

Toward a new synthesis: Major evolutionary trends in the angiosperm fossil record

David Dilcher*

Florida Museum of Natural History, University of Florida, Gainesville, FL 32611-7800

Angiosperm paleobotany has widened its horizons, incorporated new techniques, developed new databases, and accepted new questions that can now focus on the evolution of the group. The fossil record of early flowering plants is now playing an active role in addressing questions of angiosperm phylogeny, angiosperm origins, and angiosperm radiations. Three basic nodes of angiosperm radiations are identified: (i) the closed carpel and showy radially symmetrical flower, (ii) the bilateral flower, and (iii) fleshy fruits and nutritious nuts and seeds. These are all coevolutionary events and spread out through time during angiosperm evolution. The proposal is made that the genetics of the angiosperms pressured the evolution of the group toward reproductive systems that favored outcrossing. This resulted in the strongest selection in the angiosperms being directed toward the flower, fruits, and seeds. That is why these organs often provide the best systematic characters for the group.

Here I focus on the fossil record of the same plants that Stebbins did in his book, *Variation and Evolution of Plants* (1), the angiosperms. This contribution has the advantage of being written more than 50 years after Stebbins wrote about his view of the fossil record of the angiosperms. His use of the fossil record of angiosperms as a model in his evolutionary synthesis was hampered because in the 1940s the paradigm in angiosperm paleobotany was to match fossils, especially leaves, to extant genera (2). The successes of the angiosperm paleobotanists (e.g., D. Axelrod, H. Becker, E. W. Berry, R. Brown, R. Chaney, and H. MacGinitie, and many others for 100 years before them) were judged by their ability to match a high percentage of fossils to living genera (Fig. 1). Once the identifications were made to living genera, their focus was on questions of phytogeography and paleoclimate. This meant that almost no fossil angiosperms were recognized as extinct; it was quite impossible to focus questions of plant evolution on the fossil record of the angiosperms in 1950 as George Gaylord Simpson had done with the fossil vertebrate record in his classic *Tempo and Mode in Evolution* in 1944 (3).

Stebbins wrote in “Fossils, Modern Distribution Patterns and Rates of Evolution,” chapter 14 of *Variation and Evolution of Plants* (1), about the disjunct distribution of modern genera of fossil plants. His rates of evolution were based on the various modern genera described in the fossil record of North America and currently living in southeastern Asia or South America. His arguments about the rates of evolution from the fossil record may have some validity when based on fossils from the Miocene (about 25 million years) and younger. However, many of the fossils from the Paleocene, Eocene, and Oligocene reported as living genera have been subject to revisions (4) as shown in Fig. 2. This trend that had dominated angiosperm paleobotany for more than 100 years continued into the early 1970s. The supposed failure of the fossil record to contribute to understanding the evolution of the early angiosperms was still evident in 1974 when Stebbins published *Flowering Plants: Evolution Above the Species Level* (5). In chapter 10, “The

Nature and Origin of Primitive Angiosperms,” there is no substantive use of the fossil record to address this question. The theories and hypothesis presented by Stebbins are based on the comparative morphology and anatomy of living angiosperms considered primitive at that time rather than the fossil record of early angiosperms.

However, at the same time, the early 1970s, special attention was being focused on the fine features of the morphology of angiosperm leaf venation and the cuticular anatomy of living and fossil angiosperms (2, 6–8). Most of the early angiosperms from the Cretaceous and early Tertiary were being found to be extinct or only distantly related to living genera (Fig. 3). Grades and clades of relationships were being founded on the basis of careful character analysis (9, 10). During this time, it became scientifically acceptable to be unable to identify a modern genus to match a fossil. Fossil angiosperms were analyzed on the basis of multiple detailed objective characters, and degrees of relationships could be established based on the extent to which these same combinations of characters were found in living families, subfamilies, or genera (11). Analyses of the fossil angiosperm record were being constructed that included vast amounts of data based on careful anatomical and morphological analysis of the diversity of characters found in living genera and modern families. Large collections of cleared leaves and cuticular preparations were developed, and whole families were surveyed to establish their range of venation and cuticular characters and fruit and seed anatomy and morphology to research the fossil history of a family (4, 9, 11–24). This anatomical/morphological style of systematic-based angiosperm paleobotany was a distinct change from the floristic approaches that focused on paleogeographic and paleoclimatic questions and dominated the field before 1970.

