

Rates of floral turnover and diversity change in the fossil record

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DR VENKATACHALA, Dr Pascal, Dr Singh, and ladies and gentlemen. I was pleased and honored to be asked to give this lecture honoring the birthday of Professor Sahni. The work I will be talking about was done in North America, but the methods that are the heart of the talk can be applied anywhere.

Many palynologists spend much of their time examining samples from geologic sections. We accumulate a great deal of data in the form of lists of palynomorph taxa found in each sample, with the object of determining the geologic ranges of the taxa within the section, and we end up by drawing range charts. This is the beginning of the biostratigraphic process that hopefully results in our being able to make correlations of strata among different areas.

However, there is more that can be done with these data than making geologic correlations. These palynological occurrence data also have potential biological significance, and the purpose of this lecture is to discuss using presence-absence palynological occurrence data from geologic sections to make some inferences about the history of ancient floras. In particular, two aspects of floral history will be emphasized: (i) rates of floral turnover, which means rates at which pollen/spore taxa had first and last appearances, and (ii) diversity change, in which diversities (numbers of pollen/spore taxa within each stratigraphic interval) are interpreted to be directly related to the numbers of plant taxa actually present in the area at various times.

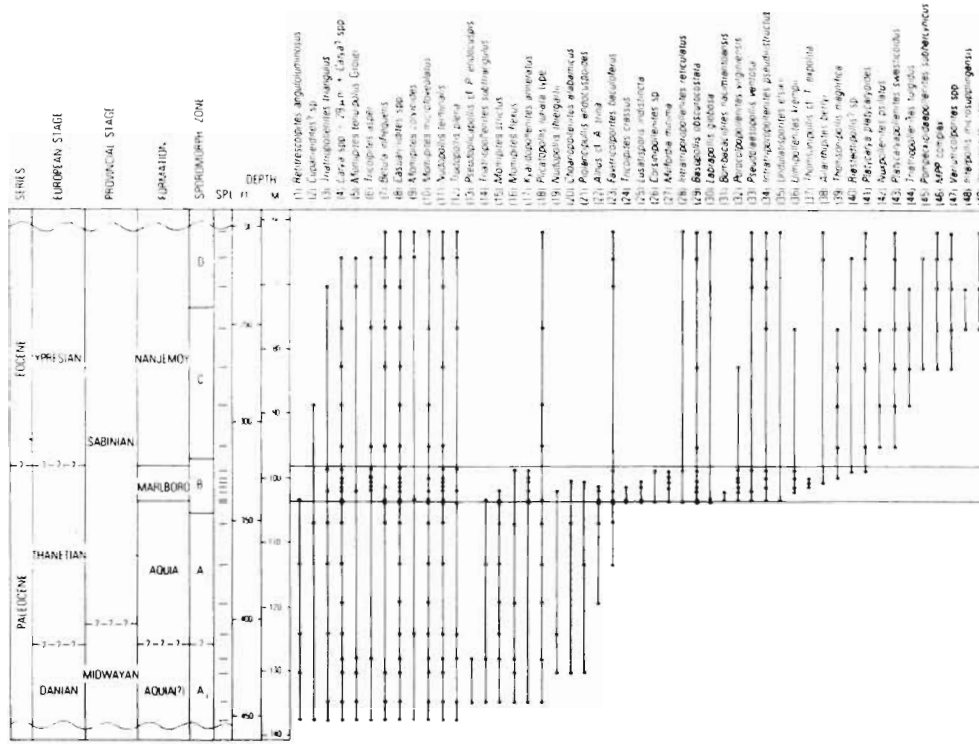
In the late 1970's and early 1980's, Karl Niklas, Andrew Knoll, and Bruce Tiffney published a number of papers in which they presented floral turnover and diversity curves based on a compilation of plant megafossil data from the literature (Niklas, 1977, 1978; Knoll *et al.*, 1979; Niklas *et al.*, 1979, 1983, 1985; Tiffney, 1981; Knoll, 1984). Although these papers are very useful for providing a generalized picture of floral changes over long

intervals of time, they have weaknesses that are inherent in using data from the literature. For example, authors may disagree about the identification of certain specimens; therefore, it is difficult to compare lists of species identified by different authors. Also, some fossil collections described in the literature are from rocks that have not been very well dated; therefore, the ages of some floral turnover events are not very well known, although if one is plotting data over long time spans, the exact ages of events are not as important as the overall trends.

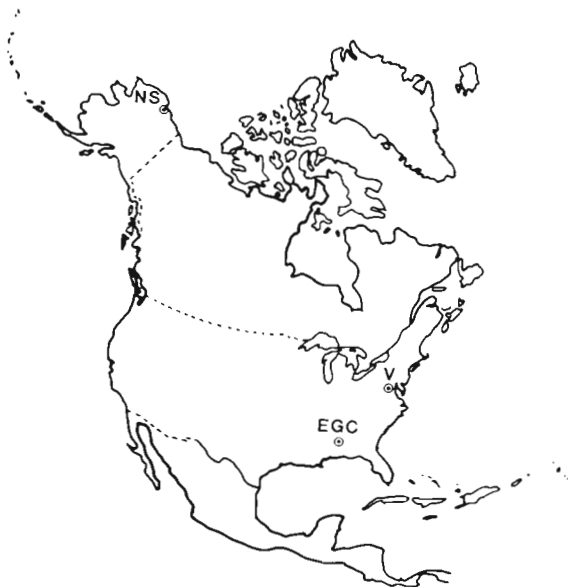
My work on floral turnover and diversity avoids some of these problems because I have made all the species identifications myself; also, I use only samples from known stratigraphic positions, so that the sequence of samples is well known. Furthermore, the sample spacing is much closer than one could get from summarizing data in the literature; therefore, the turnover and diversity diagrams (Text-figs 5, 9, 10) provide a much more detailed picture of floral changes than has previously been possible, at least for the Late Cretaceous and Early Tertiary.

PALEOCENE-EOCENE BOUNDARY, EASTERN UNITED STATES: A QUICK ESTIMATE OF FLORAL TURNOVER AND DIVERSITY CHANGES

Text-figure 1 serves as a simple example intended to introduce the subject of floral turnover and diversity changes. The figure shows stratigraphic ranges of angiosperm pollen taxa, mainly of pollen species level, in Upper Paleocene and Lower Eocene strata of the U.S. Geological Survey Oak Grove core in northern Virginia (Text-fig. 2). The region in which the core was taken is one of the few known in the eastern United States where there seems to have been continuous deposition across the Paleocene-Eocene boundary. The Aquia and Nanjemoy



Text-figure 1—Ranges of angiosperm pollen taxa (mainly pollen species) in Upper Paleocene and Lower Eocene strata of Virginia (eastern United States)—(from Frederiksen, 1979, text fig. 2, in *Palynology*).

