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11. Synaptoneurosomes were prepared by the method of Gusovsky and Daly (*26*) as described for rat neocortex (*10*). Briefly, kittens of various ages were anesthetized with a small intramuscular dose of a ketamine-xylazine mixture (20 and 2.5 mg/kg, respectively) followed by an intraperitoneal injection of sodium pentobarbital (25 mg/kg) and decapitated. The brains were rapidly removed and cortical area 17 was dissected free. The cortex was weighed and homogenized in 10 volumes of oxygenated (95% O_2:5% CO_2) Krebs-Henseleit buffer, pH 7.4 (119 m*M* NaCl, 4.7 m*M* KCl, 1.18 m*M* $MgSO_4$, 2.5 m*M* $CaCl_2$, 1.18 m*M* KH_2PO_4, 24.9 m*M* $NaHCO_3$, and 10.0 m*M* glucose), in a glass-glass homogenizer with four strokes by hand. The homogenate was centrifuged at 1000*g* for 10 min, and the supernatant was discarded. The pellet was resuspended in 20 volumes of Krebs-Henseleit buffer plus 50 m*M* Hepes (pH 7.4) and mixed with 1 μ*M* [^{3}H]inositol (15 Ci/mmol). Aliquots of 320 μl were then incubated at 37°C for 60 min to label the inositol lipid pool. Twenty microliters of 200 m*M* lithium chloride was added 10 min before the addition of agonists for a final incubation volume of 400 μl. The tubes were gassed with a ratio of 95% O_2 to 5% CO_2 and capped before each incubation. [^{3}H]Inositol was present throughout the 90-min incubation (*27*). The suspension was then centrifuged and the pellet washed once with fresh buffer and then resuspended in 6% trichloroacetic acid. After centrifugation, the supernatant was collected and mixed with Bio-Rad anion exchange resin AG 1-X8 (1 ml of a 50% slurry in water). The columns were washed four times with 1 ml of water and two times with 1 ml of a mixture containing 200 m*M* ammonium formate and 100 m*M* formic acid to elute [^{3}H]inositol-1-phosphate (IP_1) into scintillation vials. All results are from at least three experiments performed in duplicate and expressed as percentage of basal activity. Basal activity is counts per minute of samples from the same run incubated without any transmitter ligands. A condition containing 100 μ*M* carbachol was run in every experiment to assess the integrity of the assay system; comparisons between ligands were always done on samples from the same preparations. The synaptoneurosomes were unfiltered as previous reports have shown that this step makes no difference in the results of this assay (*26*). Also, because IP_3 is rapidly hydrolyzed to IP_1 in this system, accumulation of IP_1 is an accurate measure of overall phosphoinositide turnover (*26*).
12. NMDA also failed to stimulate PI turnover in synaptoneurosomes prepared from visual cortex of one kitten in which ketamine was omitted from the anesthesia. This finding is in agreement with previous work with rat neocortex (*10*) in which no anesthesia was used before decapitation.
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15. That carbachol potently stimulated phosphoinositide turnover regardless of age also indicates that the developmental changes in ibotenate-stimulated phosphoinositide turnover are not explained by changes in the initial incorporation of [^{3}H]inositol into phospholipid. Lipid phase measurements were not performed routinely because preliminary studies confirmed that [^{3}H]inositol was incorporated into phospholipid at all ages and that availability of labeled phospholipid did not limit [^{3}H]IP_1 accumulation in the assay (*27*). Nonetheless, [^{3}H]inositol incorporation was lower in tissue prepared from visual cortex of older animals, and this is reflected by a lower number of counts per minute under basal conditions (Table 2).
16. Kittens and mother were transferred within a week of birth to a standard breeding cage in a dark room.
17. It is possible that a transient rise in ibotenate-stimulated phosphoinositide turnover occurs before 5 weeks of age. This would be surprising, however, as dark rearing is thought to delay or slow visual cortical development. M. Cynader and D. E. Mitchell, *J. Neurophysiol.* **43**, 1026 (1980); G. D. Mower, C. J. Caplan, W. G. Christen, F. H. Duffy, *J. Comp. Neurol.* **235**, 448 (1985).
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27. In pilot experiments, the time course of IP_1 accumulation stimulated by 10 μ*M* ibotenate was studied in synaptoneurosomes prepared from the striate cortex of adult and 4-week-old cats. At both ages, and in agreement with F. Gusovsky, E. B. Hollingsworth, and J. W. Daly [*Proc. Natl. Acad. Sci. U.S.A.* **83**, 3003 (1986)], IP_1 accumulation did not plateau until after 90 min (our usual incubation time). The differences between ibotenate-stimulated phosphoinositide turnover in immature and adult cortex were observed at all incubation times, including those as short as 10 min.
28. We thank W. Bowen for help with the synaptoneurosome assay, A. Bohner for technical assistance, and B. W. Connors for critically reading the manuscript. Supported by grants from the Office of Naval Research, the National Eye Institute, and the Alfred P. Sloan Foundation.