This new paradigm shift opened the door for a new synthesis of the fossil record of angiosperms. New questions about the evolutionary biology of the fossil record of angiosperms could now be addressed based on detailed character-based data of living and fossil angiosperms often organized with the help of cladistic analysis. At this same time there was renewed interest in exploring the fossil plant record to determine the origin and early evolutionary history of the angiosperms (8, 25, 26). The techniques of careful analysis and the concerted effort to open up a new fossil record of early angiosperms by the use of small, often charcoalified plant remains (27), or fragments of cuticle sieved from sediment (28) from newly collected material of the Jurassic to the Upper Cretaceous were very successful. A whole new area of the study of intermediate-sized fossil plants, often termed mesofossils as opposed to microfossils or megafossils, expanded to occupy the majority of angiosperm

This paper was presented at the National Academy of Sciences colloquium “Variation and Evolution in Plants and Microorganisms: Toward a New Synthesis 50 Years After Stebbins,” held January 27–29, 2000, at the Arnold and Mabel Beckman Center in Irvine, CA.

*E-mail: dilcher@flmnh.ufl.edu.

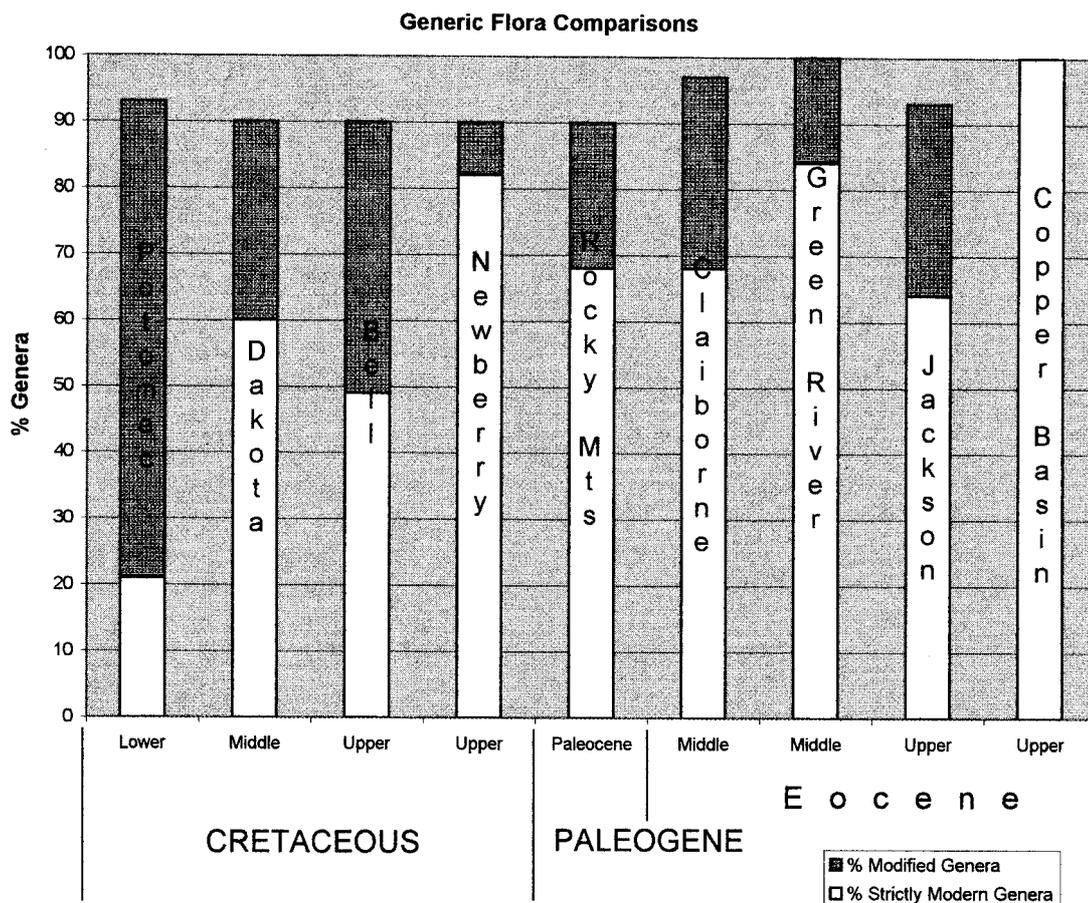


Fig. 1. Selected floras published from the late 1800s to the 1960s, ranging in time from the Lower Cretaceous to the Upper Eocene (62–69). The open area represents percent of the species in the flora that were given extant generic names. The shaded area represents the percent of species in the flora that were given fossil generic names based on a modern genus to which they were perceived to be similar. The short fall, less than 100% for each flora, represent genera perceived to be truly extinct.

research in some laboratories with good success (refs. 29–36 and references cited therein). It is the success of these new techniques applied to the fossil record of angiosperms that now provides a new database from which to analyze some of the major trends in angiosperm evolution and allows us to ask new questions.

What Is Known About Early Angiosperm Diversity During The Cretaceous?

