



Did insect pollination cause increased seed plant diversity?

ROOT GORELICK

Department of Biology, Arizona State University, Tempe, AZ 85281-1501, USA

Received 21 February 2001; accepted for publication 17 July 2001

The dominant paradigm for the disproportionate number of flowering plants is the unique coevolution that they underwent with pollinating insects. The theory underlying this biotic pollination hypothesis contradicts more generally accepted evolutionary theory. Furthermore, various lines of empirical evidence falsify the biotic pollination hypothesis: (a) several lineages of plants were insect pollinated – angiosperms, Gnetales, Bennettitales, Cheirolepidiaceae, Medullosales, and Cycadales – yet only the first four were ever diverse or underwent radiations; (b) the predicted rise in insect diversity, which was coupled with angiosperm radiation, does not appear in the fossil record; (c) the family Poaceae (grasses) are wind pollinated, yet are exceptionally diverse and species-rich; and (d) the family Formicidae (ants) were not pollinators, yet are exceptionally species-rich and ecologically dominant. I enumerate many alternate (and seldom investigated) hypotheses for these patterns of seed plant diversity, keeping in mind that although I show that insect pollination was neither a necessary nor sufficient condition for large numbers of species, it may have played a substantial role in both plant and insect speciation. Alternatively, existing theory regarding the biotic pollination hypothesis can be refined in an attempt to eliminate the aforementioned empirical anomalies and theoretical inconsistencies.

© 2001 The Linnean Society of London

ADDITIONAL KEY WORDS: pollinator–plant coevolution – angiosperm radiation – insect radiation – gymnosperm – speciation — extinction.

INTRODUCTION

Why are there so many species (and families) of flowering plants, yet so few other seed plants? There are over one hundred times more extant flowering plant (angiosperm) species than there are species of all other extant seed-bearing plants (Table 1). Similarly, three-quarters of extant animal species are insects (Ehrlich & Wilson, 1991). For 150 years, the paradigm has been that this disparity was due to flowering plants coevolving with insect pollinators (Darwin, 1862). Purportedly, angiosperms possessed a unique association with pollinating insects, which resulted in extreme radiation of both flowering plants and of their insect pollinators (Grant, 1949; Thompson, 1994; Grimaldi, 1999). In the last decade, the paradigm has slightly shifted. Coevolution of pollinators and plants is still considered the primary cause of radiations of insects and flowering plants, but in part these radiations are secondarily ascribed to coevolution of seed dispersing

Table 1. Diversity of living seed plants

	Number of families	Number of species	First appearance (million years ago)
Gingkophyta	1	1	280
Cycadophyta	3	100	300
Coniferophyta	7	500	330
Gnetales	3	100	200
Angiosperms	500	300 000	120

animals and plants and to coevolution of insect herbivores and plant chemical defences. The purpose of this paper is to review the underlying theory and test the hypothesis that insect pollination facilitated increased flowering plant (and seed plant) diversity. I also briefly describe the interrelationships between these three coevolution hypotheses, although my focus is on insect pollination because it is still considered the primary cause of the radiations.

* Corresponding author. E-mail: cycad@asu.edu

For the past 350 million years, seed plants have been the cornerstone of terrestrial ecosystems. Before the origin of seed plants in the Late Devonian, records of terrestrial fossil plants were limited to riparian areas, which form a miniscule fraction of terrestrial ecosystems (Edwards & Fanning, 1985; Retallack, 1985, 1986; Behrensmeyer *et al.*, 1992; Algeo & Scheckler, 1998; Scott & Scheckler, 1998). Immediately after their origin, seed plants colonized all these previously depauperate lands. Furthermore, until the appearance of seed plants – and, to a lesser degree, progymnosperms – almost all plants were less than 1 m tall (Gensel & Andrews, 1984; Meyer-Berthaud, Scheckler & Wendt, 1999). The colonization of most terrestrial environments by seed producing trees, the consequent soil formation and weathering, and the resulting changes in ambient atmospheric concentrations of O₂ and CO₂ (McElwain, 1988; McElwain & Chaloner, 1995) may have caused the five mass extinctions during a 20 million year period in the Late Devonian (Algeo *et al.*, 1995; Retallack, 1997; Algeo & Scheckler, 1998), forever altering terrestrial ecosystems.

The biotic pollinator coevolution hypothesis is usually phrased vaguely. It originated from Darwin's (1859, 1862, 1876) invocation of Sprengel's (1793) pioneering work on insect pollination. However, until fifty years ago, the mechanisms by which insect pollination caused radiations of plants and insects had not been explicated. Radiations are dramatic increases in speciation rate minus extinction rate. Specific flower and insect morphologies could have served as isolating mechanisms resulting in speciation of both plants and insects (Grant, 1949; van der Pijl, 1960; Thompson, 1994). This includes temporal isolation, ecological isolation, and other forms of sympatric speciation. Extinction rates may have been lower for insect pollinated plants because they can be cross-pollinated at lower densities than wind pollinated plants and thereby better able to withstand otherwise cataclysmic events, including herbivore or pathogen epidemics (Janzen, 1970; Raven, 1977).

Although I focus on the biotic pollinator hypothesis, it is related to other coevolution hypotheses, such as the hypothesis that the proliferation of secondary chemical compounds in plants to deter herbivory resulted in increased plant speciation rates and decreased extinction rates (Ehrlich & Raven, 1964; Scott, Stephenson & Chaloner, 1992). These two coevolution hypotheses are related in at least three independent ways. First, the chemicals that attract pollinators to plants may have the same precursors as those chemicals that deter herbivores (Pellmyr & Thien, 1986; Pellmyr *et al.*, 1991; Armbruster, 1997; Dobson & Bergström, 2000). The plant may even make trade-offs between synthesizing herbivore deterrents and

volatiles to attract pollinators (Fineblum & Rauscher, 1997). Second, some insects both eat and transport pollen (Darwin, 1876; Arber & Parkin, 1907; Kevan, Chaloner & Saville, 1975; Scott *et al.*, 1992). Third, insect pollination can result in sparser plant populations, which thereby become more immune from herbivore infestations (Janzen, 1970; Regal, 1977). It may not be possible to separate the effects or processes of these two coevolution hypotheses (Armbruster, 1997; Armbruster *et al.*, 1997; Strauss & Armbruster, 1997), hence I will ignore such synergistic effects between hypotheses and focus solely on the biotic pollination hypothesis.

The relationship between the biotic pollination hypothesis and the biotic seed dispersal coevolution hypothesis (Herrera, 1989) is even clearer. In both hypotheses, animals are transporting reproductive plant parts: haploid pollen or diploid seeds. Some insects both pollinate flowers and parasitize the seeds (Pellmyr, 1992; Thompson & Pellmyr, 1992; Pellmyr & Leebens-Mack, 2000). The biotic seed dispersal hypothesis has been largely rejected (Herrera, 1989).

A voluminous literature supports the biotic pollination hypothesis (Proctor, 1978; Crepet, 1983, 1984; Knoll, 1986; Friis, Chaloner & Crane, 1987; Thompson, 1994; Grimaldi, 1999), although I disagree with many of their inferences. I join the minority by arguing that either animal pollination may not have played such a large role in radiation of angiosperms (Midgley & Bond, 1991) or, alternatively, that animal pollination did play a large role but the underlying theory is not adequately developed (Waser, 1998). I provide a broad swath of empirical evidence showing that animal pollination is neither necessary nor sufficient for the evolution of large numbers of species. I also discuss how mechanisms underlying the biotic pollination hypothesis contradict more widely accepted and tested portions of evolutionary theory. For example, animal pollinated plants should have lower heterozygosity (hence lower speciation rates) and larger geographic ranges (hence less chance for allopatric speciation) than do wind pollinated plants. I conclude that researchers should (1) focus on the many oft-neglected hypotheses that have been proposed to explain the preponderance of extant angiosperms, hypotheses that I enumerate in the Appendix, and (2) attempt to refine existing theory to reconcile apparently contradictory data and theory.

THEORY UNDERLYING THE BIOTIC POLLINATOR HYPOTHESIS

Theories regarding pollinator-plant coevolution are too sweeping in that they always predict increased probability of radiation of both the plants and the pollinating animals. I first discuss existing theory and

then describe how this contradicts other, well-accepted evolutionary theories.

EXISTING MODELS

The primary proposed mechanism by which pollinating animals cause radiations is by increasing speciation rates by establishing isolating mechanisms that prevented incipient species from interbreeding with their parent species in zones of secondary contact (Grant, 1949). Without animal pollinators or without ethological specialization of the animal pollinators, the previously diverged populations might have interbred and re-combined into one large sympatric population. However, if previously diverged populations each had animal pollinators that somehow differed from each other, then interbreeding might be precluded.

Grant's notions have been extended in recent years. Ecological communities are no longer considered coherent and static entities: component species in such communities change greatly over time (Davis, 1986; Van Devender, 1990). The habitats of plants and their insect pollinators may not overlap during certain periods of time, especially as local climatic conditions fluctuate. Although such a situation would be the death knell for plants that are pollinated by a single animal species, this may not adversely affect plants that are pollinated by several species. An obligately insect-pollinated species may have a geographic range that includes several animal pollinator species, possibly with non-overlapping ranges. This could result in different plant specializations in areas where the pollinators differ. Later, there can be despecialization, when additional animal species – that are closely related to the original pollinator or are morphologically similar to the original pollinator – become pollinators of that plant. Iterated cycles of specialization followed by despecialization may have caused angiosperm and insect radiations (Thompson, 1994). This proposal has its roots in Darwin's (1862) discussion of an arms race between plants and their pollinators and Fisher's (1930) discussion of runaway sexual selection. Unfortunately, no mathematical or population genetic model exists for this model of repeated cycles of specialization and despecialization nor for Grant's model of floral isolation.

The only existing population genetic model for angiosperm radiation is one in which insect pollinators feed from and pollinate a single plant species (Kiestler, Lande & Schemske, 1984). As the authors admit, this model has limited applicability because most biotically pollinated plants and their pollinating animals are generalists (Waser *et al.*, 1996). The only angiosperms that fit this model are orchids, yuccas, figs, and globe-flowers, each with tightly linked insect pollinators and herbivores. A completely different model would be

needed to explain species-richness of all other angiosperm families. Another problem is that many extant species of Cycadales (cycads) have only a single known species of pollinator (Oberprieler, 1995b), which often needs to eat the starch of the cones (although, see Fawcett & Norstog, 1993 and Tang, 1997 citing unpublished work of Charles O'Brien for cycad species with two putative insect pollinators). The Cycadales were never a diverse lineage (Harris, 1961, 1964; Pant, 1987; Anderson & Anderson, 1989), thereby falsifying this one quantitative genetic model or inexplicably strictly limiting its applicability to angiosperms.

Other population genetic models of plant and pollinating animal coevolution may eventually be derived as corollaries of coevolutionary models of antagonistic relationships, such as between predators and prey, between disease causing organisms and hosts, or between plants and herbivores. However, it is not obvious how well these models will apply when there is a mutualism that is beneficial to both organisms. Positive and negative feedback models often give qualitatively very different results. Mathematical models that are not population genetic have also been developed for plant-pollinator coevolution (e.g. Waser *et al.*, 1996), but it is not obvious how robust or applicable these are.

The biotic pollination hypothesis and all other existing models of pollinator-plant coevolution are comparative in nature. The predicted radiations in pollinator and animal-pollinated plant lineages are relative to those lineages that are not pollinators and are not animal-pollinated. Implicit in the biotic pollination hypothesis is that with a pair of sister taxa, one of which was composed of animal-pollinated plants and the other composed of wind-pollinated plants, on average there will be far less radiation in the wind-pollinated taxon. Radiation is a relative term used to describe a higher than average rate of speciation minus extinction. The average rate is determined in comparison with the nominal case of non-pollinating animals and wind-pollinated plants. Therefore, a corollary of the biotic pollination hypothesis is that – in general – there should be a lack of radiations of non-pollinating animals and wind-pollinated plants.

Ethological isolation is a form of ecological isolation. It is generally believed that ecological isolation causes adaptive radiations via increased speciation rates, rather than decreased extinction rates (Schluter, 1998). As I show below, this distinction between speciation and extinction rates contradicts other evolutionary models.

CONTRARY MODELS

All existing verbal and mathematical models of the biotic pollination hypothesis predict that coevolution

leads to radiations of both plant and pollinator. Not only are these sweeping predictions not true (e.g. cycads and many of their pollinators), but they are contrary to the predictions of other, well-accepted evolutionary models.

Animal pollinated plants have a much lower genetic diversity of pollen alighting on their female reproductive parts than do wind-pollinated plants (Kress, 1981). Often animal pollinated plants have pollen from a single male or bisexual individual landing on a female flower or cone, whereas wind pollinated species receive pollen from hundreds of male or bisexual individuals. Unless animal pollinated plants have substantially larger effective population sizes than do wind or water pollinated sister taxa, which is unlikely (Midgley & Bond, 1991), these differences in pollen load cause populations of animal pollinated plants to have substantially lower heterozygosities than their wind pollinated sister taxa. Lower heterozygosities reduce speciation rates for animal pollinated species because genetic variation is the fodder for speciation (Dobzhansky, 1937).

Animal pollinated plants generally have substantially lower population densities than do wind pollinated plants (assuming no difference in the relative geographic ranges of animal versus wind pollinated plants). Lower densities result in lower extinction rates (Stebbins, 1981), due to populations being much less susceptible to plagues of herbivores or to microscopic pathogens. Dense populations sustain epidemics much more readily than sparse populations. Although lower extinction rates for animal pollinated plants will have the same effect on overall plant diversity as would increased plant speciation rates (Raup, 1994), the mechanism is different and is contrary to expectations from models of radiation via ecological isolation. Furthermore, these sparser plant populations would not affect insect speciation or extinction rates, contrary to the biotic pollination hypothesis.

Similarly, decreased extinction rates in plants could be due to populations being better able to withstand decimations from herbivores or other environmental shocks (Janzen, 1970; Raven, 1977). This may be due to individual male or bisexual plants being able to increase their fitness because they do not need to invest as many resources on pollen production (Midgley & Bond, 1991). This ability to withstand decimations may be accompanied by an increased geographic range for the plant species, which acts against possible allopatric speciation.

