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HOW OLD ARE THE ANGIOSPERMS?*

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ABSTRACT. The currently known paleontological evidence bearing on the time and appearance of the angiosperms in the fossil record is examined. Special attention is directed to the very considerable body of data derived from palynological studies made during the past decade in various parts of the world. It is concluded that no *bona fide* angiosperm remains, either megafossil or microfossil, have yet been described from rocks older than Early Cretaceous sediments. Their record, however, is extraordinarily and increasingly well-documented in post-Early Cretaceous sediments from the major geographic areas of the earth. Considering the efficiency of the atmospheric and fluvial media of transport of plant microfossils, and the well known instances of long distance transport of microfossils, it seems highly implausible that a major, evolving unit of the earth's terrestrial flora could have greatly antedated the Cretaceous without detection. The morphological problems in identification of "early" angiosperms and difficulties in determining their first appearance are briefly considered.

INTRODUCTION

The ancestry of the flowering plants and the place and time of their origin constitute a most conspicuous and also much discussed gap in paleontological knowledge. There is increasing agreement, in which we concur, that the original home of the angiosperms was in tropical rather than temperate extratropical regions, but the time of their differentiation is yet curiously uncertain. The rise and ultimate dominance of the angiosperms during the Cretaceous period is well documented in the geologic record despite the lack of fossil evidence regarding ancestral forms. The evolutionary advancement and diversity commonly attributed to Early Cretaceous representatives of the angiosperms has been interpreted to imply either (1) their relatively rapid evolution in middle Mesozoic time, or (2) their extended pre-Cretaceous existence.

Much of the recent speculation on the origin of the angiosperms has favored the second of these possibilities, postulating their existence as long ago as the Paleozoic (Axelrod, 1952, 1959; Camp, 1947; Eames, 1959; Lawrence, 1951; Thomas, 1957, 1958; Thompson, 1952). For example, Axelrod (1952, p. 57) summarizes his views on the early history of the angiosperms as follows:

> Geological and botanical data are adduced which support strongly the inferences that (1) angiosperms probably were in existence by Permo-Triassic time, that (2) they probably occupied upland regions remote from lowland sites of deposition, that (3) they were distributed in the diverse environments of the tropical zone, that (4) at least some of them were ancestral to modern primitive types of monocotyledons and dicotyledons which are now represented in tropical regions, and that (5) they were then undergoing quantum evolution from proangiosperms which occupied upland regions.

The present writers are not convinced that the available data indicate or even strongly suggest that the angiosperms originated as long ago as the Paleozoic. Therefore they have examined and here summarize some of the tangible evidence and inferences bearing on this problem.

PRE-CRETACEOUS RECORD OF THE ANGIOSPERMS

The only conclusive argument for the existence of pre-Cretaceous flowering plants would be concrete evidence in the form of fossil remains. A number

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of putatively angiospermous plant fossils have been described from Jurassic and older rocks, but the angiospermous affinities of most of these remains are, as Edwards (1955, p. 170) puts it, "vague and dubious." In some examples, the true relationships of the fossil material are not determinable owing to poor preservation or to the often unrecognized morphological parallelisms between flowering and non-flowering plants. In most cases, reinvestigation has shown the original assignments to have been in error, or revisions in stratigraphy have abated the situation. It is probably no overstatement to say that there has not yet been described a pre-Cretaceous plant whose angiospermous affinities are unequivocal.

Some of the most commonly cited examples of early angiosperms are discussed below:

1. *Homoxylon* Sahni

   This genus, since renamed *Sahnioxylon* (Bose and Sah, 1954), was described in 1932 for Jurassic wood from India thought to represent a vesselless dicotyledon. Hsü and Bose (1952) later showed on the basis of gross stem structure that the material represents the secondary wood of a bennettitalean plant, probably of the *Williamsonia* complex.

2. *Suevioxylon* Kräusel

   This poorly preserved specimen of fossil wood containing vessels having a ring porous arrangement, from the Brown Jura of Germany (Middle Jurassic), was described originally as angiospermous (Kräusel, 1924). Later, however, Kräusel (1950, p. 95) expressed doubt, noting that the determinable characteristics of the wood are also present in gnetalean plants.

3. *Eucommiidites* (Erdtman) Couper

   Pollen thought to resemble that of the monotypic dicotyledonous family Eucommiaceae was described by Erdtman (1948) from shale of Early Jurassic age.