New Tools of Analysis. The study of angiosperm fossils has undergone rapid and profound changes during the past 30 years as discussed in the introduction to this paper. Although the study of angiosperm fossils is only as reliable as the individual investigator, resources are now available, such as cleared leaf collections and cuticular reference slide collections from vast herbarium holdings. This allows angiosperm paleobotanists to survey the nature of characters circumscribed by a particular living family or genus before reaching a conclusion about the relationship(s) of a fossil angiosperm organ. It is now understood that some organs may contain more useful characters for determining relationships than others. It is not only acceptable, but desirable, to list the available characters and how these are distributed among several living genera in a family rather than to select only a single living genus that has such characters and on this basis refer the fossil to that genus.

New Paradigm Applied. We are moving toward a well-defined and repeatable objective character-based analysis of the angiosperm

fossil record. Much of this analysis is based on the study of the anatomy and morphology of fossil plant organs. Stebbins (1) recognized the need for this type of study when he wrote that “The method of identification is simple comparison between the fossil and the leaves of living species, but various approaches have greatly increased its accuracy.” He then cites Bandulka (37), Edwards (38), and Florin (39), all early pioneers in the use of anatomy and morphology in the study of the systematics of fossil plants. However, using the new tools, it became apparent that there were many fossils that could not be related to living taxa even when such careful analyses were applied (Figs. 2 and 3). There came a time when it was necessary to give names to the various organs of fossil angiosperms that reflected their extinct nature, recognizing them as separate from any living genus (40). With few exceptions (41), workers have not yet taken such bold steps as defining and naming extinct angiosperm plant families, orders, or classes.

Rapid Changes in the Data. The great strides in developing techniques of investigation for understanding Devonian fossil plants, on the basis of seemingly nondescript structurally compressed remains (42, 43), and the excellent application of anatomy and morphology to the study of Pennsylvanian age plants (i.e., ref. 44, and examples cited in ref. 45) influenced me to apply similar techniques to fossil angiosperms to extract as much information as possible from compressed leaves and flowers. The amount of information that can be determined about a fossil leaf, fruit, flower, pollen grain, or wood by using these techniques allows

