5 August 2010 16:9 YB110150.tex McGraw Hill Encyclopedia of Science & Technology, 10th Edition Galley Proofs
Keystroked: 25/07/2010
Initial MS Page Sequence Stamp:
Article Title: Pollination mutualism in insects before the evolution of flowers
Article ID: YB110150
1st Classification Number: 563000
2nd Classification Number:
Sequence Number:

Pollination mutualism in insects before the evolution of flowers

A preeminent association between flowering plants and insects is pollination. Pollination is a mutualism in which two interactors reciprocally benefit: a host plant receives the service of insect pollination in return for a reward provided for its insect pollinator. Typically, the reward is nectar or pollen, but occasionally the provision can be a mating site, resin for nest construction, floral aroma, or even the attraction of plant-generated heat. Evidence from the fossil record and from the inferred ecological and phylogenetic relationships between flowering plants (angiosperms) and their insect pollinators indicates that these types of associations initially were launched during the Early Cretaceous, 125–90 million years ago. It was from this interval of time that flowering plants experienced their initial radiation, as did major groups of insects, especially Thysanoptera (thrips), Coleoptera (beetles), Diptera (flies), Lepidoptera (moths and butterflies), and Hymenoptera (sawflies, wasps, ants, and bees). However, until recently, very little was known about more ancient modes of insect pollination, those that predated the appearance of flowering plants or that occurred before angiosperms became dominant in terrestrial ecosystems.

Types of evidence. There are several dietary precursors to the consumption of pollen and nectar as a reward for pollination. As far back as the Early Devonian, 416–397 million years ago, small, mandibulate (chewing) arthropods were consuming the spores of well-known, early land plants. Evidence for this feeding style consists of the sporangial contents of single species of host plants found as identifiable spores in coprolites (preserved fecal pellets) that were defecated by small arthropods. Later evidence from the Early Permian, 299–271 million years ago, includes the prepollen and pollen of seed plants found in the coprolites of insects such as booklice (see **illus.** *a*). Of course, pollen consumption by insects is a pattern that continues today. However, it is especially demonstrated by the gut contents extracted from extinct, mid-Mesozoic sawflies (illus. *b*). These sawflies typically consumed gymnosperm pollen provided by gnetaleans (illus. *c*), which are represented currently by *Ephedra* (Mormon tea), *Gnetum* (a tropical shrub or vine), and *Welwitschia* (an unusual plant of the southern African Namib Desert). Other extinct lineages that provided pollen for insect consumption included seed ferns and, notably, cheirolepidiaceous conifers, whose distinctive pollen has been found as gut contents and clumps plastered to the heads and mouthparts of insects (illus. *d*). In contrast, fluids (such as the nectarlike pollination drops of gymnosperms) are not preserved in dispersed coprolites or the guts of insects. Thus, insect feeding on fluids is inferred by distinctive, siphonlike mouthparts, such as those from extinct species of flies (illus. *e*) or scorpionflies (illus. *f*).

Several features of the ovulate and pollen organs of many gymnospermous plants directly implicate the fluid feeding by insects bearing siphonate mouthparts. These features included elongate tubular micropyles (minute openings in the integument at the tip of an ovule through which the pollen tube commonly enters; illus. *g*) that occur only in gymnosperms, deep channels through ovulate-covering tissue that allowed access to pollination-drop rewards secreted by deep-seated ovules (illus. *h*), and channels formed by the partial closure of a bivalved ovule, allowing proboscis-bearing insects to imbibe inner pollination drops (illus. *i*). This varied evidence, including coprolites and gut contents from mandibulate insects that fed on pollen grains, the distinctive long-proboscate mouthparts of insects that fed on pollination drops, and plant structures that received the size-matched proboscises of insects, collectively indicates the presence of pollination during the preangiospermous Mesozoic. Evidently, there were two major modes of insect pollination: (1) long-proboscid, fluid-feeding insects that fed on gymnosperm reproductive organs, in which the reward was principally nectar; and (2) mandibulate, chewing insects, whose adults consumed mostly pollen and whose larvae tunneled through vegetative tissue and ovules of plant hosts, including extinct bennettitaleans and the extant cycads.

Major players. The spectrum of mandibulate insect pollinators that occurred before the advent of angiosperms, during the Permian, included the Psocoptera (booklice) and Grylloblattodea (rock crawlers), as well as extinct groups related to orthopteroids (currently, grasshoppers and relatives) and hemipteroids (currently, cicadas, aphids, true bugs, and relatives). After the end-Permian extinction and during the Mesozoic, this spectrum of insects was replaced by various lineages of Coleoptera, whose life cycles were associated intimately with bennettitaleans and cycads, and some taxa that became affiliated with the large, showy flowers of basal angiosperms (for example, members of the magnolia and laurel families). In contrast, an array of small, fluid-feeding, long-proboscate insects included early forms of Trichoptera (stem-group caddisflies), Mecoptera (aneuretopsychine scorpionflies), and Neuroptera (butterfly-like kalligrammatid lacewings), as well as three or four major lineages of brachyceran Diptera (tanglevein flies, horseflies, and flower-loving flies). With the exception of the brachyceran Diptera, this gymnosperm-pollinating assemblage was replaced, during the diversification of angiosperms in the Early Cretaceous, by the Lepidoptera (glossate moths), more advanced groups of Diptera (hover flies and bee flies), many lineages of Hymenoptera (wasps and bees), and probably blister beetles with siphonate proboscises.