   Couper (1956, 1958) has restudied this and other material of the genus. He concluded that the fossil pollen has gymnospermous affinities. Single specimens of pollen from Jurassic strata of the Caucasus, thought to resemble grains of the Angiospermae, have been recorded by Naumova (1939) under the form generic names *Tryptycha* "with three folds", and *Monoptycha* "with one fold." The three-folded form appears comparable to *Eucommiidites*; *Monoptycha* is based on a monocolpate grain which could be gymnospermous.

4. Pollen resembling *Castalia, Nelumbium*, and *Magnolia* (*Simpson*, 1937).

   Simpson's material often accepted as authentically recording Jurassic angiosperms, has been re-examined by Hughes and Couper (1958). They show that all forms from the Scottish Middle Jurassic Brora Coal belong to gymnospermous taxa named since Simpson published his study. Hughes and Couper conclude that this evidence of pre-Cretaceous angiosperms must be discarded.

5. *Sporojuglandoidites* Vishnu-Mittre

   This genus is based upon a single specimen preserved in chert from the Upper Jurassic of India. Vishnu-Mittre (1955) suggests that the grain, which he regards as polyporate, is angiospermous and resembles pollen of the Juglandaceae. Preservation as shown by the figures is poor, and the pores are simple, unlike those of the Juglandaceae. Comparable openings, possibly due to degradative processes, crystal growth during diagenesis, or to fungal attack have been observed by us in undoubted spores of similar age.

6. *Poroplanites, Classopollis, Circumpollis, Canalopollis* Pflug

Pflug (1953) based these genera on Jurassic spores and pollen grains with supposed angiosperm-like germinal apertures. Krutzsch (1955) identified similar material from Liassic strata. Potonié (1954) and Couper (1955) have offered evidence that *Poroplanites* is a folded fern spore, and Couper believes that the other three genera have gymnospermous relationships.

7. *Furcula* Harris

This genus, of which Harris (1932) records some 50 specimens grouped in one species, is a curious leaf from Rhaetic deposits of east Greenland. Cuticular structure is known and is basically dicotyledonous. Stomata are of the syndetocheilic type, though this does not, as Harris implies, signify angiospermic affinity since the syndetocheilic condition prevails among the Cycadeoidales of the Mesozoic. The finer reticulate venation is strikingly dicotyledonous, though the coarse venation and over-all shape of the leaf are not. There seems no question that *Furcula* is of Rhaetic age since, according to Harris, it occurs in the same matrix with such typically Rhaetic species as *Ptilozamites nilssoni, Anomozamites minor*, etc. In the absence of any conflicting evidence, we suggest that *Furcula* be regarded as a member of the seed fern complex. The persistence of seed ferns well into the Mesozoic has been clearly established in the past few decades.

8. *Fraxinopsis* Wieland

These structures from the Rhaetic of Argentina originally were compared with winged fruits of *Fraxinus*. Kräusel (1950, p. 95) suggests that they are cone scales similar to *Cycadocarpidium* Nathorst.

9. *Propalmophyllum* Lignier

Palm-like leaves, or more restrictively, the terminal portions of the rachis of fan-shaped ridged leaves have been described as palms by Lignier. The specimens are of Liassic age and have been regarded by some authors (Seward, 1931) as evidence of the Jurassic antiquity of the Palmae. Lignier's studies were published in a somewhat obscure journal and have not been widely cited. Insofar as we know, Lignier's original specimens have not been reexamined. There is no doubt that his figured specimens appear palm-like, although their preservation, as indicated in the published figures, leaves much to be desired in making critical botanical asignment. As well as to the palms, they might also be compared to the juvenile leaves of some cycads, especially certain species of the genus *Cycas*. In Lignier's papers, his figured specimens of *bona fide* palms do not greatly strengthen his inferences regarding the affinity of *Propalmophyllum* with the palms. Until there is morphological evidence to the contrary, we feel that Lignier's material is most logically assignable to the Cycadaceae-Cycadeoidaceae complex of Mesozoic gymnosperms.

10. *Sanmiguelia* Brown

Leaves of a distinctly palm-like gross structure, preserved as impresssions on relatively coarse sandstones of Triassic age have been described as possible precursors of the palms (Brown, 1956). There is no doubt that Brown's material is the most arresting evidence of the megascopic remains of putative pre-Cretaceous angiosperms which has yet been described. The plaited, multi-ribbed leaves, in some cases attached to a very truncated rachis, are reconstructed as attached to a conical apical meristem. The restoration figured by Brown does not add significantly to the inferred relationship with modern palms. On the other hand, *Sanmiguelia* does not resemble any known early Mesozoic plant and its true affinity is certainly an open question. Unfortunately, no vestige of organic material is present in the matrix so that anatomical study is not possible. On the basis of the wide range of structure to be found within the cyadophyte line of vascular plants we suggest that the plant be regarded tentatively as a cycadeoid.