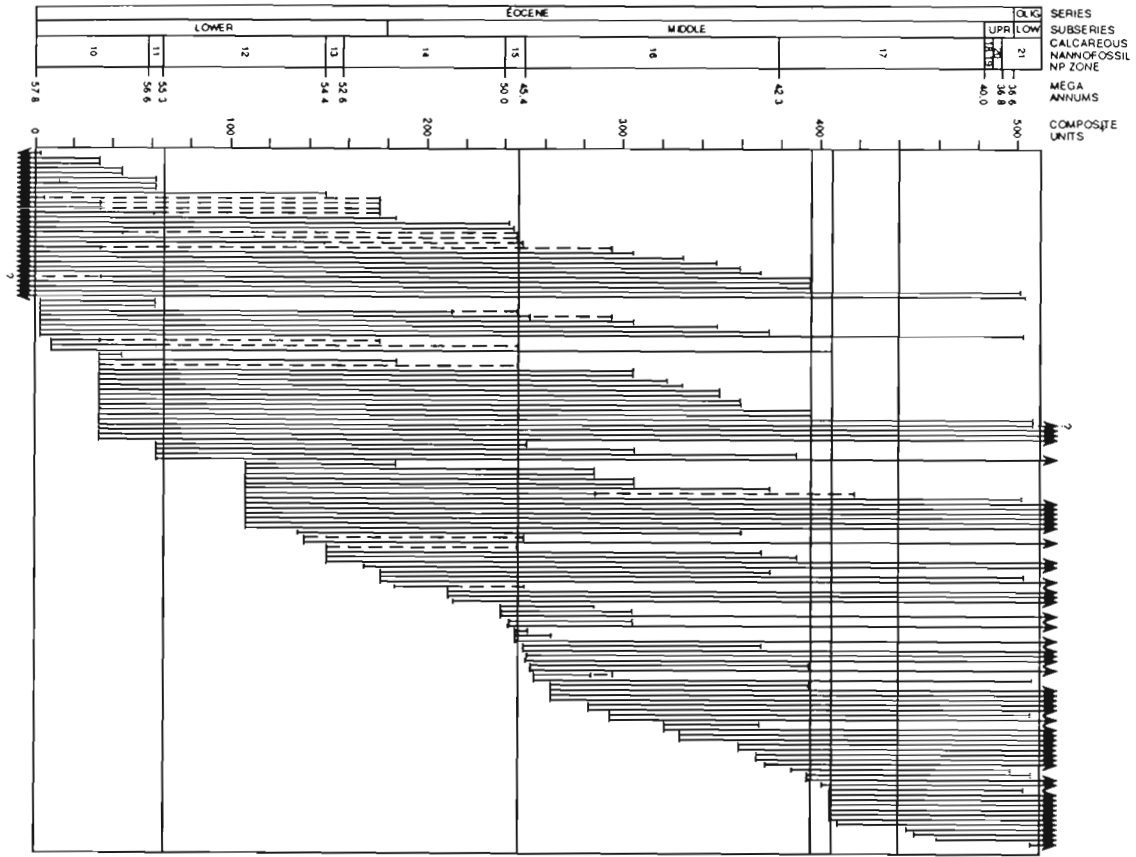


Text-figure 2—Areas discussed in this paper **NS** = North Slope of Alaska (lower Colville River area); **V** = Virginia (U.S. Geological Survey Oak Grove core); **EGC** = eastern Gulf Coast (Mississippi, Alabama, western Georgia).

formations are composed of glauconitic sand, silt, and clay rich in marine megafossils and microfossils; therefore, the Late Paleocene age of the Aquia and the Early Eocene age of the Nanjemoy are well

established (Gibson *et al.*, 1980). However, the relatively thin Marlboro Clay is a brackish-water deposit; therefore, the exact position of the Paleocene-Eocene boundary in the area is uncertain.

I have not calculated pollen diversities and rates of turnover of pollen taxa from the range data in Figure 1, but the trends of diversity change and turnover rates are easily seen. *Diversity* (the number of taxa at each stratigraphic level) increases slightly upward in the Upper Paleocene as several new taxa appear; diversities are at a maximum very close to the Paleocene-Eocene boundary because there is an overlap of typical Paleocene and typical Eocene taxa; diversity drops abruptly slightly above this maximum because of last appearances of many Paleocene species and last appearances of several species that were found only in the boundary interval; and diversity does not change greatly upward in the Lower Eocene because first appearances of some species generally compensate for last appearances of other species. The *turnover rate* of pollen taxa (that is, the number of first and last appearances per stratigraphic interval) has an abrupt maximum very near the Paleocene-Eocene boundary. As shown later in this lecture, the turnover maximum near the boundary represents evolution, extinction, and migration of taxa, and the turnover maximum was



Text-figure 3—Range chart of spore/pollen taxa, mainly spore/pollen species, in a composite section for the Eocene and lowermost Oligocene of the eastern Gulf Coast (from Frederiksen, 1988, pl. 17). Most taxa are of angiosperm pollen, but the range chart also includes a few taxa of spores and gymnosperm pollen. Taxon names have been omitted for lack of space and because, for purposes of this lecture, it is the pattern of range bases and tops that is important. Dashed portions of range lines indicate intervals of uncertainty as to where the true range base or range top of the taxon is located. Note the radiometric dates of the nannofossil zone boundaries (from Berggren *et al.*, 1985), which were used to transform the stratigraphic thickness scale (vertical axis) in this Text-figure to the time scale of Text-figures 4-6. The "Composite Unit" thickness scale is based on thicknesses (in feet) of 27 stratigraphic sections that were combined to form the single composite section shown here.

probably due at least in part to a rapid climatic change.

In summary, the Paleocene-Eocene boundary interval in the eastern United States was a time of great floral diversity and rapid floral turnover, and in this case, these floral events can be seen easily even in a simple range chart.

