Fossil Evidence for the Evolution of Biotic Pollination [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1991 **333**, 187-195
doi: 10.1098/rstb.1991.0067

Fossil evidence for the evolution of biotic pollination

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SUMMARY

The Cretaceous–Paleogene history of plants and insects reveals a discernible pattern in the evolution of floral character complexes and insects. Earliest Cretaceous flowers were small apetalous magnoliids with few parts. They co-occurred with a greater variety of anthophilous insects than has previously been supposed, and the idea that Coleoptera were the principal early insect pollinators is in need of review. By the mid-Cretaceous rosid flowers are known with well-developed corollas and the Rosidae are diverse by the late Cretaceous. The more derived asterid floral types are not firmly established until the Tertiary. Nectaries are present in many of the late Cretaceous rosids and may signal the beginning of the most significant evolutionary interaction between Hymenoptera and angiosperms. Advanced floral types in Maastrichtian and early Tertiary deposits are consistent with the appearance of meliponine Apideae (Stingless honeybees) in the late Cretaceous.

1. INTRODUCTION

The history of floral structure and insect pollination are now within reach of paleobotanists. Fossil data are particularly useful in the context of the distribution of insect pollination mechanisms in angiosperms and in the related groups, Bennettitales and Gnetales. It is most likely that angiosperms arose at a time when insect pollination was already established in sister clades. Parallelism and convergence may have been significant in the characters held in common between early angiosperms and some related non-angiospermous groups, but can be fully assessed only with careful phylogenetic analyses.

After the origin of angiosperms, the ongoing relation between angiosperms and insects undoubtedly affected angiosperm radiation and success. It is important to consider how phylogenetically informative the distribution of pollination syndromes in the angiosperms might be and the ecological or evolutionary implications that follow from this distribution.

Our present goal is to update fossil evidence on the evolution of insect pollination mechanisms, and examine in a preliminary way the possible utility and implications of these data (e.g. does fossil evidence reveal patterns relevant to insect pollination and angiosperm phylogeny, and success?). To employ fossil evidence in addressing these questions, certain assumptions are necessary about the relation between structure and mode of pollination and the phylogenetic value of fossils. We have previously considered the historical development and timing of appearance of relevant fossil structures (Crepet 1985; Crepet & Friis 1987; Friis & Crepet 1987; Friis & Endress 1990). However, the relation between fossils and phylogenetic analysis has been the subject of some controversy since the publication of what we regard as a widely misinterpreted paper by Patterson (1981). Even so, that paper has served as a focus for several subsequent expositions on the value of fossil evidence in the rigorous context of phylogeny reconstruction (Donoghue *et al*. 1989).

2. CONCEPTUAL FRAMEWORK

(*a*) *Anthophyte phylogeny*

A phylogenetic framework is necessary for the analysis of the fossil record and, ultimately, for the analysis of the distribution of pollination mechanisms in angiosperms and related groups. Cladistics has emerged as an essential tool for the understanding of phylogeny and for the testing of particular adaptational hypotheses (Coddington 1988). Parsimony analyses provide independent tests of hypothesized character transformations considered to be indicative of particular pollination syndromes.

In recent years a consensus has emerged among botanists that the Gnetales are among the closest living relatives of angiosperms, whereas Bennettitales are the closest fossil group to both angiosperms and Gnetales (Crane 1985; Doyle & Donoghue 1986). At the present time, the evidence for the exact relations of these three groups is somewhat equivocal, and we take here a conservative interpretation in which Gnetales, angiosperms and Bennettitales form an unresolved trichotomy that is probably derived from a Mesozoic seed fern group. Characters that support the monophyletic nature of the angiosperm–Gnetales–Bennettitales ('anthophyte') group include close arrangement of male and female organs (bisexuality), the second integument of the ovule, and possibly granular–columellate pollen wall structure. Numerous features of the extant Gnetales, which are not observable in fossil Bennettitales, can also be cited, and with more

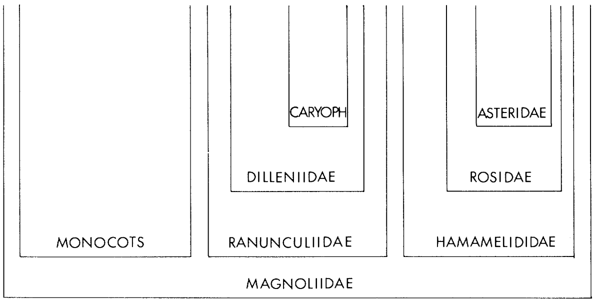

Figure 1. Generalized hierarchic relations of the angiosperm subclasses. This should not be interpreted as a final phylogeny, but only as a preliminary assessment based on very broad character distributions. Note that two major tricolpate/tricolpate-derived pollen-bearing lineages (Ranunculiidae, Hamamelididae) are derived separately from Magnoliidae in this hypothesis.