Clarno Flora Genera Middle Eocene

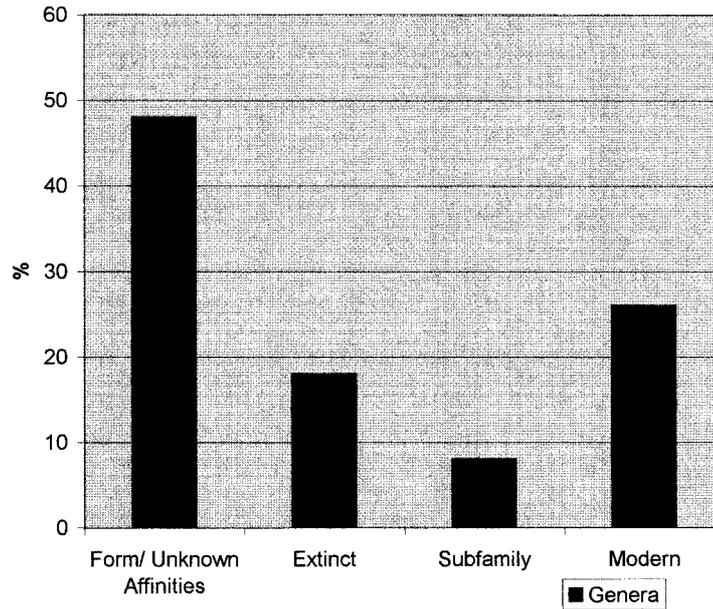


Fig. 2. Representation of the Middle Eocene Clarno Flora from eastern Oregon (4) based on several thousands of fruits and seeds collected over 60 years. The bars represent the percent of the genera identified to angiosperm genera of various degrees of similarity to living genera. Note that less than 30% of the fruits and seeds can be identified with living genera.

character-based comparisons to be made. These data have become available at the same time that cladistic-based (i.e., character-based) data were being assembled for the living angiosperms. Now, with the study of megafossils, mesofossils, and microfossils all yielding new information about the characters of the early angiosperms, there are huge amounts of new data available each year. In particular, because they had not been studied before, mesofossils are adding a new set of valuable

information that is changing our concept of early angiosperm diversity. The Lower Cretaceous sediments from Portugal have yielded 105 different kinds of flowers with 13 associated pollen types (35). The lower Upper Cretaceous sediments from New Jersey are yielding a large number of new taxa (29–34, 36). The application of character-based analyses of fossil angiosperm remains has been used (46) to demonstrate the presence of systematic groups of angiosperms through time (Fig. 4).

Rose Creek Floristic Composition

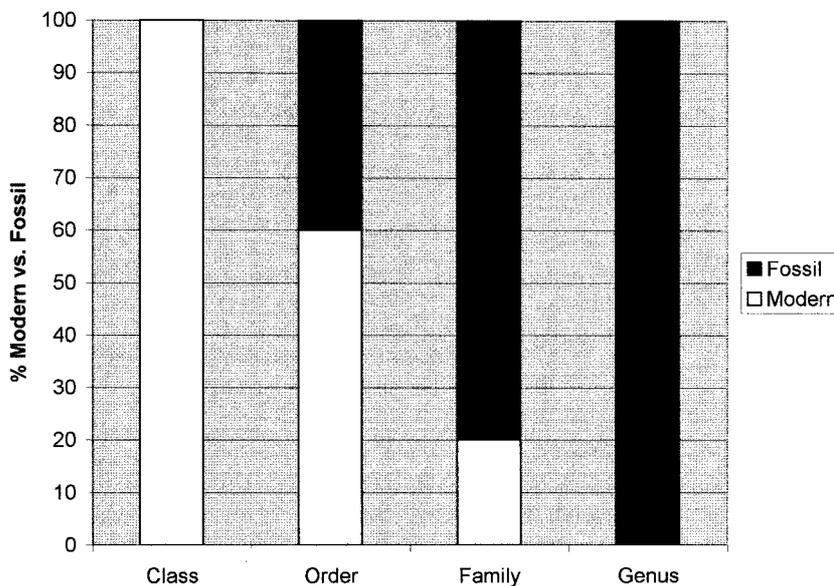


Fig. 3. Representation of modern vs. fossil taxonomic groups published for the mid-Cretaceous, Dakota Formation, Rose Creek Flora (70). This flora is based on leaves. Note no modern genera identified as opposed to the 60% identified for the same flora illustrated in Fig. 1.