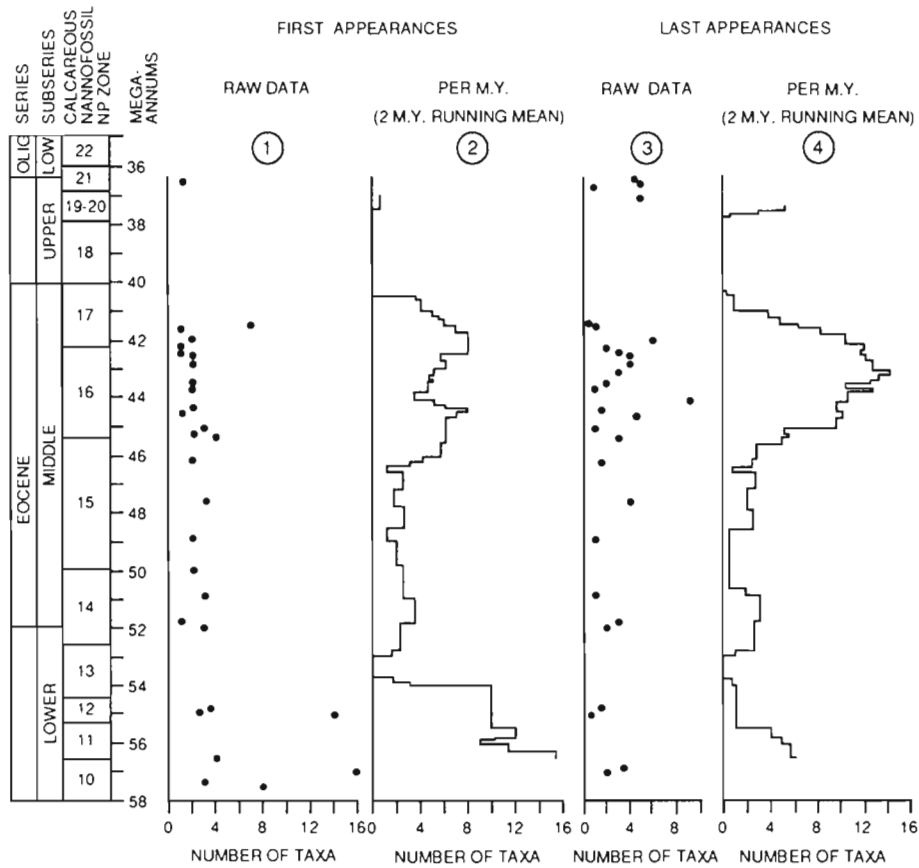
EOCENE AND LOWERMOST OLIGOCENE OF THE EASTERN GULF COAST: A DETAILED STUDY OF FLORAL TURNOVER AND DIVERSITY CHANGES PLOTTED AGAINST A TIME SCALE

This part of the lecture discusses very detailed data on angiosperm pollen from the entire Eocene and lowermost Oligocene of the eastern Gulf Coast; the work summarized here was reported by Frederiksen (1988). The geologic section and the pollen record represent a time span of about 22 m.y.

This study is based on 106 pollen-bearing samples from Mississippi, Alabama, and Georgia (Text-fig. 2); the samples are from 16 outcrop localities and 11 coreholes, but it was possible to combine all the samples into one composite section for the eastern Gulf Coast from which a composite range chart could be constructed for the Eocene and earliest Oligocene pollen taxa (Text-fig. 3).

The vertical axis of this range chart is stratigraphic thickness. In later charts relating to this study of the Gulf Coast (Text-figs 4-6), the vertical axis is geologic time; therefore, it is important to explain how a geologic time scale was derived for the section.

The eastern Gulf Coast is one of the most important areas in which to study changes of Eocene taxa through time, because much work has been done on calcareous nannofossils there (for example, Bybell, 1980; Gibson *et al.*, 1982; Siesser, 1983; Hazel *et al.*, 1984). The result of this work is that the



Text-figure 4—Numbers of first and last appearances (range bases and range tops, respectively) of angiosperm pollen taxa at each data level, and the running means calculated from the raw data, in the Eocene and lowermost Oligocene composite section for the eastern Gulf Coast (from Frederiksen, 1988, pl. 17). “Data level” means the stratigraphic position of a sample or group of samples. Compare the time scale of this figure (and Text-figures 5 and 6) with the stratigraphic thickness scale of Text-figure 3.

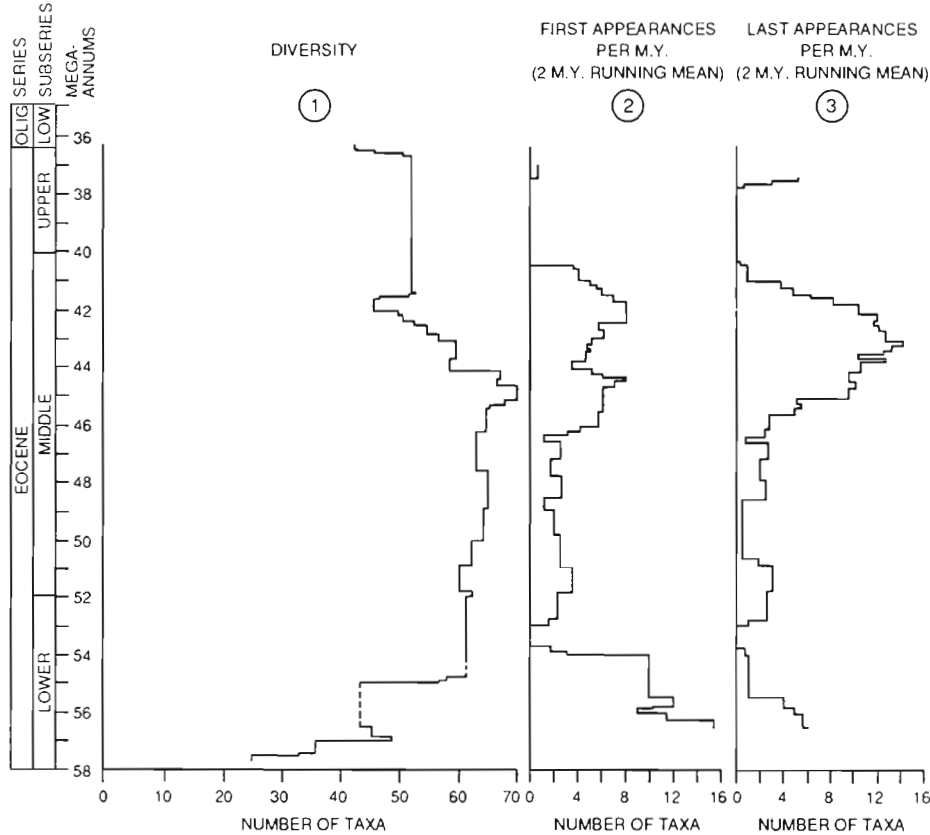
nannofossil zonation of the section is unusually well known, and there are also some data on planktic foraminifers. The range chart shows the nannofossil zones; the boundaries of these zones in the section have been quite well established.

Control points for geologic time in the eastern Gulf Coast are the radiometric ages of the nannofossil zone boundaries which were published by Berggren *et al.* (1985) based on data from all over the world. There are eleven of these control points in my section, that is, eleven nannofossil zone boundaries. I assumed uniform rates of deposition between these control points but also took into account several unconformities in the section. It is worth emphasizing again that the time control in the eastern Gulf Coast is far better than in most other Eocene areas of North America or Europe because most of the section is marine at least in Alabama and Georgia.