careful analyses, we anticipate that Gnetales, or some portion of Gnetales, may be found to be closer to the angiosperms than is Bennettitales. The inclusion of *Pentoxylon* in the 'anthophyte' clade as suggested by Crane (1985) and Doyle & Donoghue (1986) is based largely on missing values (Nixon & Davis 1991), as well as characters that reverse on the *Pentoxylon* clade. Thus, our position is that it is premature to include *Pentoxylon* and in any case so little is known about important features of this fossil taxon that it is of little interest to our discussion.

A phylogeny within the angiosperms, particularly one that outlined relations of major groups, would be desirable in the context of the analysis presented below. Unfortunately, the scope of such an analysis, character variation within the angiosperms, lack of equivalent data among the many groups, and the relatively recent emphasis on cladistic methodology applied to angiosperms, have combined to delay such analyses. In the context of this paper, we therefore must utilize a very general tentative hierarchy reflective of some established thoughts on relations among major angiosperm groups.

Based on outgroup comparison, information from published cladograms and classical phylogenetic studies, it is likely that the ancestral angiosperms had a combination of features of one or more of the modern families placed in the subclass Magnoliidae. These ancestral forms most likely had monocolpate pollen, simple pinnately-veined leaves, fleshy stamens with well-developed connective extensions, dithecal tetrasporic anthers, bitegmic ovules, and ethereal oil cells at least in the leaves. The Magnoliidae is clearly a paraphyletic assemblage within which the higher groups of angiosperms are nested, including 'higher' dicotyledons with tricolpate and tricolpate-derived pollen, as well as the basically monocolpate monocotyledons (figure 1). The evidence seems insufficient at this time to determine if the tricolpate and tricolpate-derived angiosperms are a monophyletic group. The prevailing thought recognizes at least two major lines in which the tricolpate condition arose independently from monoaperturate magnoliid ancestors, the ranunculid–dilleniid line, and the hamamelidid–rosid–asterid line (Cronquist 1981; figure 1).

Evidence supports the interpretation that the Asteridae are nested within the Rosidae, and the Rosidae in turn are nested within the Hamamelididae. Thus, these latter groups represent paraphyletic assemblages that have generalized trends of characters, and will most likely not survive careful cladistic analyses.

(*b*) ***Angiosperm sister groups***

(i) *Gnetales*

The Gnetales first appear in the Triassic. They are reported throughout the Mesozoic and Caenozoic with a maximum distribution in the early and mid-Cretaceous. They are best represented in the fossil record by dispersed pollen similar to *Ephedra*, although megafossils are rare. Such pollen has been reported *in situ* in small ovulate structures from the Early Cretaceous (Krassilov 1986). Although not fully understood, these structures support a gnetalean affinity of this pollen type.

Among characters Gnetales share with angiosperms are close association of ovulate and staminate organs. This is particularly well developed in *Welwitschia* in which staminate flowers have a central aborted ovule. Pollination is poorly understood in these taxa with the exception of *Ephedra*. *Ephedra* has one species (*E. aphylla*) which is both insect pollinated and anemophilous (Meeuse *et al.* 1990; Niklas & Buchmann 1987).

(ii) *Bennettitales*

The Bennettitales are remarkable for their superficially flower-like reproductive structures. Both bisexual and unisexual reproductive structures have been reported in early Bennettitales. Dispersed ovulate receptacles and androecia provide primary evidence that some taxa had unisexual reproductive structures, but structure and reproductive biology of these fossils are not well understood. Bennettitales show more variability in microsporophyll structure than in morphology of the ovules or ovulate receptacles. In unequivocally bisexual taxa, conical to dome-shaped multi-ovulate receptacles are subtended by whorled microsporophylls, that are in turn subtended by spirally arranged bracts. Variability in microsporophyll structure through time has been ascribed to a trend reflective of increasing predation or specialization for beetle pollination during the Mesozoic (Crepet 1974; Gottsberger 1988). The possibility that an observed trend within the fossil history of a group might reflect a transformation series related to increasing interactions with beetle pollinators may come to be better evaluated in the context of a phylogenetic analysis of variation in Bennettitales and through applying the precepts of Coddington (1988). In any case, the bisporangiate condition, universality of ovule protecting interseminal scales, direct evidence of beetle-chewing damage of microsporophylls and ovules in *Cycadeoidea*, and highly modified and variable microsporophylls in conjunction with cone position and degree of exposure are all highly suggestive of insect pollination. In *Williamsoniella*, the fleshy microsporophylls are highly reduced with only four to six synangia, and may have served as attractants or rewards.

