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HOW OLD ARE THE ANGIOSPERMS?

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ABSTRACT. Available evidence has earlier led to the inference that ancient angiosperms originated in moist tropical upland regions during Permo-Triassic time.

Recent arguments, which purport to show that there was a much briefer interval between the time of origin and appearance of angiosperms in the record, and that they evolved in lowland areas, are not consistent with evidence from morphology, evolution, paleoecology, or paleoclimate.

INTRODUCTION

The preceding paper (Chandler and Axelrod, 1960), which describes one of the oldest undoubted angiosperm fruits on record, adds a little more evidence to the few facts now available which can be used to assess the antiquity of flowering plants. At present there are two opposing views concerning the probable age of the alliance. One group has felt that data favor the inference that primitive flowering plants, representing taxa that are extinct but which gave rise to alliances (families, orders) ancestral to modern ones during the Jurassic and Early Cretaceous, probably were in existence by Permo-Triassic time (Axelrod, 1952, 1960; Camp, 1947; Eames, 1960; Němejc, 1956, Melville, 1960). More recently, Scott, Barghoorn, and Leopold (1960) documented a case for an origin during the Middle Mesozoic. The arguments which they have marshalled for such a recent history for flowering plants are in no wise decisive. The inadequacies of the major criticisms that they have leveled at inferences that favor the occurrence of ancient flowering plants in moist tropical upland regions during the Permo-Triassic are sketched here in the same order that they attacked the original theory (Axelrod, 1952). In addition, the principal weaknesses of a theory that visualizes only a brief unrecorded lowland history for the phylum are also noted.

PRE-CRETACEOUS ANGIOSPERMS

Axelrod (1952) reviewed most of the records of Jurassic and Triassic angiosperms reported up to that time and concluded that some of them probably were correctly assigned to the phylum (also see Thomas, 1936). This was considered to indicate that the alliance was already in existence during the later Triassic, some 40 million years prior to the first Cretaceous records. Hence the origin of the group was believed to have occurred somewhat earlier, probably during the Permo-Triassic transition. This conclusion that the alliance probably has considerable antiquity was not new but had been suggested earlier by Thomas (1936) on the basis of presumed rates of evolution in the group, and by Camp (1947) from morphological evidence of known Cretaceous angiosperms. More recently, Němejc (1956), Eames (1960), and Melville (1960) have summarized additional morphological data which suggest that the phylum is an ancient one and that it probably was in existence by the close of the Paleozoic.

On the other hand, Scott, Barghoorn, and Leopold (1960) take the ex-extreme position that Krausel (1956) has already enunciated: Because all

records of pre-Cretaceous angiosperms are suspect, they do not provide a means for evaluating the antiquity of the group. Their reanalysis of some of the previously reported pre-Cretaceous "angiosperms" is most welcome and deserves careful study by anyone who is sufficiently bold to describe another pre-Cretaceous flowering plant. They conclude (p. 285) that " . . . there has not yet been described a pre-Cretaceous plant whose angiospermous affinities are unequivocal". Like Krausel, they reach this decision because nearly all of the morphological features which characterize angiosperms are also represented in other alliances. Vessel-less wood indistinguishable from that attributed to primitive living angiosperms occurs in the extinct cycadeoids; vessels characterize most angiosperm woods and have also developed in six other phyla of vascular plants; leaves with reticulate venation occur not only in angiosperms but also in the Gnetales, ferns, and seed ferns; stomata of angiosperms may resemble those of cycadophytes; even the flower is difficult to define in such a way that it excludes the inflorescences of cycadophytes; and angiospermy was essentially attained by the Caytoniales and some early Mesozoic seed ferns. Thus they properly point out that until angiosperm ancestors are identified there is uncertainty as to the extent of the morphological gap between flowering plants and their predecessors. "Only double fertilization and endosperm development seem to be unique angiospermous achievements" (p. 296).

(1) They are no doubt correct when they assert that "there has not yet been described a pre-Cretaceous plant whose angiospermous affinities are unequivocal" (p. 285). However, their criticisms of all pre-Cretaceous angiosperm records are nullified because they have not demonstrated that these plants are nonangiospermous: they first have to show (somehow) that the previously reported pre-Cretaceous angiosperms did not have double fertilization and endosperm before they can be rejected as valid angiosperm records. Obviously, all presently known pre-Cretaceous "angiosperms" will always comprise unequivocal records. In fact, until we are fortunate enough to find seeds which were mineralized under extremely exceptional conditions we never will have an undoubted pre-Cretaceous angiosperm. We realize that the pre-Cretaceous fossils now in hand are not decisive as evidence for angiosperms, yet Scott, Barghoorn, and Leopold have given us no real reason to doubt that at least some of them are ancient angiosperm taxa (families, orders, possibly classes) that have been long extinct, and that they actually do provide us with evidence of the plexus from which the alliance diverged.