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Angiosperm Diversification and Paleolatitudinal Gradients in Cretaceous Floristic Diversity

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The latitudinally diachronous appearance of angiosperm pollen during the Cretaceous is well documented, but the subsequent diversification and accompanying significant changes in floristic dominance have not been assessed quantitatively for a wide range of paleolatitudes. Trend surfaces fitted to within-palynoflora diversity data from 1125 pollen and spore assemblages show that angiosperms first become floristically prominent in low paleolatitude areas (~20°N to 20°S). Non-magnoliid dicotyledons show a similar but slightly delayed pattern of increase and are the principal component of angiosperm diversity from all areas sampled. Monocotyledons and magnoliid dicotyledons are significant primarily in low to middle paleolatitude palynofloras (~50°N to 20°S) during the latest Cretaceous. As angiosperms become increasingly prevalent the importance of most non-angiosperm taxa either decreases or remains unchanged. The only apparent exception is a striking increase in gnetalean diversity concurrent with the initial angiosperm diversification at low paleolatitudes.

ALTHOUGH THE ORIGIN OF ANGIOSPERMS persists as one of the most widely debated issues in evolutionary botany (*1–4*), the paleobotanical record demonstrates unequivocally that the major early diversification of the group occurred during the mid-Cretaceous (*4–10*). Through this interval many of the characteristic reproductive features of extant flowering plants appear in the fossil record for the first time (*11*), and fossil angiosperm leaves and pollen exhibit marked, coincident, patterns of increasing diversity (*6–10*). By the Cenomanian (earliest Late Cretaceous), at least four of the eleven extant angiosperm subclasses (Magnoliidae, Hamamelidae, Rosidae, and at least one subclass of Liliopsida), as well as several distinct clades within these groups, had already differentiated (*9*). Increased abundance of angiosperm fossils parallels this rise in diversity, and together these patterns have been used to infer ecological expansion (*6, 7*), perhaps as a function of biological attributes of the angiosperm clade (*3, 12, 13*), and possibly with direct effects on other plant groups (*13*). Although detailed analyses of local stratigraphic sections provide partial resolution of such ecological effects (*7*), extrapolation to the level of angiosperms as a whole requires a more inclusive geographic and

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temporal framework, as well as clarification of large-scale patterns exhibited by angiosperm subclades and non-angiosperm components of Cretaceous vegetation.

Angiosperm pollen appears first in the fossil record at low to middle paleolatitudes, and only subsequently at higher latitudes in both hemispheres (*7, 14*). Quantitative analyses of macrofossil and palynological data from mid- to high paleolatitude assemblages in the Northern Hemisphere (Southern and Northern Laurasia) show that angiosperms were floristically dominant by the Cenomanian-Campanian and that this rise to dominance coincided with profound changes in the diversity of other plant groups (*8–10*). Previous qualitative evaluations of mid-Cretaceous floristic provinciality indicate that the details of these patterns probably vary at different paleolatitudes (*14, 15*).

Our quantitative analyses assess floristic change between paleolatitudes 80°N and 20°S and clarify the extent to which latitudinally diachronous patterns in first appearance data are also reflected in patterns of change in the relative importance of angiosperms in successive Cretaceous palynofloras. Because a latitudinally diachronous pattern is most pronounced for first appearances of triaperturate pollen (*7, 14*)—characteristic of non-magnoliid ("higher") dicotyledons (Fig. 1)—we also examine the relative importance of this clade as a component of latitudinal gradients in the diversification of flowering plants.