Another proposed theory for decreased extinction rates is that, after decimation of plant populations by some catastrophic event, plant population densities may have been too low to sustain themselves via wind pollination, but may have survived if animals carried

pollen between distant individuals (Burger, 1981). Again, lower extinction rates are contrary to the ecological isolation model of the biotic pollination hypothesis.

The possibility exists that animal pollinated plants may have larger geographic ranges than wind pollinated plants, although there is substantial debate regarding this (Midgley & Bond, 1991). However, assume for the moment that animal pollinated plants have larger ranges, then they have much less potential for allopatric (Gulick, 1890; Mayr, 1942) and parapatric (Gavrilets, Li & Vose, 2000) speciation. Less allopatric and parapatric speciation means lower speciation rates for the plants (Stebbins, 1981; Midgley & Bond, 1991), directly contradicting the biotic pollination hypothesis (although, one also has to account for the lower extinction rates associated with larger geographic range). Even in the Mesozoic, most putative pollinators had the potential for long distance dispersal, especially in macropterous stages: grasshoppers in the Mesozoic conifer family Cheirolepidiaceae (Krassilov, Zherikhin & Rasnitsyn, 1997); beetles in the Mesozoic order Bennettitales (Crepet, 1972); and bees, flies, and beetles in Mesozoic, Cenozoic, and extant Cycadales (Ornduff, 1991; Fawcett & Norstog, 1993). Consequently, if insect pollination had any effect on increasing seed plant diversity, it would have to have been via reduced extinction rates rather than raised speciation rates, especially for plants that had animal pollinators that occasionally travelled far. The constantly changing constitution of ecological communities over geologically brief periods of time (Van Devender, 1990) – especially the changing suite of insect pollinators – also reduces the possibility of allopatric speciation in insect pollinated plants.

EMPIRICAL EVIDENCE AGAINST THE BIOTIC POLLINATION HYPOTHESIS

The following four empirical arguments shed serious doubt on the biotic pollination hypothesis. The first line of evidence is that insect pollination arose independently in several lineages of seed plants, but some of these lineages were never diverse. Since several of these animal pollinated lineages are extinct, this first argument requires substantial inferences regarding insect pollination. For those readers wishing to skip the details, a summary is given in Table 2.

The other three lines of empirical evidence are that insect diversity decreased in the late Cretaceous during the origin and initial radiation of angiosperms and that some highly diverse lineages of plants and animals – namely ants and grasses – were never pollinated nor animal pollinated. These lines of evidence require fewer palaeoecological details hence I will take much less space discussing them. The arguments regarding

Table 2. Pollination mode and diversity of seed plants

	Pollination mode	When diverse	When alive
Angiosperms	Insects (mostly)	Cenozoic	Cretaceous–Present
Poaceae	Wind	Cenozoic	Tertiary–Present
Bennettitales	Insects	Cretaceous	Triassic–Cretaceous
Gnetales	Insects	Cretaceous	Triassic–Present
Coniferophyta			
Cheirolepidiaceae	Insects	Jurassic–Cretaceous	Triassic–Cretaceous
All other conifers	Wind	Never	Mississippian–Present
Cycadales	Insects	Never	Pennsylvanian–Present
‘Seed ferns’			
Medullosales	Arthropods	Never	Mississippian–Permian
Other seed ferns orders	Wind	Never	Mississippian–Cretaceous
Ginkgophyta	Wind	Never	Permian–Present
Czekanowskiales	Unknown	Never	Jurassic–Cretaceous
Pentoxylales	Unknown	Never	Jurassic–Cretaceous

diversity of ants and grasses hinge on the comparative nature of the biotic pollination hypothesis. That is, they rely on the implicit argument that non-pollinating insects and wind pollinated plants should undergo fewer radiations than related lineages of pollinating insects and animal pollinated plants.

Although the following four lines of empirical evidence imply that we should reject the biotic pollination hypothesis, they do not close the door on the possibility that insect pollination may have been partly or even largely responsible for radiations of insects and the plants they pollinate. Instead, these four lines of evidence may simply require revising or refining the mechanisms underlying the biotic pollination hypothesis, i.e. a revision of the hypothesis itself.

NOT ALL INSECT SEED PLANT LINEAGES UNDERWENT RADIATIONS

Seed plants consist of the angiosperms, Ginkgophyta (ginkgos), Coniferophyta (conifers), Gnetales (possibly subsumed under Coniferophyta), Bennettitales (cycadeoids), Cycadales (cycads), the seed fern orders Calamopityales, Caytoniales, Buteoxylonales, Lyginopteridales, Medullosales, Callistophytales, Peltaspermales, Gigantopteridales, Glossopteridales, Crystospermales, and a few other orders such as Pentoxylales and Czekanowskiales. There remains an uneasy consensus that Bennettitales are closely related to flowering plants (Crane, 1985a,b; Axsmith, Taylor & Taylor, 1998; Doyle, 1998), despite the recent demise of the anthophyte hypothesis. Recent molecular work suggests that Gnetales and Coniferales are sister taxa (Goremykin *et al.*, 1996; Chaw *et al.*, 1997; Frohlich & Meyerowitz, 1997; Frohlich, 1999; Qiu *et al.*, 1999; Samigullen *et al.*, 1999; Winter *et al.*, 1999; Chaw *et al.*, 2000; Frohlich & Parker, 2000; Kuzoff

& Gasser, 2000), which conflicts with virtually all morphological data and some older molecular data (Crane, 1985a,b; Doyle & Donoghue, 1986; Chase *et al.*, 1993; Donoghue & Doyle, 2000). Relationship of Gnetales will, however, not affect my conclusions. Cycadales either descended from Medullosales or they are sister taxa (Crane, 1985a,b; Doyle & Donoghue, 1986; Nixon *et al.*, 1994). This relationship is primarily based on pollen or prepollen with alveolate sexine and lamellate nexine, which is unique to these two orders (Taylor, 1978, 1981); a vascularized integument, which is not found in any other non-flowering seed plants (Crane, 1985b); and fibres in secondary phloem, which are not found in any other Palaeozoic seed ferns (Smoot, 1984).

Below, I discuss each of the animal pollinated lineages of seed plants separately, describing their diversity (heeding the warning of Harris (1961) regarding diversity of fossil taxa) and then describing their pollination mode. Many of the inferences about pollination mode in fossil plants are based on anatomy of the pollen or prepollen. Seed plants that are wind pollinated generally have pollen or prepollen that is round, smooth, thin-walled, unclumped, not adhesive, with shallow or non-existent furrows, between 17 and 58 µm in diameter, and produced in much larger quantities than in insect pollinated plant species (Sprengel, 1793; Wodehouse, 1935; Pederson, Friis & Crane, 1993; Ackerman, 2000; also see Darwin, 1876). Seed plants that are animal pollinated generally have pollen or prepollen that is large, sculptured, and coated with an adhesive wax or oily substance (pollenkitt) that is produced by the innermost layer of cells of the pollen sac. Pollenkitt causes pollen grains to clump to each other and to pollinating animals (Sprengel, 1793; Eames, 1960; Chaloner, 1976), deters herbivores (Dobson & Bergström, 2000), attracts pollinators (Pacini &

Franchi, 1994), and is a food source for pollinating insects (Houston *et al.*, 1993). Inferences about pollination mode are also based on other evidence, such as presence of nectaries and fossil insect remains with attached pollen.

Several seed plant lineages other than angiosperms have shown a preponderance of evidence of animal pollination in many, if not most, species: the Palaeozoic seed fern order Medullosales, extant and extinct members of the order Cycadales, the Mesozoic conifer family Cheirolepidiaceae, the Mesozoic order Bennettitales, and the Mesozoic and Cenozoic order Gnetales.

Although, nowadays, no plants other than angiosperms are diverse (Table 1), in the Mesozoic there were large radiations with substantial diversity in the Bennettitales, Gnetales, and Cheirolepidiaceae, all of which are believed to have been insect pollinated.

Angiosperms

The terms angiosperm and flowering plant are interchangeable and include the ANITA clades magnoliids, eudicots, monocots, Chloranthaceae and Ceratophyllaceae (Kuzoff & Gasser, 2000). I accept the generally, but not universally, held view that angiosperms as usually circumscribed are monophyletic (Donoghue & Doyle, 1991; Qiu *et al.*, 1999).

Based on evidence from pollen (Muller, 1984) and macrofossils (Wing, Hickey & Swisher, 1993), angiosperms were not nearly as diverse in the Cretaceous as they currently are. Most Cretaceous angiosperm diversity was in magnoliid clades and possibly in some early monocots (Friis, Pedersen & Crane, 1999). Before the Cretaceous–Tertiary extinction and certainly before the Late Cretaceous, there were very few eudicot species (Magallón, Crane & Herendeen, 1999). Cretaceous flowering plants were not ecologically dominant (Wing & Boucher, 1998). The first appearance of angiosperms in the palynological record displayed a substantial abundance and variety of pollen types, which was followed almost immediately by a drastic diminution in both abundance and variety (Hughes & McDougall, 1987). Late Cretaceous angiosperms, however, displayed a wide diversity of growth forms: from small herbs to large trees.

Amongst the earliest angiosperms, there were both biotically and abiotically pollinated taxa. Some of the earliest bona fide angiosperms belonged to the family Chloranthaceae (Walker & Walker, 1984; Dilcher, Krassilov & Douglas, 1996; Dilcher, 2000), which contained both wind and animal pollinated species (Thien *et al.*, 1985; Friis, Crane & Pedersen, 1986; Friis *et al.*, 1987). A bit further up in the stratigraphic record is a preponderance of Platanaceae and Winteraceae fossils (Doyle, Hotton & Ward, 1990; Krassilov, 1997). Both extant and extinct Platanaceae were wind pollinated. An extant genus of Winteraceae is pollinated

primarily by a moth that also eats the pollen and is secondarily pollinated by a beetle. Both the plant and the moth genus have been found in the Cretaceous (Aptian). The moth has also been found in the Neocomian, pre-dating the origin of angiosperms (Whalley, 1978; Thien *et al.*, 1985). Pollenivory is believed to be the evolutionary precursor of insect pollination (Darwin, 1876; Arber & Parkin, 1907; Kevan *et al.*, 1975; Scott *et al.*, 1992; Krassilov & Rasnitsyn, 1996) and both pollination and pollenivory are seen in non-specialized insects. Beetles are considered to be the first insect pollinators (van der Pijl, 1960 attributing these ideas to Darwin, 1876 and Müller, 1873). Much Cretaceous angiosperm pollen was highly reticulate, an indication of self-incompatibility and/or animal pollination (Doyle, Jardine & Doerenkamp, 1982; Zavada, 1984; Krassilov & Rasnitsyn, 1996). Both biotic and abiotic pollination appeared very early in the angiosperm record and have remained in those same families to the present day. About one-third of extant angiosperm species are wind pollinated, while virtually all other angiosperm species are animal pollinated (Darwin, 1876; Grimaldi, 1999).

Bennettitales

There is evidence for substantial Bennettitales diversity in the Mesozoic (Wieland, 1906; Harris, 1969; Person & Delevoryas, 1982; Delevoryas, 1991; Osborn & Taylor, 1995; Krassilov, 1997). Growth forms were primarily restricted to plants resembling extant Cycadales, along with a few more slender species (Delevoryas & Hope, 1976). Diversity of growth forms in this order would increase if Pentoxylon is also considered part of the Bennettitales (e.g. Doyle & Donoghue, 1986). Bennettitales abundance seemed to mirror that of Gnetales (and Cheirolepidiaceae?) in xeric areas throughout the Cretaceous (Doyle *et al.*, 1982).

Most Bennettitales were probably insect pollinated (Scott, 1900; Leppik, 1960). Except for some later putatively derived species, Bennettitales had reproductive structures containing both functional female and male parts (Crane, 1988). All known specimens had somatic tissue completely enveloping and separating the male and female reproductive structures. This required self-pollination, parthenogenesis, or animal pollination, the latter of which is most likely. Burrowing insects are believed to have transported pollen from male to female reproductive parts, especially on the many species with monosporangiate cones (Crepet, 1972, 1974; Crepet, Friis & Nixon, 1991). Even in monoecious species, burrowing beetles have been found in the cones (Delevoryas, 1968; Crepet, 1974), with their tunnels almost always located so that they are "ideal pathways to insure optimum pollen deposition" (Crepet, 1972). Pollen exine sculpture was

generally psilate (Osborn & Taylor, 1995), indicative of beetle pollination or wind pollination in extant angiosperms (Grayum, 1986). All but the earliest and putatively most ancestral species of Bennettitales had helically arranged perianth-like bracts (Crane, 1988), which are generally associated with animal pollination. The inner whorl of these bracts usually had no stomata (Krassilov, 1997: 31–32 attributed to Harris, 1973 but without citation), akin to typical angiosperm corollas. Resin-like structures, which may have been extra-floral nectaries, were found in male cones of one species (Harris, 1969). Most species of Bennettitales were probably insect pollinated.

Gnetales

Gnetales underwent a substantial radiation in the Middle Cretaceous, which began simultaneously with the origin of angiosperms (Hughes & McDougall, 1987; Krassilov, 1997 attributed to Pons *et al.*, 1992 but without citation). At low palaeolatitudes, this Gnetales radiation occurred in similar ecological niches as the Cretaceous angiosperm radiation (Doyle *et al.*, 1982; Crane & Hult, 1988; Crane & Lidgard, 1990; Ibrahim, 1996; Krassilov, Dilcher & Douglas, 1998). At all palaeolatitudes, diversity of Gnetales pollen forms in the Cretaceous was much greater than in extant Gnetales (Takahashi, Takai & Saiki, 1995), reflecting a larger diversity of Cretaceous Gnetales growth forms. There is already a wide range of growth forms in the three extant genera: from shrubs, to trees, to lianas, to the unique growth form of *Welwitschia mirabilis*. Some Cretaceous Gnetales resembled extant forms (Krassilov *et al.*, 1998), while others such as *Drewria* were herbaceous (Crane & Upchurch, 1987). Having herbs and other small growth forms within a lineage probably results in much higher diversity within that lineage, especially when coupled with barriers to gene flow, such as insect pollination or self-incompatibility (Levin & Wilson, 1976).