Regarding the fossil history of the palms, it should be noted that the megascopic remains of unquestionable palms are first found in the Upper Cretaceous. Extensive data exist, largely unpublished, which indicate that the earliest microfossil record of the palms is likewise Upper Cretaceous.

11. *Tetraporina* Naumova and *Triporina* Naumova

Under these generic names, Naumova (1950) described microfossils which she considers to be angiospermous from the Lower Carboniferous of the Moscow Basin. Similar forms were reported from the Lower and Middle Carboniferous of the western Don Basin by Teteryuk (1956), who notes that these forms range from Carboniferous through Cretaceous.

The Carboniferous alleged angiosperm pollen is difficult to evaluate because in most cases illustration is by drawing rather than by photomicrographs, and neither illustration nor text supplies the critical details of wall and pore morphology necessary to assess angiospermous relationships. The morphology and range of variation shown by described species of *Tetraporina* and *Triporina* bear a striking resemblance to the morphology of species of *Tetraëdron*, a unicellular green alga, in all important respects including shape, size, wall sculpture variation, and presence of thickenings and/or processes at the wall angles. Pores are absent in figures of many of the species assigned to *Tetraporina* and *Triporina*; where pores are shown, they could be analagous to the short, bifurcate processes present in some *Tetraëdron* species. *Tetraëdron* is represented in some fossil pollen assemblages (Florissant flora: Leopold, unpublished data; Stinking Water flora: Gray, 1956). Final assessment of the Russian Paleozoic forms must await an opportunity to examine the material.

The skepticism with which the listed pre-Cretaceous "angiosperms" are treated is not meant to imply that we reject the possibility that the ancestral angiosperms may have existed in Jurassic time, or indeed, earlier. We suggest only that since the fossil record is basic to paleontologic interpretation, extreme care should be taken in evaluating and accepting the actual evidence regarding so crucial an issue as the early record of the angiosperms.

UPLAND ORIGIN OF THE ANGIOSPERMS

To explain the paucity of angiosperms in the pre-Cretaceous geologic record, advocates of a Paleozoic or early Mesozoic origin for the group usually suggest that they arose and developed in upland areas of tropical regions far distant from the usual sites of deposition, it being assumed that the usual sites of deposition are in the lowlands. This inference has been made by several authors (e. g. Arnold, 1947, p. 334; Berry, 1945, p. 89; Seward, 1931, p. 366; Thomson, 1952). Three lines of evidence for the assumption have been stated by Axelrod (1952), whose views may be summarized as follows:

> 1. The majority of plant fossils accumulate at or close to the site of deposition, typically in lowland lake or streamside regions of sediment accumulation. Since upland sites of deposition, when they occur, are not likely to persist for long periods of geologic time, the probability of finding fossil leaves representing older, upland angiosperms is slight or non-existent.
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> 2. Cliseral relations demonstrated by successions of fossil floras show that higher and more specialized types were present in uplands of a region long before they entered the lowlands as replacements for the older flora.
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> 3. Diversity of physical environment in upland areas would promote rapid evolution in the ancestral angiosperm types.

Discussion

Let us consider these three lines of evidence in more detail.

I. The conclusion that fossil plants represent chiefly vegetation that grew at or near the site of deposition is based primarily upon the occurrence of fossil leaves which, in the past, have been the most studied organ of extinct plants. Other plant organs of a less fragile nature, e. g. wood, certain fruits and seeds, and pollen may withstand transport for long distances; in fact, paleoecological interpretation of these remains must be made cautiously because of the likelihood that organs representing plants from diverse habitats have been assembled.

Examples of the transport of wood from higher environments to a lower environment of deposition include the principally Devonian genus *Callixylon*, considered by Axelrod (1952) to represent an upland gymnosperm, and also other associated woods in the New Albany shale (Hoskins and Cross 1951); *Araucarioxylon* assembled in logpiles in the Petrified Forest National Monument in Arizona and elsewhere on the Colorado Plateau (Daugherty, 1941); araucarian cones in great quantities in the petrified forest of Cerro Cuadrado, Argentina (Wieland, 1935); wood of *Ginkgo* and *Betula* associated, somewhat incongruously, with endocarpal remains of tropical lianas of the families Icacinadceae and Menispermaceae in the Clarno formation of Oregon (Scott, unpublished data); the Aptian dicotyledonous woods described by Stopes (1912); seeds and fruits of unquestionably upland habitat associated with remains of swamp plants in the rich flora of the Brandon lignite of Vermont (Barghoorn, 1950, and unpublished data).