Their argument clearly lacks conviction because all of the angiosperm characters (apart from endosperm development and double fertilization), which they reject as evidence for recognizing the existence of previously reported flowering plants (p. 285-287), they also believe were present in early angiosperm evolution.

(2) Scott, Barghoorn, and Leopold believe that angiosperms diverged from an ancestral alliance during the Middle Mesozoic. This is difficult to understand because they present no evidence which might lead to the assumption that flowering plants were even in existence at this time. On the contrary, they emphatically conclude that all previously reported records of pre-Cretaceous angiosperms are suspect or at least unequivocal. They particularly emphasize

that during the past decade intensive palynological studies have failed to turn up any authentic angiospermous pollen in pre-Cretaceous rocks which . . . "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 (p. 297)." Using their own argument, we may appropriately note that, if it is "quite unlikely" that angiosperms were in the uplands prior to the Cretaceous, then it is practically certain that they were not in the lowlands: otherwise we should have Jurassic pollen. Nowhere do Scott, Barghoorn, and Leopold attempt to explain why we have no records of these plants which they maintain were evolving in the Middle Mesozoic.

UPLAND ORIGIN FOR ANGIOSPERMS

To account for the paucity of angiosperms in the pre-Cretaceous lowland record several investigators have suggested that they probably evolved in upland regions.[1] As reasons supporting such a view had not been presented, Axelrod (1952) developed three arguments favoring the inference, all of which have been rejected by Scott, Barghoorn, and Leopold (1960).

Upland Record Not Preserved

Practically all of the known pre-Cretaceous plant record was accumulated at or close to sites of deposition in lowland basins, notably in lakes, swamps, floodplains, and deltaic to nearshore marine areas. Because any pre-Cretaceous sediments which were deposited in upland basins could not have persisted for any long period of time owing to erosion, the probability of finding ancient angiosperms which may have been preserved there is very low.

To this suggestion, Scott, Barghoorn, and Leopold bring the argument that, if early angiosperms were in the uplands for an interval lasting from the Permo-Triassic to the Early Cretaceous, we should at least expect to find some evidence of pollen grains preserved in lowland record. They point out that, as water is an effective medium of transport from highland to lowland areas, pollen grains—owing to their small dimensions (silt size) and high resistance to chemical and microbiological attack—should be in the lowland record if they had existed in the uplands at this early date. A number of examples of long-distance transport are cited to support the argument. They note (p. 290) that during the past decade the emphasis on palynology "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 pollen has not yet been reported." They conclude (p. 297) that . . . "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."

[1] Since the word "upland" is not precise it may have led Scott, Barghoorn, and Leopold (1960) and others as well to misunderstand the concept. It is to be emphasized that the term was never intended to connote high montane summits or the upper zones of mountains. On the contrary, the writer has visualized rolling hilly tracts and the lower to middle slopes of mountainous terrain in the ancient tropics as an upland environment. We grant that the word lacks precision, yet in the present case it has much in its favor because we can speak about ancient angiosperm evolution only in general and vague terms.

(1) First, it is appropriate to note again that although Scott, Barghoorn, and Leopold doubt that angiosperms could have existed in the uplands for the 60-million-year period from the Permo-Triassic to the Early Cretaceous without having contributed to the pollen record, they nonetheless postulate that angiosperms were evolving in the Middle Mesozoic, which is only 30 million years later. Curiously, they provide no explanation for the absence of pollen records during the 40-million-year period of evolution which they believe occurred prior to the Early Cretaceous. Obviously, if the pollen argument has validity, and they believe it does, then it must mean either (*a*) that the whole phylum is of post-Jurassic age, or (*b*) that the absence of pollen from the record is not a crucial argument for rejecting an hypothesis that visualizes the emergence of the phylum in Permo-Triassic rather than in Middle Mesozoic time.