Many extant Gnetales are insect pollinated, especially in *Gnetum* (van der Pijl, 1953; Kato & Inoue, 1994; Kato, Inoue & Nagamitsu, 1995) and *Welwitschia* (Hooker, 1863; Bornman, 1978; Crane & Hult, 1988; Wetschnig & Depisch, 1999). All Gnetales have a pollen droplet produced on the ovuliferous (but sterile) portion of each male inflorescence at the time of pollen dehiscence. The pollen droplet has a higher sugar concentration than is typically found in wind pollinated species of seed plants, an indication of possible animal pollination (Baker & Baker, 1975; Bino, Devente & Meeuse, 1984; Tang, 1987; Kato & Inoue, 1994). All Gnetales have sticky pollen, although there is debate whether this is due to pollenkitt or to high sugar concentrations in the pollen droplets coating the pollen (Hesse, 1980, 1984).

Unlike *Gnetum* and *Welwitschia*, there is still debate whether *Ephedra* is predominantly wind pollinated (Hesse, 1984) or animal pollinated (Moussel, 1980 according to Hesse, 1984). The aerodynamics around female *Ephedra* cones indicates wind pollination (Niklas, Buchmann & Kerchner, 1986; Niklas & Buchmann, 1987; Buchmann, O'Rourke & Niklas, 1989). On the other hand, gauze around female cones of another *Ephedra* species precludes pollination when the mesh of the gauze is fine enough to allow in wind-borne pollen but not allow in putative pollinators (Bino *et al.*, 1984). No definitive enclosure experiments have been conducted with this genus. Other evidence for insect pollination in *Ephedra* (and *Welwitschia*) are coloured cones and subtending bracts.

Gnetum was first suspected of being insect pollinated because of sticky pollen that aggregates in strands, extra-floral nectaries that are high in sugar content, odour emitted by male cones, and presence of the ancient lineage of bees at nectaries (van der Pijl, 1953; Michener & Grimaldi, 1988). *Gnetum* is remarkable in having pollen tubes germinate in the micropylar canal, rather than directly on the nucellus (Krassilov, 1997). Most species of Gnetales are insect pollinated.

Cheirolepidiaceae

The Cheirolepidiaceae are unequivocally a member of the division Coniferophyta, but it is unclear how they are related to other conifer lineages. This family is beautifully defined and circumscribed by its pollen, *Classopollis*. The Cheirolepidiaceae originated in the Late Triassic (or Mid Triassic according to Scheuring, 1976) and went extinct at the Cretaceous–Tertiary boundary.

There is substantial evidence that the Cheirolepidiaceae diversified greatly in terms of both species numbers and growth forms (Watson, 1988) and that these conifers predominated ecologically in many hot climates throughout the world – in much the same way as angiosperms do today – during portions of the Upper Jurassic (Vakhrameev, 1970; Filatoff, 1975; Vakhrameev, 1981; Alvin, 1982), Early Cretaceous (Müller, 1965; Alvin, 1982), Middle Cretaceous (Douglas, 1985; Watson, 1988), and possibly even in the very Late Cretaceous (Krassilov, 1997: 112, citing Krassilov, 1979). Growth forms included small herbs (Watson, 1977), thick tangled mats (Daghlian & Person, 1977), small stem succulents (Watson, 1977; Upchurch & Doyle, 1981), large pachycauls (Watson, 1988), mangrove forests (Hughes & Moody-Stuart, 1967; Batten, 1974; Hluštík, 1984), and large woody trees (Francis, 1983). “Hluštík sees the Cheirolepidiaceae as a very large plastic group producing nearly all possible morphological variations of a coniferous habit, ecologically rather than phylogenetically controlled, with *Classopollis* [pollen] as the sole phylogenetic fixed point”

(Watson, 1988). This diversity of forms increased through time (in the Mesozoic), as indicated by increasing variety of male cone structures and increasing diversity of pollen exine structures (van Konijnenburg-van Citter, 1987; Pocock, Vasanthi & Venkatachala, 1990). Having herbs and other small growth forms within a lineage probably results in much higher diversity within that lineage, especially when coupled with barriers to gene flow, such as insect pollination or self-incompatibility (Levin & Wilson, 1976).

Most Cheirolepidiaceae were probably pollinated by insects (Alvin, 1982; Taylor & Alvin, 1984; Pocock *et al.*, 1990). Pollen grains landed on and adhered to cone scales, far from the ovule, which was itself covered by cuticle derived from the cone scale. The ovules did not possess pollen chambers (Clement-Westerhof & van Konijnenburg-van Citter, 1991). Pollen tubes had to grow far to deposit the sperm cells, which may have facilitated self-incompatibility mechanisms, in which the cone scale cuticles interacted with the growing pollen tube (Watson, 1988; Taylor & Taylor, 1993). Such self-incompatibility systems are often associated with animal pollination.

Cheirolepidiaceae pollen (i.e. *Classopollis*) also provides strong indication of self-incompatibility and animal pollination (Chaloner, 1976). Cheirolepidiaceae pollen is often found in tetrads, held together by exinal threads, and possessing a pollenkitt-like substance (Scheuring, 1976), which are strong indications of animal pollination in extant angiosperms (Heslop-Harrison, 1971; Walker & Doyle, 1975; Chaloner, 1976; Alvin, 1982; Dickinson, Elleman & Doughty, 2000; Pacini, 2000). Cheirolepidiaceae pollen had highly elaborate exines, even more so than in any extant angiosperms (Pettitt & Chaloner, 1964), highly indicative of self-incompatibility (Zavada, 1984, 1990; Zavada & Taylor, 1986). Contrary to widely held beliefs, there is limited evidence of self-incompatibility in extant conifers (Owens, Takaso & Runions, 1998; Runions & Owens, 1998) and therefore reason to believe that self-incompatibility could have existed in Cheirolepidiaceae. Pollen was probably sequestered in male cones for a considerable time after dehiscence from pollen sacs, which is indicative of animal pollination or pollen release conditioned on environmental cues (Alvin, Watson & Spicer, 1994). Two grasshopper species have been identified as putative pollinators, based on Cheirolepidiaceae pollen being the primary contents in their guts (Krassilov *et al.*, 1997). Pollen herbivory is often associated with and may have been the precursor of animal pollination (Darwin, 1876; Kevan *et al.*, 1975; Krassilov & Rasnitsyn, 1996). Cumulatively, this provides strong support for insect pollination throughout the Cheirolepidiaceae.

Individually, each aspect of the evidence for animal

pollination in Cheirolepidiaceae is open to debate. Exine structure alone (in any plants) may be insufficient proof of self-incompatibility (Gibbs & Ferguson, 1987; Gibbs, 1991), especially since self-incompatibility probably arose independently many times (Weller, Donoghue & Charlesworth, 1995). Cheirolepidiaceae pollen tetrads may have disintegrated and the exinal threads fallen away long before the pollen reached the female cones (Clement-Westerhof & van Konijnenburg-van Citter, 1991), thereby weakening arguments for insect pollination. Jurassic (and Late Triassic?) Cheirolepidiaceae all had the ancestral form of pollen in tetrads, while many Early Cretaceous species had pollen in dyads and Middle and Late Cretaceous species had pollen in monads. Dyads and especially monads are considered derived characters in Cheirolepidiaceae that are indicative of wind pollination (Pocock *et al.*, 1990). In some samples, Cheirolepidiaceae pollen constitutes between 50% and 90% (Vakhrameev, 1970) of the pollen, which is indicative of wind-pollinated species in extant ecosystems (Erdtman, 1935). However, these truly high abundances of Cheirolepidiaceae pollen only occurred in the Middle and Late Cretaceous when its pollen was predominantly found in monads, rather than tetrads or dyads.

Pollen tubes growing a substantial distance across female cone scales are not necessarily indicative of self-incompatibility or insect pollination. All extant members of the conifer family Araucariaceae (Burlingame, 1913; Eames, 1913; Owens *et al.*, 1995) have pollen tubes growing the length of female cone scales, which can take from 5 to 24 months to reach the nucellus, sometimes including growing through tissue enveloping the cone scales. Another pair of extant genera in the conifer families Pinaceae and Podocarpaceae have independently evolved incidences of pollen grains landing on cone scales and pollen tubes then growing to the ovule (Doyle & O'Leary, 1935). Yet, all extant conifers are assumed to be wind-pollinated (Owens *et al.*, 1998). Nevertheless, despite isolated evidence for wind pollination in Cheirolepidiaceae, cumulatively, the evidence is convincing that most species were insect-pollinated, especially in the Triassic through Early Cretaceous.

Cycadales

The Cycadales originated in the Pennsylvanian and were never diverse (Zhifeng & Thomas, 1989), either in terms of number of species or number of growth forms. All extinct and extant cycads have roughly the same appearance: unbranched pachycauls. Only the ultimate size of the plant and the proportions seem to have varied, with more slender stems in the Palaeozoic and Mesozoic (Delevoryas & Hope, 1971). The paucity of extant taxa is typical of cycad diversity throughout

the Palaeozoic, Mesozoic, and Cenozoic (Harris, 1961, 1964; Pant, 1987; Anderson & Anderson, 1989).

Many extant Cycadales are obligately insect pollinated (Pearson, 1906 crediting Joseph Hooker and Alice Pegler; Webster, 1910 citing unpublished work of H. G. Hubbard; Rattray, 1913; Baird, 1939 citing unpublished work of C. A. Gardner; Norstog, Stevenson & Niklas, 1986; Tang, 1987; Norstog & Fawcett, 1989; Oberprieler, 1989; Vovides *et al.*, 1993; Oberprieler, 1995a). One extant cycad species is pollinated by a bee in the genus *Trigona*, a genus that has existed since the Middle Cretaceous, adding credence to the hypothesis that insect pollination may have been an ancestral character in the Cycadales (Michener & Grimaldi, 1988; Ornduff, 1991). Many extant cycads are pollinated by beetles (e.g. Fawcett & Norstog, 1993), which are considered to be the earliest pollinators (van der Pijl, 1960; Farrell, 1998; Grimaldi, 1999). Nectaries in female cones that are not associated with pollen droplets have been found in Pennsylvanian (Mamay, 1976) and Cretaceous (White, 1986) cycads. The nectar in pollen droplets of extant cycads have ratios of fructose, sucrose, and glucose that are similar to those found in flowering plants and is rich in amino acids (Tang, 1995), which is indicative of animal pollination.

Cycad pollen is almost too large to be effectively transported by wind, especially since the pollen is sticky and grains tend to clump (Norstog & Nichols, 1997). In some extant cycad species, pollen may possibly be transported by wind to the outside of the female cone and then transported by insects from the outside of the female cone to the megagametophyte (Niklas & Norstog, 1984; Norstog, 1987) – confounding conclusions drawn from air-flow experiments over cones (e.g. Niklas, 1981, 1985). Several researchers are beginning to wonder whether any cycads are or ever were exclusively wind pollinated (Norstog, 1987; Connell & Ladd, 1993; Wilson, 1994; Donaldson, Nänni & Bösenberg, 1995; Norstog & Nichols, 1997).

Medullosales

The Medullosales are a strictly Palaeozoic order that went extinct in the Permian and were never known to be very diverse (Delevoryas, 1955; Stewart & Delevoryas, 1956), although they were widespread and abundant (Stewart & Delevoryas, 1956; DiMichele & Phillips, 1988).

It appears that all Medullosales were animal pollinated. Most Medullosales prepollen is in the pollen genus *Monoletes*, which were so large – 0.2 to 0.6 mm long and two-thirds that in width (Wodehouse, 1935 citing both Renault, 1876 and Saporta & Marion, 1885; Delevoryas, 1964; Taylor, 1971; Stidd, Leisman & Phillips, 1977) – that they would have fallen straight to the ground unless transported by animals (Wodehouse,

1935; Taylor, 1978; Dilcher, 1979; Taylor & Millay, 1979). All *Monoletes* prepollen grains possessed a luminate/alveolate wall structure that probably stored (or produced?) secondary compounds or pollenkitt (Taylor, 1971; Stidd *et al.*, 1977; Dickinson *et al.*, 2000) often associated with attracting insects and/or self-incompatibility (Zavada & Taylor, 1986). A 2 m-long myriapod has been proposed as one possible pollinator, based on leg segments containing *Monoletes* (Scott & Taylor, 1983 based on a re-examination of the specimen in Richardson, 1980) and evidence that the myriapod was herbivorous (Rolfe & Ingham, 1967). Insect pollination has also been proposed (Taylor & Millay, 1979). *Monoletes* prepollen has been found in arthropod coprolites (Baxendale, 1979), evidence of pollenivory and possible pollination.

The remaining Medullosales (i.e. the remaining two prepollen types) had much smaller prepollen grains, but were probably also insect pollinated, based on exine cavities in *Parasporites* and spines on the surface of *Nanoxanthiipollenites* that are typical of animal pollinated species (Taylor, 1979, 1981). Although *Parasporites* prepollen had sacci, they were small and virtually vestigial (Taylor, 1981). Both *Parasporites* and *Nanoxanthiipollenites* prepollen were too large to have been transported by wind (Dennis & Eggert, 1978; Millay, Eggert & Dennis, 1978; Taylor, 1979).

Possible nectaries not associated with pollen droplets have been found in association with Medullosales seed-bearing fronds (Halle, 1929). In conjunction with extensive evidence from prepollen, Medullosales were almost certainly animal pollinated.

