

THE PALEOBIOLOGY OF POLLINATION AND ITS PRECURSORS

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PERHAPS THE MOST conspicuous of associations between insects and plants is pollination. Pollinating insects are typically the first and most obvious of interactions between insects and plants when one encounters a montane meadow or a tropical woodland. The complex ecological structure of insect pollinators and their host plants is a central focus within the ever-expanding discipline of plant-insect interactions. The relationships between plants and insects have provided the empirical documentation of many case-studies that have resulted in the formulation of biological principles and construction of theoretical models, such as the role of foraging strategy on optimal plant-resource use, the advantages of specialized versus generalized host preferences as viable feeding strategies, and whether "pollination syndromes" are meaningful descriptions that relate flower type to insect mouthpart structure and behavior (Roubik, 1989; Ollerton, 1996; Waser et al., 1996; Johnson and Steiner, 2000). Much of the recent extensive discussion of plant-insect associations has centered on understanding the origin, maintenance, and evolutionary change in plant/pollinator associations at ecological time scales and increasingly at longer-term macroevolutionary time intervals (Armbruster, 1992; Pellmyr and Leebens-Mack, 1999). Such classical plant-insect association studies—cycads and cycad weevils, figs and fig wasps, and yuccas and yucca moths—were explored at modern time scales and currently are being examined through a long-term geologic component that involves colonization models based on cladogenetic events of plant and insect associates, buttressed by the fossil record (Farrell, 1998; Pellmyr and Leebens-Mack, 1999; A. Herre, *pers. comm.*). In addition to tracing modern pollination

to the earlier Cenozoic and later Mesozoic, there is a resurgence in understanding the evolutionary history of earlier palynivore taxa (spore, prepollen and pollen consumers), which led toward pollination as a mutualism (Scott et al., 1992).

Almost all terrestrial vascular plants have two opportunities during their life cycle to disperse to new localities. These events are spore or pollen dispersal to fertilize a megagametophyte at the haploid phase, and the dispersal of the fertilized, diploid megagametophyte after it has been transformed into a seed in seed-bearing plants. Agamic modes of plant colonization also occur, such as vegetative propagation through disseminules including root fragments or leaves with adventitious rootlets. However, these mechanisms lack the genetic advantages conveyed by sex. These two crucial junctures in the life-cycle of a stationary plant are indispensable for extending its geographic range, colonizing new habitats, and maintaining genetic variability through outcrossing, thus avoiding the perils of inbreeding depression. Fertilization of the female gamete by a motile male gamete is important because it establishes the gametophyte phase of the life cycle. Once fertilization has occurred, the resulting zygote develops into the ephemeral sporophyte generation, which produces spores in plants such as lycopods, ferns, and sphenopsids, or seeds and pollen in gymnosperms and angiosperms. Thus, the sporophyte generation gets a second chance for dispersal through the abiotic broadcasting of these propagules by agents such as wind, water, gravity, fire, or animals. This review will focus on the first phase of this twofold dispersal process, addressing how it originated and evolved into the assorted associations and magnificent mutualisms of today.

TYPES OF EVIDENCE

The fossil history of plant-insect associations can be viewed as three relatively distinct, but linked fossil records. The two obvious candidates are the separate plant and animal body-fossil records. The third is the record of plant-insect associations, subdivided into five principal types of evidence: (1) plant reproductive biology, (2) plant damage, (3) dispersed coprolites, (4) insect gut contents, and (5) insect mouthparts (Labandeira, 2001). A sixth type of evidence, discussed herein incidentally, is taxonomic assignment to a modern descendant for which reliable ecological data exist. Each of these five types of evidence provides data for the identities of either the plant hosts or their insect palynivores, or both, in unique circumstances. These five types of evidence are a continuum from the plant-host end member (plant reproductive biology) to an emphasis on the insect as the dominant type of evidence (mouthpart structure). Each type of evidence has a very uneven spatiotemporal distribution and taphonomic occurrence in the fossil record (Labandeira, 2001). For example, the value of dispersed coprolites, particularly in coal-ball deposits of Pennsylvanian age (Fig. 1A,B), is that they reveal the microanatomy of consumed plants in exquisite detail, albeit the identities of the palynivores are murky due to limitations in attributing coprolite shape, size, and texture to insects beyond major taxonomic divisions. Gut contents, by contrast, occur in fine-grained compression deposits where highly refractory pollen exines are resistant to degradation and preserved in a similar manner to insect chitin and plant cuticle (Fig. 1D). Occasional examples from younger amber deposits also are known (Grimaldi et al., 1994). Insect gut contents represent the most secure class of evidence, resulting in precision of taxonomic identification for both the host plant and insect culprit, particularly because pollen can be linked to a source plant clade and a palynivore is identifiable by external body characters.

Plant damage rarely reveals the exact identities of the insect associates of plants. Examples are damage by stylet-bearing paleodictyopteroid

insects in seed-fern prepollen organs such as *Bernautilia* (Fig. 1C), or the consumption by mandibulate insects of sterile megasporophyll and fertile ovular tissues in bisporangiate cycadeoid cones, involving tunneling behavior (Crepet, 1974). Because of the often highly patterned and stereotyped nature of plant damage, it also can reveal certain behavioral attributes of interacting insects, including palynivores. However, plant damage by itself is insufficient for attributing damage to a specific insect culprit, and often requires supplemental information for a more certain identification.

Plant morphology, especially the structure of reproductive units, is critical for assessing the possibility of insect palynivory or the participation of insects in pollination mutualisms. Several, often co-occurring, structures of extinct plants provide circumstantial evidence for insect pollination. Evidence from plant morphology includes: the size and surface properties of pollen; accessibility of the female reproductive structures to the ambient environment or to insects; presence of food, nesting materials, or other rewards to lure potential pollinating agents; general advertisements to potential pollinators through modifications of reproductive structures; and features that promote pollen transfer or enhance certain types of pollination. All these attributes have been found in the plant fossil record and have been inferred to indicate the presence of insect-mediated pollination. Some are linked to each other, such as the association of relatively large pollen size to reproductive structures inaccessible to wind in Paleozoic medullosan seed ferns. Similarly, in modern orchids the presence of nectaries (a nutritional reward) occurs in association with deep-throated flowers (a structural modification) and distinctive floral scents (an advertisement), attracting insects with long, projecting mouthparts (Darwin, 1877).

Structural modifications in insects indicative of palynivory and imbibation of nectar, which may result in pollination, involve principally the mouthparts and accompanying features of the head region (Fig. 1E; Labandeira, 1997a). Other relevant structures related to the acquisition of food in some

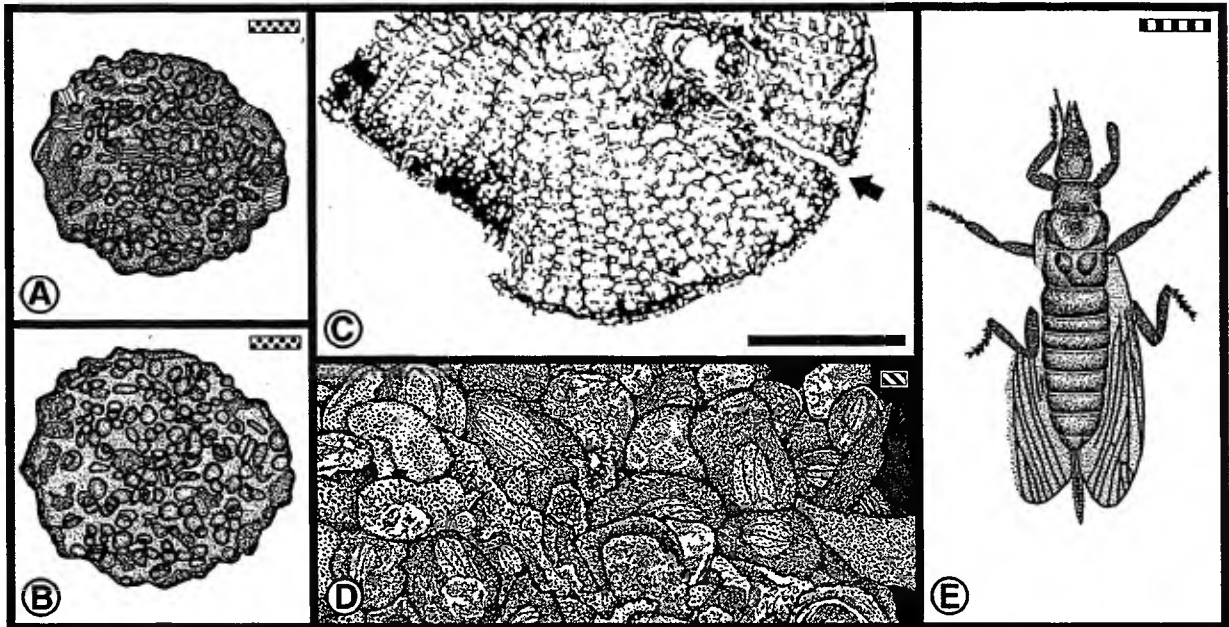


FIGURE 1.—Evidence from dispersed coprolites, plant damage, insect gut contents, and mouthpart structure for palynivory in Evolutionary Assemblage 2. These examples are from the Late Pennsylvanian Calhoun Coal of the Illinois Basin (A-C) and the late Early Permian Koshelevo Formation of the central Urals, Russia (D, E). A, Coprolite containing abundant spores (*Convolutispora* or *Apiculatosporis*) of the marattialean tree fern *Psaronius*; from NMNH peel BV9-Dtop, slide 499151. B, Coprolite containing abundant cordaite prepollen, *Florenites*; from NMNH peel BV18-Itop, slide 483986. C, Stilet track of a piercing-and-sucking paleodictyopteroid insect (arrow) on the bell-shaped prepollen organ (*Bernautia*) of the medullosan seed fern *Medullosa*. Approximately transverse section perpendicular to median axis; redrawn from Schopf (1948) plate 104, fig. 3, coal ball 129A. D, Gut contents of the insect *Idelopsocus diradiatus* (Hypoperlidae) containing pollen of *Lunatisporites* (Coniferales) and *Protohaploxylinus* (Glossopteridales); redrawn from SEM photograph in Krassilov and Rasnitsyn (1997), fig. 1b. E, The pollinivorous insect *Mycteroptila armipotens* (Hypoperlidae), redrawn from a camera lucida sketch in Novokshonov (1998), fig. 1. Scale bars: solid = 1.0 cm, striped = 0.1 cm, dotted = 0.01 cm, backslashed = 0.001 cm.

taxa include mycangial cavities on the surface of sporivorous beetles, specialized regions of body hair in pollinivorous flies and moths, pollen baskets (corbiculae) on the legs of bees, and pollen brushes on the abdominal undersides of megachilid bees (Crowson, 1981; Proctor et al., 1996). Nonetheless, it is the varied modifications of mouthparts for extracting spores and pollen and imbibing nectar that allow for the evolutionary possibility of pollination. In this context there are two basic

categories of mouthparts that are involved in consumption of spores, pollen, and nectar. First are subtle to major modifications of mandibulate mouthparts in insects such as beetles, sawflies, and caterpillars. Generalized and unelaborated mandibulate mouthparts have been considered as structures for comminuting detritus, animal prey and foliage, but also hard tissues such as seeds and wood. Fossil evidence now indicates that latest Silurian to Early Devonian spore-feeding was part

of this repertoire and may have been the earliest indurated food source consumed by insects or other arthropods, long before the appearance of seeds and wood during the Late Devonian. Pollen feeding, an extension of spore consumption, appeared later, during the Pennsylvanian. The identities of the earlier Paleozoic spore feeders are unknown, although later Paleozoic ones are much better circumscribed. Eventually modification of mandibulate mouthparts for highly specific associations became highly developed in the Coleoptera, with alteration of appendages, such as the maxillary galeae or labial glossae into brushes and rakes for sweeping spores and pollen towards the mandibles. In highly pollinivorous forms such as scarab beetles, there was conversion of normally rigid, sclerotized mandibles into structures with membranous margins or even flexible flaps with brushes for collecting pollen into the oral cavity and subsequent processing by a muscled crop (Bürgis, 1981; Picker and Midgley, 1996). For those taxa that use mandibles to fracture pollen and extract their protoplasts within the oral cavity, an opposite trend resulted in the evolution of "nutcracker" devices on mandibular molars (Crowson, 1981).