The range chart shows geologic ranges of 126 angiosperm pollen taxa, mainly pollen species. As noted in the caption of Text-figure 3, the chart also

includes a few taxa of spores and gymnosperm pollen, but the ranges of these taxa were disregarded in compiling data for the diversity and turnover diagrams; most species of spores and gymnosperm pollen have such long geologic ranges that they are not useful for floral turnover analysis, at least in the uppermost Cretaceous and Tertiary.

There were 35 sampled levels in the section at which one or more range bases or range tops (first or last appearances of taxa) appeared in the range chart (Text-fig. 3). Columns 1 and 3 of Text-figure 4 are numbers of observed first and last appearances at each sampled level. In a general way it is clear that many first appearances are present in the lower part of the section, and there is a concentration of last appearances in the upper Middle Eocene, but the raw data are difficult to interpret in detail. Therefore, the raw data (columns 1 and 3, Text-fig. 4) were converted to numbers of first and last appearances per million years, expressed as a 2 million year running mean (curves of columns 2 and 4 of Text-figure 4). Choosing the interval with which to



Text-figure 5—Diversities and rates of turnover of angiosperm pollen taxa in the Eocene and lowermost Oligocene composite section for the eastern Gulf Coast (from Frederiksen, 1988, p. 17).

calculate the running mean is somewhat arbitrary. If a larger interval is used, the curves will be smoother, and long-term trends will be emphasized, but some details will be obscured; if a smaller interval is chosen, the curves will be more detailed, but the important trends of the curves may be difficult to visualize. The section of Text-figure 4 represents about 22 m.y. of deposition; thus, the interval used to calculate the running mean was about 1/11 of the total time interval of the diagram. One disadvantage of using a running mean is that the curve cannot be calculated for the lowermost and uppermost parts of the section (note that the running mean curves in Text-fig. 4 do not extend to the bottom and top of the section).

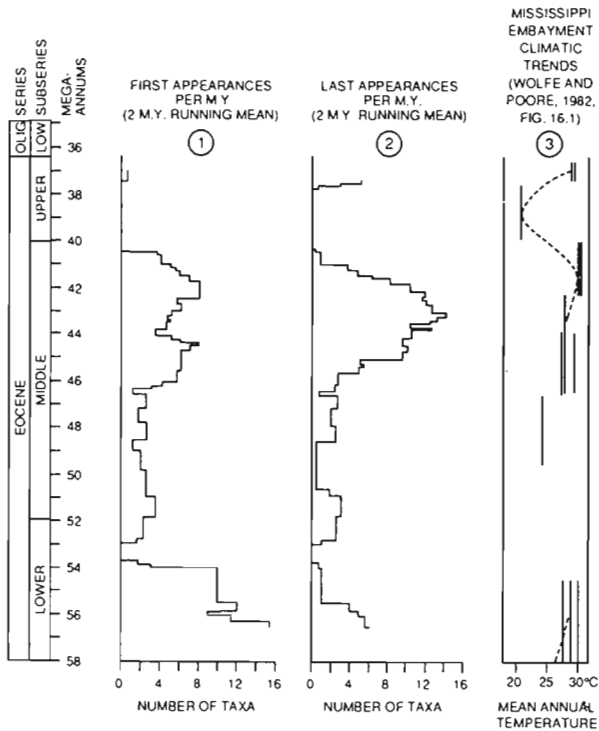
In short, it is easy to calculate rates of turnover (rates of first and last appearances) of fossil floras, if enough data points are available, that is, if the section contains enough stratigraphic horizons at which there are range bases and tops. Interpreting the significance of the rates of turnover is much more difficult, but of course the interpretation is the interesting part of the whole procedure.

In interpreting the floral turnover diagrams, for the sake of simplicity I refer to rates of first and last

appearances. First appearances are due to evolution and immigration of taxa; last appearances are due to extinction and emigration. It is desirable to determine whether first and last appearances are due more to evolution and extinction or to migration, but that determination is often difficult.

Text-figure 5 includes the same turnover curves as Text-figure 4, but it also has a curve showing diversity changes. As noted previously, diversity, as used in this lecture, is defined as the number of fossil taxa within each stratigraphic interval and is interpreted to be directly related to the number of plant taxa that actually lived in the area during the time span represented by that interval. Diversity is calculated from the range chart (Text-fig. 3) by counting the number of taxon range lines that cross each stratigraphic interval.

It is important to note that in this work, both diversity and turnover rates were calculated using the range-through method of Cheetham and Deboo (1963); this method assumes that each taxon is present in every sample between its range base and its range top, whether or not the taxon was actually seen in each sample within this interval. What is wanted is an estimate of how many plant taxa lived



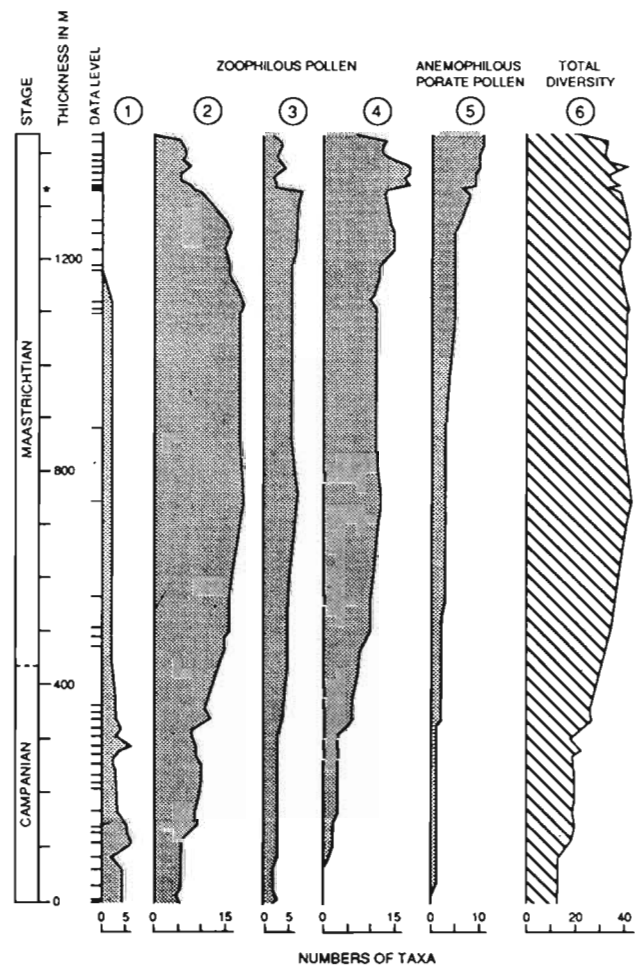
Text-figure 6—Rates of turnover of angiosperm pollen taxa in the Eocene and lowermost Oligocene composite section for the eastern Gulf Coast (from Frederiksen, 1988, pl. 17) compared with the climatic trend curve for the Mississippi Embayment of Wolfe and Poore (1982, fig. 16.1).

in the region at any particular time, and how many taxa had first or last appearances at any particular time. The strength of the range-through method is that it avoids ecological biases that strongly influence the taxon composition actually observed in each sample (Hazel, 1970). An important weakness of the method is that if climatic fluctuations occurred during deposition of the sequence being studied, some members of the flora may well have migrated out of the region and later returned, but if the range-through method is used, these migrations would not be apparent. Therefore, it is essential to be aware of this weakness of the range-through method in interpreting calculated diversities and turnover rates. In studies where distinct climatic fluctuations are likely to have occurred, for example, in the Quaternary, it might be better to calculate diversities and turnover rates based on observed taxon compositions of each sample.