We compiled data from 1125 Cretaceous pollen and spore samples (assemblages or palynofloras) predominantly from the Northern Hemisphere (Fig. 2) and in particular Europe and North America. On the basis of geographic position and sedimentological occurrence, samples represent a range of predominantly lowland depositional environments in diverse physiographic settings. Data were not compiled from assemblages with fewer than ten "species" to reduce potential effects of small sample sizes. Each sample was assigned an age equivalent to the midpoint of its possible time-stratigraphic range based on recent studies, and paleolatitude-paleolongitude coordinates were calculated with present latitude and longitude with paleomagnetic and paleogeographic data (*16*). In each sample the number of "species" of angiosperm pollen, pteridophyte and bryophyte spores, conifer pollen, ephedroid pollen, and pollen of other (non-conifer, non-ephedroid) gymnosperms was scored to the extent permitted by the systematic resolution in the original studies. The contribution of each systematic group to each sample was calculated as a percentage of the number of palynomorph

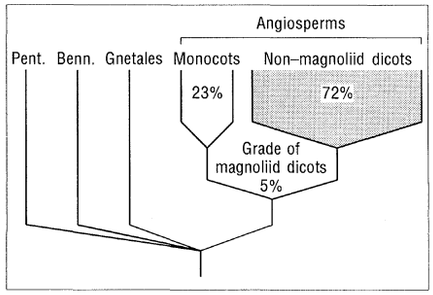

Fig. 1. Systematic relationships of angiosperm subgroups and related seed plants [Bennettitales (Benn.), Gnetales, and Pentoxylales (Pent.)] (*2, 3*). Non-magnoliid dicotyledons (subclasses Hamamelidae, Dilleniidae, Asteridae, Caryophyllidae, Rosidae) make up a clade including approximately 72% of extant angiosperm species (*28*) that is defined by the presence of triaperturate (or putatively derivative) pollen (*29, 30*). Monocotyledons (Liliopsida) and magnoliid dicotyledons (Magnoliidae) together account for 28% of extant angiosperm species (*28*) and are characterized by monosulcate (or putatively derivative) pollen (*29*). Pollen of most angiosperms is readily distinguished from that of other seed plants by the characteristic tectate, columellate pollen wall (*29*).

"species" recognized (including palynomorphs *incertae sedis*). Mean percentage values were calculated for groups of samples with the same combination of paleolatitude, paleolongitude, and geologic age. The systematic assignment of all palynomorph "species" was standardized based on the affinities of the 593 genera encountered in compiling our data. Palynomorphs *incertae sedis* make up less than 2% of the palynomorph diversity of individual samples and occur in only 42% of samples studied. Paleolatitudinal gradients and temporal trends in the palynological data are summarized graphically with a moving average method (kriging) (*17*) to fit trend surfaces to the within-palynoflora percentage values (Fig. 2).

Use of within-palynoflora diversity overcomes many of the biases associated with direct evaluation of total (summed) diversity (*8–10*), but because values for a single flora must sum to 100%, the strength of such comparisons depends on the consistency with which the floristic compositions of many floras independently conform to an overall pattern through time. Previous analyses (*8–10*) show that temporal changes in the within-flora percentages of angiosperms and other groups cannot be accounted for solely by the increase in mean palynoflora diversity that occurs during the Late Cretaceous (*10*).

The earliest widely accepted evidence of angiosperm pollen is from the Hauterivian of southern England and Israel (*18*), whereas at higher paleolatitudes, for example, western Canada and southeastern Australia (*19*), angiosperm pollen is first recorded in the Aptian. Within-palynoflora diversity results are consistent with first appearance data and indicate that the subsequent angiosperm diversification was also latitudinally diachronous (Fig. 2). Angiosperm pollen first becomes an important component of palynoflora diversity at low paleolatitudes, and only subsequently becomes important in middle and higher latitudes. Angiosperm pollen is still absent from high latitude samples well after it is diverse at low paleolatitudes. By the latest Cretaceous, angiosperms dominate the diversity of low-latitude palynofloras and typically account for 60 to 80% of the palynomorph "species" present, whereas at high latitudes typical angiosperm values are 30 to 50%. On the basis of comparison with macrofloras these values may actually underestimate the rate of angiosperm diversification (*10*).