3. FOSSIL ANGIOSPERMS

(*a*) *Fossil record*

The earliest evidence of angiosperms in the geological record is monocolpate pollen from Lower Cretaceous (Hauterivian) strata (Brenner 1984). In Hauterivian–Barremian assemblages angiosperms typically comprise less than 1% of the total plant assemblage (see, for example, Crane (1987)). Palynological data and evidence from fossil leaves indicate that the angiosperms underwent a major radiation during the later part of the early Cretaceous (Aptian–Albian) and in the course of a few million years, the group was well established at a global scale.

Cretaceous floras discovered over the past few years include extremely well preserved flowers and have provided a greater range of characters from which to infer both the relations and reproductive biology in angiosperms from this critical time interval. A summary of fossil flowers was given by Crepet & Friis (1987), Friis & Crepet (1987) and Friis & Endress (1990) and stamen features through the Cretaceous were summarized by Friis *et al.* (1991) and we refer the reader to these papers for more detailed descriptions and literature citations.

(*b*) *Characters of early Cretaceous flowers*

Although data available from dispersed pollen, leaf fossils and floral structures indicate a major radiation of angiosperms during the Aptian–Albian, these floral structures are rather uniform in general organization, and within the dicotyledons only magnoliid and hamamelidid lineages have been identified. An early establishment of rosids as indicated by leaf fossils remains to be documented by floral evidence. The presence of monocotyledons is suggested by dispersed pollen, but a more precise systematic affilation within the monocots has yet to be established for these grains. The presence of magnoliids is documented mainly by a variety of monocolpate, reticulate pollen referred to *Clavatipollenites* and related genera. Although some *Clavatipollenites* show great similarity to pollen of modern Chloranthaceae, wall ultrastructure indicates this complex may represent several distinct magnoliid families (Pedersen *et al.* 1991). A Barremian fossil from Australia with fruits and leaves preserved is described as having a mosaic of chloranthoid and piperalean characters (Taylor & Hickey 1990). A small androecium from the Albian of North America also suggests the presence of the Chloranthaceae (Crane *et al.* 1989). Winteraceous pollen tetrads have been reported from the Aptian–Albian (Walker *et al.* 1983). The Hamamelididae is represented by several kinds of pistillate and staminate platanoid inflorescences (Friis *et al.* 1988) and small unisexual flowers of possible trochodendralean–buxoid affinity (Drinnan *et al.* 1990). *In situ* pollen in these hamamelididean flowers is similar to dispersed pollen assigned to *Tricolpites* and *Retimonocolpites*, both of which have an extensive record in the early Cretaceous palynofloras.

Size: fossil flowers are typically minute (0.5–4 mm) and borne in dense inflorescences.

Distribution of sex: flowers are unisexual and arranged in monoclinous or diclinous inflorescences or more rarely bisexual.

Number of floral parts is typically low and there is only one record of a reproductive structure with many parts. The angiospermous affinity of this fossil, however, is ambiguous.

Perianth parts are free, consisting of small membranous or coriaceous tepals. There is no indication that corolla or showy bracts were present in any of the Early Cretaceous forms.

Androecium: stamens are typically fleshy with weakly differentiated filament and anther. Connective tissue between the pollen sacs is extensive and typically expanded beyond the pollen sacs. Anthers are dithecal and tetrasporangiate with relatively small pollen. Dehiscence is valvate or more rarely by longitudinal slits. Dispersed pollen and pollen grains observed in stamens are small, monocolpate or tricolpate–tricolporate with columellate, reticulate exine. A pollenkitt-like substance has been observed in a single taxon.

Gynoecium: carpels are typically free with sessile and sometimes strongly decurrent stigmatic surface, rarely syncarpous. The adaxial suture in some apocarpous forms is apparently incompletely sealed.

Position of parts: an undescribed flower from Portugal has an epigynous perianth whereas all other angiosperm flowers so far identified are completely hypogynous.

Floral symmetry is actinomorphic.

Attractants and rewards: none of the flowers have any indication of a corolla. Attraction of pollinators was most likely by the androecium as in modern magnoliid flowers with similar anthers (Endress 1990). Thus, connective tissue may have been brightly coloured and odoriferous with yellow pollen sacs. Available evidence suggests that the only major reward was pollen. Carpels in pistillate platanoid flowers show superficial resemblance to stamens from corresponding staminate flowers in having an extended apical portion, and may have had attractive function as in modern *Myristica insipida* (Armstrong & Irvine 1989).