Alternatively, there are three major directions that adult mouthpart design has followed for extraction of nectar and other fluid rewards produced by vascular plants. These are the sponging labellum of flies and analogous structures in caddisflies, the siphon of almost all moths and butterflies and equivalent structures in certain beetles, and the glossa and associated clasping structures in bees and wasps that are paralleled in some neuropterans (Smith, 1985). All three major directions of mouthpart variation have multiple origins in unrelated clades of insects and are involved principally in the uptake of fluid food, although secondary reversions to pollen feeding has recurred in each. The fly labellum is a compound organ consisting of a broad, fleshy expansion of the labium that includes the labial palps, paraglossae, and certain maxillary elements. It is applied broadly to a fluid-laden surface, and uptake is accomplished by capillary flow into pseudotracheae that are channeled by a common

food canal into the mouth. By contrast, lepidopterans have two elongate galeae that are C-shaped in cross-section and conjoined to form a tube that can be deployed by hydrostatic pressure to probe flowers for the consumption of nectar. A partial vacuum for fluid uptake is provided by a cibarial pump, which is a muscle-controlled expansion of the esophagus. However, it is among the bees that the most complicated mouthpart apparatus has originated for fluid feeding. The central organ is comprised of long, hairy, laterally conjoined labial glossae, collectively referred to as a glossa. This structure, with its densely distributed and characteristically-shaped hairs, is inserted into flowers for imbibing nectar (Alvesdos-Santos and Wittmann, 1999) and pollen (Müller, 1996). The fluid-laden glossa is then withdrawn while simultaneously a pair of galeae and sometimes maxillary palps form a clasping tube, each with an elongate, hollowed region adjacent to the glossa. After this fluid uptake, the glossa is wringed through the surrounding tubular clamp of four, adpressed, mouthpart elements. The fluid is then transferred to the mouth.

Pollen feeding occurs sporadically among these nominally fluid-feeding mouthpart types. In dipteran taxa, such as hover flies (Syrphidae) and bee flies (Bombyliidae), their terminal labellar lobes have become reduced, resulting in an elongate labellum that is thick, sclerotized, and often prolonged for consumption of pollen grains that are swallowed whole for enzymatic breakdown, with minimal digestive fragmentation (Holloway, 1976; Deyrup, 1988). By contrast, two families of butterflies use extraoral digestion by forming a pollen slurry on their siphons that results in leaching of protein-rich protoplasts when it is subsequently consumed (Gilbert, 1972; DeVries, 1979). Bees also consume pollen, which they store in their crop together with nectar, that eventually becomes transformed into honey or provided as food to their larval brood (Roubik, 1989). Many species of bees also pack pollen into their corbiculae, which gradually degrades as a mass (Klungness and Peng, 1983) and eventually is transferred to the mouth or given to their developing larvae. Analogously, other bees have a

leg structure known as a “pollen press,” which similarly transforms clumps of pollen into a moistened sticky mass for consumption.

PLANTS: SOURCES OF REWARDS FOR INSECTS

The history of land plants involves three phases in the development of the male gametophyte—spores, prepollen, and pollen—of which the transitional stage of seed-fern prepollen is extinct.

Spore-Bearing Groups.—A basic feature of the life of all land plants is an alternation of generations. This life-cycle consists of one phase, the diploid sporophyte generation, that alternates with the other phase, the haploid gametophyte generation. This condition evidently occurred in all spore-bearing, late Silurian and earlier Devonian plants—lycopsids, sphenopsids, ferns and extinct clades such as rhyniopsids and “trimerophytes” (Bateman et al., 1998). For ferns, the dominant and conspicuous portion of this cycle is the diploid sporophyte, which produces mobile haploid spores that are dispersed by wind or other means to germinate, forming the haploid prothallus. The prothallus is the growth form of the gametophyte generation, which is tied to a wet habitat. The prothallus is a fleshy, cryptic, leaf-like structure that produces the haploid sex organs of the male antheridia and the female archegonia. The antheridia produce sperm, that represent a second motile phase, and fertilize archegonial eggs in water. In some lycopod and fern groups, the gametophyte consists of male and female individuals, each producing antheridia or archegonia, respectively. Although similar or externally identical spores can give rise to male and female individuals, known as the homosporous condition in some fern groups, in other fern taxa structurally differentiated spores develop. These spores are microspores and megaspores that produce respectively male or female prothalli, known as the heterosporous condition. In a few derived lineages, the female megaspore and its constituent megagametophyte is retained within the tissues of the sporophyte, providing an inference as to how the seed originated (DiMichele et al., 1989; Bateman and DiMichele, 1994).

Nectaries occur in some marattialean and filicalean ferns (Bonnier, 1879; Fahn, 1979), and are involved in the secretion of protein-, sugar- or lipid rich fluids by specialized epidermal tissues. These extranuptial nectaries are attractants to insects, although they are not linked to spore or pollen dispersal. The best-known example is bracken fern, in which nectaries occur in the axils of the stem and petiole (Potonié, 1891). There are at least ten other fern genera housing nectaries (Koptur et al., 1982), although studies have indicated that benefits do not necessarily accrue to the host (Rashbrook and Compton, 1992). These structures always are located on the vegetative parts of the plant and are not associated with reproductive structures, even though they attract a variety of insects, especially ants (Bentley, 1977). Such nectaries produce nutritionally rewarding substances beyond what would be expected from the simple, dilute, nutritionally poor products of hydathodes, salt glands, or sap flows. Extranuptial nectaries on vegetative organs precede floral-associated nectaries in the fossil record, and suggest that the presence of specialized glands for producing nutritionally rich fluids may be earlier than once thought.

Seed ferns, Prepollen, and the Pollination Drop Mechanism.—The term “prepollen” designates a dispersible, haploid male gametophyte borne by Late Paleozoic gymnospermous plants, that has similarities to both spores and pollen (Chaloner, 1970). Prepollen, such as *Monoletes* from medullosan seed ferns, is similar to spores in overall external structure, including shape, the absence of bladder-like sacci, and the retention of an elongate, linear mark for attachment to the sporangial wall, reminiscent of the trilete mark on the proximal surface in fern spores. Additionally, prepollen are housed in organs that resemble fern sporangia but became elaborated into complex synangia. For example, the bell-shaped prepollen organ of some medullosan seed ferns, *Bernaulltia* (Fig. 1c) is a compound organ consisting of tubular sporangia multiplied and coalesced into numerous radiating elements within a large synangium. Medullosan seed ferns bear both fern-like foliage and seeds, and employ a typically gymnospermous

mechanism of pollen capture, the pollination drop mechanism (Rothwell, 1977). Thus, prepollen has been hypothesized to represent a transitional phase of the dominant sporophyte generation between heterosporous fern-like plants and true pollen-bearing seed plants. In medullosan and other seed ferns, prepollen was transported by abiotic or biotic agents to the receptive ovular surface where the pollination drop mechanism represents an early form of pollination.

The pollination drop mechanism is present in gymnospermous plants, and examples have been documented from extinct seed ferns, extant conifers (Haines et al., 1984), cycads (Norstog and Nicholls, 1997), gnetophytes (Church, 1914; Bino et al., 1984; Kato and Inoue, 1994), and *Ginkgo* (Dogra, 1964). These seed plants are characterized by ovules, either borne singly, in strobili, or other clustered arrangements, that bear a terminal, projecting beak typically at the ovular pole opposite to the attachment site. This terminal beak, the micropyle, houses a central longitudinal tube that connects the basal pollen chamber immediately above the nucellus, which contains the haploid megagametophyte, to an outer receptive surface exposed to the environment. It is on this outer, micropylar surface that pollen land. During the liberation of pollen from conspecific male cones or other pollen-bearing organs, a sugary fluid is secreted by female ovular tissues that surround the pollen chamber such that the fluid fills the micropylar tube and extends to the micropylar terminus. Concurrently, airborne or insect-disseminated pollen land or are brought to the micropylar surface, which sometimes produces a visible, extruded bubble. This is followed by evaporation or resorption of the fluid, causing the pollen grains to be drawn into the micropylar canal and eventually towards the basal surface of the pollen chamber, where pollen tubes emerge from the pollen grain to penetrate various integumentary and nucellar tissues. The natural result of this process is fertilization of the eggs borne on the megagametophyte. Undoubtedly much of the timing of pollen release, pollination fluid production and resorption, pollen tube formation, and fertilization is choreographed by hormone

concentrations, histocompatibility protein reaction, and environmental variables such as temperature and humidity. Modifications of this mechanism exist, including the absence of any micropylar fluid, resulting in "dry" pollination, and the presence of micropyles in an inverted position, whereby pollen ascends toward a pollination chamber (Tomlinson et al., 1991).

Pollen in Gymnospermous and Angiospermous Plants.—The five major clades of seed plants that exist today display an interesting combination of abiotic and biotic pollination. Of the five, all conifers and *Ginkgo* are obligately wind-pollinated, probably primarily so (Proctor et al., 1996). By contrast, cycads, gnetophytes, and angiosperms are insect pollinated, most likely an ancient entomophilous condition, although some evidence indicates that some gnetophytes experienced wind pollination (anemophily) in their history. In fact, in the case of both cycads and the three modern gnetophyte clades—Gnetaceae, Welwitschiaceae, and Ephedraceae—conventional wisdom maintained that wind pollination was the norm, probably exclusively so (e.g., Baird, 1938). For cycads, recent evidence has overturned this judgement, documenting insect pollination in every case that has been examined extensively, including *Zamia* in Central America, *Encephalartos* in southern Africa, and *Bowenia* and *Stangeria* in Australia (Wilson, 1993; Norstog et al., 1995). Currently the only genus of the 11 extant cycad genera that may be wind pollinated is *Cycas* (Ornduff, 1991; Norstog and Nicholls, 1997). The cycad *Zamia furfucaria* and its pollinating weevil, *Rhopalotria mollis*, is a classic story of detective work in sleuthing the life-cycle of a highly specific pollination system (Norstog, 1987).

Similarly insect pollination, mostly by small flies, has been documented for *Gnetum* in Indonesia (Pijl, 1953; Kato and Inoue, 1994), various species of *Ephedra* in Eurasia (Bino et al., 1984; Hult and Crane, 1988; Meeuse et al., 1990) and *Welwitschia mirabilis* in southeastern Africa (Marsh, 1982; Crane and Hult, 1988), all representing insect co-optation of the pollination drop mechanism. Fossil evidence for a sixth, seed-plant clade, the Bennettitales, strongly suggests cycad-like insect pollination as well, particularly for *Cycadeoidea*

(Crepet, 1974), and the presence of a pollination drop mechanism. Evidently, the early to mid-Mesozoic ancestors and relatives of modern angiosperms took two approaches toward pollination: the phylogenetically more distant conifers and *Ginkgo* retained wind pollination, whereas the “anthophyte” clade of bennettitaleans, cycads, gnetophytes, and basal angiosperms either retained ancestral insect pollination (entomophily) or evolved it during the Mesozoic (Lloyd and Wells, 1992).