Summary regarding seed plant pollination and diversity

Six lineages of seed plants predominantly had insect pollination: angiosperms, Gnetales, Cheirolepidiaceae, Medullosales, Cycadales, and Bennettitales. These are the only lineages that had animal pollination, except for extremely scant evidence in Lyginopteridales (nectaries not associated with pollen droplets; Oliver & Scott, 1904 attributing this suggestion to Joseph Hooker), Cordaitales (very large prepollen grains in some species; Taylor & Taylor, 1993; Poort, Visscher & Dilcher, 1996), and Caytoniales (pollen found in coprolites; Harris, 1946, 1956, 1964). *Brenneria* with *Decussosporites* pollen may have been insect pollinated (based on pollen sac anatomy and relatively low numbers of pollen grains; Pederson *et al.*, 1993), but the systematic position of this taxon is unknown. Angiosperms, Bennettitales, Gnetales, and Cheirolepidiaceae each had substantial radiations and animal pollination, which supports the biotic pollination hypothesis. The Medullosales and Cycadales, however, falsify this hypothesis because neither ever underwent radiations.

The most species-rich plant taxa had animal pollination in many species. But animal pollination was no guarantee of species richness, as evidenced by the paucity of angiosperms in the Mesozoic, Gnetales in the Cenozoic, and cycads throughout their existence.

INSECT DIVERSITY DECREASED WHEN ANGIOSPERMS ORIGINATED

The biotic pollination hypothesis also predicts that lineages of pollinating insects should have radiated along with their host plants. Thus, there should be a correlation between insect and angiosperm diversity. Insect taxa should have diversified at the time of origin of angiosperms in the Middle Cretaceous (Dilcher, 2000) or diversified contemporaneously with the rise of angiosperms to ecological dominance in the Early Cenozoic (Wing *et al.*, 1993). The fossil record shows that insect diversity remained low until the origin of seed plants in the Late Devonian and then increased at roughly a constant rate from the Late Devonian until present (Labandeira & Sepkoski, 1993) with the anticipated exception of a drastic decrease during the Permo-Triassic mass extinction and an unanticipated exception of a *decrease* in insect diversity in the Middle Cretaceous concomitant with angiosperm origin (Jarzemowski, 1989, 1995). This is the exact opposite of what the biotic pollination hypothesis predicts. After the Cretaceous-Tertiary mass extinction, the rate of insect diversity returned to and stayed at levels that were indistinguishable from those in the Triassic and Jurassic (Labandeira & Sepkoski, 1993). There is nothing in the insect diversity data to indicate coevolution of insects and *angiosperms*. If anything, insect diversity increased due to the presence of *seed plants*, whether they were biotically pollinated or not.

Although the biotic pollination hypothesis predicts radiations of both animal pollinated plants and their pollinators, the radiations of plants and animals need not be perfectly symmetrical. For example, many pollinating insects require a temporal or spatial sequence of different species of flowers from which to feed. The flowering periods of many plants are often too short to support the entire life cycle of a given pollinating animal. Similarly, many animal pollinated species are too sparsely populated to supply the complete nutritional requirements of a given pollinating animal. With such plants, there is less likelihood of animal speciation than plant speciation because of the lack of dependence of the animal upon one specific plant species. Asymmetries between plant and insect radiations may help explain the decrease in overall insect diversity during the Middle Cretaceous.

It may be too simplistic to consider overall insect diversity. There was an apparent increase in diversity of certain presumed pollinating insects in the Middle

Cretaceous, concomitant with presumed angiosperm origins (Grimaldi, 1999).

Another problem highlighted by a broad scale look at the insect fossil record throughout the Mesozoic and Cenozoic is that these extraordinary insect radiations appear to be almost entirely due to decreased extinction rates, rather than increased speciation rates (Labandeira *et al.*, 1994). Insects appear to have speciation rates comparable to virtually all other animal taxa, but have very low extinction rates. This is the exact opposite of what is predicted from radiations that are driven by ecological isolation (Schluter, 1998).

GRASSES ARE DIVERSE, YET WERE NOT ANIMAL POLLINATED

About one-third of extant angiosperm species are wind pollinated (Darwin, 1876; Grimaldi, 1999), including those in one of the most species-rich families: Poaceae (grasses) with over 10 000 extant species in over 500 genera. With few exceptions, Poaceae are exclusively wind pollinated. One exception is *Paspalum dilatatum*, which has larger pollen grains than most grasses, has over one-third of its pollen grains sticking together, and has well-documented insect pollination (Adams, Perkins & Estes, 1981). A few small genera of bamboos have exine structures indicating insect pollination (Salgado-Labouriau, Nilsson & Rinaldi, 1993) and have pollen-carrying insects found at open flowers (Davis & Richards, 1933; Soderstrom & Calderon, 1971), but definitive enclosure experiments have not been done. Despite these few exceptional species, wind pollination is undoubtedly ancestral in Poaceae, and all or most grass species were wind pollinated during the major radiations of grasses.

Such a large radiation of wind pollinated plants implies that there exist mechanisms other than animal pollination generating plant radiations. Likewise, ants show that there must be mechanisms other than biotic pollination generating animal radiations.

Grasses are not the only example of a flowering plant lineage that has radiated despite insect pollination. However, it is the largest such family and has the most striking absence of insect pollination. Likewise, although the discussion below is on ants being a large family of insects that are virtually never pollinators, other less poignant examples of such non-pollinating insect taxa exist.

ANTS ARE DIVERSE, YET WERE NOT POLLINATORS

If pollinating insect and angiosperm radiation were truly linked, then those lineages of insects that were not pollinators should have very few species with little diversity. The ant family, Formicidae, originated at roughly the same time as angiosperms (Middle Cretaceous) and radiated in the very early Cenozoic as

did angiosperms (Hölldobler & Wilson, 1990). Ants secrete antibacterial and antifungal compounds from metapleural glands that also inhibit pollen germination and retard pollen tube growth (Beattie *et al.*, 1984). Very few ants are pollinators, and these associations are derived. Winged male ants cross pollinate a few species of Orchidaceae (Peakall, Beattie & James, 1987; Peakall, Angus & Beattie, 1990) and a few species in other families (Hickman, 1974; Wyatt, 1981; Peakall & Beattie, 1991; Gómez & Zamora, 1992; Gómez *et al.*, 1996; Gómez, 2000). Wingless worker ants apparently only self pollinate plants; walking takes longer than flying, allowing time for metapleural secretions to render pollen inviable (Ramsey, 1995; Gómez, 2000). Although not nearly as species-rich as other more ancient insect lineages such as beetles, ants form one of the most successful and diverse insect families, with approximately 9600 species in 300 genera (Bolton, 1995). Such success runs contrary to the predictions of the biotic pollination hypothesis.

CONCLUSION

Coevolution with animal pollinators appears to be neither a *necessary* nor *sufficient* condition for large-scale diversification of seed plants. Several unrelated plant lineages – angiosperms and Bennettitales (i.e. the remaining anthophyte lineages), Gnetales, and Cheirolepidiaceae – underwent major radiations in the Late Mesozoic, although only the initial Cretaceous radiations of angiosperms and Gnetales appeared to be concomitant. These are the only four truly species-rich seed plant lineages. Each of these lineages was predominantly insect pollinated. By itself, this implies that animal pollination is a necessary condition for high species diversity.

The conclusion that animal pollination is a *necessary* condition for high species diversity is, however, dispelled by the family Poaceae (grasses), which has an extraordinary number of species, is well-circumscribed (i.e. there is no question as to whether species belong to this family), yet is virtually exclusively wind pollinated. There is no evidence that anything but wind pollination was ancestral in grasses. The enormous success of the ant family, Formicidae, also dispels the notion that insect pollination is a *necessary* condition for high species numbers of plants and insects. Although ants have not been pollinators, ants originated and radiated almost simultaneously with angiosperms. I have focused on grasses and ants because they are large, important lineages that are exceptional cases. Grasses and ants show that animal pollination is not a *necessary* condition for high species numbers.

There is also a preponderance of evidence dispelling the notion that animal pollination is a *sufficient* condition for high species diversity. Several seed plant

lineages were predominantly insect pollinated, yet were only diverse for a time or were never diverse. The Gnetales are no longer diverse. The once diverse Cheirolepidiaceae and Bennettitales went extinct at or around the Cretaceous–Tertiary boundary. The seed fern order Medullosales was never diverse and went extinct at the Permo–Triassic boundary. Most persuasive, is the order Cycadales, which was never diverse and was probably pollinated by insects since its origin in the Palaeozoic. Insect pollination is no guarantee of plant diversity.

Several researchers claim that animal pollination does not by itself guarantee species diversity, but that animal pollination coupled with one or more other factors, such as animal dispersal of seeds, does guarantee species diversity (Regal, 1977; Burger, 1981). Medullosales, Cycadales, and Cheirolepidiaceae provide readily available tests for such hypotheses. For example, extant Cycadales have seeds that are primarily dispersed by animals (Jones, 1993). Furthermore, cycads may be involved in a coevolutionary arms race with herbivores detoxifying or sequestering novel plant chemical defences (reviewed in Norstog & Nichols, 1997). Thus, even if all three of these principal coevolution hypotheses are concurrently evoked, radiations are still not guaranteed.

A factor that has never been explicitly considered in seed plant species diversity is siphonogamy, in which sperm cells travel down a pollen tube to the egg cell (as opposed to zoidogamy, in which flagellated sperm cells swim from the pollen or prepollen grain to the egg cell). Animal pollination coupled with siphonogamy may be enough to guarantee species diversity, with the caveat that diversity of animal pollinated lineages may not recover from mass extinctions. Medullosales and Cycadales are zoidigamous (Stewart, 1951; Norstog & Nichols, 1997) and never were diverse, while diversity of the siphonogamous Gnetales, Bennettitales (Rothwell & Stockey, 2001) and Cheirolepidiaceae were great in the Jurassic and Cretaceous, until plummeting precipitously at the Cretaceous–Tertiary mass extinction. Such an explanation would remove the exceptional cases of the Medullosales and Cycadales. Pollen tube competition provides a possible causal mechanism by which siphonogamy may result in increased speciation rates. Zoidigamous plants either lack pollen tubes or have very different looking pollen tubes than do siphonogamous plants. Unlike pollen tubes in most siphonogamous taxa, zoidigamous pollen tubes are always branched (except when just germinated) and never carry sperm cells. My conjecture that pollen competition is limited to siphonogamous plants is an extension of Mulchay's (1979) hypothesis that only angiosperms experience pollen tube competition.

Any hypothesis should be considered suspect if it is

not sufficiently explicated or if it yields predictions that are incommensurate with hitherto well-tested theory. The biotic pollination hypothesis predicts increased speciation rates for both pollinators and the plants that they pollinate. However, homozygous pollen loads on animal pollinated plants implies lower speciation rates for plants and no change in speciation rates for pollinators. Lower densities for animal pollinated plants results in lower extinction rates (not higher speciation rates) for the plants and no change in extinction or speciation rates for the pollinators. Larger geographic ranges for animal pollinated plants results in lower speciation rates for the plants due to smaller probabilities of allopatric speciation and, again, no change in speciation or extinction rates for the pollinators. Since the biotic pollinator hypothesis and these other evolutionary hypotheses yield diametrically opposite predictions given the same premises, we should question each of the hypotheses, but especially the biotic pollinator hypothesis because it is the least parsimonious, least well tested, and least general.

Another problem with existing theory is that quantitative models have not been proposed for any of the verbal models of angiosperm radiation, with the exception of one model that is of very limited applicability (pollinating insect specialized to a single plant species). And, that one quantitative model yields predictions that are incommensurate with cycad diversity. The theory underlying coevolution of plants and animal pollinators is inconsistent with other better-established theories and incommensurate with data. One of two things can be done to resolve this conundrum: abandon the biotic pollination hypothesis or refine the biotic pollinator hypothesis so that it accounts for the inconsistencies (Lakatos, 1970).

Refinements of the biotic pollination hypothesis should explain angiosperm and insect radiations and explain anomalies, such as lack of diversity of the animal pollinated Medullosales and Cycadales. Two-locus population genetic models of floral isolation or quantitative genetic models of repeated and alternating cycles of specialization and despecialization may provide such refinements.

There are several alternatives to the biotic pollination hypothesis waiting to be tested (refer to Appendix for a detailed summary). The hypothesis that plant radiations were primarily caused by polyploidy is potentially testable, although this has never been done. Extant angiosperms show relatively high incidences of polyploidy and have undergone radiations, while extant Cycadophyta and Ginkgophyta have not. Coniferophyta and Bennettitales provide crucial tests for this polyploidy hypothesis. Bennettitales underwent substantial radiations and were probably closely related to angiosperms. Therefore, Bennettitales may

have experienced polyploidy events, which could be inferred if one were to find increased cell size in closely related individuals over geologic time, especially larger stomatal guard cells as chromosome numbers doubled (Masterson, 1994). In the Mesozoic, Coniferophyta contained two species-rich lineages: Gnetales and Cheirolepidiaceae, whose fossil remains should show a progression of larger guard cells in closely related individuals over time through the Mesozoic if the polyploidy hypothesis is correct. By contrast, there should be no systematic change in guard cell size through time in the species-poor Cycadales and Medullosales.

Other hypotheses seem even easier to test, such as the hypothesis that angiosperms had increased capacity for cell elongation following hormonal exposure, especially with root hairs and trichomes (Stebbins, 1981), thereby gaining a selective advantage over other seed plants. Yet, such a test has never been performed.

Further investigations into the extraordinary modern preponderance of flowering plants and insects should proceed along two different tracks. First, there are many alternative hypotheses to explain the preponderance of angiosperms, most of which do not invoke coevolution with insects. These other hypotheses (Appendix) are seldom mentioned, let alone investigated. Although beyond the scope of this paper, it is time to unearth them – remembering that they may act in tandem – and give them the consideration they deserve. They may prove to be the key to explaining some anomalies, such as the concomitant radiations of ants and angiosperms. Second, because of the corpus of knowledge regarding pollinator-plant coevolution accumulated at least since Darwin, it is time to explore models of pollinator-plant coevolution that are more quantitative than the current verbal models of the biotic pollination hypothesis, thereby continuing a 150-year-old research programme.