Triaperturate, or triaperturate-derived, pollen occurs in the almost three-quarters of extant angiosperm species that make up the non-magnoliid dicotyledons (Fig. 1). Latitudinally diachronous first appearances of triaperturate pollen are particularly pronounced (*7, 14*), and this pattern is also reflected in the increase of triaperturate pollen "species" as a proportion of within-palynoflora diversity. In samples over the full range of paleolatitudes examined, triaperturate pollen typically accounts for the majority of angiosperm pollen "species" except during the earliest (pretriaperturate) phases of the angiosperm diversification (Fig. 2). In contrast, monosulcate and monosulcate-derived pollen of magnoliid dicots and monocots is generally a relatively minor component of the palynofloras sampled except at low paleolatitudes in the latest Cretaceous (Fig. 2). Qualitative assessments of palynofloras from these areas show that this relatively high diversity of monosulcate or monosulcate-derived pollen largely reflects the diversification of palms (Arecaceae) (*15*). Our data provide insufficient systematic resolution within the monocot-magnoliid group to test the hypothesis, based on extant taxa and fossil pollen data, that the initial diversification of monocotyledons was centered primarily in middle paleolatitudes of the Northern Hemisphere (*22*).

Within-flora diversity measures for non-angiosperm groups show various temporal and latitudinal trends complementary to the angiosperm pattern. "Species" of conifer pollen and bryophyte-pteridophyte spores are the major systematic components of Early Cretaceous palynofloras. Spores show the most pronounced decline in diversity, particularly through the mid-Cretaceous, although they remain a consistently important floristic component at high latitudes. Conifer pollen shows only a slight decline in

relative diversity through the mid-Cretaceous, and is also consistently better represented in higher, rather than lower, paleolatitude palynofloras. Other (non-conifer, nonephedroid) gymnosperms show a minor decline in percentage diversity through the Cretaceous and typically account for less than 20% of the species in palynomorph samples. In contrast to conifers and free-sporing plants (bryophytes and pteridophytes), they are most significant as components of low to mid-latitude palynofloras.

Among non-angiosperm taxa, the most striking paleolatitudinal pattern is shown by a group of distinctive polyplicate ephedroid pollen grains probably produced by extinct Gnetales (*21–24*). These grains range in morphology from simple plicate types (for example, *Ephedripites*) to more complex forms with club-shaped or elater-like projections (for example, *Elaterocolpites* and *Galeacornea*), and are particularly diverse in Barremian to Santonian low latitude samples (Fig. 2). Their gnetalean affinities are indicated by comparisons with pollen of extant *Ephedra* and *Welwitschia*, as well as unequivocal gnetalean pollen from middle paleolatitudes (*21–24*). Current phylogenetic hypotheses place Gnetales as the extant seed plants most closely related to angiosperms (Fig. 1) (*2, 3*), and it has long been recognized that taxa in the two groups share important biological characteristics, including the occurrence of vessels, reticulate-veined laminar leaves, insect pollination, and a tendency toward "progenetic" development of micro- and megagametophytes (*2, 3, 9*).

The mid-Cretaceous diversity of ephedroid grains at low paleolatitudes (Northern Gondwana) is documented in palynofloras ranging from Peru to South China (*25*). In samples from South America and West Africa relatively high abundances of angiosperm and ephedroid pollen are often positively correlated (*23, 26*), and in probable Aptian sediments from eastern North America macrofossils of Gnetales and early angiosperms co-occur in a low diversity plant assemblage (*24*). These data complement the large-scale similarities between the latitudinal and temporal patterns of increasing angiosperm and ephedroid diversity and suggest that angiosperms and Gnetales may have occurred, both locally and regionally, in similar habitats (*23, 24*).