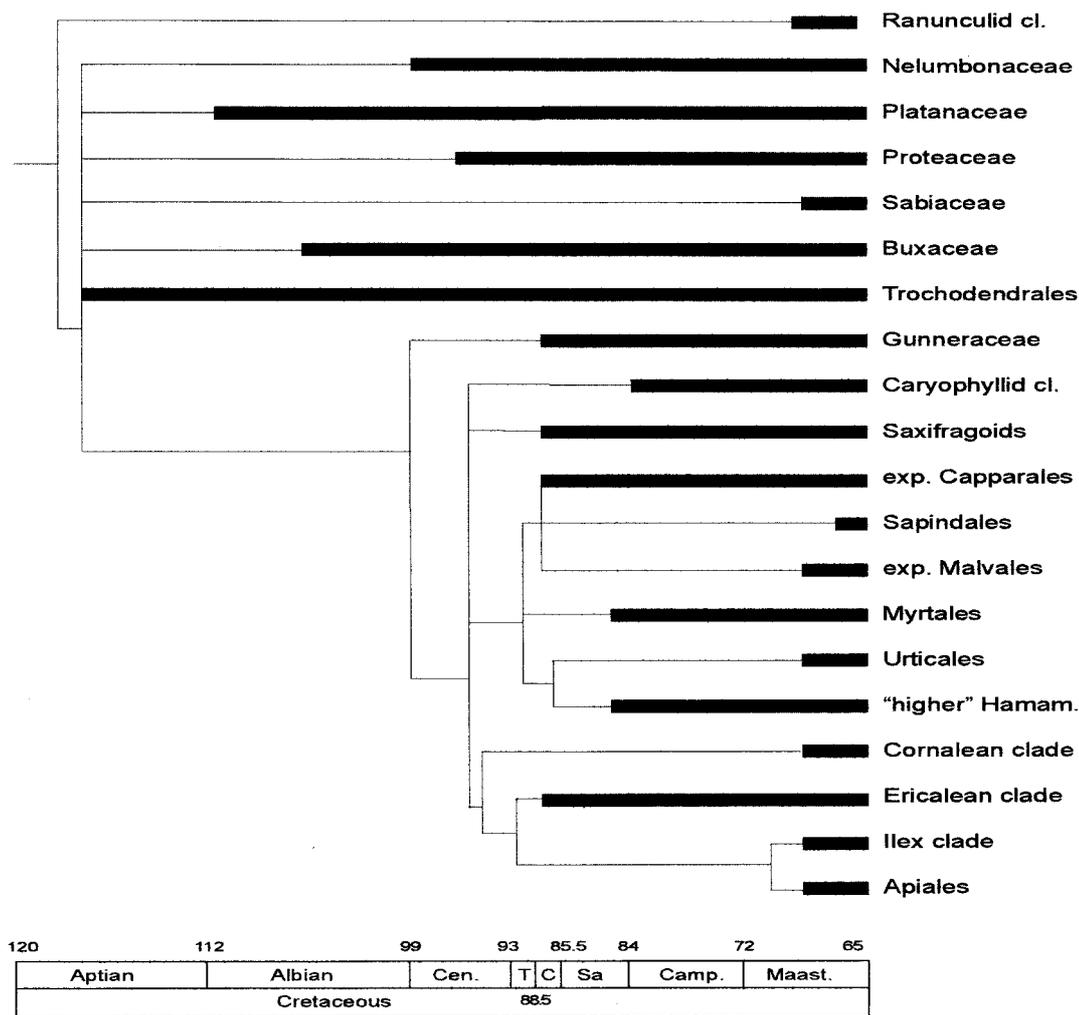


Fig. 4. Angiosperm diversity as recognized through Cretaceous time. The solid bars extend from the earliest identified fossils of the clades listed on the right side. Modified from refs. 46 and 71.