(2) The absence of undoubted pollen grains (though some have been reported) in the record from the Late Paleozoic to the Early Cretaceous may be owing to any one or all of the following four factors:

(A) Most pre-Cretaceous angiosperms may have produced pollen that was not yet wholly distinctive of the alliance. In all phyla of vascular plants different parts of the plant body show evolution toward increased complexity, as illustrated by the evolution of woody tissues, stems, sporangia and spores, fronds, leaves, flowers, etc. In some taxa, however, primitive structures may persist for long intervals of time. Thus certain primitive living angiosperms still have open carpels (*Degneria*), vessel-less wood (*Trochodendron*), and foliar stamens (*Himantandra*).

Angiosperm pollen grains show morphological evolution into more complex forms, and the more primitive living alliances have also preserved ancient pollen morphology. For instance, some ranalian taxa still produce pollen that is generally regarded as primitive. Those with 1-sulcoidate aperatures (Austrobaileyaceae, Cannelaceae, Degneriaceae, Himantandraceae, Myristicaceae) and those that are nonaperaturate (Lauraceae) are in this category. The fact that nonaperaturate grains, which are represented in the ranalian alliance as well as in other groups (Cannaceae, Juncaceae, Marantaceae, Musaceae, Zingiberaceae), could be mistaken for nonsaccated grains of conifers, and that those with 1-sulcoidate aperatures could be taken for certain pteridophytes or gymnosperms, is a significant point. If pre-Cretaceous angiosperms were largely producing "gymnospermous" pollen we might well regard them as coniferous. In fact, it is to be noted that although some investigators have described pre-Cretaceous pollen (see records discussed by Scott, Barghoorn, and Leopold, 1960, p. 285-287), they believe that several of them represent gymnosperms. The belief that pollen grains underwent considerable morphological evolution during pre-Cretaceous time seems a reasonable assumption, although Scott and co-authors appear to favor the view that angiosperm pollen scarcely evolved at all during the pre-Cretaceous history of the phylum. In view of the nature of the evolution of other plant structures this would be a most remarkable phenomenon if it could be proven.

(B) The pollen of pre-Cretaceous angiosperms may not yet have evolved an exine sufficiently resistant to permit easy preservation. For example, genera

of such families of the woody ranalian plexus as Lactoridaceae, Lauraceae, and Himantandraceae have a very thin exine and hence are generally not preserved even in the Tertiary record. A number of others have grains that are not resistant to chemical (acid) or microbiological attack, for instance, Cannaceae, Juancaceae, Marantaceae, Zingiberaceae, and Thurniaceae, and they also are but rarely preserved. Thus it seems more reasonable to infer that many pre-Cretaceous angiosperms also produced pollen that had not yet developed an exine sufficiently strong to withstand either the rigors of long transport or later chemical and microbiological attack, rather than to suppose that most of them had pollen grains as resistant as those which lived much later in the history of the alliance.

(C) Every higher (and lower) category comes into existence in some local area. During its early evolution, which may involve some tens of millions of years, populations are comparatively small, and the alliance maintains a generally restricted occurrence. In view of the inferred small size of early angiosperm populations and their spotwise distribution (Axelrod, 1952, 1960), the possibility of contributing pollen to the sedimentary record was greatly reduced in pre-Cretaceous as compared with Middle Cretaceous and later times when angiosperms were nearly everywhere dominant. Clearly, local distribution and small numbers would tend to limit their entry into the pre-Cretaceous lowland record, whether in the Permo-Triassic or the Middle Mesozoic transition.

(D) Early angiosperm evolution may have occurred in moist tropical regions, which no longer exist as land areas, and hence all records of their early history may be lost forever. The evidence that links the origin of the alliance to tropical rather than to temperate regions has been discussed elsewhere (Bews, 1927; Axelrod, 1952, 1959, 1960). In brief, the phylum is basically adapted to moist tropical forests today; the derived alliances commonly comprise the more specialized taxa of both tropical and extratropical regions; modern distribution patterns show that three-fourths of all angiosperm families are primarily adapted to tropical regions; and the fossil record shows that they migrated from lower to higher latitudes as they initially invaded lowland areas during the Early Cretaceous.