(*c*) *Characters of mid-Cretaceous flowers*

The Cenomanian record of angiosperms documents a further diversification of magnoliid and hamamelidid taxa (Dilcher 1979), and the establishment of several rosid lineages. The major diversification of the rosids, however, did not appear until later in the Cretaceous. Within the Magnoliidae, Lauraceae and Magnoliales have their first appearance. Small fruits with *Clavatipollenites*-type pollen share several characters with fruits of modern Chloranthaceae but differ by their anatropous ovules (Pedersen *et al.* 1991). Floral structures of Hamamelididae show little innovation, but dispersed pollen of the extinct *Normapolles*-complex records a major radiation by the mid-Cenomanian.

Size: fossil flowers are typically small as seen in earlier flowers, but larger floral structures, about 1–2 cm in diameter, have also been reported, as well as larger fruiting structures.

Distribution of sex: unisexual flowers remain common, but bisexual flowers are also diverse.

Number of floral parts: although number of parts was generally low in early Cretaceous flowers several multiparted taxa are present in the Cenomanian. Most flowers, however, have few parts, and lineages having flowers with trimerous, tetramerous or pentamerous arrangements are known.

Perianth parts are free and may be differentiated into calyx and corolla, although forms with undifferentiated perianths remain common.

Androecium: stamens with only slightly differentiated filaments and anthers, massive connective tissue and apical expansions of the connective are common, but several taxa show distinct filament and anthers with little connective tissue developed. These types typically dehisce by longitudinal slits whereas valvate dehiscence prevails in the fleshy stamens. Staminodea and lateral appendages at the base of the stamens are present in a lauraceous flower (Drinnan *et al.* 1991). Monocolpate and tricolpate–tricolporate pollen are diverse and include reticulate forms as well as forms with continous tectum.

Gynoecium: several taxa with syncarpous ovaries suggest that fusion of carpels was established and diverse.

Position of parts: most flowers are hypogynous, but epigynous taxa are also present.

Floral symmetry is mostly actinomorphic and flowers are shallow and open.

Attractants and rewards: the androecium continues to play a role as attractant in many magnoliids and hamamelidids in which perianth is undifferentiated and pollen was the main reward. Modifications occur in the lauraceous flower in which the lateral stamen appendages probably functioned as food bodies. In several rosids the attractive function had shifted to the corolla. Although nectaries have been recorded in a single flower this is poorly documented and pollination rewards may still have been mainly pollen.

(*d*) *Characters of late Cretaceous flowers*

The late Cretaceous record of fossil flowers documents a major radiation particularly within the rosids, dilleniids and higher hamamelidids (excluding the Asteridae, figure 1). The latter includes the diversification of the *Normapolles*-complex also documented by an extensive record of fossil pollen. Within the rosids, several lineages of saxifragalean and myrtalean affinities are known. There is also increased diversity within the monocotyledons with flowers, fruits and seeds related to the Liliidae and Arecidae.

Size: flowers are typically very small and larger reproductive organs are preserved in fruiting stage only.

Distribution of sex: most of the flowers are bisexual. Unisexual flowers prevail in the hamamelididean taxa although both bisexual and unisexual flowers have been identified within the Normapolles-complex.

Number of floral parts is typically low and arrangement of parts mostly cyclic.

Perianth is well differentiated into a calyx and a corolla in most flowers. Parts are typically free, but fusion of petals into a short tube has been documented for a single taxon.

Androecium: stamens typically have clearly differentiated filament and anther with weakly developed connective tissue. Pollen is typically small and often clumped together by a pollenkitt-like substance.

Gynoecium: syncarpous gynoecia with well-developed stylar tissue prevail.

Position of parts: there is a remarkably high proportion of epigynous forms. This was reported by Crepet & Friis (1987) and has been further supported by new findings in Portugal. In one flora relative position of perianth and gynoecium could be established in 15 different taxa and in 12 of these, gynoecium is inferior.

Nectaries are present in a variety of taxa typically formed as a disk inserted between androecium and gynoecium. Septacular nectaries were reported in a monocotyledonous taxon from Japan.

Floral symmetry is typically actinomorphic, but the presence of bisymmetrical and zygomorphic forms is documented by floral evidence and implied by indirect evidence from other organs.

Attractants and rewards: the main attractive feature apparently was the corolla. Nectaries are common in many different taxa and nectar had probably become an important reward in the rosid lineages.