How Has Angiosperm Reproductive Biology Changed Through Time?

Evolution of the Closed Carpel. The closed carpel is the one major feature that separates the angiosperms from other vascular seed plants. The closure most often is complete and entirely seals off the unfertilized ovules from the outside environment. Suggestions that this provided protection for the vulnerable ovules from beetles or other herbivores have been proposed as a reason for the closure of the carpel. However, I think that the closure of the carpel may be more directly related to the evolution of the bisexual flower (47). During the evolution of the flower, as the male and female organs of the flower were brought into proximity, the need for protection against self-fertilization was so important that biochemical and mechanical barriers were developed very early in flowering plant ancestors. The mechanical barrier is the closed carpel and the biochemical barrier is the incompatibility systems that developed to prevent the successful growth of pollen tubes. Some living angiosperms have loosely closed carpels or lack any firm closure at all. It has been suggested that these have sufficient exudates to fill the carpel opening so that the carpel has a biochemical barrier against self-fertilization (48).

Although the closed carpel is the fundamental strategy for preventing self-pollination, the addition or loss of sepals, petals, and stamens must have been important events ensuring out-

crossing. It is reasonable to assume that the development of attractive colored organs and nectaries, the clustering together of female (ovule-bearing) organs and male (pollen-bearing) organs, and, finally, the association of the female and male organs together on the same axis were all changes designed to increase the effectiveness of insect pollination. The closed carpel and biochemical incompatibility are natural early steps that followed or took place at the same time as the evolution of the floral features just mentioned. The closed carpel in a showy flower ensured outcrossing by animal pollinators while increasing pollen exchange with bisexual flowers. The closed carpel serves as a plant's control mechanism to guarantee that outcrossing happens. Any mechanical protection it offered probably always has been of secondary importance and can be easily overcome by insects.

Evolution of Floral Form and Patterns. Radial symmetry. The floral organs of all early angiosperms are radially symmetrical, a symmetry exhibited by all of the floral organs and flowers whether they are small or large, unisexual or bisexual. The earliest known angiosperm flowers suggest that individual carpels were borne helically on an elongated axis with pollen organs if present, either subtending and helically arranged on the same axis (41). Similarly, the early small flowers (35), unisexual or

bisexual, have axes with radially arranged organs. In small flowers the elongation of many early flowering axes is compressed so that the organs appear radially arranged. This organization is clearly seen in larger flowers such as *Archaeanthus* (40) and the Rose Creek flower (49). This radial arrangement of organs persisted until late into the Late Cretaceous or the Paleocene.

Bilateral symmetry. By Paleocene and Eocene time, there are several evidences in the fossil record of bilateral flowers. This evolution probably began during the Upper Cretaceous. The evolution of bilateral flowers is associated with the evolution of social insects and happened in the angiosperms at different stages in the evolution of several living families. In some angiosperm families, bilateral symmetry may be present in only a part of the family, while in other families the entire family, is characterized by bilateral symmetry. As discussed below, this must relate to the time at which different groups evolved.

Evolution of Small and Large Flowers. Flower size in living angiosperms is quite variable. Only during the past 25 years have numerous new fossil flowers been discovered from the Cretaceous. The record that has been developed demonstrates that both medium- and small-sized flowers are present very early. Certainly, flower size must relate to pollinator size. The variability in size of the early flowers suggests that a variety of pollinators were involved in their pollination biology. In addition to insect pollinators, both wind and water were important in the pollination of early angiosperms. Because the wind and the water have changed very little since the Cretaceous, there has been little change in the floral anatomy and morphology of these plants. Therefore, they are examples of some of the most ancient lines of living flowering plants. Those angiosperms that have modified their pollination biology to accommodate insect pollinators have been plants that have undergone the most extensive changes whose fossil ancestors are most different from their modern descendants.