Based on the structure of ovulate and pollen organs consistent with a pollinator function, gymnospermous plant hosts for these lineages were predominantly cycads, bennettitaleans, seed ferns, cheirolepidiaceous conifers, and gnetaleans. Cycads

and bennettitaleans typically were composed of fleshy, thick stems that were predominantly beetle-pollinated and involved sacrifice of internal tissues to larvae for completion of their life cycle. Various seed fern groups included caytonialeans, corystosperms, and lepidostrobaleans that bore ovulate organs (illus. *g–i*), which secreted pollination drops for imbibation by insects, and produced pollen that may have been consumed as particles by insects with siphons that bore accommodating food tubes. Gnetaleans were considerably more diverse during the Mesozoic and undoubtedly were insect-pollinated, based on a variety of reproductive features, including pollen consistent with insect vectoring. A plant host with the most distinctive and bizarre type of insect pollination was the cheirolepidiaceous conifer, *Alvinia bohemica*. This ovulate cone bore a trichome- and nectary-lined funnel that was directed outward and connected by a "pipe" to an inward-placed ovule that secreted a pollination drop. The deep funnel structure was surrounded by various conspicuous appendages that may have served as a lure to small insects or to large insects with elongate mouthpart siphons.

Evolutionary biology. The earliest significant evidence for insect pollination is from the Permian, even though earlier occurrences extending to the Early Devonian indicate the presence of spore and pollen consumption by mandibulate insects. Permian pollination was mediated overwhelmingly by mandibulate insects, although there is some evidence for small, caddisfly-like insects with extended proboscises designed for fluid uptake. After the demise of this assemblage at the end-Permian mass extinction, new lineages of both mandibulate chewing and long-proboscid fluid-feeding insects originated by the mid-Mesozoic. Although mandibulate beetles were associated predominantly with bennettitaleans and cycads, the former hosts became extinct during the Cretaceous, whereas the latter survive today, probably with similar life cycles. A distinctively different evolutionary trajectory was followed by the long-proboscate lineages of scorpionflies, lacewings, true flies, and others that diversified during the Middle Jurassic and experienced an approximately 60-million-year duration as pollinators, principally on a variety of seed ferns, cheirolepidiaceous conifers, and gnetalean hosts. However, this assemblage of gymnosperm pollinators came to a close with the global turnover of gymnosperm to angiosperm floras that commenced during the mid–Early Cretaceous and was mostly completed during the early Late Cretaceous. Their replacements, on angiosperms, are long-proboscid lineages that are familiar to us today: glossate moths, bee flies and hover flies, wasps and bees, and a broad range of other holometabolous insects that independently evolved siphonate mouthparts.

For background information *see* DIPTERA; FLOWER; INSECTA; MAGNOLIOPHYTA; MUTUALISM; PALEOBOTANY; PALYNOLOGY; PLANT-ANIMAL INTERACTIONS; POLLEN; POLLINATION in the McGraw-

Hill Encyclopedia of Science & Technology.

Conrad C. Labandeira

Key Words: Cretaceous; fly; gymnosperm; insect; Jurassic; mutualism; nectar feeding; pollen drop; pollination; seed fern

Bibliography. R. Gorelick, Did insect pollination increase seed plant diversity?, *Biol. J. Linn. Soc.*, 74:407–427, 2001; V. A. Krassilov, A. P. Rasnitsyn, and S. A. Afonin, Pollen eaters and pollen morphology: Co-evolution through the Permian and Mesozoic, *Afr. Invert.*, 48:3–11, 2007; H. W. Krenn, J. D. Plant, and N. U. Szucsich, Mouthparts of flower-visiting insects, *Arthropod Struct. Devel.*, 34:1–40, 2005; C. C. Labandeira, The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects, *Ann. Missouri Bot. Gard.*, 96, 2010; C. C. Labandeira, J. Kva, and M. B. Mostovski, Pollination drops, pollen, and insect pollination of Mesozoic gymnosperms, *Taxon*, 56:663–695, 2007; M. P. Proctor, P. Yeo, and A. Lack, *The Natural History of Pollination*, 2d ed., Timber Press, Portland, OR, 1996; D. Ren et al., A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies, *Science*, 326:840–847, 2009.

Additional Reading. F. G. Barth, *Insects and Flowers: The Biology of a Partnership*, Princeton University Press, Princeton, NJ, 1985; D. A. Grimaldi, The co-radiations of pollinating insects and angiosperms in the Cretaceous, *Ann. Missouri Bot. Gard.*, 86:373–406, 1999; V. A. Krassilov and A. P. Rasnitsyn, Plant remains from the guts of fossil insects: Evolutionary and paleoecological inferences, pp. 65–72, in *Proceedings of the First International Palaeoentomological Conference, Moscow, 1998*, AMBA Projects, Bratislava, 1999; V. A. Krassilov, A. P. Rasnitsyn, and S. A. Afonin, Pollen morphotypes from the intestine of a Permian booklouse, *Rev. Palaeobot. Palynol.*, 106:89–96, 1998; K. J. Norstog and T. J. Nicholls, *The Biology of the Cycads*, Cornell University Press, Ithaca, NY, 1997.