However, in the record of upland vegetation preserved in sedimentary basins, it is microfossils rather than megafossils which are most likely to be encountered. Although the representation of wind-borne pollen in sediments is determined by the interaction of a complex of factors of the physical and biological environments (Leopold and Scott, 1958; Muller 1959), a pollen assemblage typically contains forms from diverse ecological situations. The large numbers of pollen grains produced. together with their suitability for preservation under a variety of geologic conditions make it statistically far more probable that pollen will be incorporated in sediments than leaves or other organs. The small size and buoyancy of most pollen make it especially suitable for distribution by either wind or moving water.

Examples of long distance transport of modern pollen by wind are common. Grayson (1960. oral communication) discovered *Quercus* and *Acer* pollen in several moss polsters from Labrador. He concludes that these occurrences represent wind transport from deciduous forests hundreds of miles to the south. The most extraordinary example is that of Hafsten (1951) who reports *Nothofagus* pollen in a modern peat profile from the islands of Tristan da Cuhna in the center of the south Atlantic basin. Geographic relationships and effective wind directions indicates that the *Nothofagus* grains were transported from southern South America, a distance of 4500 kilometers. Pollen of *Podocarpus* from upland habitats on the island of Trinidad has been transported by wind to marine sites as far as 75 miles from the island (Muller, 1959).

In fossil floras, Kosanke (1950) suggests that winged gymnospermous pollen of the genus *Illinites* in Pennsylvanian coal swamp deposits may have originated from plants growing in uplands. Study of the pollen from the Eocene Green River formation (Wodehouse, 1933) added several upland genera to the warm-temperature streamside assemblage known from leaves. Traverse (1955) identified pollen of such upland genera as *Pterocarya* and *Quercus* (in part) in the dominantly swamp assemblage of the Brandon lignite of Vermont. *Podocarpus*, now limited in Venezuela to mountainous sites above 2000 meters, occurs sporadically as pollen in sediments of Eocene age and younger, and increases markedly in sediments of Oligocene and Miocene age (Kuyl, Muller and Waterbolk, 1955) in Venezuela.

As noted above, water is likewise an effective medium for transport of pollen. Because of their small size, equivalent to silt particles, and extreme resistance to chemical and microbiological degradation, pollen grains may be carried for long distances as a part of the sediment load of streams before incorporation in lowland flood plains or even in marine deposits. Muller (1959) in his intensive study of pollen distribution in sediments of the Orinoco delta, shows by specific examples that, depending on the various factors, the pollen obtained in a single dredge sample may have been derived from cosatal vegetation bodering the estuaries or transported by air or water from inland montane environments. An example of long distance transport by water is the occurrence of *Alnus* pollen, which must have been carried more than 500 miles from mountain habitats by the Orinoco system.

Objection to the likelihood of the pollen of early upland angiosperms entering the sedimentary record has been raised on the ground that they may have been pollinated by insects rather than wind. The geologic history of Coleoptera dates from the Permian, and the existence of beetle pollination in the woody ranalian complex has led some investigators to link their rise and to suggest co-existence (Grant, 1950; Eames, 1959). Modern members of the Magnoliales known to be pollinated by beetles, e. g. *Magnolia, Illicium, Calycanthus*, have pollen that is also well suited to transport by wind, being of small to medium size and produced in numbers. Ranalian floral characters, particularly the numerous stamens borne on an open flower and the medium to small sized pollen, which is within the range (17-58μ) of the majority of anemophilous plants (Dyakowska and Zurzycki, 1959), favor the representation of their pollen in the regional pollen rain regardless of the functional vector in pollination.

The absence or paucity of pollen of some ranalian genera in recent (i.e. post-glacial) sediments, including peat deposits, may be ascribed to lack of resistance to chemical and microbiological factors in the depositional environment. Thus pollen of the Lauraceae and many genera of the Magnoliaceae are quite ephemeral in modern sediments owing to feeble development of their exines and, more important, the chemical instability of the exine to oxidative and microbial attack. The pollen of many of the more primitive surviving ranalian forms, however, are featured by massive exines, and the grains with stand rigorous treatment with a variety of reagents as may be demonstrated in laboratory preparations.

That insect or bird pollinated plants may indeed have their pollen preserved in sediments is demonstrated by the fossil record of the Proteaceae in Australia, where Cookson (1950) has found a variety of grains assignable to this family in a number of Tertiary deposits.