ACKNOWLEDGEMENTS

I thank Sue Bertram, David Dilcher, Jennifer Fewell, Greg Pollock, Pat Fall, Bob Johnson, Wendy Marussich, Bill Crepet, and three anonymous reviewers for generously reading and commenting on earlier versions of this paper, regardless of any differences they may have had with my assertions. I also thank Dan Howard, Jeremy Midgley, and V.S. Krishnan for their encouragement.

REFERENCES

- Ackerman JD, 2000. Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. *Plant Systematics and Evolution* **222**: 167–185.

- Adams DE, Perkins WE, Estes JR. 1981. Pollination systems in *Paspalum dilatatum* Poir (Poaceae) – an example of insect pollination in a temperate grass. *American Journal of Botany* **68**: 389–394.
- Algeo TJ, Berner RA, Maynard JB, Scheckler SE. 1995. Late Devonian oceanic anoxic events and biotic crisis: rooted in the evolution of vascular land plants? *GSA Today* **5**: 45, 65–66.
- Algeo TJ, Scheckler SE. 1998. Terrestrial–marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events. *Philosophical Transactions of the Royal Society of London Series B* **353**: 113–128.
- Alvin KL. 1982. Cheirolepidiaceae: biology, structure and paleoecology. *Review of Palaeobotany and Palynology* **37**: 71–98.
- Alvin KL, Watson J, Spicer RA. 1994. A new coniferous male cone from the English Wealden and a discussion of pollination in the Cheirolepidiaceae. *Palaeontology* **37**: 173–180.
- Anderson JM, Anderson HM. 1989. *Palaeoflora of Southern Africa, Molteno Formation (Triassic), Volume 2: Gymnosperms (excluding Dicroidium)*. Rotterdam: A.A. Balkema.
- Arber EAN, Parkin J. 1907. The origin of angiosperms. *Journal of the Linnean Society, Botany* **38**: 29–80.
- Armbruster WS. 1997. Exaptations link evolution of plant–herbivore and plant–pollinator interactions: a phylogenetic inquiry. *Ecology* **78**: 1661–1672.
- Armbruster WS, Howard JJ, Clausen TP, Debevec EM, Loquvam JC, Matsuki M, Cerendolo B, Andel F. 1997. Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with *Dalechampia* vines. *American Naturalist* **149**: 461–484.
- Axsmith BJ, Taylor EL, Taylor TN. 1998. The limitations of molecular systematics: a palaeobotanical perspective. *Taxon* **47**: 105–108.
- Baird AM. 1939. A contribution to the life-history of *Macrozamia reidleyi*. *Journal of the Royal Society of Western Australia* **25**: 153–163.
- Baker HG, Baker I. 1975. Studies of nectar constitution and pollinator–plant coevolution. In: Gilbert LE, Raven PH, eds. *Coevolution of animals and plants*. Austin: University of Texas Press, 100–140.
- Batten DJ. 1974. Wealden palaeoecology from the distribution of plant fossils. *Proceedings of the Geologists' Association* **85**: 433–458.
- Baxendale RW. 1979. Plant-bearing coprolites from North American coal balls. *Palaeontology* **22**: 537–548.
- Beattie AJ, Turnbull C, Knox RB, Williams EG. 1984. Ant inhibition of pollen function: a possible reason why ant pollination is rare. *American Journal of Botany* **71**: 421–426.
- Behrensmeyer AK, Damuth JD, DiMichele WA, Potts R, Sues H-D, Wing SL. 1992. *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. Chicago: University of Chicago Press.
- Bino RJ, Devente N, Meeuse ADJ. 1984. Entomophily in the dioecious gymnosperm *Ephedra aphylla* Forsk. (= *E. alta* C.A. Mey) with some notes on *E. campylopoda* C.A. Mey. II. Pollination droplets, nectaries, and nectarial secretions in *Ephedra*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C* **87**: 15–24.
- Bolton B. 1995. A taxonomic and zoogeographic census of the extant ant taxa (Hymenoptera, Formicidae). *Journal of Natural History* **29**: 1037–1056.
- Bond WJ. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* **36**: 227–249.
- Bornman CH. 1978. *Welwitschia*. Cape Town: C. Struik Publishers.
- Brown JH, Gibson AC. 1983. *Biogeography*. St. Louis: C.V. Mosby.
- Buchmann SL, O'Rourke MK, Niklas KJ. 1989. Aerodynamics of *Ephedra trifurca*. 3. Selective pollen capture by pollination droplets. *Botanical Gazette* **150**: 122–131.
- Burger WC. 1981. Why are there so many kinds of flowering plants? *Bioscience* **31**: 572–581.
- Burlingame LL. 1913. The morphology of *Araucaria brasiliensis*. I. The staminate cone and male gametophyte. *Botanical Gazette* **55**: 97–114.
- Chaloner WG. 1976. The evolution of adaptive features in fossil exines. In: Ferguson IK, Muller J, eds. *The evolutionary significance of the exine*. London: Linnean Society/Academic Press, 1–14.
- Chase MW, Soltis DE, Olmstead RG, Morgan D, Les DH, Mishler BD, Duvall MR, Price RA, Hills HG, Qiu YL, Kron KA, Rettig JH, Conti E, Palmer JD, Manhart JR, Sytsma KJ, Michaels HJ, Kress WJ, Karol KG, Clark WD, Hedren M, Gaut BS, Jansen RK, Kim KJ, Wimpee CF, Smith JF, Furnier GR, Strauss SH, Xiang QY, Plunkett GM, Soltis PS, Swensen SM, Williams SE, Gadek PA, Quinn CJ, Eguiarte LE, Golenberg E, Learn GH, Graham SW, Barrett SCH, Dayanandan S, Albert VA. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene *rbcL*. *Annals of the Missouri Botanical Garden* **80**: 528–580.
- Chaw S-M, Parkinson CL, Cheng YC, Vincent TL, Palmer JD. 2000. Seed plant phylogeny inferred from all three genomes: monophyly of extant gymnosperms and the origin of Gnetales from conifers. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 4086–4091.
- Chaw S-M, Zharkikh A, Sung H-M, Lau T-C, Li W-H. 1997. Molecular phylogeny of gymnosperms and seed plant evolution: analysis of 18S rRNA sequence. *Molecular Biology and Evolution* **14**: 56–68.
- Clement-Westerhof JA, van Konijnenburg-van Citter JHA. 1991. *Hirmeriella muensteri*: new data on the fertile organs leading to a revised concept of the Cheirolepidiaceae. *Review of Palaeobotany and Palynology* **68**: 147–179.
- Connell SW, Ladd PG. 1993. Pollination biology of *Macrozamia reidleyi*: the role of insects. In: Stevenson DW, Norstog KJ, eds. *The biology, structure, and systematics of the*

- Cycadales: proceedings of CYCAD 90, the second international conference on cycad biology*. Milton: Palm & Cycad Societies of Australia, 89–95.
- Cox PA. 1990.** Pollination and the evolution of breeding systems in Pandanaceae. *Annals of the Missouri Botanical Garden* **77**: 816–840.
- Crane PR. 1985a.** Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden* **72**: 716–793.
- Crane PR. 1985b.** Phylogenetic relationships in seed plants. *Cladistics* **1**: 329–348.
- Crane PR. 1988.** Major clades and relationships in “higher” gymnosperms. In: Beck CB, ed. *Origin and evolution of gymnosperms*. New York: Columbia University Press, 218–272.
- Crane PR, Hult CD. 1988.** *Welwitschia the wonderful*. *Bulletin of the Field Museum of Natural History* **1988**: 22–29.
- Crane PR, Lidgard S. 1990.** Angiosperm radiation and patterns of Cretaceous palynological diversity. In: Taylor PD, Larwood GP, eds. *Major evolutionary radiations*. Oxford: Clarendon Press, 377–407.
- Crane PR, Upchurch GR. 1987.** *Drewria potomacensis* gen. et sp. nov., an Early Cretaceous member of Gnetales from the Potomac Group of Virginia. *American Journal of Botany* **74**: 1722–1736.
- Crepet WL. 1972.** Investigations of North American cycadeoids: pollination mechanisms in *Cycadeoidea*. *American Journal of Botany* **59**: 1048–1056.
- Crepet WL. 1974.** Investigations of North American cycadeoids: the reproductive biology of *Cycadeoidea*. *Palaeontographica, Abteilung B* **148**: 144–169.
- Crepet WL. 1983.** The role of insect pollination in the evolution of angiosperms. In: Real L, ed. *Pollination biology*. New York: Academic Press, 29–50.
- Crepet WL. 1984.** Advanced (constant) insect pollination mechanisms: pattern of evolution vis-à-vis angiosperm diversity. *Annals of the Missouri Botanical Garden* **71**: 607–630.
- Crepet WL, Friis EM, Nixon KC. 1991.** Fossil evidence of the evolution of biotic pollination. *Philosophical Transactions of the Royal Society of London Series B* **333**: 187–195.
- Cronquist A. 1968.** *The evolution and classification of flowering plants*. Boston: Houghton Mifflin.
- Daghlian CP, Person CP. 1977.** The cuticular anatomy of *Frenelopsis varians* from the Lower Cretaceous of central Texas. *American Journal of Botany* **64**: 564–569.
- Darwin CR. 1859.** *On the origin of species by natural selection or the preservation of favoured races in the struggle for life*. London: John Murray.
- Darwin CR. 1862.** *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of interbreeding*. London: John Murray.
- Darwin CR. 1876.** *The effects of cross and self fertilisation in the vegetable kingdom*. London: John Murray.
- Davis MB. 1986.** Climatic instability, time lags, and community disequilibrium. In: Diamond J, Case TJ, eds. *Community ecology*. New York: Harper & Row, 269–284.
- Davis TAW, Richards PW. 1933.** The vegetation of Moraballi Creek, British Guiana: an ecological study of tropical rain forest (Part I). *Journal of Ecology* **21**: 350–384.
- Delevoryas T. 1955.** The Medullosae – structure and relationships. *Palaeontographica, Abteilung B* **97**: 114–167.
- Delevoryas T. 1964.** A probable pteridosperm microsporangiate fructification from the Pennsylvanian of Illinois. *Palaeontology* **7**: 60–63.
- Delevoryas T. 1968.** Investigations of North American cycadeoids: structure, ontogeny and phylogenetic considerations of cones of *Cycadeoidea*. *Palaeontographica, Abteilung B* **121**: 122–133.
- Delevoryas T. 1991.** Investigations of North American cycadeoids: *Weltrichia* and *Williamsonia* from the Jurassic of Oaxaca, Mexico. *American Journal of Botany* **78**: 177–182.
- Delevoryas T, Hope RC. 1971.** A new Triassic cycad and its phyletic implication. *Postilla* **150**: 1–21.
- Delevoryas T, Hope RC. 1976.** More evidence for a slender growth habit in Mesozoic Cycadophyta. *Review of Palaeobotany and Palynology* **21**: 93–100.
- Dennis RL, Eggert DA. 1978.** Parasporotheca gen. nov., and its bearing on the interpretation of the morphology of permineralized medullosan pollen organs. *Botanical Gazette* **139**: 117–139.
- Dickinson HG, Elleman CJ, Doughty J. 2000.** Pollen coatings: chimaeric genetics and new functions. *Sexual Plant Reproduction* **12**: 302–309.
- Dilcher DL. 1979.** Early angiosperm reproduction: an introductory report. *Review of Palaeobotany and Palynology* **27**: 291–328.
- Dilcher DL. 2000.** Toward a new synthesis: major evolutionary trends in the angiosperm fossil record. In: Ayala FJ, Fitch WM, Clegg MT, eds. *Variation and evolution in plants and microorganisms: toward a new synthesis 50 years after Stebbins*. Washington DC: National Academy Press, 255–270.
- Dilcher DL, Krassilov VA, Douglas JG. 1996.** Angiosperm evolution: fruits with affinities to Ceratophyllales from the Lower Cretaceous. *Abstracts from the 5th conference of the International Organization of Paleobotanists (Santa Barbara)*. Santa Barbara, 23.
- DiMichele WA, Phillips TL. 1988.** Paleocology of the Middle Pennsylvanian-age Herrin Coal swamp (Illinois) (USA) near a contemporaneous river system, the Walshville paleochannel. *Review of Palaeobotany and Palynology* **56**: 151–176.
- Dobson HEM, Bergström G. 2000.** The ecology and evolution of pollen odors. *Plant Systematics and Evolution* **222**: 63–87.
- Dobzhansky TG. 1937.** *Genetics and the origin of species*. New York: Columbia University Press.
- Donaldson JS, Nänni I, Bösenberg JD. 1995.** The role of insects in the pollination of *Encephalartos cycadifolius*. In: Vorster P, ed. *Proceedings of the third international conference on cycad biology*. Stellenbosch: Cycad Society of South Africa, 423–434.
- Donoghue MJ, Doyle JA. 1991.** Angiosperm monophyly. *Trends in Ecology & Evolution* **6**: 407.

