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A review of brood-site pollination mutualism: plants providing breeding sites for their pollinators

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Abstract In this paper, I review pollination systems in which plants provide breeding sites as a reward for pollination. I divide the pollinators into three groups based upon ovipositing sites and the larval food of insects. The first group consists of ovule parasites found in only five plant lineages, e.g., the fig wasps and yucca moths, pollination systems in which pollinator specificity is very high. The second group is pollen parasitism, primarily by thrips (Thysanoptera), but specificity of the pollinators is low. In the third group, pollinator larvae (Coleoptera and Diptera) develop in decomposed flowers and inflorescences of plants and these adaptations evolved repeatedly via different pathways in various plant taxa. Pollinator specificity varies, and shifts in pollinators may occur between related or unrelated insects.

Key words Herbivore · Plant reproduction · Pollination · Speciation · Tropical forest

Introduction

Pollination is the process whereby pollen is transferred from anthers and deposited onto the stigma(s) of flowers resulting in fertilization and the production of fruits and seeds (sexual reproduction). Interactions between animal vectors, primarily between insects and flowers, has produced an amazing array of pollination mechanisms (Proctor et al. 1996; Kato 2000). This mutualism (pollination by insects) is hypothesized to be one of the driving forces in the evolution of angiosperms (Burger 1981; Grimaldi 1999). The flowers of many angiosperms have evolved many intricate mechanisms to attract pollinators including highly scented floral parts, insect pheromones, color patterns, structural morphologies.

Floral fragrance (including pollen odors) is hypothesized to be an ancient insect attractant that preceded color (Porsch 1950, 1954; van der Pijl 1960). Pellmyr and Thien (1986) hypothesized that floral fragrances arose from secondary compounds in plants that originally functioned as insect deterrents. Some insects could bypass some of these chemicals, and the life cycles of insects and plants meshed. It is not uncommon to find such chemicals in the floral fragrances of extant flowers (Thien et al. 2000). The meshing of the sexual life cycles of insects with plants may have promoted the diversity of insects and plants.

In addition to floral fragrance, thermogenesis possibly played a major role in early plant reproductive systems (Thien et al. 2000). Thermogenic flowers have been reported in only ten angiosperm families, primarily in the basal angiosperms (Patiño et al. 2000; Thien et al. 2000). Of the several hypotheses explaining heat production in flowers, the following are correlated with pollinators: a direct energy reward for insects, to increase diffusion rates of carbon dioxide and volatilization of specific chemicals, mimicry of mammalian feces and carrion to attract scavengers and carrion flies, and to enhance development of pollinator larvae on the flower (Patiño et al. 2000; Thien et al. 2000).

Evidence of interactions between arthropods and the reproductive structures of terrestrial plants dates to the Upper Silurian and Lower Devonian periods. Undigested land-plant spores found in coprolites (fossil feces) of arthropods, indicate spore feeding on litter (as detritus) and from intact sporangia (Edwards et al. 1995; Edwards 1996). Insect coprolites provide evidence that consumption of pollen by insects was already established at the end of the Carboniferous period (Labandeira 1998; Grimaldi 1999). Feeding on reproductive organs may have been common and predated consumption of vegetative organs (Selden and Jeram 1989). The fossil record also suggests that insects became increasingly specialized for feeding on plant reproductive structures during the Late Carboniferous-Mesozoic interval (Scott and Taylor 1983; Crepet 1984).

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Insect pollination evolved before the origin of Angiosperms (Crepet and Friis 1987). Many extant cycads, an important terrestrial plant group in the Mesozoic, are pollinated by beetles and thrips that lay their eggs on the plant and form close pollination mutualisms. Thrips are exclusive pollinators of *Macrozamia* (Zamiaceae, Cycadales; Mound and Terry 2001), and beetles of *Zamia* (Tang 1987; Norstog and Fawcett 1989) and *Encephalartos* (Zamiaceae) (Donaldson 1997). In the Gnetales, moth pollination occurs in *Gnetum* (Kato and Inoue 1994; Kato et al. 1995). The hermaphroditic fructifications of the extinct Bennettitales from the Mesozoic appear similar in structure to extant Magnoliidae flowers, and may have been pollinated by beetles and dipterans (Crepet and Friis 1987). Beetles, flies, and thrips first occur in the fossil record from Early to Mid Permian (Kukalova-Peck 1991) and are thought to be significant early (preangiosperm) insect pollinators. These insects also play important roles in the pollination of extant basal angiosperms, e.g., Winteraceae and Degeneriaceae (Thien 1980).