It is unlikely that pollination in the primitive angiosperms was limited to insect vectors. Stebbins (1951) has pointed out that various means of pollination are utilized within most major taxa. He states that (p. 299): " . . pollination by flies, birds, wind and water is likewise scattered through the angiosperms with little relationship to the boundaries of the higher categories".

Thus for both the largest and the smallest of angiosperm organs, their woody trunks and their pollen, there exist prevalent, competent and demonstrated means for the representation of upland plants in lowland sediments. Emphasis on palynology in the last decade has resulted in the examination of thousands of samples of sediments of Mesozoic age from the major geographic regions of the earth including many from the tropics; but authentic pre-Cretaceous angiosperm pollen has not yet been reported. Although the leaves of upland dicotyledons cannot ordinarily nor logically be expected in lowland deposits, there is ample reason to give careful scrutiny as to why their pollen is consistently absent from pre-Cretaceous sediments if the group had actually been evolving in the uplands since the Paleozoic.

II. In cliseral relationships among floras, migration is by no means limited to the downslope path of movement, and the source and nature of the replacing flora is ecologically determined largely by the nature of the climatic change. Cooling would cause upland, more temperate plants to move into lower latitude lowland regions; a widespread and consistent warming trend provides an opportunity for lowland plants to extend their ranges at the expense of the more temperate plants previously occupying the area. The first situation is illustrated by the southward retreat of the warm temperate and subtropical flora of late Eocene and early Oligocene time in temperate regions of Europe and North America; the converse is shown by the northward movement in the early Tertiary of elements of the Poltavian tropical or subtropical flora to the latitude of present-day southern England (Chandler, 1954; Edwards, 1955).

The fossil record provides exceptions as well as agreements to the thesis that higher, more specialized types of plants were present in the uplands of a region long before they entered the lowlands as replacements for the older flora. The first vascular plants, the Psilophytes, almost certainly arose from aquatic or semi-aquatic environments to dominate and replace the prostrate non-vascular land flora of the earlier Paleozoic lowland basins. There is no evidence nor implication in the fossil record that either the early or advanced arboreal members of the Lycopsida and Sphenopsida entered the lowland environment from the uplands to become a part of the dominant forests of the Carboniferous. In fact, their anatomical structure suggests the opposite. In the case of more highly specialized groups of plants of known Paleozoic origin, the Coniferales are of much interest in connection with the hypothesis that evolutionary specialization is fostered by high altitudes in tropical environments. The ancestors of the entire group of coniferophytes (including probably also the Ginkgoales), the Cordaitales, were among the most abundant representatives of the lowland Carboniferous swamp forests. It seems in accord with currently known facts of the fossil record that the major units or phylogenetic derivatives of the Cordaitales had diverged by the early Mesozoic; most probably the taxonomically recognizable families of the Coniferales were morphologically distinct by Jurassic time. It may well be argued that the Coniferales represent a major and, in the existing flora, a well-represented group of plants whose origin has been in lowland tropical regions and whose diversification has been in upland and cool temperate regions. In this connection it is of interest to note their present phytogeographic and evolutionary status. The conifers are a moribund group of plants in terms of the late Mezozoic and Cenozoic history of the earth's vegetation. Presently, their phyletic as well as geographic distribution is featured by a high degree of endemism, especially in higher altitudes of warm temperate and tropical regions. In fact, 15 genera of conifers are each represented in the surviving flora by only one species, and these species are chiefly limited to isolated upland localities in austral tropical areas. It would appear that the geographic origin and phylogenetic diversification of the Coniferales has been one of origin in lowland environments and progressive moribundity in upland environments, chiefly in tropical regions.

If the primitive angiosperms had become established in, and remained restricted to, uplands during all or a major portion of the time interval from the Permian to the Cretaceous, a widespread, major climatic deterioration presumably would have been required to initiate their invasion of the tropical lowlands to displace the established gymnosperm flora on the extensive scale that occurred in the Early Cretaceous. Evidence from other paleoecologic considerations and groups of organisms (e. g. marine invertebrates: Gignoux, 1950, p. 392; and vertebrates: Colbert, 1953, p. 265) indicates that climatic conditions then, while not so uniform as in the Jurassic, were equable over large portions of the earth during Early Cretaceous time. If minor or localized ecologic changes were adequate to initiate the migrational capacities of the primitive angiosperms, it would be remarkable that this group of plants should be restricted geographically for such an extended period of geologic time as elapsed between the late Paleozoic and the Early Cretaceous.