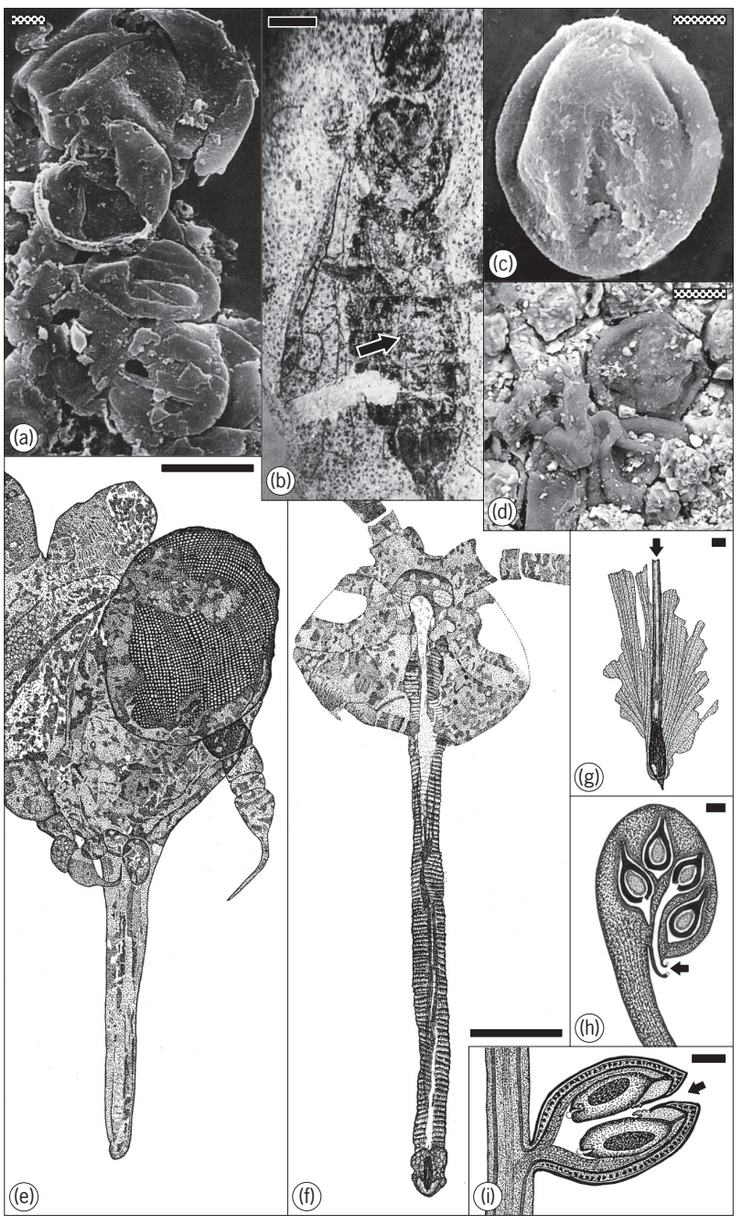
URLs

Palynological Database

http://www.paldat.org

Palynology

http://www.kew.org/science/palyn.html



Plant mutualism displayed. (*a*) Pollen grains of the early conifer, *Lunatisporites* sp., and the glossopterid, *Protohaploxypinus perfecta*, from the gut of the booklouse, *Parapsocidium uralicum*, from the Early Permian Chekarda site of Russia. (*b*) The sawfly, *Ceroxyela dolichocera*, from the Lower Cretaceous of Baissa, Transbaikalia, Russia, with *Eucommiidites* type pollen (gnetalean?) in its midgut (indicated by an arrow). (*c*) The *Eucommiidites* type pollen extracted from the midgut of the sawfly in panel *B*. (*d*) Pollen of the cheirolepidiaceous conifer, *Classopollis* sp., found smeared on the head of a small brachyceran fly, from the same locality as panel *B*. (*e*) Head, proboscis, and associated mouthparts of the nemestrinid fly, *Florinemestrius pulcherrimus*, from the mid–Early Cretaceous of Liaoning, China. (*f*) The head and proboscis of the aneuretopsychid scorpionfly, *Jeholopsyche liaoningensis*, from the same formation as panel *e* (*g*) *Problematospermum ovale*, an enigmatic seed with a 12-mm (0.48-in.) micropyle, from the late Middle Jurassic of Inner Mongolia, China. (*h*) *Caytonia sewardi*, with a 4-mm (0.16-in.) integumental tube, from the mid-Jurassic deposits at Yorkshire, United Kingdom. (*i*) *Leptostrobus cancer*, with an intervalve, 4.5-mm (0.18-in.) channel allowing access to concealed pollination drops, from the same site as panel *h*.