Angiosperms are distinguished structurally from other seed plants by reproductive apomorphies such as a triploid endosperm, double integumentary layers enclosing the ovule, and stigmatic pollen germination (Crane et al., 1995). The basic pollination mechanism in angiosperm ancestors can be viewed as a modification and elaboration of the pollination drop mechanism from related gymnospermous plants. The presence of a nontubular style and a stigma of solid tissue replaced the micropyle of related seed plants, perhaps as a consequence of ovular protection (Proctor et al., 1996). Also the presence of an elongate style and stigmatic surface is hypothesized to be a mechanism for maintaining self incompatibility, eliminating the negative genetic consequences associated with self pollination (Scott et al., 1992). Regardless, the generation of an elongate pollen tube by the male gametophyte was a requisite development for pollen on the stigmatic surface to reach the megagametophyte. This feature is related to the increased distance between the two haploid nuclei that was minimized in the pollination drop mechanism. The transition from the pollination drop mechanism to fluid substances secreted by floral nectaries can be considered as nutritionally equivalent and functionally similar (Baker and Hurd, 1968). Interestingly, both sugary sources coexist on modern *Ephedra* and *Gnetum* (Porsch, 1916; Kato and Inoue, 1994), and evidently existed on some cycadeoids (Harris, 1973; Bino et al., 1984). Floral nectaries, very similar to those of angiosperms (Fahn, 1979), are used in the pollination of extant *Gnetum* by siphon-bearing moths (Kato and Inoue, 1994). Additionally, the production of honey from *Ephedra* pollen by bees (Ordetx, 1952) is

functionally mirrored by the attraction of flies to *Welwitschia* by sugary fluids flooding the micropylar tube (Marsh, 1982; Crane and Hult, 1988).

INSECTS: CONSUMERS OF SPORES, POLLEN AND NECTAR

The fossil insect record commences during the Early Devonian (Hirst and Maulik, 1926; Labandeira et al., 1988) but does not become significant until the Early Pennsylvanian when 13 orders of insects appear principally in equatorial wetlands representing both mineral and peat substrates in Euramerica, Angara, and western Gondwanaland (Wootton, 1990). These insects include predominantly predaceous forms such as protodonatan dragonflies, “protorthopterans,” grylloblattodeans, detritivores such as monurans, silverfish and blattodeans, but also many phytophagous forms such as piercing-and-sucking paleodictyopteroids, hypoperlids, and probably orthopterans. Scattered among these Pennsylvanian taxa are spore, prepollen, and pollen consuming species—a dietary trend that was extended to other major groups of insects in more xeric and vegetationally different environments of the Early Permian, particularly in Angara.

Extinct Palynivores of the Late Paleozoic.—Evidence for identifiable insect taxa associated with the consumption of spores, prepollen, or pollen originates from gut contents of two of the best-preserved Late Paleozoic insect localities: Mazon Creek, from the late Middle Pennsylvanian of the Illinois Basin (Moscovian), and Chekarda, from the later Early Permian (Kungurian) of the central Urals in Russia (Carpenter, 1997; Novokshonov, 1998). From Mazon Creek, spores of an unknown pteridophyte (lycopsid, sphenopsid, or fern) in the gut of an unidentifiable diaphanopterid nymph was noted by Kukalová-Peck (1987), as well as lepidodendrolean spores in the gut of the hypoperlid *Eucaenus* (Scott and Paterson, 1984). Related data from dispersed coprolites originate from the Calhoun Coal of the Illinois Basin, although other occurrences are known. For example, indicative of the large size of some arthropod palynivores are Upper

Mississippian and Lower Permian coprolites in which entire sporangia were consumed, initially confused for primary plant structures, but now attributed to unknown arthropod consumers (Meyen, 1984; Rothwell and Scott, 1988).

The most profound data originate from the late Early Permian of Russia, at Chekarda, where five species of insects, representing three orders, have revealed superbly preserved gut contents of pollen and prepollen. Their intestinal contents are referable to peltasperm and glossopterid seed ferns, cordaites, *Ulmannia*-like conifers, and gnetophytes (Rasnitsyn and Krassilov, 1996a, 1996b; Krassilov et al., 1997, 1999), occurring either as largely monospecific accumulations or as mixed assemblages of a few morphotypes, both representing selectivity of prepollen or pollen types. The greatest representation of palynivores is the Grylloblattodea (rock crawlers), a relict order of insects that today are represented by four, monofamilial, wingless genera that feed on insects in cool to alpine, often periglacial habitats of the Northern Hemisphere (Vrsansky et al., 2001). Their current refugial status is distinct from a much greater diversity during the Late Paleozoic and Early Mesozoic, in which they occupied many major habitats, bore wings, inhabited warm-temperate environments, and were palynivores. Forms with gut contents are represented by three families: Ideliidae, Tillyardemiidae, and Tschekardaenigmatidae (Rasnitsyn and Krassilov, 1996a, 1996b; Krassilov and Rasnitsyn, 1999). The second group of insects are the Psocoptera (barklice), which currently are dominantly detritivores and subordinately herbivorous, consist of approximately 33 families, and occur under bark or other cryptic habitats. One member of the Psocoptera at Chekarda, assigned to the Psociidae, contained the pollen of conifers (*Lunatisporites*), cordaites (*Florinites*), and glossopterids (*Protohapoxypinus*) in its gut (Krassilov et al., 1999). The third group of insects, the Hypoperlida, are stem-group hemipteroid ancestors (Kukalová-Peck and Brauckmann, 1992), represented by *Idelopsocus* of the family Hypoperlidae, which were predicted by their prominent rod-like lacinial mouthparts to be pollinivorous (Rasnitsyn, 1980).

Pollen grains in this insect include taxa representing a conifer, a glossopterid, and an unknown gnetophyte (Rasnitsyn and Krassilov, 1996a). The next occurrences of insect gut contents are from the Late Jurassic to mid-Cretaceous, culprits of which are largely referable to modern lineages (Krassilov and Rasnitsyn, 1999).

From a deposit slightly younger than Mazon Creek, there is superb anatomical evidence for the consumption of spores and spore-associated tissues from dispersed coprolites in the Late Pennsylvanian Mattoon Formation (Calhoun Coal) of the Illinois Basin. Excellently-preserved, distinctively shaped coprolites with oxidation rinds, indicating subaerial exposure, occur in coal balls within this deposit and exhibit many features documented in the intestines and fecal pellets of extant pollinivorous insects (Barker and Lehner, 1972; Peng et al., 1985; DeBuck, 1990). These coprolites consist of marattialean fern spores of *Convolutispora* and *Apiculatosporites*, the probable medullosan seed-fern prepollen *Monoletes*, and proportionately very abundant cordaite pollen attributed to *Florinites* (Labandeira, 1998a). The palynomorphs in these coprolites are almost always unfragmented and are recognizable by characteristic internal structure and exine ornamentation. Some coprolites exhibit considerable unidirectional packing, suggesting a final phase of rectal compaction prior to voiding as a fecal pellet. Occasional trichomes, sporangial wall elements, microsporophyll elements, and even foliar tissue indicate the larger context of fructifications and source plants from which the consumed material originated. Most coprolites consist of monotaxic constituents, with some but limited admixture of other palynomorph types. Some coprolites contain fern spores in the tetrad phase, indicating consumption of immature sporangia, a feeding habit found in extant insects (Lawton, 1984). Interestingly, although cordaites are a very minor constituent in the Calhoun Coal flora, they are the overwhelmingly dominant population of palynomorph-bearing coprolites. Marattialean ferns, the dominant floral element, are represented by a relatively small percentage of coprolites. Coprolites with inferred medullosan prepollen, the subdominant floral element, are very

rare, but are consistent with evidence from a paleodictyopteran insect consuming seed-fern prepollen from the bell-shaped sporangium *Bernautilia* (Schopf, 1948; Labandeira, 1998b).

The Current “Big Five”.—Virtually all of the present-day consumers of spores and pollen, as well as the pollinators of seed plants, are members of only five of the 32 orders of insects. They are the Thysanoptera (thrips), an hemipteroid group of small, flower-inhabiting insects, and the four dominant holometabolous orders: Coleoptera (beetles), Diptera (true flies), Lepidoptera (moths and butterflies), and Hymenoptera (sawflies, wasps, ants and bees). This taxonomic spectrum probably has been present since the early Mesozoic, although the proportional representation of each group has varied, of which the most notable is the absence of macrofossil evidence for butterflies, ants and bees before the mid-Cretaceous.

Thysanoptera. Once thought to be relatively unimportant in the consumption of spores or pollen, and pollination, several major studies have documented the importance of thrips as principal pollinators of some plants (Grinfel'd, 1959, Ananthakrishnan, 1993). The range of thrips-pollinated plants include the cool-temperate heaths of northern Europe (Hagerup, 1950), tropical Malaysian dipterocarps (Appanah and Chan, 1981), and modern representatives of Early Cretaceous plesiomorphic lineages such as the Chloranthaceae and Winteraceae (Gottsberger et al., 1980; Luo and Li, 1999), and possibly cycads (Mound and Palmer, 1990; Mound, 1991). In fact, many species of these tiny insects spend their entire life-cycle in flowers transporting pollen grains between flowers by their body hairs (Kirk, 1996). Following the work of Grinfel'd (1959), Kirk (1984) demonstrated a stereotyped punch-and-sucking technique of feeding by thrips on spores and pollen. These minuscule insects bear asymmetrical, stylate mouthparts that have the ability to puncture the grain walls for extraction of protoplasts (Ananthakrishnan and James, 1983; Kirk 1996). The fossil record of thrips extends to the Early Permian (Vishniakova, 1981) and they are represented in Cretaceous and Cenozoic ambers (Zur Strassen, 1973; Larsson, 1978).

Coleoptera. Beetles are the most speciose order of insects and have the oldest fossil record of any major holometabolous group, making their first documented appearance in the Early Permian (Sakmarian). This, together with their consummate associations with varied vascular plants, makes mandibulate beetles the premier group that is associated with fern sporangivory and pollinivory of cycads and many basal clades of angiosperms, particularly tropical to warm-temperate taxa with large, showy, dish-shaped flowers such as the Magnoliaceae, Winteraceae and Nymphaeaceae (Kuschel, 1990). Beetle pollinators often are associated with short-tongued flies, and have perfected the “mess-and-soil” pollination technique in which the transfer of pollen incurs significant structural damage to floral structures, including ovules. Pollination biologists historically have preferred medium- to large sized, flower-loving, adult beetles as the ancestral pollinators of relatively large-flowered, basal angiosperms during their initial ecological expansion (Diels, 1916; Leppik, 1963; Baker and Hurd, 1968). Candidates such as the Staphylinidae (rove beetles), Scarabaeidae (June beetles), Nitulidae-Meligethinae and Brachypteridae (pollen beetles), Buprestidae (metallic wood-boring beetles), Curculionioidea (weevils and relatives), and Chrysomelidae (leaf beetles) have been cited (Grinfel'd, 1975; Crowson, 1981), particularly as they lack the highly-honed pollinator sophistication of advanced flies, butterflies, or bees that includes cues such as petal guide marks, subtle differences in floral aroma, and recognition of ultraviolet and other corollar colors indicating receptivity (Faegri and Pijl, 1980; Proctor et al., 1996). Although the hypothesis of the ancestral angiosperm pollinator as a relatively large-sized beetle is true for a particular suite of floral characters (Grant, 1950; Heiser, 1962), it was displaced in favor of an alternative hypothesis emphasizing small-tongued and bodied flies and, to a lesser extent, thrips, micropterygid moths and tiny beetles as pollinators of even more basal and diminutive angiosperms as Chloranthaceae, Piperaceae, Schisandraceae and other “paleoherbs” (Crepet and Nixon, 1994, 1996;