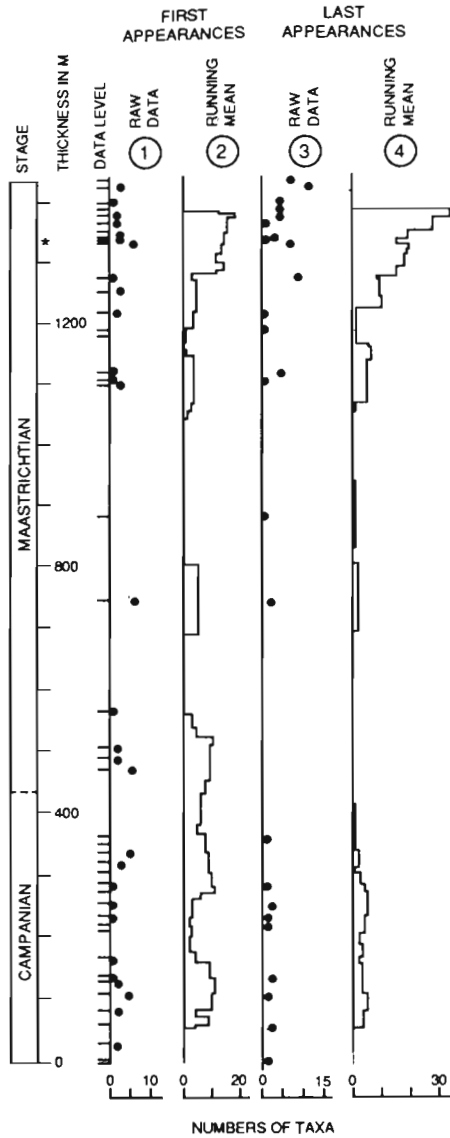
A second weakness of the range-through method is that the number of "observed" range tops and range bases at each horizon depends on the number of samples examined above and below this horizon; therefore, the number of supposed range tops tends to artificially increase toward the top of

the studied section, whereas the number of supposed range bases tends to artificially increase toward the base of the section, seriously distorting calculations of diversities and turnover rates (Boltovskoy, 1988). In the examples of floral diversity and turnover discussed in this lecture, this type of potential error is minimized because other palynologists and I have examined many samples from above and below the sections actually discussed here; thus, the range bases and tops plotted in the diagrams are believed to be reasonably reliable.

A series of changes in diversities and rates of floral turnover can be observed in Text-figure 5. First is an Early Eocene event, a rapid turnover of the flora



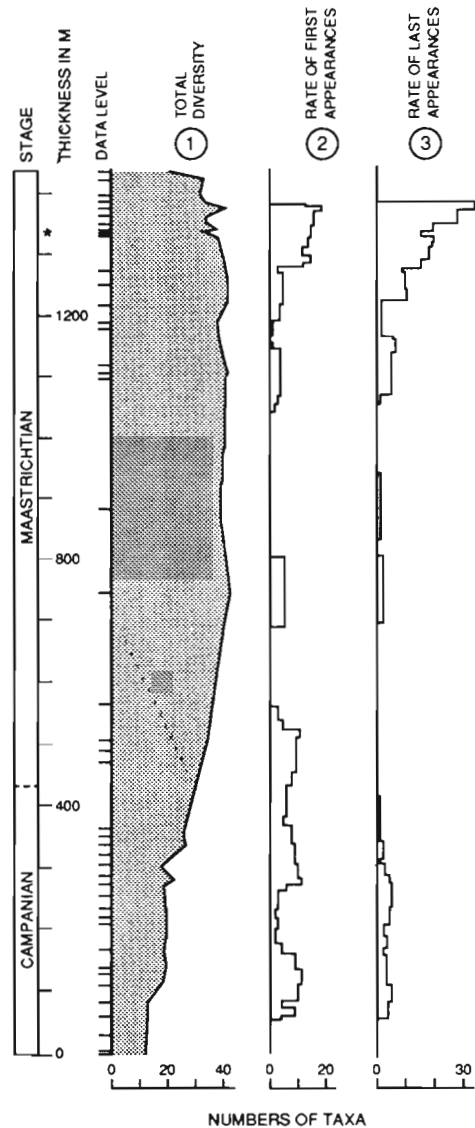
Text-figure 7—Six kinds of angiosperm pollen diversity data for the mid(?)-Campanian to Maastrichtian section of the lower Colville River region, North Slope of Alaska (from Frederiksen, 1989, fig. 2, in *Cretaceous Research*). Columns are as follows: 1-4, diversities of four zoophilous pollen groups; 5, diversity of anemophilous porate pollen; 6, total angiosperm pollen diversity (which is plotted against a smaller horizontal scale than the other columns). The level marked by an asterisk is a stratigraphic unit that is approximately mid-Maastrichtian in age (Frederiksen and others, 1988).