- Donoghue MJ, Doyle JA. 2000.** Seed plant phylogeny: demise of the anthophyte hypothesis? *Current Biology* **10**: R106–R109.
- Douglas JG. 1985.** The Albian extinctions in the great Aust–Antarctic Trough. *New Zealand Geological Survey Record* **9**: 38–40.
- Doyle J, O’Leary M. 1935.** Pollination in *Tsuga*, *Cedrus*, *Pseudotsuga*, and *Larix*. *Scientific Proceedings of the Royal Dublin Society* **21**: 191–204.
- Doyle JA. 1998.** Molecules, morphology, fossils, and the relationship of angiosperms and Gnetales. *Molecular Phylogenetics and Evolution* **9**: 448–462.
- Doyle JA, Donoghue MJ. 1986.** Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Botanical Review* **52**: 321–431.
- Doyle JA, Hottel CL, Ward JV. 1990.** Early Cretaceous tetrads, zonasulculate pollen, and Winteraceae. 2. Cladistic analysis and implications. *American Journal of Botany* **77**: 1558–1568.
- Doyle JA, Jardín S, Doerenkamp A. 1982.** *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and paleoenvironments of northern Gondwana. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* **6**: 39–117.
- Dudley R. 1998.** Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. *Journal of Experimental Biology* **201**: 1043–1050.
- Eames AJ. 1913.** The morphology of *Agathis australis*. *Annals of Botany* **27**: 1–38.
- Eames AJ. 1960.** *Morphology of the angiosperms*. New York: McGraw-Hill.
- Edwards D, Fanning U. 1985.** Evolution and environment in the late Silurian–early Devonian: the rise of the pteridophytes. *Philosophical Transactions of the Royal Society of London Series B* **309**: 147–165.
- Ehrlich PR, Raven PH. 1964.** Butterflies and plants: a study in coevolution. *Evolution* **18**: 586–608.
- Ehrlich PR, Wilson EO. 1991.** Biodiversity studies: science and policy. *Science* **253**: 758–762.
- Erdtman G. 1935.** Pollen statistics: a botanical and geological research method. In: Wodehouse RP, ed. *Pollen grains: their structure, identification and significance in medicine*. New York: McGraw-Hill.
- Farrell BD. 1998.** “Inordinate fondness” explained: why are there so many beetles? *Science* **281**: 555–559.
- Farrell BD, Dussord DE, Mitter C. 1991.** Escalation of plant defense: do latex and resin canals spur plant diversification? *American Naturalist* **138**: 881–900.
- Fawcett PKS, Norstog KJ. 1993.** *Zamia pumila* in South Florida: A preliminary Report on its pollinators *R[hopalotria] slossoni*, a snout weevil, and *P[haraxantha] zamia*, a clavicorn beetle. In: Stevenson DW, Norstog KJ, eds. *The biology, structure, and systematics of the Cycadales: proceedings of CYCAD 90, the second international conference on cycad biology*. Milton: Palm & Cycad Societies of Australia, 109–119.
- Filatoff J. 1975.** Jurassic palynology of the Perth Basin, Western Australia. *Palaeontographica, Abteilung B* **154**: 1–113.
- Fineblum WL, Rauscher MD. 1997.** Do floral pigmentation genes also influence resistance to enemies? The W locus in *Ipomoea purpurea*. *Ecology* **78**: 1646–1654.
- Fisher RA. 1930.** *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Francis JE. 1983.** The dominant conifer of the Jurassic Purbeck Formation, England. *Palaeontology* **26**: 277–294.
- Friedman WE. 1990.** Double fertilization in *Ephedra*, a nonflowering seed plant: its bearing on the origin of angiosperms. *Science* **247**: 951–954.
- Friis EM, Chaloner WG, Crane PR. 1987.** Introduction to angiosperms. In: Friis EM, Chaloner WG, Crane PR, eds. *The angiosperms and their biological significance*. Cambridge: Cambridge University Press, 1–15.
- Friis EM, Crane PR, Pedersen KJ. 1986.** Floral evidence for Cretaceous chloranthoid angiosperms. *Nature* **320**: 163–164.
- Friis EM, Pedersen KR, Crane PR. 1999.** Early angiosperm diversification: The diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. *Annals of the Missouri Botanical Garden* **86**: 259–296.
- Frohlich MW. 1999.** MADS about Gnetales. *Proceedings of the National Academy of Sciences of the United States of America* **96**: 8811–8813.
- Frohlich MW, Meyerowitz EM. 1997.** The search for flower homeotic gene homologs in basal angiosperms and Gnetales: a potential new source of data on the evolutionary origin of flowers. *International Journal of Plant Sciences* **158**: S131–S142.
- Frohlich MW, Parker DS. 2000.** The mostly male theory of flower evolutionary origins: from genes to fossils. *Systematic Botany* **25**: 155–170.
- Gavrilets S, Li H, Vose MD. 2000.** Patterns of parapatric speciation. *Evolution* **54**: 1126–1134.
- Gensel PG, Andrews HN. 1984.** *Plant life in the Devonian*. New York: Praeger.
- Gibbs PE. 1991.** The “Zavada hypothesis” – a rebuttal rebutted. *Taxon* **40**: 583–595.
- Gibbs PE, Ferguson IK. 1987.** Correlations between pollen exine sculpturing and angiosperm self-incompatibility systems – a reply. *Plant Systematics and Evolution* **157**: 143–159.
- Gómez JM. 2000.** Effectiveness of ant pollinators of *Lobularia maritima*: effects of main sequential fitness components of the host plant. *Oecologia* **122**: 90–97.
- Gómez JM, Zamora R. 1992.** Pollination by ants: consequences of the quantitative effects on a mutual system. *Oecologia* **91**: 410–418.
- Gómez JM, Zamora R, Hodar JA, García D. 1996.** Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. *Oecologia* **105**: 236–242.
- Goremykin V, Bobrova V, Pahnke J, Antonov AS, Martin WF. 1996.** Noncoding sequences from the slowly evolving chloroplast inverted repeated in addition to rbcL data do not support affinities of angiosperms. *Molecular Biology and Evolution* **13**: 383–396.
- Grant V. 1949.** Pollination systems as isolating mechanisms in angiosperms. *Evolution* **3**: 82–97.

- Grayum MH. 1986.** Correlations between pollination biology and pollen morphology in the Araceae, with some implications for angiosperm evolution. In: Blakemore S, Ferguson IK, eds. *Pollen and spores: form and function*. London: Academic Press, 313–327.
- Grimaldi D. 1999.** The co-radiation of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* **86**: 373–406.
- Gulick JT. 1890.** Indiscriminate separation under the same environment, a cause of divergence. *Nature* **42**: 369–370.
- Halle TG. 1929.** Some seed-bearing pteridosperms from the Permian of China. *Kungl. Svenska Vetenskapsakademiens Handlingar* **6**: 2–24.
- Harris TM. 1946.** Notes on the Jurassic flora of Yorkshire, 19–21. 19 *Klukia exilis* (Phillips) Raciborski; 20 *Otozamites bunburnyanus* Zigno; 21 a coprolite of *Caytonia* pollen. *Annals and Magazine of Natural History* **12**: 357–378.
- Harris TM. 1956.** The investigation of a fossil plant. *Notices of the Proceedings of the Royal Institution of Great Britain* **36**: 456–468.
- Harris TM. 1961.** The fossil cycads. *Palaeontology* **4**: 313–323.
- Harris TM. 1964.** *The Yorkshire Jurassic flora. II. Caytoniales, Cycadales and Pteridosperms*. London: British Museum (Natural History).
- Harris TM. 1969.** *The Yorkshire Jurassic flora. III. Bennettitales*. London: British Museum (Natural History).
- Herrera CM. 1989.** Seed dispersal by animals: a role in angiosperm diversification? *American Naturalist* **133**: 309–322.
- Heslop-Harrison J. 1971.** Sporopollenin in the biological context. In: Brooks Jea, ed. *Sporopollenin*. London: Academic Press, 1–30.
- Hesse M. 1980.** Pollenkitt is lacking in *Gnetum gnemon* (Gnetaceae). *Plant Systematics and Evolution* **136**: 41–46.
- Hesse M. 1984.** Pollenkitt is lacking in Gnetatae – *Ephedra* and *Welwitschia* – further proof of its restriction to the angiosperms. *Plant Systematics and Evolution* **144**: 9–16.
- Hickman JC. 1974.** Pollination by ants: a low energy system. *Science* **184**: 1290–1292.
- Hluštík A. 1984.** Did fossil mangrove forests exist? *International Organization of Palaeobotany (IOP) Newsletter* **23**: 9–10.
- Hölldobler B, Wilson EO. 1990.** *The ants*. Cambridge: Harvard University Press.
- Hooker JD. 1863.** On *Welwitschia*, a new genus in the Gnetaceae. *Transactions of the Linnean Society* **24**: 1–48.
- Houston TF, Lamont BB, Radford S, Errington SG. 1993.** Apparent mutualism between *Verticordia nitens* and *V. aurea* (Myrtaceae) and their oil-ingesting bee pollinators (Hymenoptera, Colletidae). *Australian Journal of Botany* **41**: 369–380.
- Hughes NF, McDougall AB. 1987.** Record of angiospermid pollen entry into the English Early Cretaceous succession. *Review of Palaeobotany and Palynology* **50**: 252–272.
- Hughes NF, Moody-Stuart JC. 1967.** Palynological facies and correlation in the English Wealden. *Review of Palaeobotany and Palynology* **1**: 259–268.
- Husband BC, Schemske DW. 1997.** The effect of inbreeding depression in diploid and tetraploid populations of *Epi-lobium angustifolium* (Onagraceae): implications for the genetic basis of inbreeding depression. *Evolution* **51**: 737–746.
- Ibrahim MIA. 1996.** Aptian–Turonian palynology of the Ghazalat-I Well (GTX-I), Qattara Depression, Egypt. *Review of Palaeobotany and Palynology* **94**: 137–168.
- Janzen DH. 1970.** Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**: 501–528.
- Jarzewowski EA. 1989.** Cretaceous insect extinction. *Mesozoic Research* **2**: 25–28.
- Jarzewowski EA. 1995.** Early Cretaceous insect faunas and palaeoenvironment. *Cretaceous Research* **16**: 681–693.
- Jones DL. 1993.** *Cycads of the world*. Frenchs Forest: Reed Books.
- Kato M, Inoue T. 1994.** Origin of insect pollination. *Nature* **368**: 195.
- Kato M, Inoue T, Nagamitsu T. 1995.** Pollination biology of *Gnetum* (Gnetaceae) in a lowland dipterocarp forest in Sarawak. *American Journal of Botany* **82**: 862–868.
- Kevan PG, Chaloner WG, Saville DBO. 1975.** Interrelationships of early terrestrial arthropods and plants. *Palaeontology* **18**: 391–417.
- Kiester AR, Lande R, Schemske DW. 1984.** Models of coevolution and speciation in plants and their pollinators. *American Naturalist* **124**: 220–243.
- Klekowski EJ, Kazarinova-Fukshansky N, Mohr H. 1985.** Apical meristems and mutation: stratified meristems and angiosperm evolution. *American Journal of Botany* **72**: 1788–1800.
- Knoll AH. 1986.** Patterns of change in plant communities through geological time. In: Diamond J, Case TJ, eds. *Community ecology*. New York: Harper Row, 126–141.
- Krassilov VA. 1979.** *Cretaceous flora of Sakhalin*. Moscow: Nauka.
- Krassilov VA. 1997.** *Angiosperm origins*. Sophia: Pensoft.
- Krassilov VA, Dilcher DL, Douglas JG. 1998.** New ephedroid plant from the Lower Cretaceous Koonwarra Fossil Bed, Victoria, Australia. *Alcheringa* **22**: 123–133.
- Krassilov VA, Rasnitsyn AP. 1996.** Pollen in guts of Permian insects: first evidence of pollenivory and its evolutionary significance. *Lethaia* **29**: 369–372.
- Krassilov VA, Zherikhin VV, Rasnitsyn AP. 1997.** *Classopollis* in the guts of Jurassic insects. *Palaeontology* **40**: 1095–1101.
- Kress WJ. 1981.** Sibling interactions and the evolution of pollen unit, ovule number and pollen vector in angiosperms. *Systematic Botany* **6**: 101–112.
- Kuzoff RK, Gasser CS. 2000.** Recent progress in reconstructing angiosperm phylogeny. *Trends in Plant Science* **5**: 330–336.
- Labandeira CC, Dilcher DL, Davis DR, Wagner DL. 1994.** 97 million years of angiosperm–insect association: paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 12278–12282.
- Labandeira CC, Sepkoski JJ. 1993.** Insect diversity in the fossil record. *Science* **260**: 310–314.