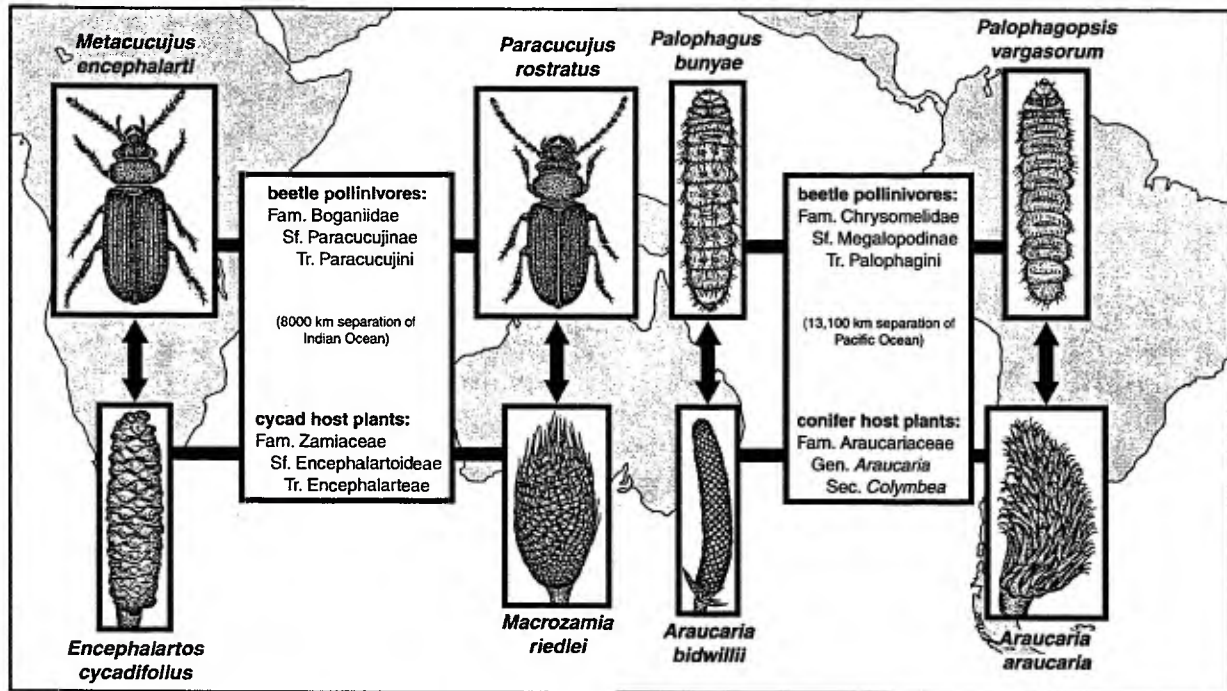


FIGURE 2.—Relict associations between extant beetle pollinators and their cycad and conifer host-plants, indicative of the persistence of Evolutionary Assemblage 3 to the present. These Gondwanan distributions occur on basal clades of both plant and beetle associates that are traceable to the mid-Mesozoic based on various phylogenetic, biogeographical and fossil evidence. Note the relatively low taxonomic level (tribes) of the assignments of the two paired associations at left, between western Australian and South African boganiid beetles and their cycad host plants; as well as the two paired associations at right (tribe, section), between eastern Australia and southern South America chrysomelid beetles and their conifer host plants. Associations are documented in Enrödy-Younga and Crowson (1986) and Crowson (1990) for western Australia/South African couplet, and in Kuschel and May (1990, 1996) for the eastern Australia/southern South American couplet. Abbreviations: Fam = family, Sf = subfamily, Tr = Tribe, Gen = Genus, Sec. = Section.

Dilcher, 1995). These taxa bear small, white, or drab-colored flowers, exhibit a general absence of fragrance and elevated pollen production, bear ovaries located below the level of the petal disk, possess a limited petal and sepal number, and have pollenkitt-covered pollen grains (Lloyd and Wells, 1992; Endress, 1994; Crane et al., 1995). However, this hypothesis emphasizes the pollination of "paleoherbs" which are neither a natural group nor the most basal of angiosperms (Qui et al., 1999),

indicating that insight into primitive modes of angiosperm pollination may reside among even more primitive clades such as the Amborellaceae. Given the generalization of these pollination patterns (see also Waser et al., 1996), they should not be mistaken for the absence of host fidelity during the mid-Mesozoic: cycads and their cycad-weevil pollinators are some of the most specialized and specific of associations known (Norstog and Nicholls, 1997), lineages of which existed prior to

the documented advent of angiosperms based on a variety of evidence (Morrone, 1996; Farrell, 1998; Windsor et al., 1999).

Spore feeding in extant beetles is an important diet that has involved many phylogenetically disparate taxa at both the larval and adult stages (Leschen and Lawrence, 1991; Srivastava et al., 1997). Targeted plant taxa include all major fern groups. Beetle sporivores typically are host-specific and select for either individual spores or entire sporangia; historically they have opted for a nutritionally superb diet compared to more common plant foods such as foliage or sap (Southwood, 1973). Obligate fern sporivory by both larvae and adults occurs significantly among the Cryptophagidae (silken fungus beetles), Mycetophagidae (hairy fungus beetles), and especially among several lineages of the Curculionoidea (weevils and relatives), many of which are primitively fungal-spore feeders and engage in associations that are predominantly secondary reversions to sporivory and not ancestral commitments. Many of the sporivorous beetle lineages associated with fern hosts occur in mid-oceanic islands such as Rapa, Juan Fernandez, and New Zealand (May, 1973; Paulay, 1985; Leschen and Lawrence, 1991), but also occur on continental mainlands (Board and Burke, 1971; Loyal and Kumar, 1977) where evidence indicates that this feeding niche is vacant or undersaturated (Srivastava et al., 1997).

Among the most interesting of biogeographical relationships indicating the antiquity of pollen-consuming beetles are closely related, primitive taxa feeding on the pollen of similarly ancient gymnospermous hosts that are separated by vast oceanic distances (Fig. 2). One example is Chrysomelidae, of which closely-related species from the same tribe feed as larvae and adults on the pollen cones of the same infrageneric section *Colymbea* of *Araucaria* in eastern Australia (*Palophagus bunyae* on *Araucaria bidwillii*) and in the southern Andean region of South America (*Palophagopsis vargasorum* on *Araucaria araucana*) (Kuschel and May, 1990, 1996). These beetle sister-genera are poor dispersers, separated by approximately 13000 km of oceanic distance,

and are distinguished from each other by subtle morphological features (Fig. 2). Similarly, in western Australia, the pollen of the cycad *Macrozamia riedlei* is consumed by *Paracucujus rostratus*, whereas in southern Africa there is a parallel association that exists between the host cycad *Encephalartos cycadifolius* and its pollinivore *Metacucujus encephalarti* (Enrödy-Younga and Crowson, 1986, Donaldson et al., 1995). These two cycad host-plant genera are closely related, belonging to the same tribe (Encephalarteae), as are the two beetle pollinators that are assigned to the same tribe (Paracucujini) of the Boganiidae, even though collectively they are separated by 8000 km and are poor dispersers (Fig. 2; Crowson, 1991; Norstog and Nicholls, 1997). These paired, intercontinental patterns of relatively basal beetle lineages occurring on gymnospermous host plants are duplicated in several other beetle pollinivore lineages, such as relict weevil taxa of the Nemonychidae, Belidae, Brentidae and Curculionidae occurring variously on conifers and cycads, indicating that these associations are ancient and of Mesozoic origination (Kuschel, 1983; Crowson, 1991; Morrone, 1996; Farrell, 1998). These case-studies are particularly compelling because most of these pollinivores or pollinators have low vagility and are intimately, often monospecifically, linked to particular plant hosts.

Diptera. True flies represent a complex spectrum of varied pollination strategies. Spore consumption has not been documented, and only a few lineages are regular and obligate pollen consumers. By far the most anthophilous forms are highly visual nectar consumers from almost every major group within the order and representing virtually every type of angiosperm blossom type, as well as associations with cycads (Breckon and Ortiz, 1983) and gnetaleans (Moussel, 1980; Bino et al., 1984). The suborder Nematocera consists predominantly of delicate, small-bodied forms that bear stylate mouthparts for piercing animal tissues for blood, though many possess a modestly-sized labellum for sponging surface fluids from flowers (Proctor et al., 1996). This is particularly true for taxa such as crane flies (Tipulidae), march flies

(Bibionidae), and virtually all blood-feeding flies with stylate mouthparts in which males lack the requirement of a protein (blood) meal that is essential for egg development. Field observations have established that nectar feeding is present in almost all blood-feeding forms, including black flies, mosquitoes, biting midges, and horse flies (Downes, 1955; Young et al., 1984); additionally, pollen feeding has been documented in the biting midge *Forcipomyia* (Billes, 1941), a regular pollinator of cacao, and the horse fly *Tabanus* (Wilson and Lieux, 1972). Interestingly, the consumption of pollen from wind-pollinated plants is not uncommon (Goot and Grabant, 1970; Stelleman and Meeuse, 1976).

The suborder Brachycera contains some remarkable mouthpart modifications capable of imbibing both nectar and pollen (e.g., Nicholson, 1994). Exemplars are bee flies (Bombyliidae) and hover flies (Syrphidae), which are highly specialized, hovering feeders that are known to imbibe pollen with or without a nectar suspension through a short, expanded proboscis (Leereveld, 1982; Deyrup, 1988; Gilbert, 1981). Fecal pellets of these flies contain concentrated, intact, pollen contents that lack protoplasts (DeBuck, 1990; Haslett, 1989). By contrast, obligate nectar imbibers bear a longer, tubular proboscis with an abbreviated labellum (Gilbert, 1981). Several studies have examined the mouthpart processing and digestion of pollen by syrphid flies, concluding that grain fragmentation is minimal and extraction of nutrients is by enzymatic leaching in the intestine (Gilbert, 1981; Haslett, 1983), similar to bees. Hover flies have been the most investigated dipteran pollinator and exhibit high flower constancy, differential visitation rates, and frequently resemble co-occurring wasps by a convergent black-and-yellow coloration (Kugler, 1950; Parmenter, 1956; DeBuck, 1990). These groups should be placed in a larger dipteran context whereby the overwhelming majority of flies contained in the more apomorphic clades of Brachycera have relatively short mouthparts typically ranging from 0.3 to 1.2 cm long, and bear an expanded, fleshy labellum for sponging exposed and concealed

surface fluids (Grinfel'd, 1955; Gilbert and Jervis, 1998). These anthophilous families are nectar consumers of short-throated flowers. However, it is the "sapromyophilous pollination syndrome" that is the most intriguing of these brachyceran pollination types. This pollination strategy involves flowers that are the color, textural consistency, and odor of carrion, replete with a shimmering surface resembling liquefying flesh. Flies that are lured by all these indicators of rotting flesh often become trapped in the inflorescence from a few hours to days, assuring pollination. This type of flower has originated independently in families as unrelated as the Araceae (arums and relatives), Asclepiadaceae (milkweeds), Aristolochiaceae (birthworts), and members of the family that produces the largest known flower, the Malaysian Rafflesiaceae (Faegri and Pijl, 1980; Ollerton and Leide, 1997).

