northern continents at middle latitudes into the Late Miocene.

4) The factors involving transport and preservation may explain the absence of angiosperms from the record in some cases. For example, the Aptian Glen Rose flora of Texas is preserved in the marine Glen Rose limestone. The plant collection represents drifted material composed chiefly of structures well suited to transport, such as stems, twigs, and cones. Thus, it is possible that angiosperms, which were only moderately common at this latitude (32°N) during the Aptian, did not survive transport to this marine site of deposition. This would be particularly true if the low, swampy shores (coal is found in the section) were dominated by coniferophytes, cycadophytes, and ferns which were persisting in a favorable relict site, and if flowering plants were on more distant, well-drained slopes sufficiently remote—perhaps only a few miles away—to preclude their occurrence in the marine section.

5) A combination of these factors may also explain the slightly different times of appearance of angiosperms in the record in a given region. For instance, some of the Albian floras of Alaska (see 7) are reported to occur in well-dated marine sections, but the percentage of angiosperms in them deviates from the idealized curve in the diagram (Fig. 1). We must not forget, however, that this region is very complex structurally, that the sections are incompletely exposed, and that many of the collections were

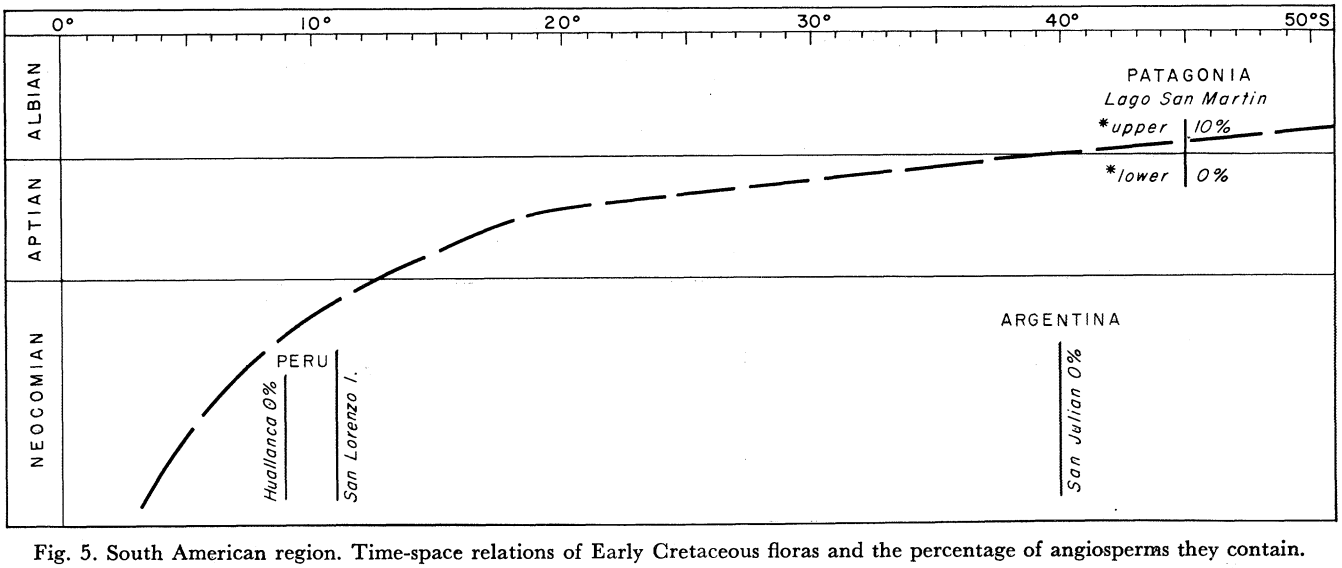

Fig. 5. South American region. Time-space relations of Early Cretaceous floras and the percentage of angiosperms they contain.

secured by early reconnaissance expeditions. Thus, some of these Alaskan floras may actually have stratigraphic positions other than those to which they have been assigned. Pertinently, Martin (*8*) notes that some of the marine fossils may come from older rocks which were erroneously correlated with the plant-bearing beds.