(*e*) *Characters of early Tertiary flowers*

An extensive innovation in floral organization took place during the early part of the Tertiary period and families representing all major subclasses of angiosperm have been identified. In addition to the taxa that persist after the Cretaceous, there are several major groups of taxa that radiate in the early Tertiary, including the legumes and Euphorbiaceae. Higher Hamamelididae and grasses appear early in the Tertiary or in the uppermost Cretaceous and radiate in the Tertiary.

Size: direct evidence from fossil flowers and indirect evidence from other organs indicate that there is a considerable size range in the early Tertiary flowers.

Distribution of sex: bisexual flowers prevail and this is reflected in the more modern flora of the early Tertiary. Higher Hamamelididae are very well represented as are other wind pollinated dicots.

Number of floral parts is typically low and arranged in whorls of 3, 4 or 5. Evidence from fossil fruits and seeds indicates that an increase in the number of stamens took place in several separate lineages.

Perianth parts are typically differentiated into calyx and corolla. Sepals are mostly free. Petals are free or laterally fused to form funnel-shaped or wider corolla tubes.

Androecium: flowers exhibit a wider range of stamen morphology than seen in the Cretaceous although forms with distinct filaments and simple tetrasporangiate anthers are the most common forms.

Exserted brush like androecia occur in several taxa and stamen arrangements exhibit various modifications that have not been seen in earlier fossils (e.g. bilaterally arranged partially-fused stamens of papilionoid legumes).

Gynoecium: carpels are typically fused to form syncarpous ovaries with distinct styles. Fruits vary widely in morphology. Fleshy fruits as well as various winged fruits were diverse, indicating more specialized dispersal systems than seen in the Cretaceous angiosperms.

Position of parts: epigynous flowers are present but less common than hypogynous types.

Floral symmetry: the Tertiary record of flowers provides the earliest floral evidence of strongly zygomorphic types formed by differentiation of corolla lobes. Indirect fossil evidence indicates that zygomorphy was established in several lineages.

Attractants and rewards: the attractive function was mainly by the corolla, or in some brush flowers, the attractive function was probably by the stamens. Stamens in these flowers were not massive as in many Cretaceous forms, but protruding from the flowers by long thin filaments. Reward was most likely nectar and to some extent pollen.

4. INSECT FOSSIL RECORD

There have been interesting developments in our knowledge of the fossil record of anthophilous insects since we last reviewed the history of insect pollination (Crepet & Friis 1987). In that review, we predicted the presence of bees in the late Cretaceous based on the fossil record of angiosperm floral characters and families with particularly distinctive combinations of characters. Meliponinae have subsequently been reported from the late Cretaceous of New Jersey (Michener & Grimaldi 1988). The records of other orders of anthophilous insects have improved and some spectacular new fossil insect localities have been reported and their faunas described.

(*a*) *Coleoptera*

Beetles are well established in the Permian with several flower-visiting orders present by the Jurassic (including Nititulidae, Elateridae and Buprestidae). They continue to diversify in the Mesozoic with many families associated with pollen- and nectar-feeding present throughout that era (Handlirsch 1906–1908; Carpenter 1976; Crowson 1981). Phylogenetic relations among certain 'primitive' groups of beetles (Boganiidae (modern pollen feeders on cycads and shrubby angiosperms where cycads do not occur; Endrody-Younga & Crowson 1986), Hobartiinae and others), suggest an interesting relation between mycophagy and pollen feeding early on in Coleoptera (Wheeler, personal communication). Recent reports include Staphylinidae with both pollen and nectar feeders from the early Jurassic and late Cretaceous, and Chrysomelidae (leaf chewing beetles) that are typically pollen feeders. Beetle-like borings have been reported in the reproductive structures of Cretaceous *Cycadeoidea* (Crepet 1974).

In addition to the highly derived syndromes (Gottsberger 1988) associated with complex large-flowered Magnoliidae, beetles may pollinate small flowers with exposed nectar or with nectar shallowly hidden in addition to pollen. Some exceptional beetles are well suited to nectar feeding, with modified maxillae up to 12 mm long (Proctor & Yeo 1973).

(*b*) *Diptera*

Flower visiting Diptera are distributed among all three suborders of flies: Nematocera (usually considered the most primitive), Brachycera and Cyclorrhapha. The fossil record of families that include flower-visiting flies is good and includes a significant number of new discoveries (Grimaldi 1990). In Nematocera there have been additional reports of Cretaceous Tipulidae, a family that extends to the Jurassic and pollinates Saxifragaceae today (Raynder & Waters 1990). Bibionidae have been reported throughout the Cretaceous, Mycetophilidae from Jurassic through Cretaceous and Chironomids from the early Cretaceous. The Ceratopogonidae are now known from the late Cretaceous and Pycodidae from the early Cretaceous.