In this paper, I review pollination systems in which plants provide breeding sites as a reward for pollination. In these pollination systems, pollinators visit and oviposit on flowers, and pollinator larvae grow on the flowers feeding on pollen, ovules, or other floral parts. Studies conducted on the fig–wasp pollination mutualism (e.g., Yokoyama 1995; reviewed in Janzen 1979; Wiebes 1979; Machado et al. 2001) and the yucca–yucca moth pollination mutualism (e.g., Baker 1986; Pellmyr and Thompson 1992; Pellmyr et al. 1996a, 1996b; Pellmyr and Leebens-Mack 1999, 2000) indicate very specialized interactions involving ovule parasitism. However, figs and yuccas are only a small fraction of the plants that provide pollinating insects with breeding sites. I divide pollinators that use flowers as breeding sites into three groups based upon sites of oviposition and larval food. Then, I utilize the pollination systems of *Aristolochia* spp. (Aristolochiaceae) in a seasonal tropical forest of Panama to illustrate how pollinators and nonpollinating parasites breed on flowers after pollination. Lastly, I discuss pollinators breeding on decomposing plant reproductive organs after pollination (third group).

Three groups of pollinators breeding on flowers

Group 1. Ovule parasites

Pollination by ovule parasites has been recorded in only five plant lineages: figs (*Ficus*, Moraceae) pollinated by fig wasps (Agaonidae, Hymenoptera) (Janzen 1979; Wiebes 1979), yuccas (Yucca, Agavaceae) by the yucca moth (Prodoxidae, Lepidoptera) (Baker 1986; Pellmyr and Thompson 1992), *Lithophragma* (Saxifragaceae) by moths (Prodoxidae, Lepidoptera) (Thompson and Pellmyr 1992), *Trollius* (Ranunculaceae) by flies *Chiastochaeta* (Anthomyidae, Diptera) (Pellmyr 1989, 1992), and *Lophocereus* (Cactaceae) by the moth *Upiga* (Pyralidae, Lepidoptera) (Fleming and Holland 1998; Holland and Fleming 1999). In all cases, specificity of pollinator to the host plant is very high (a one-to-one species relationship). Rarity of pollination by ovule parasites and high plant-to-insect specificity is probably due to the high cost of seed loss as a reward to pollinators. In some groups (figs, yuccas and *Lophocereus*), pollinators actively deposit pollen grains on stigmas to assure pollination (active pollination), because development of their larvae depends upon the growth of ovules after pollination to insure food for the larvae. Active pollination has not been recorded in any other pollination systems.

Inflorescences of figs, the “syconium” is an urn-shaped closed structure with staminate and pistillate flowers on the inner surface. Female fig wasps, the pollinators, crawl into a syconium through a small hole at the top enclosed by bracts, and deposit pollen grains from their pollen pockets and oviposit on ovules. Subsequently, in some pollinated pistillate flowers the larvae of pollinators develop, while ovules of other flowers grow into seeds. When the larvae mature, staminate flowers in the same syconium shed pollen. The new female fig wasps then emerge from the syconium after copulation, with pollen in their pollen pocket, and search for a syconium suitable for oviposition (Janzen 1979; Wiebes 1979). *Ficus* species (more than 700, mostly in the tropics) have very specialized relationships with their pollinator wasps: each species is pollinated by only one species of wasp (“one-to-one”). Since nonpollinating wasps parasitic on fig ovules are ancestral and closely related to pollinating species, fig wasps are thought to have arisen only once from nonpollinating ovule parasites (Yokoyama 1995; Machado et al. 2001).