A considerable body of evidence indicates that during the pre-Cretaceous, and into the Late Cretaceous and Early Tertiary as well, angiosperms migrated extensively over land areas which have since subsided (Axelrod, 1960). The evidence supporting this view lies in the present and past distributional relations of angiosperm families and genera that are confined chiefly to the moist tropics of America, Africa, and Australasia. Today there are 54 pantropic families common to these regions, and they comprise the larger and more characteristic alliances of the tropics. These intertropical ties are strengthened when we note that an additional 125 families, although represented in the temperate and drier regions by derivative taxa, attain optimum diversity and development in the moist tropics and are chiefly of pantropic occurrence. Further, a number of tropical families have discontinuous occurrences: 12 of them link the American and African regions, 8 the tropics of America and Australasia, and 16 are common to the tropics of Africa and Australasia. Significantly,

there is good fossil evidence to show that an even larger number of families and genera were common to these tropical regions in the past and that the discontinuous and endemic occurrences of the present day are more recent (Axelrod, 1960, p. 247-249).

These relations can not be explained by postulating migration around the higher latitudes during the Cretaceous and Early Tertiary: those areas were occupied by temperate climates during this long interval, and in pre-Cretaceous time as well. Transtropic migration is therefore required in order to account for both the present and past distribution of tropical taxa. Migration appears to have been across land areas that occupied the West Indian Ocean, the mid-Atlantic, and greater Melanesia. The geological evidence which indicates that these are continental—not oceanic—regions has been summarized in some detail elsewhere (Axelrod, 1960). Clearly, if early angiosperms evolved in some ancient tropical land area which has subsequently foundered, we could not expect to recover any records of them.

(3) The authors point out that "the occurrence, due to parallel development, of many of the advanced features of angiosperms in (other) taxa 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 (p. 296)". This is a reasonable suggestion, yet it raises a problem relating to the site of early evolution that Scott and others (1960) have not considered: if forerunners of the alliance that had already evolved typical angiospermous features were living in the lowlands during the Middle Mesozoic, as they believe, then we might reasonably suppose that the record would already have provided evidence of the gradual emergence of the phylum from this proangiosperm plexus. However, Scott and others not only carefully note that all previously reported pre-Cretaceous "angiosperms" may well belong to other phyla but nowhere do they report any Middle Mesozoic ancestral plants that "had already evolved in their structural organization features now characteristic of the angiosperms". The fact that angiosperm ancestors have not yet been recovered from the abundant lowland record seems best explicable by the inference that they probably were living in the distant uplands, in areas too remote for preservation in the lowland record. If they were living in the lowlands, as Scott and others (1960) believe, then why is it that we still have no records of these ancestral plants which in most ways were already angiospermous?

Cliseral Relations

A second argument supporting the idea that early angiosperms may have existed in upland regions during pre-Cretaceous time comes from the cliseral relations of sequences of fossil floras (Axelrod, 1952, 1960). They show that often the more specialized and advanced taxa, as well as younger floras, were present in the uplands of a region long before they entered the lowlands to replace the older flora.

Scott and others concede that the record provides agreements with the general thesis as well as some exceptions; I disagree with some of their supposed exceptions, but this is no place to argue details. They then state that if angiosperms had been in the uplands 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 older Gymnophyte Paleoflora (1960, p. 291-292). As they point out, paleoclimatic consideration of plants as well as other groups of organisms indicate that conditions remained generally equable over most of the world during the Early Cretaceous.

(1) These criticisms are based on a misinterpretation of the significance of the basic idea, which they concede is largely true: the record does support the inference that higher categories, such as flowering plants, often have evolved in upland areas. Nowhere in the original theory (Axelrod, 1952), or in an extension of it (Axelrod, 1960), has a worldwide climatic change been called upon to account for their entry into the lowland record.

(2) Present evidence suggests that it took flowering plants all of Early Cretaceous time to assume dominance over the lowlands throughout the world (Axelrod, 1959). They are encountered first in the lowland record at lower-middle latitudes in the Neocomian, they reached generally middle to high-middle latitudes in the Aptian, they appeared at high latitudes in small numbers only in the Albian, and did not dominate there until Early Cenomanian time. The gradual poleward migration of angiosperms during this 35-million-years interval may reflect gradual climatic change. If Early Cretaceous climate was slightly cooler than that of the Jurassic—and some evidence suggests that it was—angiosperms may well have responded by migrating into the lowlands. However, replacement of the Gymnophyte Paleoflora may be owing to other factors as well, biologic, ecologic, etc. The argument which Scott and others (1960) present obviously does not discount the likelihood that they may have evolved in the uplands long before they entered the lowland record.