Evolution of Floral Presentation. In flowers that are insect pollinated, the display of the flower is critical. There seem to be clear distinctions between the presentation of the large *Archaeanthus* flower and the small fossil dichasial (50) flowers. The large *Archaeanthus* flower appears to have been terminal on a moderately large axis similar to the flowers of *Liriodendron* or *Magnolia* today. This allows for sturdy support and a colorful display to attract a pollinator. The dichasial flower, in contrast, is small and clustered into an umbel-like arrangement. This allows for a showy display of flowers in different stages of maturity and a broad area of clustered flowers upon which a pollinator can land and move about. However, small unisexual florets such as those of platanoid-like inflorescences and ceratophylloid-like plants have been little affected by animal pollinators. For this reason, they persist today only slightly changed from their form in the Early Cretaceous.

Unisexual vs. Bisexual Flowers. The earliest flowers now known appear to be gynodioecious. One axis has only carpels with a clear indication that no other organs subtended them, while an attached axis has both carpels and pollen-bearing organs (51). So, was the first flower unisexual or bisexual? It appears to have had the potential to be both. Some early flowers, such as the platanoids and ceratophylloids, appear to be unisexual and never to have had a bisexual ancestry. Others such as *Archaeofructus*, many of the small flowers from Portugal and the larger flowers from the Dakota Formation, are certainly bisexual. I suggest that the ancestral lineage of the angiosperms was most likely unisexual, and that with the availability of insect pollinators the efficiency of bisexual flowers won the day.

What Are the Significant Nodes of Angiosperm Evolution?

There are three major nodes or events through time that resulted in major radiations of the angiosperms. These nodes include the evolution of showy flowers with a closed carpel, the evolution of bilateral flowers, and the evolution of nuts and fleshy fruits. At each of these events, there is a burst of adaptive radiation within the angiosperms that can be interpreted as an attempt to maximize the event for all of the diversity possible and to use the event for increased reproductive potential.

The evolution of the closed carpel and the evolution of the showy radial flower must have occurred at nearly the same time. This was the first adaptive node marking a distinct coevolution of early flowering plants and animal (insect) pollinators. The success of this involvement of insects in the reproductive biology of plants was not new. Dating back into the Paleozoic, insects most probably were involved in pollination of some of the seed ferns such as *Medullosa* (25, 52). During the Mesozoic, several plants were certainly using animals for pollination as part of their reproductive biology. These include plants such as the Cycadoidea, *Williamsonia*, *Williamsoniella*, and, perhaps, some seed ferns such as *Caytonia*. Insect diversity increased parallel to the increasing diversity of the angiosperms during the Mesozoic (46, 53, 54). This node of evolution corresponds to the initial coevolution of animals and flowering plants in gamete transport. These early showy flowers came in many sizes, were displayed on the plant in many different ways, and were uniform in the types of organs they contained and the radial symmetry of these organs. They must have accommodated many different types of pollinators as evidenced by the variety of their anthers, stigmatic surfaces, nectaries, and the sizes and positions of the floral organs (25, 29–35, 55). It was through the success of this coevolution that the angiosperms became the dominant vegetation during the early Late Cretaceous. Ordinal and family clades began to become identifiable during the later Early Cretaceous and the early Late Cretaceous (29–34, 46). However, at the same time, some of the angiosperms never developed showy flowers and used other means of gamete transport for cross-pollination such as wind (early platinoids) and water (early ceratophylloids).