The most pronounced difference between the diversification of gnetalean and angiosperm pollen is that ephedroid "species" never became diverse at mid- to high paleolatitudes and decline significantly in the Late Cretaceous. However, the ephedroid increase at low paleolatitudes indicates clearly that mid-Cretaceous floristic change did not uniformly result in decrease or stability in the diversity of non-angiosperm groups of Mesozoic plants (*8–10, 13*). Competitive effects between early angiosperms and non-angiosperm groups may have been important (*13*), but are not manifested initially in the ephedroid pattern and need to be interpreted in the context of marked mid-Cretaceous changes in the physical environment (*27*). The extent to which the parallel increase in angiosperm and ephedroid diversity reflects biological similarities between the two groups remains uncertain in the absence of a more detailed understanding of these critical mid-Cretaceous seed plants from low paleolatitudes.

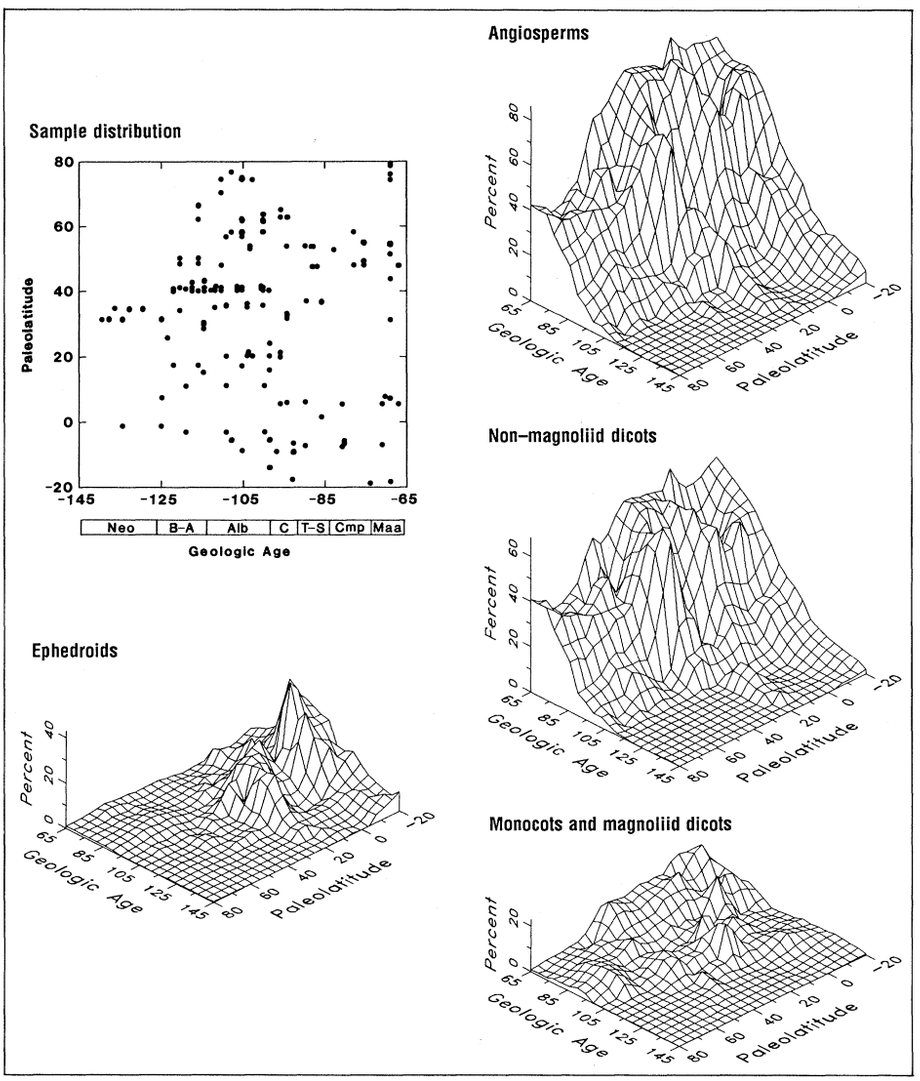

Fig. 2. Temporal and paleolatitudinal changes in relative "species" diversity within Cretaceous palynofloras for angiosperms, angiosperm subgroups (non-magnoliid dicotyledons, monocotyledons and magnoliid dicotyledons), and ephedroids. Inaperturate and polyporate angiosperm grains (a consistently minor component of within-palynoflora angiosperm diversity) are included in the total angiosperm analysis but not in either of the angiosperm subgroups considered here. Sample distribution incorporates 252 distinct combinations of