- Lakatos I. 1970.** Falsification and the methodology of scientific research programmes. In: Lakatos I, Musgrave A, eds. *Criticism and the growth of knowledge*. Cambridge: Cambridge University Press, 91–316.
- Landis GP, Rigby JK, Sloan RE, Hengst R, Snee LW. 1994.** Pele hypothesis: ancient atmospheres and geologic-geochemical controls on evolution, survival, and extinction. In: Keller G, MacLeod N, eds. *Cretaceous-Tertiary mass extinctions: biotic and environmental changes*. New York: W. W. Norton, 519–556.
- Leppik EE. 1960.** Early evolution of flower types. *Lloydia* **23**: 72–92.
- Levin DA, Wilson AC. 1976.** Rates of evolution in seed plants: net increase in diversity of chromosome numbers and species numbers through time. *Proceedings of the National Academy of Sciences of the United States of America* **73**: 2086–2090.
- Magallón S, Crane PR, Herendeen PS. 1999.** Phylogenetic pattern, diversity, and diversification of eudicots. *Annals of the Missouri Botanical Garden* **86**: 297–372.
- Mamay SH. 1976.** Paleozoic origin of cycads. *U.S. Geological Survey Professional Paper* **934**: 1–48.
- Marcotrigiano M. 2000.** Herbivory could unlock mutations sequestered in stratified shoot apices of genetic mosaics. *American Journal of Botany* **87**: 255–361.
- Masterson J. 1994.** Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* **264**: 421–424.
- Mayr E. 1942.** *Systematics and the origin of species*. New York: Columbia University Press.
- McElwain JC. 1988.** Do fossil plants signal palaeo-atmospheric CO₂ concentrations in the geological past? *Philosophical Transactions of the Royal Society of London Series B* **353**: 83–96.
- McElwain JC, Chaloner WG. 1995.** Stomatal density and index of fossil plants track atmospheric carbon dioxide in the Paleozoic. *Annals of Botany* **76**: 389–395.
- McKey D. 1975.** The ecology of coevolved seed dispersal systems. In: Gilbert LE, Raven PH, eds. *Coevolution of animals and plants*. Austin: University of Texas Press, 159–191.
- Meyer-Berthaud B, Scheckler SE, Wendt J. 1999.** *Archaeopteris* is the earliest known modern tree. *Nature* **398**: 700–701.
- Michener CD, Grimaldi D. 1988.** The oldest fossil bee: apoid history, evolutionary stasis, and antiquity of social behavior. *Proceedings of the National Academy of Sciences of the United States of America* **85**: 6424–6426.
- Midgley JJ, Bond WJ. 1991.** How important is biotic pollination and dispersal to the success of the angiosperms? *Philosophical Transactions of the Royal Society of London Series B* **333**: 209–215.
- Millay MA, Eggert DA, Dennis RL. 1978.** Morphology and ultrastructure of four Pennsylvanian prepollen types. *Micropaleontology* **24**: 303–315.
- Moussel B. 1980.** Gouttelette réceptrice du pollen et pollinisation chez *Ephedra distachya* L. Observations sur le vivant et en microscopies photonique et électronique. *Revue de Cytologie et Biologie Vegetales le Botaniste* **3**: 65–89.
- Mulchay DH. 1979.** The rise of the angiosperms: a genealogical factor. *Science* **206**: 20–23.
- Mulchay DH. 1981.** Rise of the angiosperms. *Natural History* **90**: 30–35.
- Müller H. 1873.** *Die befruchtung der blumen durch Insekten*. Leipzig.
- Müller H. 1965.** Palynological investigations of Cretaceous sediments in northwestern Brazil. *2nd West African Micropaleontological Colloquium*, Ibadan, 123–136.
- Muller J. 1984.** Significance of fossil pollen for angiosperm history. *Annals of the Missouri Botanical Garden* **71**: 419–443.
- Niklas KJ. 1981.** Airflow patterns around some early seed plant ovules and cupules: implications concerning efficiency in wind pollination. *American Journal of Botany* **68**: 635–650.
- Niklas KJ. 1985.** The aerodynamics of wind pollination. *Botanical Review* **51**: 328–386.
- Niklas KJ, Buchmann SL. 1987.** The aerodynamics of pollen capture in two sympatric *Ephedra* species. *Evolution* **41**: 104–123.
- Niklas KJ, Buchmann SL, Kerchner V. 1986.** Aerodynamics of *Ephedra trifurca*. I. Pollen grain velocity fields around stems bearing ovules. *American Journal of Botany* **73**: 966–979.
- Niklas KJ, Norstog KJ. 1984.** Aerodynamics and pollen grain depositional patterns on cycad megastrobili: implications on the reproduction of three cycad genera (*Cycas*, *Dioon*, and *Zamia*). *Botanical Gazette* **145**: 92–104.
- Nixon KC, Crepet WL, Stevenson DW, Friis EM. 1994.** A reevaluation of seed plant phylogeny. *Annals of the Missouri Botanical Garden* **81**: 484–533.
- Norstog KJ. 1987.** Cycads and the origin of insect pollination. *American Scientist* **75**: 270–279.
- Norstog KJ, Fawcett PKS. 1989.** Insect-cycad symbiosis and its relation to the pollination of *Zamia furfuracea* (Zamiaceae) by *Rhopalotria mollis* (Curculionidae). *American Journal of Botany* **76**: 1380–1394.
- Norstog KJ, Nichols TJ. 1997.** *The biology of cycads*. Ithaca: Cornell University Press.
- Norstog KJ, Stevenson DW, Niklas KJ. 1986.** The role of beetles in pollination of *Zamia furfuracea* L. fil. (Zamiaceae). *Biotropica* **18**: 300–306.
- Oberprieler RG. 1989.** *Platymerus*, the forgotten cycad weevil. *Pelea* **8**: 50–54.
- Oberprieler RG. 1995a.** The weevils (Coleoptera: Curculionoidea) associated with cycads. 1. Classification, relationships, and biology. In: Vorster P, ed. *Proceedings of the third international conference on cycad biology*. Stellenbosch: Cycad Society of South Africa, 295–334.
- Oberprieler RG. 1995b.** The weevils (Coleoptera: Curculionoidea) associated with cycads. 2. Host specificity and implications for cycad taxonomy. In: Vorster P, ed. *Proceedings of the third international conference on cycad biology*. Stellenbosch: Cycad Society of South Africa, 335–365.
- Oliver FW, Scott DH. 1904.** VII. On the structure of the Palaeozoic seed *Lagenostoma lomaxi*, with a statement of

- the evidence upon which it is referred to *Lyginodendron*. *Philosophical Transactions of the Royal Society of London Series* **197**: 193–247.
- Ornduff R. 1991.** Size classes, reproductive behavior, and insect associates of *Cycas media* (Cycadaceae) in Australia. *Botanical Gazette* **152**: 203–207.
- Osborn JM, Taylor TN. 1995.** Pollen morphology and ultrastructure of the Bennettitales: *in situ* pollen of Cycadeoidea. *American Journal of Botany* **82**: 1074–1081.
- Owens JN, Catalano GL, Morris SJ, Aitken-Christie J. 1995.** The reproductive-biology of kauri (*Agathis australis*). 1. Pollination and prefertilization development. *International Journal of Plant Sciences* **156**: 257–269.
- Owens JN, Takaso T, Runions CJ. 1998.** Pollination in conifers. *Trends in Plant Science* **3**: 479–485.
- Pacini E. 2000.** From anther and pollen ripening to pollen presentation. *Plant Systematics and Evolution* **222**: 19–43.
- Pacini E, Franchi GG. 1994.** Role of the tapetum in pollen and spore dispersal. *Plant Systematics and Evolution* **7**: S1–S11.
- Pant DD. 1987.** The fossil history of the Cycadales. *Geophytology* **17**: 125–162.
- Peakall R, Angus CJ, Beattie AJ. 1990.** The significance of ant and plant traits for ant pollination in *Leporella fimbriata*. *Oecologia* **84**: 457–460.
- Peakall R, Beattie AJ. 1991.** The genetic consequences of worker ant pollination in a self-compatible, clonal orchid. *Evolution* **45**: 1837–1848.
- Peakall R, Beattie AJ, James SH. 1987.** Pseudocopulation of an orchid by male ants: a test of two hypotheses accounting for the rarity of ant pollination. *Oecologia* **73**: 522–524.
- Pearson HHW. 1906.** Notes on South African cycads. *Transactions of the South African Philosophical Society* **16**: 341–354.
- Pedersen KJ, Friis EM, Crane PR. 1993.** Pollen organs and seeds with *Decussosporites* Brenner from Lower Cretaceous Potomac Group sediments of eastern USA. *Grana* **32**: 273–289.
- Pellmyr O. 1992.** The phylogeny of a mutualism: evolution and coadaptation between *Trollius* and its seed-parasitic pollinators. *Biological Journal of the Linnean Society* **47**: 337–365.
- Pellmyr O, Leebens-Mack J. 2000.** Reversal of mutualism as a mechanism for adaptive radiation in yucca moths. *American Naturalist* **156**: S62–S76.
- Pellmyr O, Tang W, Groth I, Bergström G, Thien LB. 1991.** Cycad cone and angiosperm floral volatiles: inferences for the evolution of insect pollination. *Biochemical Systematics* **19**: 623–627.
- Pellmyr O, Thien LB. 1986.** Insect reproduction and floral fragrances: keys to the evolution of the angiosperms? *Taxon* **35**: 76–85.
- Person CP, Delevoryas T. 1982.** The Middle Jurassic flora of Oaxaca, Mexico. *Palaeontographica, Abteilung B* **180**: 82–119.
- Pettitt JM, Chaloner WG. 1964.** The ultrastructure of the Mesozoic pollen *Classopollis*. *Pollen et Spores* **6**: 611–620.
- Pocock SAJ, Vasanthy G, Venkatachala BS. 1990.** Pollen of *Circumpolles* – an enigma of monotetrads showing evolutionary adaptation. *Review of Palaeobotany and Palynology* **65**: 179–193.
- Poort RJ, Visscher H, Dilcher DL. 1996.** Zoidogamy in fossil gymnosperms: the centenary of a concept, with special reference to prepollen of late Paleozoic conifers. *Proceedings of the National Academy of Sciences of the United States of America* **93**: 11713–11717.
- Proctor MCF. 1978.** Insect pollination syndromes in an evolutionary and ecosystemic context. In: Richards AJ, ed. *The pollination of flowers by insects*. London: Linnean Society/Academic Press, 105–123.
- Qiu YL, Lee JH, Bernasconi-Quadroni F, Soltis DE, Soltis PS, Zanis M, Zimmer EA, Chen ZD, Savolainen V, Chase MW. 1999.** The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature* **402**: 404–407.
- Ramsey J, Schemske DW. 1998.** Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* **29**: 467–501.
- Ramsey M. 1995.** Ant pollination of the perennial herb *Blandfordia grandiflora* (Liliaceae). *Oikos* **74**: 265–272.
- Ratray G. 1913.** Notes of the pollination of some South African cycads. *Transactions of the Royal Society of South Africa* **3**: 259–270.
- Raup DM. 1994.** The role of extinction in evolution. *Proceedings of the National Academy of Sciences, USA* **91**: 6758–6763.
- Raven JA. 1991.** Plant responses to high O₂ concentrations: relevance to previous high O₂ episodes. *Palaeogeography, Palaeoclimatology, Palaeoecology* **97**: 19–38.
- Raven PH. 1977.** A suggestion concerning the Cretaceous rise to dominance of the angiosperms. *Evolution* **31**: 451–452.
- Raven PH, Evert RF, Eichorn SE. 1992.** *Biology of plants (5th edition)*. New York: Worth Publishers.
- Regal PJ. 1977.** Ecology and evolution of flowering plant dominance: interplay of seed and pollen dispersal systems may explain angiosperm versus gymnosperm dominance. *Science* **196**: 622–627.
- Renault B. 1876.** *Bassin houiller et Permien d'Autun et d'Épinac*. Paris: Imprimerie Nationale.
- Retallack GJ. 1985.** Fossil soils as grounds for interpreting the advent of large plants and animals on land. *Philosophical Transactions of the Royal Society of London Series B* **309**: 105–142.
- Retallack GJ. 1986.** The first record of soils. In: Wright VP, ed. *Paleosols: their recognition and interpretation*. Boston: Blackwell Scientific, 1–57.
- Retallack GJ. 1997.** Early forest soils and their role in Devonian global change. *Science* **276**: 583–585.
- Richardson ES. 1980.** Life at Mazon Creek. In: Langenheim RL, Mann CJ, eds. Middle and Late Pennsylvanian strata on margin of Illinois Basin. *10th annual field conference: Great Lakes section*, University of Illinois, 217–224.
- Robinson JM. 1989.** Phanerozoic O₂ variation, fire, and terrestrial ecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **75**: 223–240.

- Robinson JM. 1990.** Lignin, land plants, and fungi: biological evolution affecting Phanerozoic oxygen balance. *Geology* **18**: 607–610.
- Rolfe WDI, Ingham JK. 1967.** Limb structure, affinity and diet of the Carboniferous 'centipede' *Arthropleura*. *Scottish Journal of Geology* **3**: 118–124.
- Rothwell GW, Stockey R. 2001.** Pollen tubes, contractile tissue, and pollination biology in Cycadeoidales/Bennettitales. *Botany 2001, abstracts from the annual meeting of the Botanical Society of America*, Albuquerque, 25.
- Runions CJ, Owens JN. 1998.** Evidence for pre-zygotic self-incompatibility in a conifer. In: Owens SJ, Rudall PJ, eds. *Reproductive biology: in systematics, conservation and economic botany*. Kew: Royal Botanic Gardens, 255–264.
- Salgado-Labouriau ML, Nilsson S, Rinaldi M. 1993.** Exine sculpture in *Pariana pollen* (Gramineae). *Grana* **32**: 243–249.
- Samigullen TK, Martin WF, Troitsky AV, Antonov AS. 1999.** Molecular data from the chloroplast rpoC1 gene suggest deep and distinct dichotomy of contemporary spermatophytes into two monophyla: gymnosperms (including Gnetales) and angiosperms. *Journal of Molecular Evolution* **49**: 310–315.
- Saporta G de, Marion AF. 1885.** *L'évolution du règne végétal. Les phanérogames*. Paris: G. Baillière.
- Scheuring BW. 1976.** Proximal exine filaments, a widespread feature among Triassic *Protosaccites* and *Circumpolles* to secure the dispersal of entire tetrads. *Pollen et Spores* **18**: 611–639.
- Schluter D. 1998.** Ecological causes of speciation. In: Howard DJ, Berlocher SH, eds. *Endless forms: species and speciation*. Oxford: Oxford University Press, 114–129.
- Scott AC, Scheckler SE. 1998.** Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events – discussion. *Philosophical Transactions of the Royal Society of London Series B* **353**: 128–130.
- Scott AC, Stephenson J, Chaloner WG. 1992.** Interaction and coevolution of plants and arthropods during the Paleozoic and Mesozoic. *Philosophical Transactions of the Royal Society of London Series B* **335**: 129–165.
- Scott AC, Taylor TN. 1983.** Plant/animal interactions during the Upper Carboniferous. *Botanical Review* **49**: 259–307.
- Scott DH. 1900.** *Studies in fossil botany*. London: Adam & Charles Black.
- Smoot EL. 1984.** Phloem anatomy of the Carboniferous pteridosperm *Medullosa* and evolutionary trends in gymnosperm phloem. *Botanical Gazette* **145**: 550–564.
- Soderstrom TR, Calderon CE. 1971.** Insect pollination in tropical rain forest grasses. *Biotropica* **3**: 1–16.
- Soltis DE, Soltis PS. 1993.** Molecular data and the dynamic nature of polyploidy. *Critical Reviews in Plant Sciences* **12**: 243–273.
- Soltis PS, Soltis DE. 2000.** The role of genetic and genomic attributes in the success of polyploids. In: Ayala FJ, Fitch WM, Clegg MT, eds. *Variation and evolution in plants and microorganisms: toward a new synthesis 50 years after Stebbins*. Washington DC: National Academy Press, 310–329.
- Sprengel CK. 1793.** *Das entdeckte geheimnis der natur im bau und der befruchtung der blumen*. Berlin: Frederick Vieweg.
- Stebbins GL. 1981.** Why are there so many species of flowering plants? *Bioscience* **31**: 573–577.
- Stewart WN. 1951.** A new *Pachytosta* from the Berryville locality of southeastern Illinois. *American Midland Naturalist* **46**: 717–742.
- Stewart WN. 1983.** *Paleobotany and the evolution of plants*. Cambridge: Cambridge University Press.
- Stewart WN, Delevoryas T. 1956.** The medullosan pteridosperms. *Botanical Review* **22**: 45–80.
- Stidd BM, Leisman GA, Phillips TL. 1977.** *Sullitheca dactylifera* gen. et sp. n.: a new medullosan pollen organ and its evolutionary significance. *American Journal of Botany* **64**: 994–1002.
- Strauss SW, Armbruster WS. 1997.** Linking herbivory and pollination – new perspectives on plant and animal ecology and evolution. *Ecology* **78**: 1617–1618.
- Takahashi M, Takai K, Saiki K. 1995.** Ephedroid fossil pollen from the Lower Cretaceous (Upper Albian) of Hokkaido, Japan. *Journal of Plant Research* **108**: 11–15.
- Tang W. 1987.** Insect pollination in the cycad *Zamia pumila* (Zamiaceae). *American Journal of Botany* **74**: 90–99.
- Tang W. 1995.** Pollination drops in female cycad cones. *Palms & Cycads* **48**: 20–21.
- Tang W. 1997.** Pollination in *Dioon*. *Palms & Cycads* **57**: 12–15.
- Taylor TN. 1971.** *Halletheca reticulata* gen. et sp. n.: a synangiate Pennsylvanian pteridosperm pollen organ. *American Journal of Botany* **58**: 300–308.
- Taylor TN. 1978.** The ultrastructure and reproductive significance of Monoletes (Pteridospermales) pollen. *Canadian Journal of Botany–Revue Canadienne De Botanique* **56**: 3105–3118.
- Taylor TN. 1979.** Ultrastructural studies of pteridosperm pollen: *Nanoxanthiipollenites* Clending and Nygreen. *Review of Palaeobotany and Palynology* **29**: 15–21.
- Taylor TN. 1981.** Pollen and pollen organ evolution in early seed plants. In: Niklas KJ, ed. *Paleobotany, paleoecology, and evolution (volume 2)*. New York: Praeger, 1–26.
- Taylor TN, Alvin KL. 1984.** Ultrastructure and development of Mesozoic pollen: *Classopollis*. *American Journal of Botany* **71**: 547–587.
- Taylor TN, Millay MA. 1979.** Pollination biology and reproduction in early seed plants. *Review of Palaeobotany and Palynology* **27**: 213–238.
- Taylor TN, Taylor EL. 1993.** *The biology and evolution of fossil plants*. Englewood Cliffs: Prentice Hall.
- Thien LB, Bernhardt P, Gibbs GW, Pellmyr O, Bergström G, Groth I, McPherson G. 1985.** The pollination of *Zygogynum* (Winteraceae) by a moth *Sabatinka* (Micropterigidae): an ancient association? *Science* **227**: 540–542.
- Thompson JN. 1994.** *The coevolutionary process*. Chicago: University of Chicago.