The evolution of bilateral flowers happened about 60 million years after the origin of the angiosperms. This node in coevolution never affected the water- or wind-pollinated groups that were already established. The evolution of the bees late in the Late Cretaceous was a coevolutionary event with the evolution of bilateral flowers. This occurred independently in many different clades of flowering plants that were already established by the mid-Late Cretaceous. The potential for flowers to further direct the behavior of insects to benefit their pollination had a profound influence on those clades that evolved during the late Upper Cretaceous and early Tertiary. Flowers not only presented their sex organs surrounded by sterile floral organs with attractive patterns and colors, exuding attractive fragrances and filled with nectar and pollen for food, but the bilateral flowers could show the animals which way to approach them and how to enter and exit them. This allowed flowers to maximize the potential for precise gamete exchange that was impossible with radially symmetrical flowers. Such clades as the Papilionoideae (legume subfamily), Polygalaceae, and Orchidaceae, among others, demonstrate this coevolution. The success of these clades and especially the Orchidaceae, with its vast number of species, demonstrates the potential of this coevolutionary event.

The evolution of large stony and fleshy fruits and seeds is the last major coevolutionary node of the angiosperms. This is not to say that there were not the occasional attractive fruits produced earlier, but a large radiation of fruit and seed types of the angiosperms occurred during the Paleocene and Eocene. The change in angiosperm fruit size was noted by Tiffney (56)

who associated this change with the radiation of rodents and birds. This coevolutionary node allowed for both the further radiation of the angiosperms and the radiation of the mammals and birds. Stone (57) noted that there was a tendency to develop animal-dispersed fruit types in the Juglandaceae several times in different clades of this family. Many angiosperm families took advantage of the potential to disperse their fruits and seeds by bird and mammal vectors during the early Tertiary as evidenced by the bursts of the evolution of fruits and seeds during this time (4, 58). It is interesting to note that at this same time the angiosperms also were experiencing a radiation of wind-dispersed fruits and seeds (59). This radiation of fruit and seed dispersal strategies in the angiosperms, late in their evolution (early Tertiary), is yet one more example of a means to promote outcrossing for the group.

Why Did Angiosperms Evolve?

Coevolutionary events are largely responsible for the origin and subsequent nodes of evolution and radiation of the angiosperms. As we begin to find reproductive material of very early angiosperms (35, 41, 60), it becomes clear that some or most angiosperms developed bisexual insect-pollinated flowers very early, while some lines also maintained unisexual flowers with abiotic means of pollination (25). The coevolution with insects sparked a tremendous potential for plants to outcross by co-opting animals to carry their male gametes (pollen) to other individuals and other populations of the same species.

Each node of angiosperm evolution established genetic systems that favor outcrossing. The showy bisexual flower, the more specialized bilateral flower, and the nutritious nuts and fleshy

fruits all are means by which the flowering plants increase their potential for outcrossing. The majority of angiosperm evolution is centered on this increased potential for outcrossing through coevolution with a wide variety of animals. In most cases the animals benefited as well from this coevolutionary association. Wind and water pollination syndromes also allowed for outcrossing and have continued to exist since the Early Cretaceous. However, they have never developed the diversity of those angiosperms pollinated by animals. Also several abiotically pollinated angiosperms, for example the Fagaceae (*Quercus* or oaks) and the Juglandaceae (*Carya* or pecans), later accommodated themselves for animal dispersal of their fruits or seeds. The importance of outcrossing cannot be underestimated as a driving force in the evolution of the angiosperms (47, 61).

The ability of the angiosperms to accommodate and maximize benefits from animal behavior has been responsible for the evolutionary success of the group. As individual clades made use of particular coevolutionary strategies the diversity of both the angiosperms and animal groups increased. The benefits to the angiosperms were the benefits of the genetics of outcrossing. Because this is a sexual process, it was accomplished by means of evolutionary changes to flowers and fruits and seeds. This is why these particular organs have been centers of angiosperm evolution and why they are so useful in angiosperm systematics today.

I acknowledge with thanks the help of Terry Lott and Katherine Dilcher in the preparation of this manuscript. Thanks to Peter Raven who read and commented on this paper and also to the many students and colleagues who shared their perspectives of angiosperm evolution with me. I thank the organizers of the symposium at which this paper was presented: Francisco Ayala, Walter Fitch, and Michael Clegg.

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