Diversity of Upland Environment Promotes Rapid Evolution

Evolutionary theory (Simpson, 1953; Stebbins, 1950) indicates that diversity of environment in the uplands would tend to favor the rapid evolution of early angiosperms. This environment would not only include a diversity of physical conditions owing to varying slope and climatic relations but the accompanying biotic diversity in these areas would also help promote the rapid evolution of the group during its early history. Scott, Barghoorn, and Leopold attempt to discount the idea of an upland origin for angiosperms in several ways.

(1) As noted earlier, their argument with respect to the absence of pollen of pre-Cretaceous angiosperms that may have been living in the distant uplands is irrelevant. If they were not in the uplands, they certainly were not in the lowlands either: from their interpretation of the evidence we may just as well conclude that the entire history of the phylum is post-Jurassic. As we have seen, at least four factors probably contribute to the absence of recognizable pollen grains in the pre-Cretaceous record.

(2) They state that "flowering plants have . . . found the tropical lowlands favorable for diversification; floras of the tropical rain forest are probably the richest plant assemblages known. . . ." (p. 292).

The argument that angiosperms have diversified in the tropical lowlands is true, but only in part. The bulk of the flora that now comprises the moist

lowland tropical rain forest is relict. The areas occupied by the rain forests of America, Africa, and Indomalaya comprise refugia for numerous ancient taxa that were gradually confined to these areas during the middle and later Tertiary as climates became cooler and drier over regions of their former occurrence. The present luxuriant rain forests are analogous to the temperate mixed hardwood forests of northeastern Asia and North America that are surviving relicts of the Arcto-Tertiary Geoflora.

Scott, Barghoorn, and Leopold (1960) present no evidence to indicate flowering plants initially evolved in the lowlands. On the contrary, some data clearly lead to the inference that they did not. In the first place, it is necessary to note that, owing to the nature of later Cenozoic climatic change, the lowland tropical rain forest now lives in an environment that is hotter and wetter than it has ever been. It is the forests on the bordering slopes (uplands) that appear to survive under a climate more like that of Eocene and earlier (pre-Cretaceous) times. Thus it becomes understandable that many of the more primitive living angiosperms persist in upland areas. This applies to the rare woody ranalian relicts in New Caledonia-Fiji and to a host of woody ranalian plants that live in the mountains of southeastern Asia, centering in the subtropical valleys of Yunnan and upper Burma (see Takhtajan, 1957, for examples). Since they are ancient bradytelic taxa, they probably have persisted under generally similar conditions for long periods of time. Thus the upland tropical to subtropical environments in which they occur may well resemble, at least in a general way, those under which angiosperms originated. This suggestion is consistent with taxonomic studies (Camp, 1947, 1952, 1956), which indicate that of the genera that have a fairly wide altitudinal range in the tropics, the more primitive living species usually occupy the mountain slopes, not the hot humid lowlands. It would thus appear that there has been considerable evolutionary deployment into the hot and humid tropical lowlands, not early evolution there.

(3) Scott and others (1960) note that Richards (1957, p. 346), in his fine discussion of modern tropical forests, shows that the tall, luxuriant tropical rain forest of the lowlands is replaced by other communities in the uplands that are also evergreen, but lower in stature, simpler in structure, and floristically poorer. The purely tropical flora is left behind and gives way to 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 in the tropics, and the general features of their altitudinal zonation appear similar in both the New and Old Worlds. From these valid observations of modern tropical forests, Scott and others then conclude that this five-zoned altitudinal distribution . . . "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 eivdence points (p. 293)".

(A) These assertions with respect to the existence of several vertical zones of tropical forests in the past are at variance with paleoclimatic evidence. Dur-

ing the time under consideration, the Earth had no regional polar, tundra, taiga, desert, or mediterranean climates. The margins of the moist tropics lay near Lat 45° N and S during the interval when flowering plants are supposed to have been evolving, whether from the Middle Mesozoic (Scott and others) or the Permo-Triassic (Axelrod). At these times the tropical and temperate zones were much broader than they are today. As latitudes now supporting tundra, polar and taiga climates were temperate, the tropical zone must have been somewhat cooler (though still tropical) than it now is in order to maintain the normal heat budget of the earth. Obviously, under such conditions vertical zonation in the tropics would have been much less than it is today, even if extreme topography like that of the present existed, and there is ample evidence to show that it did not.