III. There is little question that, in general, the variety of physical environments existing in uplands provides a favorable setting for rapid evolution and diversification (Simpson, 1944; Stebbins, 1950). The flowering plants also have found the tropical lowlands favorable for diversification; floras of the tropical rain forests are probably the richest plant assemblages known (Good, 1947, p. 192). The great variety of plants and their vast speciation in the tropics may be related to the fact that the majority of arboreal dicotyledons are basically similar vegetatively; important differences among them are more likely to involve aspects of reproductive structures and adaptations for seed dispersal. The presence of rich, rapidly evolving faunas of insects or other animals might well have been more fundamental to differentiation of taxa than stresses of the physical environment in the early stages of angiosperm evolution (Stebbins, 1950, p. 502). For example, some members of the Hymenoptera and Diptera, insect orders containing many forms now effective in flower pollination, existed in Jurassic time (Carpenter, 1955). The diversification of the angiosperms may be linked, at least in part, to the rise of these groups.

Little of the known background of the angiosperms relates them to temperate upland situations. On the contrary, there is much evidence linking the group to lowland, tropical conditions (Bews, 1927). Axelrod (1952), in summarizing Bews' work, comments that: "The evidence reviewed by Bews makes it seem reasonably certain that the phylum was basically adapted to moist tropical forests, and that it has become adapted to the more specialized environments of the tropical and extratropical regions".

This evidence, in extremely skeletonized form, includes in part the following: members of the ranalian complex, including the most primitive extant angiosperms, are primarily adapted to the environment of the moist tropical lowlands. Within the major taxa of flowering plants, the more primitive floral types are most commonly present in tropical environments, the derived types are associated with more specialized tropical and extra-tropical environments. Based on modern distribution patterns, three-fourths of all angiosperm families apparently are primarily adapted to tropical regions. It may be noted in this connection that the pollination mechanism of incompletely closed carpels, which yet exists among the most primitive surviving angiosperms (Bailey and Nast, 1943; Bailey and Swamy, 1951) would seemingly require the atmospheric environment of the humid tropics for effective operation. The persistence in the humid tropics of the primitive vesselless dicotyledons of the ranalian families Winteraceae, Amborellaceae and Sarcandraceae is therefore quite in accord with their presumed morphological dependence on a humid tropical environment.

Studies of changes in modern tropical vegetation with increasing altitude have been summarized by Richards (1957, p. 346) who states that: "The tall luxuriant Tropical Rain forest of the lowlands gives place to other communities also evergreen, but lower in stature, simpler in structure, and floristically poorer. The purely tropical flora is left behind and is replaced by a montane flora in which many of the genera, or even the species, are temperate." Five major zones of vegetation, often sharply delimited, can be distinguished. The general features of this altitudinal zonation appear similar in both Old and New World tropics, and must have existed in the past.

The existence of this zonation suggests that, had the early angiosperms been restricted from the Permian to the Cretaceous to upland habitats of sufficient altitude to furnish environmental diversity of effective contrast to that of the tropical lowlands, the resultant flora would have developed a more temperate aspect rather than the lowland character to which the available evidence points.

SOME ASPECTS OF EARLY ANGIOSPERM FLORAS

In marked contrast to the uncertainty surrounding their existence in pre-Cretaceous rocks, there is positive and widespread evidence from Cretaceous sediments of the entry and increase of angiosperms in the fossil record. Leaf floras documenting the transition from dominantly gymnospermous to dominately angiospermous plants have been compiled by Axelrod (1959, p. 203), who interprets them 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."

There is further evidence based on palynological studies of Mesozoic sediments which bears out the genuineness of the Cretaceous entry of the flowering plants. As pointed out earlier, fossil pollen is especially pertinent evidence as to the time of the first appearance of the angiosperms because of the likelihood that it will record upland as well as lowland vegetation.

Angiosperm pollen has been found to be lacking in Late Jurassic and earliest Cretaceous sediments in both eastern and western hemispheres. Quantitative studies of pollen currently known from Cretaceous sedimentary sequences, however, consistently record the appearance and increase of the angiosperm population and their ultimate dominance.