Lepidoptera. Moths and butterflies are the most phytophagous of all of the four major holometabolous insects. Larvae are typically feeders on leaf tissues, whereas adults are almost exclusively fluid feeders on nectar or other nutrient-rewarding fluids, but rarely on pollen (Downes, 1968; DeVries, 1979). Secondary reversions to almost exclusively spore feeding occurs among the larvae of several externally-feeding lineages, including Oecophoridae, Coleophoridae (casebearers), Tineidae (clothes moths), and Arctiidae (tiger moths) (Needham, 1947; Gibbs, 1979; Owen, 1993; Weintraub et al., 1995). A probable primitive diet of fern spores is known from the basalmost lepidopteran lineage, the mandibulate Micropterygidae (Powell et al., 1999; Sims, 1999), which has a fossil record extending to the Lower Jurassic (Whalley, 1986). Virtually all non-micropterygid adults have mouthparts consisting of a galeal siphon that is relatively uniform throughout the order and designed for uptake of fluids. However, the siphon commonly is lost or de-emphasized throughout the order in nonfeeding species. Functional siphons are coiled at rest due to cuticular ultrastructure, and are extruded, as in the dipteran labellum, by hemolymph pressure (Eastham and Eassa, 1955). A characteristic "knee bend" facilitates penetration

of deep floral tubes, which often ends in head-thrusting movements for extracting the bottom nectar pool, resulting in dusting of the head and proboscis base with pollen (Proctor et al., 1996). This covering of pollen on the lepidopteran body is essential for pollination.

Typical proboscis lengths range from a few millimeters to a few centimeters in small-to-medium sized moths. The longest proboscides are among hawkmoths (Sphingidae), of which the Madagascan species, *Xanthopan morgani* subspecies *praedicta* is 24 cm long. This moth was discovered 40 years after Charles Darwin (1877) predicted that a hawkmoth had to exist that possessed a nectar-seeking proboscis approximately 29 cm long, based on the spurs of the Madagascan orchid, *Angraecum sesquipedale*, that were of equivalent length (Nilsson et al., 1987). Together with functionally similar hummingbirds, hawkmoths are major pollinators of orchids worldwide, and are classic examples of functionally coupled and coevolved flower/pollinator system (Nilsson et al., 1987, also see Jermy, 1999). Whereas the hawkmoth fossil record only extends to the Miocene (Zeuner, 1927), butterflies (Papilionoidea) appear in Late Paleocene deposits (Durden and Rose, 1978), even though the fossil record of all Lepidoptera is atypically poor (Labandeira and Sepkoski, 1993). Butterflies are the other conspicuous group of nectar-consuming Lepidoptera. Unlike large moths, butterflies are diurnal and are more active fliers. They have well-developed color vision, exhibit flower constancy, and respond to color, scent, or physical outline of flowers. The plants pollinated by butterflies or large moths originated during the mid-Cenozoic, during the origin of many extant herbaceous angiosperms.

Hymenoptera. The most specialized group of insect pollinators, with the most wide-ranging mouthpart structures, are the Hymenoptera. Basal groups of this order are included in the Symphyta, some of which possess impressive, mandibulate mouthparts, such as common sawflies (Tenthredinidae) that ingest fern spores (Naito, 1988), xyelid sawflies that consume conifer pollen (Burdick, 1961), and others that house a wealth of

elongate mouthparts for imbibing concealed nectar (Jervis and Vilhelmsen, 2000). Most of the species-level diversity of flower-frequenting taxa are various small wasps (Leius, 1960; Jervis et al., 1993; Tooker and Hanks, 2000), which may represent opportunistic feeding rather than the stereotyped pattern observed in bees (Patt et al., 1997; Jervis, 1998). The larvae of these small wasps overwhelmingly are parasitoids of other insects but as adults feed on floral and extrafloral nectar using a collapsible labiomaxillary complex positioned under the head that bears a short glossa less than a few mm long (Jervis, 1998). This nectar-gathering apparatus independently evolved at least seven times among wasp lineages. One particular group of wasps, the Ichneumonidae, are larger than typical parasitoid wasps and pollinate milkweeds and orchids. Some orchids can explosively eject packets of pollen (pollinia) using a spring-loaded system and a rapidly-setting cementing substance when they contact an ichneumonid body surface. Ichneumonids and other clades of small wasps originated and diversified during the Jurassic (Rasnitsyn, 1988), resulting both in the expansion of parasites and parasitoids attacking insect larvae, as well as the exploitation of sugary exudations of seed plants by the adults (Labandeira, 1997a). Most research, however, indicates that these small parasitic wasps are ineffective pollinators, although one of the classic examples of a highly-honed mutualism is the numerous species of fig wasps (Agaonidae) and their typically monospecific fig hosts (Moraceae: *Ficus*), which are widespread in the tropics (Berg and Wiebes, 1992).

Advanced wasps such as potter wasps, pollen wasps, and hornets of the Vespidae are similar to bees in many respects. They are relatively large, feature hairy bodies, have nesting material requirements, and bear a conspicuously striped abdomen that resembles certain bees. Some of these wasps either consume pollen for nutrition or collect the grains for provisioning their larvae (Hunt et al., 1991; Gess, 1996). Those that provision their brood with pollen use it as a protein meal, which evolutionarily is a replacement for feeding larvae with paralyzed insects, a diet that also occurs

among sphecoids (digger wasps and cicad killers) (Krombein et al., 1999). Wasp clades phylogenetically closest to bees—Vespoidea, Pompiloidea and Sphecoidea—appear during the Late Jurassic to Early Cretaceous (Rasnitsyn, 1988; Carpenter and Rasnitsyn, 1990).

Ants (Formicidae) are a conspicuous and omnipresent group of social insects that dominate the insect ground traffic in almost all tropical and temperate ecosystems. Ants are poor pollinators, lacking body hairs, bearing mouthparts more appropriate for predation or folivory, deficient in essential pollinator behaviors, and secrete antibiotic chemicals that kill pollen (Beattie et al., 1984). In general, ants bypass pollination mutualisms by acting as thieves—robbing plants of foliage, pollen and nectar without transferring pollen to plant-host conspecifics (Beattie, 1985). Nevertheless, ants are notoriously fond of sweet substances, including nectar, honeydew, and evaporating sap flows, and there are ant-pollinated flowers. Ant-pollinated flowers occur in hot, dry climates and typically are self-compatible. Such plants, although rare, are prostrate or low-growing shrubs and herbs that produce flowers adjacent to the stem where cursorial ants have access for limited transfer of pollen during their daily foraging rounds (Peakall et al., 1991). Other ant-pollinated flowers include a few examples of orchids pollinated by winged male ants via pseudocopulation (Peakall et al., 1987). Primitive ants are documented during the mid-Cretaceous (Wilson et al., 1967; Dlussky, 1975) and represent a major transformation in the course of plant-insect associations by offering plant hosts protection from herbivores by virtue of their intrinsically combative nature, in exchange for a domicile. Thus, the absence of ants as pollinators is overshadowed by their defense-guard mutualisms with plants.

No group of pollinating insects has been more researched and written about than bees, and only a cursory review can be provided. Bees, the most important extant group of insect pollinators (Michener, 1974; Roubik, 1989), apparently originated during the mid-Cretaceous. The earliest bee body fossil is an amber stingless bee, *Cretotrigona prisca* (Michener and Grimald, 1988;

Engel, 2000), of probable Turonian age, that is a highly apomorphic taxon of the most derived lineage of bees, the Apidae, which includes bumblebees and honeybees. Additionally, presumptive bee burrows have been described from the Early Cenomanian of Arizona (Elliott and Nations, 1998). This indicates a prior cladogenetic history that is unrepresented as body fossils. This history, however, is documented by Late Cretaceous charcoalfied fossils that are consistent with pollination by several bee clades (Crepet, 1996; Crepet and Nixon, 1998). Additionally, biogeographic evidence suggests an Early Cretaceous radiation for the bees (Michener, 1979), which is supported by the Gondwanan distribution of stingless bees (Apidae: Meliponinae) in tropical Australia, Africa, and Central and South America (Roubik, 1989). The most plesiomorphic lineages of bees are the families Colletidae (plasterer bees) and Andrenidae (andrenid bees) which typically possess short glossae and stereotyped behavior (Linsley and McSwain, 1959), unlike the most apomorphic families, Megachilidae (leafcutting bees), Anthophoridae (carpenter bees) and Apidae, which have long glossae for probing into deep flowers and have varied behaviors (Roubik, 1989). However, the mapping of colony organization does not correspond to an apomorphic-to-plesiomorphic axis, and varies from solitary, communal, subsocial, and eusocial types across the larger bee clade. Evidently all of the types of colony organization, major behavioral repertoires, and mouthpart types were in existence during the Eocene (Zeuner and Manning, 1976; Taylor and Crepet, 1987).

Pollen is the principal source of protein, fats, minerals, and vitamins for bees and many vespid wasps (Parker, 1926; Grogan and Hunt, 1977; Jones and Bryant, 1996). The fate of pollen and nectar after removal from a flower has been investigated intensively by apiculturists (Crailsheim, 1988). Ironically, knowledge of the degradation of modern pollen, particularly in the intestinal tract of the domesticated honeybee, *Apis mellifera*, one of the most specialized of pollen consumers, can be informative about the origin of primitive palynivores during the Late

Pennsylvanian and Early Permian. In nectar-seeking bees, angiosperm pollen frequently is attached to the upper mouthparts, head, various parts of body vestiture, and packed in femoral corbiculae (Thorp, 1979). Entomophilous pollen frequently is highly ornamented with teflon-like structures such as spines and rods, contains sticky pollenkitt coatings for clumping (Hesse, 1978), and often is connected to special structures such as viscin threads that facilitate attachment to insects (Faegri and Pijlk, 1980). Once grains are removed from the flower, they are degraded by ultraviolet radiation, desiccation, and the rigors of physical transport. After mixture with nectar and enzymes secreted by the bee's salivary glands, pollen protoplasts can leach out of their pollen grains without interruption of the pollen wall (Barker and Lehner, 1972). Although much of the examined intestinal pollen in honeybees remains mechanically intact and even unabraded, each grain is enzymatically degraded by having their protoplasts emerge through germination pores or other comparatively thin sites (Whitcomb, 1929; Peng et al., 1985). The sources of this enzymatic breakdown can be external from proteolytic salivary secretions in the gut (Hunt et al., 1991) or internal from the pollen protoplasts (Grogan and Hunt, 1979). There is evidence for "osmotic shock," which is caused by the transfer of pollen from the crop rich in nectar or honey, characterized by high osmolarity, to the much lower osmolarity of the ventricular region in the anterior intestine, resulting in some pollen wall fragmentation (Kroon et al., 1974). However, this may be relatively uncommon because most pollen types have sturdy, thick walls and are not susceptible to osmotic shock (Klungness and Peng, 1984), including fern spores and wind-dispersed pollen that can form a significant dietary component (Sharma, 1970; Chaloner, 1976). Additionally, the prolonged presence of pollen in the crop can impart a certain wall flexibility, such that movement to the ventriculus avoids fragmentation. After this pollen bolus is passed to the rectum before voiding as a fecal pellet, the presence of wall flexibility allows for compressed packing.

Lesser Players.—Many adult insects from orders other than the five mentioned above are visitors to flowers, only some of which regularly consume pollen or imbibe nectar (Faegri and Pijl, 1980). The association of insects with flowers extends to predators that use camouflage and concealment to ambush prey and to nonpredaceous species that inhabit flowers as convenient domiciles. Thus, for biotic pollination to occur, there must be a definite relationship between flower host and potential pollinator, rather than a serendipitous possibility for pollination by wind or other abiotic agents. Some of the best documented pollinivores are springtails (Collembola) based on gut-content examinations (Marshall, 1978; Waldorf, 1981), but are poor pollinators. Certain tropical cockroaches (Blattodea) are known to imbibe nectar (Proctor et al., 1996) and are documented as pollinators (Nagamitsu and Inoue, 1997). Grasshoppers (Orthoptera) occasionally feed on pollen (Grinfel'd, 1957; Schuster, 1974), and can consume 100 percent of their diet as pollen (Grinfel'd 1962), particularly for the plesiomorphic Tettigonoidea (Grinfel'd, 1957). Stoneflies (Plecoptera) may be significant in the pollination of several unspecialized European flowers, including rose and buttercup (Porsch, 1958). Caddisflies (Trichoptera) are surface-fluid feeders that occasionally feed on nectar (Peterson and Hasselrot, 1994; Nozaki and Shimada, 1997) and possess fleshy proboscises that structurally parallel the dipteran labellum. Scorpionflies (Mecoptera) bear small mandibulate mouthparts set on the terminus of a hypognathous rostrum. The mecopteran rostrum is an extension of the cranium and mouthparts, and scorpionflies have been observed to feed on deep-seated nectar in tubular flowers (Pigott, 1958). Perhaps this inventory of flower visitors, some nectarivorous and others pollinivorous, is indicative of a potential for favoring anthophily that resides in many insect taxa that are not considered "typical" pollinators.