(B) Their assertions with respect to the altitudinal zonation of tropical forests in the past are also at variance with paleobotanical evidence. There is no basis for projecting the existence of the present five zones of tropical forests into the pre-Cretaceous. No doubt there were zones wherever there was sufficient altitude, but studies of the evolution of Tertiary Geofloras into modern communities clearly demonstrate that altitudinal zonation of communities developed as new subclimates appeared owing to intense orogeny at the close of the Tertiary. Generalized plant communities were then segregated climatically into more specialized associations adapted to new subclimatic zones (for example, see Braun, 1935; Axelrod, 1950, 1957). To suppose that the present altitudinal zonation in the tropics "must have existed in the past" is obviously erroneous. The present is not always the key to the past. Communities and climates have evolved in time, and modern forest zones do not give us a clue to those of the ancient past.

(C) As for the temperate aspect which they think that upland angiosperms would have developed during the pre-Cretaceous, this idea has already been discussed (Axelrod, 1952, 1960). Plants in the high uplands (i.e. highlands) and also those toward middle latitudes near the margins of the ancient tropics certainly were evolving under the influence of more temperate conditions: it was here that the remote, pre-Cretaceous ancestors of taxa that ultimately gave rise to the Arcto-Tertiary and Antarcto-Tertiary Geofloras evolved. In other words, some of these pre-Cretaceous upland angiosperm populations were adapted to both tropical and warm temperate climates, and from them evolved alliances adapted to more temperate areas. Analogous relations exist at present in the upper montane rain forest in the tropics, where typically temperate and tropical taxa still live in proximity.

RATE OF EARLY EVOLUTION

Having noted that all records of previously reported angiosperms are unequivocal and asserted that the absence of angiosperm pollen from pre-Cretaceous rocks makes it unlikely that the phylum could have been evolving at a time as remote as the Permo-Triassic, Scott, Barghoorn, and Leopold (1960) then conclude that angiosperms were evolving rapidly just prior to their appearance in the record, apparently in the Middle Mesozoic. "If several of these (angiosperm characters), e.g. vessels, reticular leaf venation, [etc.], had al-

ready evolved in precursors, the evolutionary steps that differentiated flowering plants may not have been very great, and the geologic time required for their diversification not extreme (p. 296)." They allude to great diversification and wide distribution attained by herbaceous dicotyledons during Miocene and later time as an example of rapid evolution to support the idea that angiosperms may have had only a brief pre-Cretaceous history.

(1) From an evolutionary standpoint there is no doubt that several angiospermous features were already evolving in precursors of flowering plants, or that the evolutionary steps which finally differentiated true flowering plants probably were not very great. In this connection, an excellent paper by Mayr (1960) deals with the origin of higher categories, much of which seems applicable to the problem in hand.

But the example which Scott, Barghoorn, and Leopold present for asserting that the emergence of full-fledged angiosperms did not take much time has no bearing on the problem of rate during their early evolution. They intimate that rates of evolution in herbs which were evolving 100 million years *after* the first well-documented angiosperms appeared may represent the rate when the phylum was initially differentiating. Earliest angiosperm evolution involved the emergence of a wholly new way of life, the most successful ever achieved by land plants. Initially, it adapted the alliance to living more successfully in the moist tropics, a zone that unquestionably has been the most stable and persistent of all terrestrial environments. By contrast, the herbaceous dicotyledonous evolution to which Scott, Barghoorn, and Leopold refer only represented adaptive radiation into the more rigorous environments that developed during the middle and later Cenozoic over areas of the former occurrence of more widely distributed mesophytic ancestral herbs of closely similar character. In this connection we may also recall that herbs have an annual life cycle as compared with the earliest primitive angiosperm trees (or shrubs), which certainly required a much longer time to mature: woody ranalian taxa not only grow very slowly as compared with most other woody angiosperms, they also require a longer time for flowering and fruiting. Scott, Barghoorn, and Leopold give us no reason to believe that the rate of diversification of herbs from mesophytic ancestors, which involved only minor change on an already well-established pattern, provides us an index to the rate of diversification of early flowering plants at a time when major categories (orders, classes, etc.) were being blocked out.

There is no basis for supposing that the rate of herbaceous dicotyledonous evolution since the Oligocene indicates the time required for the emergence of full-fledged angiosperms. Measuring downward from the basal Cretaceous, the 30 million years involved would place their origin in the Late Triassic. If it took twice as long, as seems more probable, then angiosperms would have been in existence in the Permian. Evidence has already been assembled (Simpson, 1953; Axelrod, 1952) which suggests that the emergence of a category of the sort that we are considering here requires fully 50-60 million years. Scott, Barghoorn, and Leopold have not demonstrated that angiosperms emerged from their ancestral alliance any more rapidly.