One study is that of Couper (1958), who examined 100 samples from Jurassic and Lower Cretaceous Wealden and Aptian beds in Great Britain and Scotland. He found the Jurassic and Cretaceous floras to be distinct, but noted no definite angiospermous pollen grains in either. Delcourt and Sprumont (1955) found no angiosperm pollen among plant microfossils from Wealden beds in Belgium. Angiosperm pollen is absent from a rich assemblage in the Morrison formation, of Upper Jurassic age in Utah (Scott, unpublished data). A survey of some 20 pollen-bearing samples of Triassic and Jurassic age from various localities in Europe, North America, and South America has failed to turn up any angiosperm pollen (Scott, unpublished data). Pollen and spore assemblages from the Upper Triassic Keuper of Germany (Leschik, in Kräusel and Leschik, 1956) and in the Upper Triassic Chinle formation of Utah and Arizona (Scott, unpublished data) lack angiospermous pollen as does also a Jurassic pollen flora from India (Vishnu-Mittre, 1954). Examination of microfossil floras of Jurassic and Upper Triassic age from such diverse areas as Greenland, equatorial Africa, Sweden, Great Britain, Central Europe and eastern North America have likewise failed to reveal any evidence of the existence of angiosperms (Barghoorn, unpublished data).

Palynological examination of sequences of Cretaceous sediments ranging from the lower Trinity (Aptian) through the Navarro (Maastrichtian) and into the Midway (Paleocene) in central Texas has been made by Grayson and Pierce (1959, personal communication, and also communicated to the 9th International Botanical Congress, Montreal, 1959). Their work shows a progressive increase in both the absolute and relative number of angiosperms represented, from their absence in the lowest beds to a predominance (75% of the total pollen and spores present) by the end of Cretaceous time. Krutzsch (1957) records that typical angiosperm pollen is not present in Middle European sediments until Albian and Cenomian time. Angiosperm pollen first apepars in the fossil record of New Zealand in Cretaceous time (Couper, 1953). In a detailed palynological study Steeves (1959) has found that in the Cretaceous sediments represented on Long Island, New York, there is a progressive increase in the representation of angiosperm pollen from the lowermost (Raritan age) beds to the later (Magothy age) sediments. Concomitant with the increase in angiosperms there is a progressive decline, both in absolute and relative proportions, of gymnosperms and ferns. The data presented by Steeves (1959) are based on samples secured from continuous subsurface cores extending from below the drift to the bedrock (saprolite, of unknown age) on eastern Long Island. The borings penetrated approximately 1400 feet of non-marine Cretaceous sediments and hence constitute a representative sample of the known middle to Upper Cretaceous section of the coastal plain of eastern North America.

A factor in the extrapolation of the angiosperms far into the geologic past is the belief that the forms found in Early Cretaceous rocks were highly evolved representatives of modern families or even genera; hence, they must necessarily have had an extended past history. For the most part this conclusion is based upon the identification of fossil leaves. The problems involved in the identification of detached leaves have been discussed by Bews (1927 p. 4-5), Good (1947, p. 264-265) and Stebbins (1950, p. 515-516). The latter author concludes that "forms similar to modern species and genera are recognized with relative ease, while radically different types, including those which might have formed connecting links between existing genera or families, could not be recognized or assigned to their correct phylogenetic position even if they were found." Stebbins (1951, p. 301) further points out with reference to floral structures the likelihood " . . that in the remote period of geologic time, probably the Cretaceous period, when the ancestors of the modern families became differentiated from each other, their interrelationships were much like those between modern species and genera, and were governed by similar selective factors". This conclusion would seem to be applicable to leaf as well as floral morphology, and points up the possibly misleading nature of many early dicotyledonous leaves. If there are criteria by which fossil leaves from the Early Cretaceous can be assigned reliably to modern families, they have not been delineated in the literature despite the many definite assignments that have been made.

The aura of modernity surrounding the Early Cretaceous dicotyledons is created in no small part by the practice of erecting names for form genera based upon supposed resemblances to modern genera, *e.g. Quercophyllum*, and the use of modern generic names for leaves which would better be placed in form or organ genera. An example of the effect of this practice is the common, uncritical acceptance of the increasing percentage of angiosperm species in successively younger beds of the Lower and Upper Cretaceous Potomac formation of Maryland as evidence for the rapid rise of the angiosperms at this time. Although forms in the lower beds of the Patuxent and Arundel have been given such names as *Juglandiphyllum* and *Ficophyllum*, there is reason to doubt whether most of the leaves are even angiospermous (Berry, 1911).

The dicotyledonous woods from the Aptian beds of England are another example pointing to the supposed modernity or high level of specialization of Early Cretaceous angiosperms. The Aptian woods were described before many of the criteria for phylogenetic advancement of the secondary xylem of woody dicotyledons were formulated. Bailey (1949) has observed that the full range of morphological expression from primitive to advanced can be found among the extant dicotyledons. The Aptian woods exhibit much of this range; it is not surprising therefore that the Aptian woods have a "modern" aspect. The possibility exists, unfortunately, that the specimens described by Stopes were from beds other than Aptian since they were selected from museum specimens which may or may not have been authentically placed stratigraphically (Couper 1958). There is need for further study of Aptian age beds in England before the significance of the Aptian woods can be established firmly. As previously noted, angiosperm pollen is absent from the Aptian beds of Great Britain (Couper, 1958).