In Brachycera, Rhagioniidae have been reported from the early Jurassic, but this has been regarded as insufficiently substantiated (Grimaldi 1990). Empididae have a suggested Jurassic origin and more reliable post mid-Cretaceous fossil record and are thought to be primtively predatory with specialization for nectar feeding following angiosperm radiation. The earliest known fossil empids appear to be flower visitors (Negrobov 1978). Asilidae and possible ancient sister groups are known to the Jurassic. Bombyliidae have a much improved fossil record with three new genera each with a relatively short proboscis known from the early Cretaceous (Zaitzev 1986), suggesting an origin of the family in the Jurassic (Grimaldi 1990). There have been recent reliable reports of Phoridae from the early Cretaceous leading to the suggestion that they originated much earlier (Grimaldi 1989).

Cyclorrhapha Syrphidae have a poor fossil record, but it has been suggested that they were diverse by the Tertiary.

Nematoceran pollinators typically pollinate flowers that are relatively small with exposed nectar. There are some taxa that pollinate flowers with small tubular flowers or with partially concealed nectar. Brachyceran families pollinate a wider variety of floral types and sizes from small flowers to large flowers; from those with exposed nectaries to concealed nectar (unusual), from small tubular to large tubular flowers.

(*c*) *Lepidoptera*

There have been more reports of fossil Lepidoptera since our last review, but few of them offer direct fossil evidence that alter our present understanding of timing in lepidopteran evolution. The earliest reports of Lepidoptera are from the Jurassic but Lepidoptera are thought to have diverged from their sister group, the Trichoptera, in the Permian. New records of micropterygid moths (pollen chewing) have been reported from the early Cretaceous and fossils have now also been discovered in the southern Hemisphere (Martens-Neto & Vulcano 1989). A new heteroneuran (Heteroneura are nectar feeders) moth has been reported from the early Cretaceous (Skalski 1984). If this is accurate, it may represent the first generally accepted evidence of the group. Whalley (1986) questioned the nature of Campanian eggs of Noctuidae (Gall & Tiffney 1983) and recognizes no Noctuidae earlier than the Miocene. Recent reports and analyses on the whole suggest an earlier origin for Lepidoptera, including butterflies, than is presently reflected by the fossil record. Lepidoptera mines on seed fern foliage of the late Jurassic are reported as suggestive of Nepticulidae (Grogan & Szadziewski 1988), but they are poorly preserved and must be interpreted with some caution. Phylogenetic analysis of Papilioninae suggest a mid-Cretaceous origin for some groups (Miller 1987). Even Whalley (1986), suggests that Heteroneura must be missing from the Cretaceous fossil record. Unequivocal butterflies appear during the Lower Tertiary (Papilionideae, Nymphalidae, Satryidae, Lycaenidae) and are well represented by the Eocene. The moth superfamilies Gelechioidea, Cossoidea, Pyraloidea, Geometroidea and Copromorphoidea are present in Eocene–Oligocene deposits.

(*d*) *Hymenoptera*

There have been important discoveries of fossil Hymenoptera since our last review. Symphyta are well known from The Triassic on and are well represented in Cretaceous sediments. Cretaceous Symphyta have even been found preserved with pollen of seed ferns in their guts (Krassilov & Rasnitsyn 1982). There has been a dramatic increase in the number of reports of Apocrita in the past five years (see, for example, Darling & Sharkey (1990)). Among the parasitic wasps, there have been Cretaceous reports of ichneumonids and Cynipidae. There have been numerous new and well-founded reports of Aculeata from the Cretaceous. Chrysididae now have a Cretaceous record and scoliids and pompilids are also known from the Cretaceous. Vespoids appear in the Lower Cretaceous (cf. Carpenter & Rasnitsyn 1990). Specidae, the paraphyletic stem group of bees, are now well known from the early Cretaceous. The most dramatic fossil discovery in recent years is the discovery of Apidae (*Trigona*, Meliponini) from the late Cretaceous (Michener & Grimaldi 1988).

5. MAJOR STAGES IN THE EVOLUTION OF INSECT POLLINATION

There is a discernible pattern in the evolution of floral structure and insect pollination based on the fossil history of plants and insects. In the anthophytes, Bennettitales and Gnetales appear before the flowering plants and overlp with them chronologically. The Bennettitales may be interpreted on the basis of several kinds of evidence as having been pollinated by beetles (Crepet 1974), and flies and Hymenoptera cannot be ruled out in certain taxa. We interpret Gnetales as basally bisexual (with close association of staminate and pistillate organs) and infer that insect pollination is basal in the group. Insect pollination was in place at the time of angiosperm origin and in early angiosperms the androecium probably served as the sole reward and attraction for pollinators as in Bennettitales. There is even parallelism (or homology pending further analysis) between the fleshy microsporophylls of *Williamsoniella* and those of early angiosperms.