These limitations, as well as the general scarcity of fossil floras in the Southern Hemisphere, must be taken into account, but the evidence nonetheless suggests that, for a given stage, angiosperms had penetrated farther north than south. For instance, they are represented in the Neocomian of California, Virginia, and Portugal, but no Neocomian flora now known from the Southern Hemisphere contains them. Similarly, during the Aptian they had ranged northward to latitude 50°N in Ussuriland, western Canada, and England, yet in the Southern Hemisphere they occurred only at low latitudes during this stage.

Furthermore, whereas angiosperms had reached latitude 70°N in the Albian (Greenland, northern Alaska, northern Siberia), they were only commencing to appear at middle latitudes (45°S) in the Southern Hemisphere (New Zealand, Patagonia) at this time. By contrast, at middle latitudes in the Northern Hemisphere, most Albian floras have a dominant angiosperm element. These geographic relations are sufficiently striking to suggest that flowering plants may have evolved chiefly in the tropical parts of the Northern Hemisphere. However, since angiosperms may already have been in existence in upland areas by the Permian (*4*), and because the record of the group is exceedingly fragmentary into the Early Cretaceous, the data obviously do not permit us to suggest any one area as the cradle of origin.

Apart from these relationships, which indicate that flowering plants evolved in generally tropical latitudes, the evidence demonstrates that age analysis of Early Cretaceous floras must take into account time-space relations analogous to those shown by Tertiary forests (*9*). The numerous differences in apparent age which have existed for nearly a century as deduced from the testimony of fossil plants and from that of marine invertebrates—often recovered from the same section—seem chiefly due to the fact that the time-space factor has not previously been considered by paleobotanists. As we have seen, typically Jurassic-type vegetation persisted in scarcely modified form at high northern and middle southern latitudes well into the closing stage (Albian) of the Early Cretaceous. This survival clearly accounts for Knowlton's (*10*) assignment of the Corwin flora from the Arctic seacoast of Alaska to the Jurassic, though recent evidence shows that the plant-bearing beds overlie conformably a marine section containing later Albian ammonites (*11*).

Similarly, we can now understand Halle's (*12*) uncertainty over the age of the Lago San Martin flora from Patagonia. Halle felt that it was Jurassic but assigned it to the Early Cretaceous (Neocomian) because fragments of Cretaceous-type ammonites were found in the section; more recent collections show that these marine fossils are transitional Aptian-Albian (*13*). Arber (*14*) also noted the Jurassic character of the flora from Waikato Head, New Zealand, but pronounced it Neocomian because two species of angiosperms were included in the collection. We now know that the specimens studied by Arber were mixed from two different localities and that the angiosperms are from much younger rocks (*15*); further, the Waikato Head flora apparently is underlain by rocks of Neocomian age. Lastly, we may recall that the floras from Spitzbergen, Franz Josef Land, King Karl Island, and Kotelny Island in the Arctic Ocean, as well as many of those in arctic Siberia, originally were assigned to the Jurassic, though they occur in sections which yield Cretaceous marine invertebrates (*16*).

Summary

1) During the opening phase of the Early Cretaceous (Neocomian), angiosperms commenced to invade lowland basins of deposition at generally lower latitudes. They reached high northern and middle southern latitudes at the close of the epoch (Albian) and only replaced the relict Jurassic-type vegetation at high latitudes during the early part of Late Cretaceous time.

2) This poleward migration of angiosperms is consistent with the theory that the phylum had its center of origin and dispersal at tropical latitudes, which ranged between 45°N and 45°S in pre-Cretaceous time.

3) Recognition of the time-space factor involved in the Early Cretaceous poleward migration of angiosperms removes most of the conflicts in the testimony on age supplied by fossil plants and by marine invertebrates—conflicts which have persisted for nearly a century (*17*).

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