There is morphological evidence from reproductive structures which indicates that Cretaceous angiosperm floras may have had a much less modern aspect than is commonly attributed to them. For example, Cretaceous pollen assemblages, particularly those from the early Late Cretaceous, contain a wealth of angiosperm forms whose detailed pollen morphology is unlike that of known living plants (Steeves, 1959). In many cases pollen cannot be assigned to families; where families can be recognized, modern generic assignments may be difficult or impossible. Although there is great variety in wall and aperture morphology in Cretaceous angiosperm pollen, grains representing certain major morphological classes do not appear until the Tertiary (Kuyl, Muller and Waterbolk, 1955).

Angiosperm fruits provide highly reliable guides to systematic affinities.

An angiosperm fruit from the Lower Cretaceous of France could not be related by Chandler (1958) to any modern genus or family. Chandler (1954) notes that Upper Cretaceous fruits from Egypt are difficult to relate to modern genera and families. Even as late as the early Tertiary, fossil reproductive structures, where known, show that the modernity of the floras was diluted by a significant admixture of extinct forms (genera). In the lower Eocene London Clay flora, Reid and Chandler (1933) found 75% of the genera to be extinct. Extinct genera represented by fruits and seeds have been recognized in the Tertiary brown coals of Germany (Kirchheimer, 1957), in Clarno flora (Eocene) of Oregon (Scott, 1954, 1956) and in the Brandon lignite (Oligocene?) of Vermont (Barghoorn, 1950; Barghoorn and Spackman, 1950).

Although the angiosperms constitute the most highly evolved group of vascular plants, many of the morphological features which characterize them also developed in other groups. Thus vesselless wood indistinguishable from that attributed to primitive angiosperms existed in the extinct cycadophytes (Hsü and Bose, 1952); even vessels, which characterize most modern angiospermous woods, have evolved independently in six groups of vascular plants (Bailey, 1949; Bierhorst, 1958). Leaves having reticulate venation are known in diverse groups, e.g. Gnetales, ferns, pteridosperms. The flower is difficult to define in a manner that excludes the highly organized infloresceneses of the cycads, and angiospermy was approached in the Caytoniales and in early Mesozoic seed ferns. Only double fertilization and endosperm development seem to be truly unique angiospermous achievements, and for the origin and significance of this the fossil record can provide no clue.

Until the angiosperm ancestors are identified, there remains uncertainty as to the extent of the morphological gaps between the flowering plants and their predecessors. The occurrence, due to parallel development, of many of the advanced features of the angiosperms in separate taxa of vascular plants raises the possibility that, whatever the relationships of these elusive ancestors, they had already evolved in their structural organization features now characteristic of the angiosperms. If several of these features, e.g. vessels, reticulate leaf venation, and bisexual reproductive organs, had already evolved in precursors, the evolutionary steps that differentiated the flowering plants may not have been great, and the geologic time required for their diversification not extreme. In this connection it is of interest to note the extraordinary diversification and ubiquitous distribution of herbaceous dicotyledons whose evolution has apparently been a phenomenon of post early Miocene time, as deduced from abundant palynological evidence.

SUMMARY

A number of lines of evidence suggest that there may be a shorter interval of geologic time between the origin of the angiosperms and their first appearance as fossils in the Cretaceous than is allowed by any theory postulating their existence in tropical uplands since the late Paleozoic. This evidence includes the lack of unequivocal angiospermous plant fossils in rocks of pre-Cretaceous age and a consistent record, based upon pollen as well as leaves and other organs, of their entry into and rapid numerical increase in Lower Cre-

taceous sediments. The common intermingling in sediments of pollen derived from plants growing in diverse habitats, including uplands, makes it quite unlikely that angiosperms could have persisted in upland regions from the Paleozoic to the Cretaceous without having contributed microfossils to sedimentary basins. Additionally, known primitive angiosperms as well as a majority of all angiosperm families basically are adapted to equable tropical conditions rather than to more extreme, upland environments.

The time of the origin of the angiosperms, whether Paleozoic, Cretaceous, or, as is more probable, intermediate between them, is not known. The fascinating potentialities of the paleontological record make it possible and even likely that tomorrow's discoveries will outmode today's speculation. Despite its vagaries and imperfections, the fossil record remains our best index to relationships involving geologic time; and it does not bear out speculations on the origin of the angiosperms in the Paleozoic era.

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