The Cretaceous and early Tertiary fossil record is broadly consistent with the generalized hierarchical relations of the major angiosperm groups as presented in figure 1, and suggests that the earliest angiosperms may have been small-flowered, apetalous magnoliids with few parts, either asymmetric or cyclically arranged. By the mid-Cretaceous, rosid flowers are known, as well as larger multiparted magnoliids. The more derived asterid floral types are not firmly established until the Tertiary, when numerous modern families appear. This pattern suggests that the hamamelidid–rosid–asterid line is probably a very early offshoot of small-flowered magnoliids, and that the larger-flowered magnoliids, long considered indicative of the most primitive angiosperms, may mostly belong to later lineages that might be considered evolutionary cul-de-sacs.

Earliest Cretaceous floral types co-occurred with a greater variety of anthophilous insects than has previously been supposed. Representatives of the four ‘major orders’ of anthophilous insects present in the early Cretaceous now pollinate a variety of simple, usually small floral types in mutli-flowered inflorescences with exposed rewards. Thus, the idea that Coleoptera were the earliest insect pollinators is in need of review because the efficacy of other anthophilous insect groups present at the time in the context of their contemporary angiosperms is either proven (cf. references) or cannot be dismissed.

The early Cretaceous (Aptian–Albian) angiosperms are poorly represented by floral structures, but remains of Chloranthaceae, Trochodendrales–buxoid fossils and platanoids are present in Albian deposits. Older pollen of chloranthaceous and winteraceous affinity suggests early pollination by beetles, flies and micropterygids consistent with the insect fossil record. Some chloranthoids may have been wind pollinated, based on dispersed pollen similar to *Ascarina*, but in the absence of overall floral structure, such interpretations should be made with caution. Cenomanian fruits with abundant *Clavatipollenites* pollen adhering to the sessile stigma indicate that at least some chloranthoids were insect pollinated.

Meristic stabilization of floral parts in cycles of threes (Lauraceae) or four to five (Rosidae) occurs by the Cenomanian. Large meristically indeterminate flowers (of Magnoliales affinity) appear at the same time. The first specialization for beetle pollination in angiosperms is represented in the Cenomanian Magnoliales. Lauraceae are frequently pollinated by bees today, but many of these reports are somewhat equivocal, as they involve *Apis mellifera* pollination of cultivated species (House 1989). However, flies and beetles have been documented as pollinating Lauraceae in their natural setting. Thus, the occurrence of Lauraceae cannot be considered strong evidence for earliest bee pollination.

According to Darling & Sharkey (1990) apparent stasis in proportions of higher level taxa in Hymenoptera throughout the Mesozoic implies a disconnection between angiosperm and hymenopteran radiations. This may be a premature conclusion, because it is not the only explanation of observed patterns in Hymenoptera in the fossil record, nor does it take into account what is known about the evolution of floral structure in the Cretaceous. From the fossil evidence of the Early Cretaceous it seems apparent that there was a general similarity in attractant and reward structures in angiosperms until the Cenomanian specialization for beetle pollination in Magnoliales and the appearance of the corolla as an attractant in Lauraceae and Rosidae. Although stabilization of cyclical 4-5-merous floral parts in the latter set the stage for the evolution of the floral tube and other corolla characters now associated with pollination in Apidae (and Lepidoptera), no specializations that can be associated with pollination by Apidae appeared before Santonian–Campanian flowers with corolla tubes. Nor do pollinators in the early Cretaceous–Campanian interval exhibit features or taxonomic affiliations that suggst any breakthroughs in attractants or rewards on the parts of the plants. It is the Cenomanian that marks the appearance of the Rosidae with its associated character complex related to pollination by generally more advanced insect pollinators. In the late Cretaceous Santonian–Campanian discoveries of numerous rosid taxa with well-developed nectaries and well-developed corollas accompany the specimens with fused corolla tubes and may signal the beginning of the most significant evolutionary interaction between Hymenoptera and angiosperms. The proliferation of advanced floral types in the Maastrichtian and Early Tertiary is consistent with this possibility as is the dramatic appearance of meliponine Apidae in the Late Cretaceous. Thus, the interpretation of apparent stasis in the hymenopteran line in the face of angiosperm radiation may be due to failure to recognize the strong relation between the character complex embodied in early rosids and the Hymenoptera. It is important to point out that these late Cretaceous rosids were possibly pollinated by other groups of insects as well because a high proportion of them are epigynous, a condition Grant (1950) associates with beetle pollination, but this hypothesized correlation invites confirmation based on more extensive data on pollination in extant epigynous flowers.