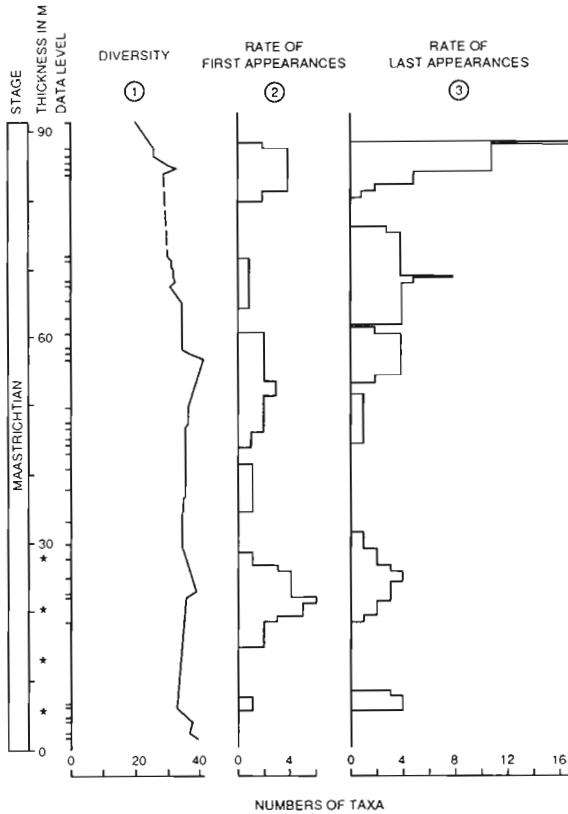
Text-figure 8—Numbers of first and last appearances (range bases and range tops) of angiosperm pollen taxa at each data level, and the running means calculated from the raw data, in the mid(?) -Campanian to Maastrichtian section of the lower Colville River region, North Slope of Alaska (from Frederiksen, 1989, fig. 2, in *Cretaceous Research*). Rates of first and last appearances (columns 2, 4) calculated as numbers of taxa per 100 m of stratigraphic thickness. The level marked by an asterisk is a stratigraphic unit that is approximately mid-Maastrichtian in age (Frederiksen and others, 1988).

in which some holdovers from the Paleocene became extinct but many more new taxa appeared, leading to a very rapid increase in diversity. This is by far the highest rate of first appearances known for the Eocene flora of the Gulf Coast, and much of it was probably due to immigration of taxa from western Europe by way of the North Atlantic land bridge across or north of Greenland (McKenna, 1975, 1983). This immigration of plants from Europe

to North America took advantage of a sudden warming of the climate possibly at the very end of the Paleocene and at the beginning of the Eocene (Wolfe & Poore, 1982; Wolfe, 1985) that allowed the plants to actually cross the bridge. For example, six of the pollen species that have first appearances in the Early Eocene of the Gulf Coast are known from the Paleocene of Europe; thus, it is evident that they came to North America from Europe at the beginning of the Eocene. The most prominent of these



Text-figure 9—Total angiosperm pollen diversity (column 1) and running mean rates of first appearances (column 2) and last appearances (column 3) of angiosperm pollen taxa, in the mid(?) -Campanian to Maastrichtian section of the lower Colville River region, North Slope of Alaska (from Frederiksen, 1989, fig. 2, in *Cretaceous Research*). Rates of first and last appearances (columns 2, 3) calculated as numbers of taxa per 100 m of stratigraphic thickness. The level marked by an asterisk is a stratigraphic unit that is approximately mid-Maastrichtian in age (Frederiksen and others, 1988).



Text-figure 10—Total angiosperm pollen diversity (column 1) and running mean rates of first appearances (column 2) and last appearances (column 3) of angiosperm pollen taxa, in the “middle” to Upper Maastrichtian section of the lower Colville River region, North Slope of Alaska (from Frederiksen, 1989, fig. 3, in *Cretaceous Research*). Rates of first and last appearances (columns 2, 3) calculated as numbers of taxa per 7 m of stratigraphic thickness. The interval marked by asterisks is a stratigraphic unit that is approximately mid-Maastrichtian in age (Frederiksen and others, 1988).

immigrants was *Platycarya* (Juglandaceae), a genus that now has only two species and is found only in eastern Asia. However, following the immigration from Europe, this genus spread so rapidly that it is found in Lower Eocene deposits throughout the United States and Canada, and along with the migration there was an explosion of evolution of the *Platycarya* complex in North America (Frederiksen, 1979; Wing, 1984; Wing & Hickey, 1984).

The rise in Early Eocene diversity observed in the eastern Gulf Coast (Text-fig. 5) appears to contrast with the stability of the Early Eocene diversity observed in Virginia (Text-fig. 1). This contrast cannot be discussed here in detail, but it does suggest several questions, not yet resolved, that illustrate some typical difficulties encountered in interpreting and correlating floral diversity and turnover diagrams:

1. Is the observed pollen diversity in the Lower

Eocene Nanjemoy Formation of Virginia (Text-fig. 1) too low because the formation was deposited too far offshore for some pollen to be transported to the sites of deposition?

2. Is the brackish-water Marlboro Clay of Virginia (Text-fig. 1), with its high diversity, earliest Eocene rather than latest Paleocene in age? That is, is the high-diversity Marlboro Clay correlative with the high-diversity Lower Eocene samples from the Gulf Coast (Text-fig. 5)? Is the drop in diversity between the Marlboro Clay and Nanjemoy Formation in Virginia (Text-fig. 1) equivalent to the relatively small drop in diversity at about 56.5 Ma (millions of years ago) in the Gulf Coast (Text-fig. 5)?
3. Are the lowest Eocene samples from the eastern Gulf Coast (Text-fig. 5) younger than the lower part of the Nanjemoy Formation of Virginia (Text-fig. 1)? That is, did the distinct rise in Early Eocene diversity in Text-figure 5 actually occur later than the stable Early Eocene diversity shown in Text-figure 1?

The Early Eocene event in the eastern Gulf Coast (Text-fig. 5) was followed by a period of low floral turnover lasting about the first half of Middle Eocene time. Next was a Middle Eocene event, in the second half of Middle Eocene time, including a burst of first appearances, a burst of last appearances, and a second burst of first appearances. This turnover event included a rise in diversity to the maximum for the Eocene and then a fall in diversity.

The Middle Eocene turnover event lasted about 4.5 m.y. The climatic implications of the Middle Eocene event are not certain, but a drying trend may have been involved, because four species of *Ephedra* (Ephedraceae) had first appearances in the Gulf Coast at the middle of Eocene time. *Ephedra* is a shrubby gymnosperm that is found mostly on dry soil.

In the lower of the two Middle Eocene peaks in the rate of first appearances, four or five of the new species are known from older rocks in southern California; therefore, this first peak may partly represent plant immigration from the southwest. The peak in the rate of last appearances was presumably due to a climatic deterioration because it led to a rapid drop in diversity. The second peak in first appearances is likely to have been due to evolution and immigration of taxa that were adapted to the new, more severe climate, because many of these new pollen taxa were produced by herbs and shrubs—for instance, this was the first appearance of grasses—whereas most of the pollen taxa originating between the Paleocene and the early Middle Eocene

were produced by trees that would do best in warm, moist climates, such as Bombacaceae, Sapotaceae, and Alangiaceae.

Next was a remarkable period of practically no floral turnover from late in the Middle Eocene to the end of the Eocene. This period of no turnover lasted for nearly 5 m.y. The level of diversity during this period was lower than at any time since the earliest part of the Eocene.