POLLINATION AS A MUTUALISM

Pollination is the process by which a spore containing a male gametophyte (pollen grain) is

transferred from a microsporangium or pollen organ to the receptive area of an organ containing the female gametophyte (ovule). In both gymnosperms and angiosperms, pollination can be effected by wind, water, or animals, although zoophilous pollination typically requires certain rewards that are provided to pollinators. These rewards include nectar, pollen itself, resins, oils, food bodies, fragrances, and concealed structures for shelter and mating (Simpson and Neff, 1983; Belokobylskij and Jervis, 1998). Most statements indicate that pollen historically was the initial reward that resulted in the pollination mutualism (Crepet, 1979). However, for the pollination mutualism to be successful, rewards ("alternative bait") for insects had to be balanced by a plant-host defense system to contend with unacceptable levels of insect damage (Eisikowitch, 1988). This tradeoff was compounded by the juxtaposition within a hermaphroditic flower of transportable pollen and consumable ovular and other tissues, resulting in an intricate balancing act that was elaborated by reciprocal genetic feedback between the plant host and insect pollinator (Crepet, 1979; Dilcher, 1995). Among modern seed plants that have fine-tuned this system of simultaneous predation and pollen transfer are the classically studied pollination systems of yuccas and yucca moths, cycads and cycad weevils, and most recently tanglevein flies and their deep-throated host plants. All three are exemplars of the role of intricacy in the evolution of mutual benefit. These finely-tuned examples illustrate the view by Schoonhoven and his colleagues (1998, p. 315) that pollination "...is probably the most spectacular large-scale example of mutualism in the living world."

Yuccas and Yucca Moths.—Yuccas are shrubby or arborescent, monocotyledonous plants in the family Agavaceae that occur typically on the deserts and xeric grasslands of southwestern North America. They are pollinated by several genera of the lepidopteran family, Prodoxidae (yucca moths), and are a textbook example of a mutualism in which the adults are highly host-specific, beneficial pollinators while their larvae are predators on the seeds of the same *Yucca* species (Fig. 3). Interestingly, adult yucca moths do not feed even

though nectar is produced; however, they do have specialized mouthparts, including a specialized and prehensile appendage of the maxillary palp, that gather *Yucca* pollen and mold it into clumps to be deposited on other conspecific host plants. The pollination cycle of the yucca moths involves pollen extraction followed by flight from the flower, the seeking of another conspecific inflorescence, the subsequent insertion of an egg in a suitably mature and non-oviposited ovule, and followed by ascent to the stigma of the same flower, on which previously collected pollen is deposited on its surface. Considerable recent work has established several new associations between newly described yucca moths and their *Yucca* hosts, including bogus yucca-moth species that cheat on host species by depositing eggs on seeds during earlier or later stages of ovary development, without effecting pollination.

Based on mtDNA phylogenies of the Prodoxidae and *Yucca*, Pellmyr and Leebens-Mack (1999) have been able to trace associations between these two coevolving taxa to 41.5 ± 9.8 Ma (Fig. 3). The earlier phylogenetic split between the Prodoxidae and its sister-group lineage, both endophytic seed or bud borers, occurred at approximately 95 Ma, during the Cenomanian. After this event, several new prodoxid lineages evolved on dicots, principally Rosaceae and Saxifragaceae, during the Late Cretaceous (Pellmyr et al., 1996a). The third bifurcation within the prodoxid lineage colonized woody monocots during the early Paleogene, currently represented by *Mesepiola* on *Nolina* (Nolinaceae) and *Dasyilirion* (Agavaceae), and the fourth shortly thereafter with colonization of *Yucca* during the Eocene with the emergence of *Prodoxus* pollinators. Subsequently, new genera of *Yucca* pollinators, first *Parategeticula* and then *Tegeticula*, rapidly came into existence between 35.6 ± 9.0 to 3.2 ± 1.8 Ma. Within *Tegeticula*, highly apomorphic species associated with capsular rather than berry fruits quickly evolved cheating behaviors that circumvented pollination while maintaining larval consumption of plant-reproductive tissues either early (early cheaters) or late (late cheaters) during ovular maturation

(Pellmyr et al., 1996b). The latest round of prooxid diversification is associated with *Yucca* hosts at the northern periphery of their geographical range and has been linked to Pliocene aridification. The most likely model of this plant-insect association is initial host-plant speciation followed by colonization by yucca-moth pollinators (Pellmyr and Leebens-Mack, 1999). This pattern shows plant and pollinator codiversification, but no congruent phylogenetic topology owing to delays in pollinator colonization of *Yucca* hosts. This conclusion rejects one-for-one parallel cladogenesis documented in other studies, but strongly demonstrates the evolutionary stability of such mutualisms over tens of millions of years.

Cycads and Cycad Weevils.—By contrast with yuccas and yucca moths, other pollinator associations are much older, based on biogeography, phylogenetic evidence, or fossil documentation. The most notable of these ancient associations are cycads and their host-specific pollinators. Although several other phylogenetically basal and otherwise relict taxa from holometabolous groups occur on conifers, such as the Agathiphagidae (Lepidoptera, on *Agathis*) and Xyelidae (Hymenoptera, on *Pinus*), it is among the herbivorous and especially pollinivorous Coleoptera where most of the associations between nonangiospermous seed plants and basal insect clades occur. Previous examples have been mentioned from the Boganiidae on Zamiaceae and the Chrysomelidae on Araucariaceae (Fig. 2), although there are many taxa from other basal families of the Chrysomelidae (Aulacoscelinae) and Curculionoidea (Belidae-Pachyurinae, Nemonychidae, Allocoryninae) that occur on conifer and cycad taxa (Forster et al., 1994; Morrone, 1997; Farrell, 1998).

The life-cycles of many cycad-associated beetles have common themes in localities as wide-ranging as Central America, Australia, and southern Africa. Cycads produce nutritional rewards to beetles, especially their larvae, in the form of foliage and especially male or female cone tissues. These cone tissues occur in the receptacular axis, sporophylls, and ovular structures including the integumentary layers and even megagametophytes

(Donaldson, 1992; Fawcett and Norstog, 1993; Oberprieler, 1999). Either the male or female cones of a species can serve as the locus of larval feeding and later pupation, with subsequent emergence of the pupated adult evidenced by an exit hole, usually on the base of a sporophyll. Male and female cones occur on separate plants and are essentially closed structures, although the sporophylls of a few species open briefly and expand outward, exposing the ovules. For male cones, typically a pupated female beetle emerging from its pupal chamber in the cone tissues negotiates through the basal region of the cone and collects pollen on her hairy integument as she brushes along pollen sacs prior to a flight to other male cones for oviposition or feeding. Frequently the female beetle is diverted to nearby female cones, often by attraction to fruity or other odors. This insures pollination, after which the female beetle oviposits into other conspecific male cones to resume the beetle life cycle. In cases where the female cone is the center of larval development, larvae frequently feed on ovular integumentary tissue, and often the host plant sacrifices some megagametophytic tissue—the nutritional equivalent of endosperm in angiosperms—for pollinator survival. The process is modified after beetle emergence, with visits to occasional male cones, resulting in the collection of pollen before females oviposit on other female cones. In cycads, the specific site at which pollination occurs is among the spaces between the base of the megasporophylls and the adjacent receptacular surface, where beetles “tunnel” once they have gained access through landing on sterile, open sporophylls usually at the base of the cone (Norstog et al., 1995, fig. 5). The presence of a pollination drop mechanism may serve as a nutritional inducement to the beetle and as a sticky substance removing pollen from the insect’s body.

This configuration of an enclosed space between the ovular micropyles and the cycad megasporophyll bases is similar in position to that found in the enclosed bisporangiate cones of the Bennettitales, especially the family Cycadeoidaceae (Crepet, 1974; Donaldson, 1992). In *Cycadeoidea*, the cones had a central conical to columnar receptacle, but unlike cycads, they bore