- Thompson JN, Pellmyr O. 1992.** Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. *Ecology* **73**: 1780–1791.
- Tiffney BH, Mazer SJ. 1995.** Angiosperm growth habit, dispersal and diversification reconsidered. *Evolutionary Ecology* **9**: 93–117.
- Upchurch GR, Doyle JA. 1981.** Paleocology of the conifers *Frenelopsis* and *Pseudofrenelopsis* (Cheirolepidiaceae) from the Cretaceous Potomac Group of Maryland and Virginia. In: Romans RC, ed. *Geobotany (volume 2)*. New York: Plenum Press, 167–202.
- Vakhrameev VA. 1970.** Range and palaeoecology of Mesozoic conifers, the Cheirolepidiaceae. *Paleontological Journal* **4**: 12–25.
- Vakhrameev VA. 1981.** Pollen *Classopollis*: indicator of Jurassic and Cretaceous climates. *Palaeobotanist* **28–29**: 301–307.
- van der Pijl L. 1953.** On the flower biology of some plants from Java with general remarks on fly-traps (species of *Annona*, *Artocarpus*, *Typhonium*, *Gnetum*, *Arisaema* and *Abroma*). *Annales Bogoricensis* **1**: 77–99.
- van der Pijl L. 1960.** Ecological aspects of flower evolution. I. Phyletic aspects. *Evolution* **14**: 403–416.
- Van Devender TR. 1990.** Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. In: Betancourt JL, Van Devender TR, Martin PS, eds. *Packrat middens: the last 40,000 years of biotic change*. Tucson: University of Arizona Press, 134–163.
- van Konijnenburg-van Citter JHA. 1987.** New data on *Pagiophyllum maculosum* Kendall and its male cone from the Jurassic of North Yorkshire. *Review of Palaeobotany and Palynology* **51**: 95–105.
- Vovides AP, Norstog KJ, Fawcett PKS, Duncan MW, Nash RJ, Molsen DV. 1993.** Histological changes during maturation in male and female cones of the cycad *Zamia furfuracea* and their significance in relation to pollination biology. *Botanical Journal of the Linnean Society* **111**: 241–252.
- Walker JW, Doyle JA. 1975.** The bases of angiosperm phylogeny: palynology. *Annals of the Missouri Botanical Garden* **62**: 664–723.
- Walker JW, Walker AG. 1984.** Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Annals of the Missouri Botanical Garden* **71**: 464–521.
- Waser NM. 1998.** Pollination, angiosperm speciation, and the nature of species boundaries. *Oikos* **81**: 198–201.
- Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1996.** Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–1060.
- Watson J. 1977.** Some Lower Cretaceous conifers of the Cheirolepidiaceae from the U.S.A. and England. *Palaeontology* **20**: 715–749.
- Watson J. 1988.** The Cheirolepidiaceae. In: Beck CB, ed. *Origin and evolution of gymnosperms*. New York: Columbia University Press, 382–447.
- Webster PJ. 1910.** Pollination experiments with *Anonas*. *Bulletin of the Torrey Botanical Club* **37**: 529–539.
- Weller SG, Donoghue MJ, Charlesworth D. 1995.** The evolution of self-incompatibility in flowering plants: a phylogenetic approach. In: Hoch PC, Stephenson AG, eds. *Experimental and molecular approaches to plant biosystematics*. St. Louis: Missouri Botanical Garden, 355–382.
- Wetschnig W, Depisch B. 1999.** Pollination biology of *Welwitschia mirabilis* Hook. f. (Welwitschiaceae, Gnetales). *Phyton* **39**: 167–183.
- Whalley PES. 1978.** New taxa of fossil and recent Micropterigidae with a discussion of their evolution and a comment on the evolution of Lepidoptera (Insecta). *Annals of the Transvaal Museum* **31**: 71–86.
- White ME. 1986.** *The greening of Gondwana*. Frenchs Forest: Reed Books.
- Whitehouse HLK. 1950.** Multiple-allelomorph incompatibility of pollen and style in the evolution of angiosperms. *Annals of Botany* **14**: 199–216.
- Wieland GR. 1906.** *American fossil cycads*. Washington DC: Carnegie Institute.
- Willson MF, Burley N. 1983.** *Mate choice in plants*. Princeton: Princeton University Press.
- Wilson GW. 1994.** Initial observations on the reproductive behavior and an insect pollination agent of *Bowenia serrulata* (W. Bull) Chamberlain. *Encephalartos* **23**: 295–335.
- Wing SL, Boucher LD. 1998.** Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth and Planetary Sciences* **26**: 379–421.
- Wing SL, Hickey LJ, Swisher CC. 1993.** Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature* **363**: 342–344.
- Winter K-U, Becker A, Munster T, Kim JT, Saedler H, Theissen G. 1999.** MADS-box genes reveal that gnetophytes are more closely related to conifers than to flowering plants. *Proceedings of the National Academy of Sciences, USA* **96**: 7342–7347.
- Wodehouse RP. 1935.** *Pollen grains: their structure, identification and significance in medicine*. New York: McGraw-Hill.
- Wyatt R. 1981.** Ant-pollination of the granite outcrop endemic *Diamorpha smallii* (Crassulaceae). *American Journal of Botany* **68**: 1212–1217.
- Zavada MS. 1984.** The relationship between pollen exine sculpturing and self-incompatibility mechanisms. *Plant Systematics and Evolution* **147**: 63–78.
- Zavada MS. 1990.** Correlations between pollen exine sculpturing and angiosperm self-incompatibility systems – a rebuttal. *Taxon* **39**: 442–447.
- Zavada MS, Taylor TN. 1986.** The role of self-incompatibility and sexual selection in the gymnosperm-angiosperm transition: a hypothesis. *American Naturalist* **128**: 538–550.
- Zhifeng G, Thomas BA. 1989.** A review of fossil cycad megasporophylls, with new evidence of *Crossozamia* Pomel and its associated leaves from the Lower Permian of Taiyuan, China. *Review of Palaeobotany and Palynology* **60**: 205–223.

APPENDIX

ALTERNATE HYPOTHESES FOR ANGIOSPERM DIVERSITY

I list 20 hypotheses for angiosperm radiation and the apparent lack of radiation in other seed plants. I have categorized these hypotheses as coevolution models, breeding system models, and all other models. Many of these hypotheses may be related to each other (especially the coevolution models). Many of the mechanisms may, in reality, be occurring in tandem. Each of these hypotheses has been previously published, except for hypotheses 10 and 11, below, which I have not seen in the literature and which I have devised.

Many of these are multiple hypotheses subsumed under an umbrella. For example, the hypothesis regarding self-incompatibility (hypothesis 6) is comprised of at least four separate hypotheses, each of which should be tested separately: (1) self-incompatibility reduced extinction rates by suppressing inbreeding depression; (2) self-incompatibility reduced extinction rates by precluding abortion of carpels/cupules; (3) self-incompatibility increased speciation rates by inducing sexual selection; and (4) self-incompatibility was only found in angiosperms.

Throughout the appendix, I use the term 'gymnosperm' to refer to all seed plants other than angiosperms.

Coevolution models

- (1) Insect pollination resulted in increased speciation rates (Grant, 1949) and decreased extinction rates (Janzen, 1970; Raven, 1977; Burger, 1981).
- (2) Coevolution of flowering plants and seed dispersing animals resulted in increased speciation rates (McKey, 1975; Regal, 1977; Herrera, 1989) and decreased extinction rates (Tiffney & Mazer, 1995).
- (3) Proliferation of secondary chemical compounds in plants to deter herbivory resulted in increased plant speciation rates (Ehrlich & Raven, 1964; Raven, 1977; Pellmyr & Thien, 1986; Farrell, Dusord & Mitter, 1991; Pellmyr *et al.*, 1991; Scott *et al.*, 1992) and decreased extinction rates.
- (4) Closed carpels precluded animals from eating ovules (Arber & Parkin, 1907; Mulchay, 1981; Stewart, 1983), thereby decreasing extinction rates.
- (5) Speciation rates increased with increased stratification of shoot apices when in the presence of specialized meristematic herbivores, especially with clonal plants (Klekowski, Kazarinova-Fukshansky & Mohr, 1985; Marcotrigiano, 2000). Angiosperms have greater stratification than other seed plants.

Breeding system models

- (6) Self-incompatibility reduced extinction rates by suppressing inbreeding depression (Whitehouse, 1950; Husband & Schemske, 1997) and precluding abortion of carpels/cupules (Zavada & Taylor, 1986). Self-incompatibility also increased speciation rates by inducing sexual selection (cf. Willson & Burley, 1983). Self-incompatibility was only found in angiosperms.
- (7) Obligate dioecy reduced extinction rates by precluding inbreeding depression and carpel/cupule abortion. Most angiosperms are monoecious; while

most gymnosperms are dioecious. Obligate dioecy may have also limited speciation (Cox, 1990).

- (8) Polyploidy caused higher speciation via quantum speciation and lower extinction rates via reduced inbreeding depression and increased heterozygosity (Soltis & Soltis, 1993; Ramsey & Schemske, 1998; Soltis & Soltis, 2000). Most angiosperms were polyploid or of polyploid origin, whereas no gymnosperms were.
- (9) Pollen tube competition on styles caused higher speciation rates (Mulchay, 1979). Only angiosperms have styles and closed carpels.
- (10) Pollen tube competition caused higher speciation rates and only siphonogamous plants had pollen tube competition.
- (11) Speciation rates were inversely proportional to duration between pollination and fertilization, which was accelerated by styles and closed carpels.
- (12) Speciation rates were inversely proportional to female gametophyte size (Norstog, 1987). Angiosperms have had much smaller megagametophytes with many fewer nuclei than gymnosperms.
- (13) Double fertilization conferred a selective advantage (Brown & Gibson, 1983; Friedman, 1990). All angiosperms had double fertilization; all Gnetales had a modified form of double fertilization; no other seed plants had double fertilization.

Other life history trait models

- (14) There was a selective advantage to having large seeds – food storage in cotyledons and endosperm of angiosperms allowed colonization of many habitats (Stebbins, 1981). On average, angiosperms had larger seeds with more nutritive tissue than gymnosperms.
- (15) There was a selective advantage to having deciduous leaves (Raven, Evert & Eichorn, 1992; Labandeira *et al.*, 1994). Angiosperms usually had deciduous leaves; gymnosperms usually did not.
- (16) Gymnosperms had lower photosynthetic rates than angiosperms due to lack of vessels, hence were at a selective disadvantage in mesic environments (Cronquist, 1968).
- (17) Angiosperms had many more stem architectures than did gymnosperms, which conferred selective advantages on angiosperms (Stebbins, 1981). These advantages included more subapical meristems, intercalary meristems, and more body plans, such as lianas and stem succulents.
- (18) Angiosperms produced less lignin (wood) than gymnosperms (Robinson, 1990). Lignin is expensive to synthesize and hence resulted in increased extinction rates in gymnosperms.
- (19) Quicker maturation times and precocious seed set resulted in higher speciation rates and lower extinction rates (Robinson, 1989; Raven, 1991; Landis *et al.*, 1994). This mechanism was especially noticeable in palaeoenvironments with high ambient O₂ concentrations and high incidence of fires (Dudley, 1998). Angiosperms had quicker maturation times than did gymnosperms (Bond, 1989).
- (20) Angiosperms had increased capacity for cell elongation following hormonal exposure, especially with root hairs and trichomes (Stebbins, 1981).