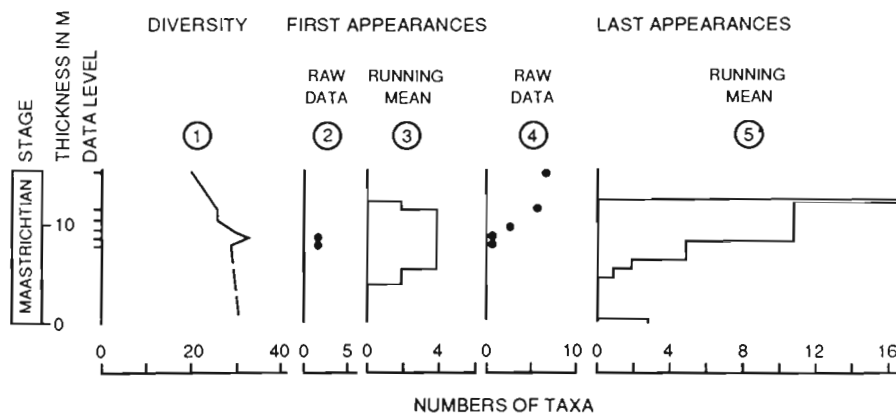
At this point it is appropriate to summarize briefly two current models of evolution, the Red Queen and Stationary Models. The Red Queen Model (Van Valen, 1973) supposes that evolution is driven primarily by interactions within the biota. Therefore, the model predicts that evolution will continue even in the absence of physical change in the environment, because organisms will always affect one another. The model derives its name from a character called the Red Queen in the children's book *Alice in Wonderland*. In the book, the Red Queen must run continuously just in order to stay in the same place. In terms of the model of evolution, because some species in the ecosystem will always be evolving, all the others must evolve also, just to keep up. The Stationary Model of evolution (Stenseth & Maynard Smith, 1984) supposes that evolution is driven primarily by physical factors of the environment such as climatic change. The stationary Model derives its name from its assumption that evolution and extinction will stop if the environment stops changing. In the late Middle Eocene and Late Eocene of the Gulf Coast, the observed stasis or cessation in the evolution of angiosperm pollen species supports the Stationary Model of evolution.

The last event recorded in Text-figure 5 is a fall

in diversity at the beginning of the Oligocene. This diversity change cannot be compared with the floral turnover curves of Text-figure 5 because, as noted previously, running mean curves cannot be calculated for the uppermost and lowermost parts of a section. However, the raw data on numbers of first and last appearances at each stratigraphic level (columns 1 and 3, Text-fig. 4) are useful because they show that many last appearances but only a few first appearances characterized the beginning of Oligocene time in the Gulf Coast. This earliest Oligocene event in North America is known as the Oligocene Deterioration (Wolfe, 1971), and at least on the Gulf Coast, the burst of last appearances was probably caused by a cooling and perhaps a drying trend in the climate.

The most important of the taxa to become extinct near the Eocene Oligocene boundary of this region was *Nypa*, a tropical, brackish-water palm. This genus was widespread in the Eocene of the Northern Hemisphere (Tralau, 1964), but it became extinct in North America, the Caribbean, and Europe at the end of the Eocene or the beginning of the Oligocene (Germeraad *et al.*, 1968; Gruas-Cavagnetto & Barbin, 1989), and today it is found only in tropical southeast Asia.

Text-figure 6 compares the floral turnover curves based on pollen data (columns 1 and 2) with a climatic curve for the same region calculated on the basis of megafossil data, mainly from percentages of entire vs. nonentire fossil leaves (column 3). The vertical bars in column 3 are the ranges of uncertainty as to stratigraphic positions of the individual leaf collections, and the curve appears to be based on data from 12 localities. The leaf collections are not very precisely dated because, of



Text-figure 11—Total angiosperm pollen diversity (column 1), numbers of first and last appearances of angiosperm pollen taxa at each data level (columns 2, 4), and the running means calculated from the raw data (columns 3, 5), in the uppermost Maastrichtian section of the lower Colville River region, North Slope of Alaska (from Frederiksen, 1989, fig. 3, in *Cretaceous Research*). Rates of first and last appearances (columns 3, 5) calculated as numbers of taxa per 7 m of stratigraphic thickness.

necessity, they were collected from nonmarine rocks for which, at that time, no good pollen zonation existed. The climatic curve drawn on the basis of leaf data is out of phase with the climatic curve interpreted on the basis of the pollen data, probably because the leaf collections were not very well dated. Finally, the number of leaf collections is only a fraction of the number of pollen samples.

Text-figure 6 illustrates strengths and weaknesses of both the pollen and leaf data. The strengths of pollen data are that many more pollen-bearing than leaf-bearing samples can usually be collected from a section; pollen samples can be collected from marine rocks, which can be dated by means of marine fossils, whereas plant megafossils are usually available only in nonmarine rocks which may not be so well dated; and the climatic trend curves based on pollen may have much more accurate and detailed time resolution than the climatic trend curves based on leaf data. Furthermore (although this is not shown directly in Text-fig. 6), pollen samples often contain many more taxa than plant megafossil samples. However, the strength of the leaf data is that they allow quantitative estimates to be made of climatic parameters, especially paleotemperatures; in contrast, at least for pre-Neogene samples, pollen data can usually be interpreted only in terms of generalized climates. In short, both pollen and leaf data are very valuable in determining the history of terrestrial climates.

CAMPANIAN AND MAASTRICHTIAN, NORTH SLOPE OF ALASKA : A DETAILED STUDY OF FLORAL TURNOVER AND DIVERSITY CHANGES PLOTTED AGAINST A STRATIGRAPHIC THICKNESS SCALE

Stratigraphic sections are normally scaled in thickness units. But it is very desirable to convert the thickness scale to a time scale so that floral turnover and diversity changes can be plotted against geologic time. To convert from a thickness scale to a time scale it is necessary to have time markers in the section, such as radiometrically dated ash beds, or fossil zone boundaries that have been tied elsewhere to a radiometric time scale. In the examples previously cited, of the Paleocene-Eocene boundary in Virginia and the Eocene and earliest Oligocene of the Gulf Coast, both stratigraphic sections had generally been well zoned on the basis of calcareous nannofossils, and the nannofossil zone boundaries had been radiometrically dated elsewhere in the world. However, my last example of floral turnover and diversity is a case where the

time control is not very good, and therefore, there is no choice but to plot the floral turnover rates and the diversity changes against a stratigraphic thickness scale; this example will demonstrate how such a plot can lead to some problems of interpretation and has to do with Late Cretaceous floral and climatic changes in the North American Arctic.