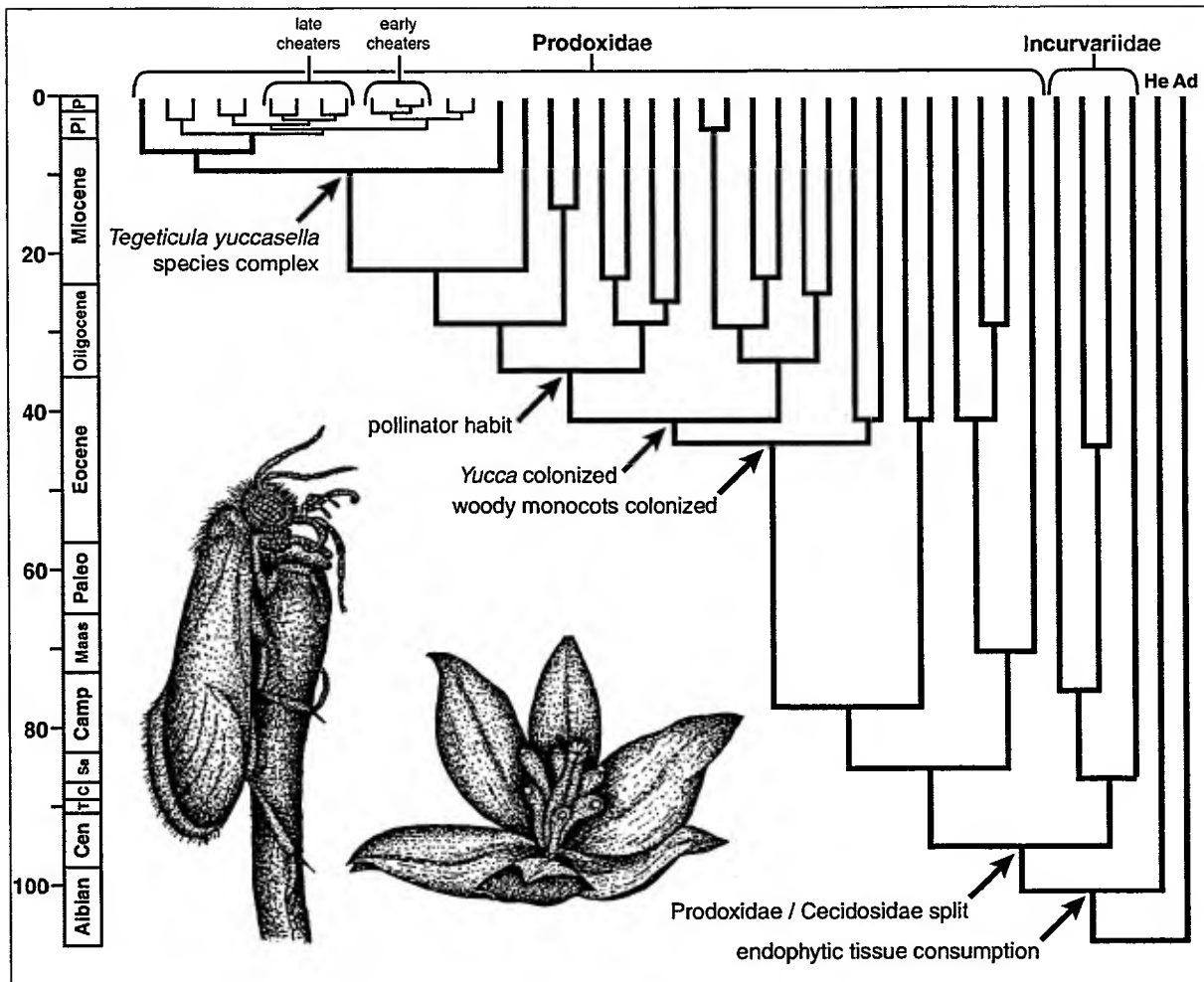


FIGURE 3.—The major phylogenetic events leading to various yucca-yucca moth associations in southwestern North America, indicative of an association assignable to Evolutionary Assemblage 4 (from Pellmyr and Leebens-Mack 1999). The phylogeny of the moth superfamily Incurvarioidea is shown, based on mitochondrial DNA sequence data, with neighbor-joining and maximum-likelihood trees having identical topology (see Pellmyr and Leebens-Mack [1999] for details). The family Cecidosidae is omitted because of its evolution at a high rate when compared to other taxa of the analysis. Note various associations between yucca moths (Prodoxidae) and their host plants, dicots for basal taxa, monocots for more derived taxa, and culminating in the varied associations between *Yucca* (Agavaceae) and the pollinating genera *Prodoxus*, *Parategeticula*, and *Tegeticula*, including the evolution of two, highly derived lineages of nonpollinating cheating moths (bogus yucca moths). Illustrations display the pollination of *Yucca* by *Tegeticula* at left and the receptive stigmatic surface of *Yucca* at right. Dates of clade bifurcations are based on rate substitution data that were calibrated to fossil occurrences. Abbreviations: Ad, Adelidae; Camp, Campanian; Cen, Cenomanian; C, Coniacian; He, Heliozelidae; ; Maas, Maastrichtian; Paleo, Paleocene; P, Pleistocene; PI, Pliocene; Sa, Santonian; T, Turonian.

pedunculate ovules interspersed among sterile interseminal scales. Emerging from the base of the ovular receptacle were large pinnate microsporophylls that extended outward from the cone's median axis, but loop back toward the receptacle, each clasping its base and revealing numerous pollen-laden microsporangia attached to lateral pinnae. This structure evidently remained closed and enveloped the central ovulate receptacle. Surrounding the cone were adpressed bracts, which, together with the enrolled microsporophylls, indicate that *Cycadeoidea* cones were closed and not susceptible to wind pollination. This interpretation is bolstered by evidence of insect-damaged tissues adjacent to the normal space between the micropylar tips of the ovules and the adjacent microsporophyll parenchymatic tissue, indicating beetle pollination (Delevoryas, 1968; Crepet, 1974). This implies entry into the cones via openings between adjacent bracts and microsporophylls, consumption or at least transportation of pollen, and then feeding on microsporophyll parenchyma or excess pollination drop fluid along the ovulate receptacular surface. This condition of a closed reproductive structure—curved microsporophylls and bracts and ovules with only micropyles exposed internally—is typical of beetle pollination in basal angiosperms (Heiser, 1962; Gottsberger, 1988; Armstrong and Irvine, 1989). It also may have assured faithful pollination rather than protecting the microsporophylls from predation (Crepet, 1979). This pattern of damage is geographically widespread and probably represents a beetle/cycadeoid association during the Late Jurassic to mid-Cretaceous. Repeated and similarly damaged cycadeoid tissues have been documented from cones found in the western United States (Delevoryas, 1968; Crepet, 1974); Japan (Saiki and Yoshida, 1999), Poland (Reymanowna, 1960), and India (Bose, 1968). Interestingly other extinct gymnospermous lineages had similar beetle associations including a probable pentoxylalean from the Late Cretaceous of Japan, in which a beetle larva was found within a seed (Nishida and Hayashi, 1996), and an extinct lineage of Pinaceae from the Early Cretaceous of Russia that bears

frass-filled galleries within its cone axis, caused probably by a bark beetle (Falder et al., 1999).

Angiosperms and Tanglevein Flies.—One of the most amazing associations, with implications for the preangiosperm fossil record of pollination, is the relationship between long-tongued tanglevein flies (Nemestrinidae) and their southern African host plants, members of the Iridaceae, Geraniaceae, and Orchidaceae. The most studied taxa, *Prosoeca peringueyi* and *Moegistorhynchus longirostris*, are active in late Winter and Spring of the Cape Province, pollinating purple to crimson, odorless flowers with exceptionally long perianth tubes that contain copious, sugary nectar at their bases (Manning and Goldblatt, 1996). Tanglevein flies in this region have a labellum from 20 to 90 mm long that is often considerably greater than total body length. Twenty-seven species from the *Iris*, *Geranium*, and orchid families are pollinated obligately by these two nemestrinid species rendering them as “keystone” species. Pollen deposition on their bodies occur on five exclusive sites, each of which may be competitively favored or disfavored based on the presence of pollinating competitors. Other long-tongued brachyceran flies comprise this pollinator guild, including the pangioniine tabanids (horse flies), acrocerids (small-headed flies), and vermilionids (wormlions) (Ludwig et al., 1996; Manning and Goldblatt, 1996, 1997). Apparently this guild of long-tongued flies is the local pollinator equivalent of hawkmoths. Members of these plesiomorphic brachyceran families occur in other regions and are nectar feeders, although they typically lack elongated mouthparts (Mackerras, 1925; Bernardi, 1973).

This spectrum of long-tongued pollen foragers is encountered in several deposits from the Late Jurassic and Early Cretaceous that contain long-tongued Nemestrinidae, Tabanidae, and Apioceridae (also designated as “protapiocerids”) (Yeates and Wiegmann, 1999). These deposits are the earlier Late Jurassic of Karatau, in Kazakhstan; later Late Jurassic Solenhofen from Germany; the earlier Early Cretaceous from the Yixian Formation of northeastern China; and the later Early Cretaceous from Baissa in the Transbaikalian Region of

Russia (Handlirsch, 1906-1908; Rohdendorf, 1968; Bernardi, 1973; Ren, 1998; Mostovsky, 1998). The proboscides of these fossil flies, when present, typically are elongate and designed for nectar imbibation; additionally, the recurved marginal veins of the wing apex suggest hovering flight, also indicative of nectarivory. Their bodies often bore a hairy vestiture typical of pollinators. Notably, these mid-Mesozoic forms occur in deposits that either antedate the advent of angiosperms, or if contemporaneous with angiosperms (Sun et al., 1998), were relict Late Jurassic holdovers (Luo, 1999) that occur in deposits lacking deep-throated angiosperm flowers (Labandeira 1998c). Deep-throated flowers do not occur until a few tens of millions of years later during the Late Cretaceous (Rayner and Waters, 1991; Zaitzev, 1998). The temporal occurrence of these brachyceran flies most likely indicates pollination of seed plants with a pollination drop mechanism (Labandeira, 1998c).

EVOLUTIONARY ASSEMBLAGES

One way of assembling and interpreting the wealth of fossil data on insect consumption of spores, prepollen and pollen, and of evidence for pollination, is to produce a matrix of insect consumers and source plant hosts using all five types of evidence (Fig. 4, Table 1). While not exhaustive, this matrix indicates that the history of palynivory and pollination can be characterized as four discrete evolutionary assemblages, initially suggested by Labandeira (1998b). These temporal suites of associational data are essential for illuminating the historical fits and starts of palynomorph consumption among a wide variety insect lineages, representing distinctive higher-level taxa from the extinct Paleozoic and extant Modern Insect Faunas. These assemblages also temporally delimit clusters of higher-level plant-host taxa associated with these insect lineages.

Assemblage 1: Primitive Vascular Plants and Unknown Arthropods.—Recent data from the latest Silurian to mid-Devonian land floras has revealed that live plant-spore consumption is one of, if not the earliest, primary feeding habit in terrestrial

arthropods. This contrasts with Southwood's (1973) proposal in which detritivory is primitive and predation on the protein- and lipid-rich contents of spores is thought to be the principal dietary conduit to the nutritionally challenging and subsequent hurdle of herbivory (Shear and Kukalová-Peck, 1990). The consumption of spores during this early interval is revealed by the presence of well-preserved, dispersed coprolites that occur among the earliest, well-documented sediments containing some of the earliest known land plants. These coprolites, from Wales in Europe and Gaspé in Quebec (Edwards et al., 1995; Hotton et al., 1996), are distinctively shaped fusiform and cylindrical structures of granulose texture, some of which are almost monotaxic assemblages of spores, as opposed to other coprolites from the same deposits that are more erratically-shaped and consist of platy or twisted plant fragments representing resistant stem or root tissues and occasional spore material (Edwards 1996). Contents of the spore-bearing coprolites are attributable to rhyniophytes, lycopsids, "trimerophytes," and unknown plant taxa. The arthropod consumers of these spores remain unknown, in part, because of the absence of suspect, co-occurring insects, myriapods or other arthropods. Modern descendants of arthropod taxa that are known to occur in similar penecontemporaneous deposits consume fungal spores and pollen, including Collembola (springtails) and Zygentoma (silverfish) (Kevan and Kevan, 1970; Kraus and Kraus, 1994).

Assemblage 2: Ferns, Seed Plants and the Paleozoic Insect Fauna.—The interval during the Early Carboniferous to Late Permian consists of considerably more evidence for spore feeding, but also provides direct data for the consumption of prepollen and pollen, and suggestions that pollination mutualisms also may have been present (Fig. 1). The type of evidence for Assemblage 2 is diverse, but principally dispersed coprolites in Late Pennsylvanian Euramerican coal-ball deposits, especially the Illinois Basin (Scott and Taylor, 1983; Labandeira 1998a), and gut contents in the mid-Permian Chekarda locality of Uralian Russia. The list of targeted later Pennsylvanian plants

consists of spore-bearing lycopsids, marattialean ferns, prepollen-bearing medullosan seed ferns and cordaites. For the mid-Permian, the consumed seed plants include conifers, glossopterids, peltasperms, and gnetophytes. The differential representation of source plants between their abundance within the local community and their representation as coprolites is striking during the Late Pennsylvanian, indicating palynivore specificity on rare cordaite plants within a swamp forest dominated overwhelmingly by marattialean tree ferns. Many of the populations of these dispersed coprolites consist of almost monotaxic contents, with occasional “extraneous” grains of other palynomorphs and incorporation of foliar or other reproductive organ tissues such as sporangial annuli, microsporophyll fragments, and trichomes. Insect culprits responsible for consumption of Middle and Late Pennsylvanian palynomorphs are known poorly because of the dispersed nature of the coprolites. These insects probably are diaphanopteroideans, “protorthopterans,” and ancestral hemipteroid groups such as the Eucenidae and Geraridae, based on mouthpart structure and poorly-preserved gut contents from soft-bodied insect fossils from the slightly older Mazon Creek deposit (Richardson, 1980; Scott and Taylor, 1983; Kukalová-Peck 1987).

By contrast, the pollen contents retrieved from the guts of insects at Chekarda, Russia, have resulted in exact identifications for insect culprits. This list includes five species of insects with mandibulate mouthparts, two of which were predicted to be pollinivorous prior to their discovery of gut contents (Rasnitsyn, 1977, 1980; Rohdendorf and Rasnitsyn, 1980; Labandeira, 1997b). The suggestion was made by Rasnitsyn and Krassilov (1996b) that some of these pollinivores also pollinated seed plants. This evidence for this is largely circumstantial. The presence of probable aromatic glands near the reproductive organs of certain Permian cycads and seed ferns (Halle, 1929; Mamay, 1976), and the occurrence of a specialized tissue that probably decomposed to form fluids that collected in the pollen chamber below the micropyle of the conifer *Fergliocladus*, also lends support to the presence

of pollination mutualisms (Archangelsky and Cuneo, 1987).