paleolatitude, paleolongitude, and geologic age (Ma). Note that samples are numerous and closely spaced through the critical mid-Cretaceous interval, but are more sparse at low and high paleolatitudes, particularly during the Neocomian. Surfaces were constructed from percentage estimates for evenly spaced points calculated from the unevenly spaced values with the use of a kriging moving-average method (*17*). This technique is sensitive to unevenness in the "spatial" distribution of samples and maintains high fidelity to local changes in percentage values. Thus, values for single floras may deviate from the fitted surface, but the surface nonetheless provides an accurate "best fit" of the overall trends. A limitation of the kriging technique and other surface fitting methods is the potential for error inherent in estimating percentage values where sampling is sparse. For example, Neocomian levels of angiosperms and ephedroids at paleolatitudes 5° to 20°S are estimates derived from nearby sample data rather than observations within those temporal and paleolatitudinal limits. In order to test the robustness of the kriging model, surfaces were also fitted by locally weighted least-squares moving-average methods and low-order polynominal trend surface methods (*31*), and these corroborate the patterns shown here. Neo, Neocomian; B-A, Barremian-Aptian; Alb, Albian; C, Cenomanian; T-S, Turonian-Santonian; Cmp, Campanian; Maa, Maastrichtian.

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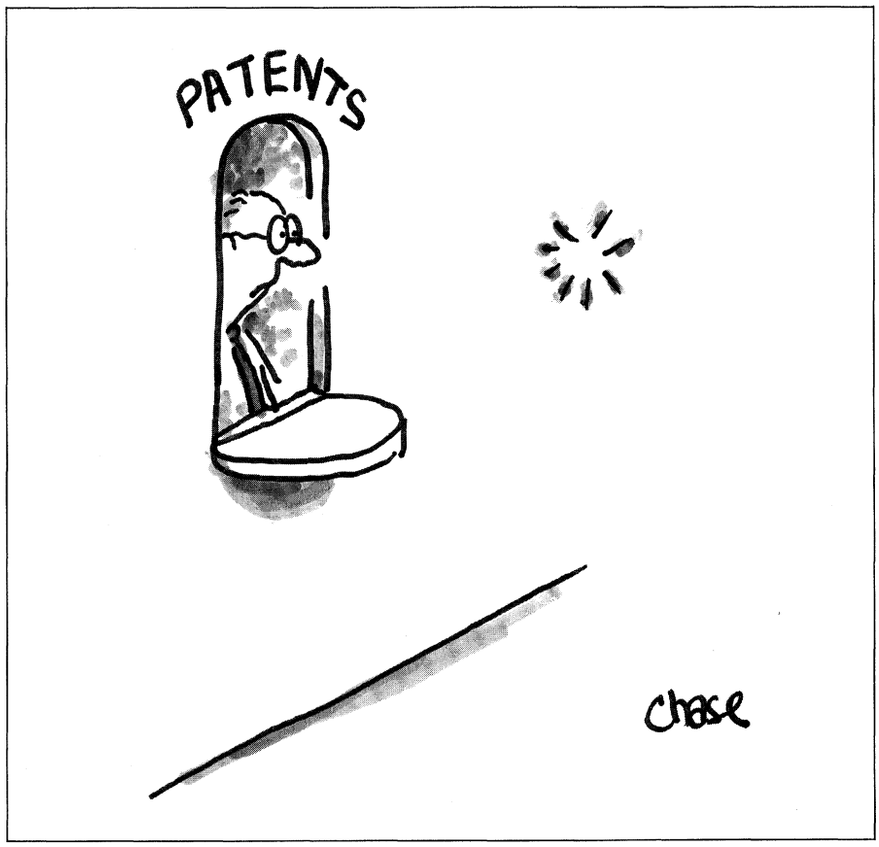

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