The samples to be discussed here are from Campanian and Maastrichtian rocks along the lower Colville River on the North Slope of Alaska (Text-fig. 2), and the interpretation of the pollen assemblages from these samples has been presented by Frederiksen *et al.* (1988) and Frederiksen (1989). The studies were based on 133 pollen-bearing samples. The stratigraphic section is on the order of 1,400 m thick. This is mainly a nonmarine section; only a few horizons are present at which marine fossils have been found. The section is known to be approximately mid-Campanian to latest Maastrichtian in age; thus, it represents approximately the last 12.5 m.y. of Cretaceous time (Kent & Gradstein, 1985).

The North Slope of Alaska was at a very high paleolatitude, approximately 80° N, toward the end of the Cretaceous, and during this time span North America was moving toward the pole (Smith *et al.*, 1981; Ziegler *et al.*, 1983). Thus, during the last part of Cretaceous time, the climate of the North Slope of Alaska should have become progressively colder, which must have been an important influence on evolution, extinction, and migration of floras in northern Alaska toward the end of the Cretaceous.

Diverse plant megafossil assemblages have not been found in the Upper Campanian to Maastrichtian part of the Colville River section; thus, the pollen assemblages are critical for determination of latest Cretaceous climatic trends in the region.

This study is based on 110 angiosperm pollen taxa, almost entirely pollen species. Most of the pollen species were zoophilous; however, a relatively small number of Late Cretaceous pollen species were anemophilous. Text-figure 7 shows diversities of four zoophilous pollen groups (columns 1-4); the group of anemophilous porate pollen (probably representing Betulaceae, Ulmaceae, and Myricaceae—column 5); and total angiosperm pollen diversity (column 6). The curves show that most of the zoophilous pollen groups became richer in species from Campanian into Maastrichtian time but decreased significantly in diversity toward the end of the Maastrichtian. The zoophilous group in column 1 decreased in diversity through this time span and apparently became extinct, at least in this region, before the end of the

Maastrichtian. In contrast, anemophilous pollen (column 5) increased gradually in diversity during the Campanian and Maastrichtian; this pollen group then composed much of the angiosperm pollen flora during the Paleocene at high northern latitudes (Doerenkamp *et al.*, 1976; Frederiksen *et al.*, 1988; Sweet *et al.*, 1989).

In Text-figure 8, columns 1 and 3 are numbers of first and last appearances at each sampled level, which reflect the numbers of range bases and range tops at each horizon in the pollen taxon range chart for the Colville River section (not shown here). Columns 2 and 4 of Text-figure 8 are running means for the first and last appearances, calculated from the raw data. However, in Text-figure 8, because the vertical axis is a stratigraphic thickness scale (as opposed to the time scale in Text-fig. 4), the running means had to be calculated in terms of thickness. As stated previously, the section is approximately 1,400 m thick, and I chose to calculate turnover rates as numbers of range bases and range tops per 100 m of stratigraphic thickness. Thus, the interval used to calculate the running mean was about 1/14 of the total thickness of the section.

In Text-figure 9, total diversity (from Text-fig. 7) is combined with rates of floral turnover (from Text-fig. 8). During the Late Campanian and Early Maastrichtian, first appearances of taxa were more abundant than last appearances, leading to an increase in angiosperm diversity. This episode was followed by a late Early Maastrichtian period of little taxon turnover.

The asterisk to the right of the Stage column indicates a stratigraphic unit probably of mid-Maastrichtian age (Frederiksen *et al.*, 1988); thus, it is clear that in the study area the Upper Maastrichtian rocks are much thinner than the Lower Maastrichtian rocks, and the stratigraphic thickness scale (vertical axis) of Text-figure 9 is far from being equivalent to a time scale. Because the floral turnover rates were plotted as running means per interval of stratigraphic thickness, the magnitudes of peaks in the curves are very sensitive to rates of deposition. Therefore, the apparent peak in floral turnover rates in the uppermost Maastrichtian is likely to be a distortion caused by the fact that the rate of deposition of Upper Maastrichtian strata was very slow compared with earlier depositional rates.

As a result of mistrusting the Late Maastrichtian peaks in turnover rates in Text-fig. 9, I constructed a diagram (Text-fig. 10) that is based on the same data as Text-figure 9, but Text-figure 10 only includes strata that represent approximately the second half of the Maastrichtian, that is, approximately only the last 5 m.y. of Cretaceous time. In Text-figure 10,

columns 2 and 3 are running means for numbers of first and last appearances at each data level. This section is approximately 91 m thick, and I chose to calculate turnover rates as numbers of range bases and range tops per 7 m of stratigraphic thickness. Thus, the interval used to calculate the running means was 1/13 of the section thickness.

Text-figure 10 shows greater detail of turnover rates near the top of the Cretaceous section than Text-figure 9. The uppermost part of this section, representing the very end of the Cretaceous, is the most interesting part, because floras at this time underwent rapid turnover at least at high latitudes (Sweet, 1988). As pointed out previously, the calculation of running means cannot be made for the lowermost and uppermost parts of a sequence. However, the raw data on numbers of first and last appearances can be used in these parts of the section, and these data are shown, with the curves from the uppermost part of Text-figure 10, in Text-figure 11.

During most of the Late Maastrichtian, first appearances of taxa generally kept pace with last appearances; therefore, pollen diversity remained relatively constant (Text-fig. 10). Later, the rate of last appearances increased while the rate of first appearances stayed about the same as earlier, leading to a decrease in diversity (Text-fig. 10), and the surge in last appearances of taxa reached a maximum at the end or close to the end of Cretaceous time in the high Arctic (Text-fig. 11). The pollen turnover curves also show that, for the most part, angiosperm turnover appears to have occurred in small bursts toward the very end of the Cretaceous (Text-fig. 10). The pollen turnover data from northern Alaska appear to agree with Kemper's (1987) climatic curve for the latest Cretaceous, based on marine data, in which the existence of distinct cold pulses was inferred.

Several types of mass extinction patterns are possible (Kauffman, 1986), including (i) a single catastrophic event, (ii) stepwise extinctions, that is, several closely spaced extinction events, and (iii) a very rapid but more or less continuous rate of extinction. Pollen turnover data (Text-fig. 10) suggest that, for the latest Cretaceous of the high Arctic, floral extinctions fit the stepwise model.

CONCLUSION

Data from both pollen/spores and plant megafossils are needed to demonstrate and understand floral and climatic changes in the fossil record. Fossil leaves have morphological features from which paleotemperatures can be estimated

directly: pollen grains and spores do not have such features. However, this lecture summarizes ways in which presence-absence of pollen occurrence data from geologic sections can be used to prepare floral diversity and turnover diagrams. This kind of pollen data has several important advantages over plant megafossil occurrence data: the large number of samples that contain pollen; the richness of the samples in taxa; and the possibility of obtaining pollen from marine rocks that can be dated by their fossils. Therefore, pollen and spore data are especially valuable for determining in detail the nature and timing of changes in floral diversities and turnover rates, two features that are often linked to climatic change.

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