(2) To judge from our present understanding of the evolutionary process, Permo-Triassic probably would have been a far more propitious time for the splitting off and rapid evolution of an early angiosperm plexus than would the Middle Mesozoic which Scott, Barghoorn, and Leopold (1960) favor. It was partly for this reason that the presumed history of the phylum was extended down into this interval (Axelrod, 1952, p. 45-46). At present, it is generally conceded that (a) the rate of evolution occurring at any particular time is largely a function of the genetic variability of the population as it is interacting with the environment, and that (b) very rapid rates of evolution accompany the shift from one adaptive norm to another that marks major evolutionary advance. Thus for major shifts to take place, an ancestral population of high genetic variability must enter an environment (physical and biotic) that is rapidly changing and which offers the population numerous opportunities in the form of new zones (or ecologic niches) into which it can deploy successfully. It seems more likely that rapid evolution of early angiosperms would occur in the Permo-Triassic when environments were diverse, than in the Middle Mesozoic interval, one of the most equable periods of geologic time.

This diversity of environment was not only physical, but biotic as well. Insects, which surely have been involved in the evolution of flowering plants, show an important outburst at this time which may well have stimulated the differentiation—at least in part—of early angiosperm orders. During the Jurassic and Cretaceous modern insect families appear, and by the Early Tertiary many insects can be referred to living genera. There is ample reason to suppose that angiosperms closely followed insect evolution and that they developed in concert (Axelrod, 1960). Birds and bats have also been involved in their history.

(3) One other criticism may be leveled at any theory that purports to show that flowering plants diverged from an ancestral stock during an interval as brief as 30 million years. The rate of evolution of angiosperm reproductive structures has been much more rapid than the diversification of the plant body, which in general has remained conservative. Leaves of such plants as sycamore, sassafras, maple, oak, magnolia, alder, cinnamon, and many others—representing diverse orders and families—have remained basically unchanged since the early Cenomanian 140 million years ago. Cretaceous woods also are closely similar to those produced by living alliances. By contrast, many of the fruits and seeds of Late Cretaceous and Early Tertiary woody plants can not be assigned to modern genera, and family relations often are obscure.

Now, if angiosperms came into existence in the Middle Mesozoic, the vegetative plant body would have had to evolve at a rate many times (possibly 40-50 times) faster than reproductive structures during this early interval, and then essentially stagnate. This not only applies to the usual plant body, whether trees, shrubs, or herbs, but poses a particularly difficult problem in the case of *Didieria*, *Pachypodium*, *Idria*, *Pachycereus*, *Cleistoyucca*, and a host of other "weird" taxa that are largely monotypic. The suggestion has been made, however, that plants of this sort may well be the bradytelic descendants of ancient

Permo-Triassic or early Triassic alliances that evolved on the drier margins of the tropics (Axelrod, 1952, 1960).

SUMMARY

A theory of angiosperm evolution has proposed that the alliance probably was in existence in the Permo-Triassic, and that it occupied upland (not highland) tropical areas remote from lowland sites of deposition. Recent arguments which purport to disprove these inferences, and to show that angiosperms had a much more recent origin in the lowlands, are largely fallacious: (1) Evidence marshalled to discredit the nature of previously reported pre-Cretaceous angiosperms is based on circular reasoning. (2) Absence of pollen in the pre-Cretaceous is no more of an obstacle to inferring their presence in the Permo-Triassic than in the Middle Mesozoic: at least four factors appear to account for the phenomenon. (3) The argument that the present five altitudinal zones of tropical forests existed in analogous form in the ancient past—and that the early angiosperms corresponded in altitudinal position to the lower wet luxuriant rain forest—is based on misconceptions of ancient climate, the manner in which modern forest communities have evolved, and the phyletic relations of modern taxa. (4) The extraordinary rate of evolution demanded for the plant (vegetative) body by a Middle Mesozoic emergence for the phylum makes such a recent development seem highly improbable. (5) The rate of evolution displayed by herbaceous dicotyledons during their later Tertiary adaptive radiation into more extreme zones does not provide a clue to the rate of early differentiation of major angiosperm categories.

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