The Paleogene signals the modernization of angiosperm families and reveals a proliferation of floral types with highly adapted corollas as well as families whose radiations have been intimately associated with bees (Leguminosae, Euphorbiaceae) or which have highly modified perianths as attractants or novel rewards (e.g. elaiophores in Eocene Malphigiaceae). Haustellate Lepidoptera including diverse moths and butterflies appear in the Paleogene. The fossil evidence at this time illustrates an uppermost Cretaceous–Paleogene radiation of highly modified corollas associated with pollinators (bees) that by correlation and mechanism (fidelity as a potential isolating mechanism, efficiency, etc.) are thought to have contributed greatly to diversification in angiosperms. This is also a time of the greatest rate of appearance of new angiosperm taxa. We suggest that the fossil record as now understood reflects a rapid late Cretaceous radiation of bees and the types of flowers and families associated with them that extends well into the Paleogene. The higher Lepidoptera and higher Diptera (Cyclorrhapha) and Coleoptera (Chrysomelidae) have a similar temporal relation with the angiosperms. It is also possible that the relation between the apparent time of appearance of bee pollination and rate of angiosperm diversification reflects a causal relation of some dimension. This is plausible based on available evidence but is a hypothesis that can be tested only with the greatest difficulty.

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Discussion

A. J. Lack (*School of Biological and Molecular Sciences, Oxford Polytechnic, U.K.*). The authors emphasized early insect pollination in the fossils. Many extant Chloranthaceae, however, are said to be wind pollinated. This includes *Ascarina* with pollen very similar to fossil *Clavatipollenites*. Is wind pollination as primitive as insect pollination or are all the earliest plants insect pollinated.

E. M. Friis. The only megafossil evidence of the plants that produced pollen of the *Clavatipollenites* type is the small fruits of *Couperites mouldinensis* from the early Cenomanian of eastern North America (Pedersen *et al.* 1991). These fruits have a single anatropous seed and have an elongated, sessile stigmatic surface. Clumps of *Clavatipollenites* pollen have been observed adhering to the stigmatic area in several specimens. Their abundant occurrence may indicate insect pollination rather than wind pollination. SEM and TEM studies of pollen wall ultrastructure document a close resemblance with modern pollen of *Ascarina*. Fruit and seed morphology of *Couperites*, however, indicate that although *Couperites* is more closely related to members of the Chloranthaceae than to any other modern magnoliid family, its anatropous seeds preclude an inclusion in the Chloranthaceae as currently circumscribed.

E. A. Jarzembowski (*Booth Museum of Natural History, Brighton, U.K.*). In the search for interactive models, the rapid radiation of angiosperms during the Cretaceous is perhaps best explained by major innovations in insects rather than by postulating general pollination. The fast accumulating evidence of Cretaceous insect life suggests significant evolution in the aculeate Hymenoptera. Generalized aculeates such as Baissodidae are first found in the early Cretaceous (Rasnitsyn 1975) but specialized groups such as stingless bees had already evolved by the late Cretaceous (Michener & Grimaldi 1988); that is, the important switch from prey catching to pollen collecting in wasps occurred during this period (Jarzembowski 1991 *a*). There is little evidence of honeydew producing insects and extrafloral nectaries in the early Cretaceous (Jarzembowski 1989) which could have increased the value of floral nectaries as a source of liquid carbohydrate rather than protein. The hypothesis could be tested by studying pubescence in fossil insects.

The fossil record of Lepidoptera is probably poor (with the possible exception of microlepidopterans in amber) because like other scaley insects, Lepidoptera trap air and are less likely to become waterlogged and incorporated in aquatic sediments in an undecayed form (E. A. Jarzembowski, personal observation). In addition, there are problems in distinguishing primitive Lepidoptera from Trichoptera in the fossil record (see comments in Jarzembowski (1991 *b*).

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Note added in proof (*26 July 1991*):

Recently discovered fossils germane to our analysis from a North American Cenomanian locality were not available until this chapter was in press. The novel fossils include hamamelidaceous flowers with staminodal nectaries, staminal tubes and sepal cups. At the same locality are fossils of two dilleniid taxa with fused corollas. These fossils therefore are the oldest examples of certain characters critical to the evolution of advanced insect pollination, and add support to our model for the timing of the relationship between angiosperms and advanced pollinators.