Assemblage 3: Seed Plants and the Earlier Phase of the Modern Insect Fauna.—The existence of pollen consumption and pollination has been demonstrated for Assemblage 3. This is based on biogeographical distributions, phylogenetic analyses, and ecological evidence of surviving lineages (Fig. 2), but especially on the presence of gut contents, mouthpart morphology and floral reproductive structures from the relevant fossil plant hosts and pollen-associated insects. Much of this assemblage, spanning the Middle Jurassic to the present, is extinct, particularly plant hosts such as: the Bennettitales; the seed-fern lineages of *Crystospermales*, *Caytonales* and *Pentoxylales*; the conifer groups *Cheirolepidaceae* and *Voltziales*; and various high-ranked gnetophyte taxa (Fig. 4). The best case for earlier, Triassic, occurrences of insect pollination in advanced seed plants has been offered by Cornet (1989, 1996), who proposes a suite of reproductive characteristics in two advanced anthophyte species consistent with the insect transfer of pollen.

By contrast, almost all of the higher-level and many of the lower-level insect lineages that have persisted to the present indicate palynivore, nectarivore or pollinator host switching rather than a parallel demise with ancient host plants. These surviving insect taxa include nemestrinid, tabanid and apiocerid flies, chrysomeloid and curculionoid beetles, and xyelid sawflies (Krassilov and Rasnitsyn, 1983; Ren, 1998; Farrell, 1998), although an exception is a proplangiopsid grasshopper with cheirolepidaceous *Classopollis* pollen in its gut (Krassilov et al., 1997a, 1997b). The associations between these pollinivorous or nectarivorous insect taxa and extinct seed plants may have been generalized, opportunistic, and readily transferable to angiosperms as they diversified during the mid-Cretaceous (cf. Labandeira et al., 1994, but see Willemstein 1987). Character-state evidence from mouthpart structures supports the presence of pollinivory as a plesiomorphic feeding style in some basal holometabolous groups (Kristensen, 1995), features of which have occur in basal Coleoptera

(Lawrence, 1999), Hymenoptera (Vilhelmsen, 1996), and Lepidoptera (Kristensen, 1984). Also, the three major lineages of modern seed plants—conifers, cycads, and gnetophytes—provide understanding of how the preangiospermous associations of Assemblage 3 may have functioned: the instructive consumption by flies, wasps and moths of fluids exuded by pollination drop mechanisms, and beetle pollinivory and pollination in strobili where external access is limited. Although only four extant lineages of nonangiospermous seed plants persist today, based on fossil evidence alone, the variety of pollination strategies was undoubtedly much greater than extant descendants would suggest (Harris, 1973, Pederson et al., 1993).

Assemblage 4: Angiosperms and the Later Phase of the Modern Insect Fauna.—The most recently evolved and familiar assemblage of host-plants and their insect palynivores and pollinators are angiosperms and their corresponding associations with the “big five” insect groups previously discussed (Grant and Grant, 1965; Armstrong, 1979; Ollerton, 1999). The importance of these major interacting plants and insects has been profound during the past 130 million years, if for

no other reason than flowering plants and holometabolous insects essentially have monopolized almost all of the terrestrial (and many freshwater) habitats during this interval. This expansion was launched during the radiation of the earliest angiospermous clades, including the Amborellaceae, Winteraceae, and Chloranthaceae—also encompassing the most plesiomorphic of extant angiosperms (Crane et al., 1995; Soltis et al., 1997; Qiu et al., 1999)—and probably pollinated by small flies with short proboscides, thrips, primitive moths and occasionally small beetles, based on knowledge from the pollination ecology of their extant descendants (Gottsberger et al., 1980; Pellmyr et al., 1990; Lloyd and Wells, 1992; Dilcher, 1995). (Curiously in some analyses [e.g., Qiu et al., 1999] the Ceratophyllaceae (hornworts), a water pollinated group, are the basalmost angiosperm lineage.) Soon thereafter, more conspicuous, comparatively large, and heavily scented flowers of the Magnoliales and Laurales established the large-beetle, mess-and-soil, pollination strategy (Grant, 1950; Gottsberger, 1988).

All of the known early associations of Assemblage 4, documented from the mid-Cretaceous to the K/T boundary are still extant at

Figure 4 (Opposite).—A matrix of vascular plants, insects, and their associations for palynivory and pollination, placed in geochronological context. This matrix details the four evolutionary assemblages of palynivores, pollinators, and their host plants that are distinct at the highest taxonomic levels, discussed in Labandeira (1998b). Fossil plant and animal taxa at top are those that display evidence for plant-insect associations, based on direct or indirect evidence from dispersed coprolites, gut contents, plant reproductive biology, insect mouthpart structure, plant damage, and modern taxonomic affiliation. Thin horizontal connectors are well-supported associations from identified insects with known plant palynomorphs as gut contents. Plant taxa with asterisks are spores or pollen; a few Paleozoic taxa refer to form-genera of plant organs with known whole-plant taxonomic attributions. Taxa persisting to the present are indicated by bold vertical links, solid for confident and dashed for probable identifications; grey and black links are assignable to Assemblages 3 and 4, respectively. The arthropod culprits of Assemblage 1 remain unknown and probably include arthropods other than insects. This compilation is not complete for reasons of space but includes most of the prominent studies. Time scale abbreviations: Silur. = Silurian; Miss. = Mississippian (or Early Carboniferous); Penn. = Pennsylvanian (or Late Carboniferous); Neog. = Neogene.

TABLE 1.—Evolutionary Assemblages of Insect Palynivores and Pollinators and Their Host Plants.

Assemblage	Known Intervals	Major Interacting Taxa		Major Type of Evidence	Localities	References
		Plants	Insects			
1	Late Silurian to Mid-Mississippian	rhyniopsids ferns	[unknown]	dispersed coprolites	Wales, UK; Gaspe, Quebec	Edwards et al. 1995; Hottone et al. 1996
2	Middle Pennsylvanian to Late Permian	ferns medullosans glossopterids cordaites gnetophytes	Diaphanopteroidea Protorthoptera Grylloblattida Hypoperlida Psocoptera	gut contents, dispersed coprolites, mouthpart morphology	Chekarda, Russia; Mazon Creek & Berryville, Illinois	Kukalová-Peck 1987; Scott et al. 1992; Rasnitsyn & Krassilov 1996a; Labandeira 1998
3	Late Jurassic to Recent	cycads bennettitaleans gnetophytes conifers	Orthoptera Coleoptera Diptera Hymenoptera	gut contents, plant damage, mouthpart morphology	Karatau Kazakhstan; Baisa, Russia; Black Hills, South Dakota	Delevoryas 1968; Crepet 1972, 1974; Krassilov et al. 1997; Ren 1998; Farrell 1998
4	Early Cretaceous	angiosperms	Thysanoptera Coleoptera Diptera Lepidoptera Hymenoptera	floral morphology, gut contents, mouthpart morphology	Orapa, Botswana; Skane, Sweden; New Jersey & Tennessee, USA; Dominican Republic	Crepet & Taylor 1985; Friis 1985; Michener & Grimaldi 1988; Rayner & Waters 1991; Grimaldi et al. 1994

lower taxonomic levels (Fig. 4; Crepet, 1996; Crepet and Nixon, 1998; also see Ollerton, 1996), indicating persistence in the face of major angiosperm host turnover (Johnson et al., 1989) and insect herbivore extinction (Labandeira et al., 1999). This includes both earlier small-flowered “paleoherb” and later larger-flowered magnolialean pollination types, inferred to be insect pollinated (Basinger and Dilcher, 1984; Crepet and Friis, 1987; Endress, 1994). During the Late Cretaceous there is strong evidence for associations such as resin collecting by pollinating leafcutting and stingless bees on clusiaceous flowers (Crepet and Nixon, 1998); the presence of pollinator-associated viscin threads draped over pollen clumps on stigmatic surfaces of ericalean flowers, suggesting bee pollination (Crepet and Nixon, 1998); *Calycanthus*-type flowers indicating beetle pollination; and ericalean-thealean-ebenalean taxa

with floral nectaries, enlarged stigmas, and pollen in loose clusters, indicating buzz-pollination by bees (Crepet, 1996; Crepet and Nixon, 1996, 1998). This interval, based mostly on floral data from the Turonian of New Jersey, is associated with expanding angiosperm diversification that involved the earliest known occurrences of some relatively specialized pollinator associations (Crepet, 1996), although family-level insect-diversity data indicate that these associations occurred earlier (Labandeira and Sepkoski, 1993). Many of the highly specialized, largely faithful mutualisms of today, including yuccas and yucca moths, the intricate variations of orchid pollination, and others probably originated during the Early Cenozoic (Fig. 3; Taylor and Crepet, 1987; Pellmyr and Leebens-Mack, 1999), although they are in the minority (Waser et al., 1996). Lastly, there have been secondary reversions in numerous

phylogenetically unrelated lineages to spore feeding on ferns, especially in Coleoptera, Lepidoptera, and some basal Hymenoptera, reflecting use of a typically Paleozoic food resource made possible by the radiation of polypodiaceous ferns during the later Mesozoic and Paleogene.

CONCLUSIONS

There are five major conclusions that result from this review. They address the origin, timing of diversification, and participants involved in the fossil history of spore, prepollen, and pollen consumption, as well as the emergence of pollination as a mutualism.

(1) The consumption of spores is an ancient feeding strategy of terrestrial arthropods and extends from the latest Silurian to the present day. The earliest evidence for prepollen and pollen consumption by insects is Late Pennsylvanian, at which time there was considerable targeting of certain plant hosts such as cordaites and marattialean tree ferns.

(2) There were multiple and iterative origins of feeding by disparate insect taxa on spores, prepollen, and pollen that were produced by diverse lineages of vascular plants. Numerous lineages of interacting insect consumers and consumed plant hosts have developed in time and space, although virtually all Paleozoic groups are extinct and most Mesozoic groups have survived to the present.

(3) The fossil record of spore, prepollen, and pollen consumption is divisible into four distinctive evolutionary assemblages. The first and earliest is poorly known, consists of primitive land plants, and lacks any credible arthropod suspects. The second is better documented and is represented by ferns and early seed plants as hosts, and taxa of the Paleozoic Insect Fauna as spore, prepollen, and pollen consumers. The third assemblage documents more advanced seed plants and an earlier phase of the Modern Insect Fauna, whereas the fourth assemblage has angiosperms as plant hosts and a later phase of the Modern Insect Fauna that is still dominant today. The last two of these assemblages have mid-Mesozoic origins and are associated with

pollination, including highly specific and faithful plant-host associations.

(4) It is debatable whether pollination mutualisms between seed plants and insects occurred during the Late Paleozoic. All of the evidence is circumstantial, highly varied, but mutually consistent. Thus, varied plant-reproductive associated features, large prepollen and pollen size in some seed ferns, and stylet marks into medullosan prepollen organs, collectively suggest the presence of insect pollination.

(5) The probable origin of pollination involved a co-optation of the pollination drop mechanism that occurs ubiquitously in extinct and extant gymnospermous seed plants. Nutrient-laden fluids occurring in the micropyle of modern and fossil taxa are, and presumably were, imbibed by insects, resulting in a type of "nectar theft." This imbibition of sugar-rich ovular fluids is functionally identical to the nectar reward in angiosperm flowers to potential insect pollinators.

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