The pollination system of yuccas in North America is similar to that of figs, but different in that the pollinator leaving a flower with pollen is not a daughter of the individual which pollinated the flower, but the pollinator herself. Yucca moths visit a flower and scrape pollen into a lump under their head using the maxillary palps, and deliver the pollen to other flowers. If the moth finds a suitable flower, it bores into the ovary with its ovipositor and lays an egg. Then it climbs the stigmas united into a tube, and pushes pollen grains into the stigmatic tube. Yucca–yucca moth mutualism is thought to have evolved from a plant–ovule parasite relationship. However, changes in the opposite direction may also have occurred. Simple ovule parasites, which do not pollinate their hosts, occur among relatives of yucca moths (Pellmyr et al. 1996a, 1996b; Pellmyr and Leebens-Mack 2000). A close relative of the yucca moths, *Greya*, are moth pollinators and ovule parasites of *Lithophragma* (Saxifragaceae). However, in contrast to the yucca moths, *Greya* parasitizes the ovules but does not actively pollinate the host plant (Pellmyr and Thompson 1992).

Community studies of ovule parasitism, indicate that some interactions between plant and pollinator, e.g. the presence or absence of copollinators and predators of pollinators, can affect the outcome of these interactions (Pellmyr 1989, 1992; Thompson and Pellmyr 1992; Herre 1996; West et al. 1996; Thompson 1997; Holland and Fleming 1999). In fig–fig-wasp and yucca–yucca-moth interactions, the ovule parasites are the only pollinators for the host plant, and the pollinators can survive only on the single host species. Existence of their partners is essential for reproduction of both the pollinators and host plants. On the other hand, *Lithophragma* secretes nectar and copollinators other than ovule parasites can serve as pollinators. In addition, the relative importance of the ovule parasites as pollinators changes through time and places. Thus, their relationship has not evolved into a specialized relationship involving active pollination (Thompson and Pellmyr 1992; Pellmyr et al. 1996b).

Group II. Pollen parasites

In this group, the larvae of pollinators feed on pollen grains of fresh flowers attached to the plant and without exception these insects are thrips (Thysanoptera). Thrips are tiny insects (1–2 mm in length) that reproduce in great numbers (explosively) and feed on floral tissue, pollen, and are common pests of many cultivated plants; they also pollinate native tropical and temperate plants (Mound and Marullo 1996). The primary host of most thrips species, namely, plants on which they reproduce, are usually difficult to identify (Mound and Marullo 1996). Host-specificity of various thrips species is difficult to determine since many feed on a variety of different plants. Even specialized species of thrips have been observed to reproduce on more than one plant species in a genus of plants (Mound and Marullo 1996). The following plants are pollinated primarily by thrips: *Bocageopsis*, *Popowia* (Annonaceae; Webber and Gottsberger 1995; Momose et al. 1998), *Arisaema* (Araceae; Rust 1980), *Shorea* (Dipterocarpaceae; Appanah and Chan 1981), *Calluna* (Ericaceae; Hagerup 1950), *Macaranga* (Euphorbiaceae; Moog et al. 2002), *Castilla* (Moraceae; Sakai 2001), *Mollinedia* (Monimiaceae; Gottsberger 1977), *Belliolum* (Winteraceae; Thien 1980; Pellmyr et al. 1990), and *Macrozamia* (Zamiaceae; Mound and Terry 2001).

An outstanding characteristic of thrips is their high rate of reproduction. They can grow from an egg to adult in 1–2 weeks, and produce several generations within a single flowering season. As a result, large numbers of individuals are produced and can function as pollinators even if the original pollinator populations were small. On the other hand, due to their small body, the number and size of pollen grains they carry tend to be small in comparison to other pollinators (D.W. Roubik, personal communication). The relatively small range of movement of thrips may limit distances of pollen dispersal in small trees such as *Popowia pisocarpa* (Annonaceae) (Momose et al. 1998). Appanah and Chan (1981), however, maintain that thrips visiting flowers of emergent trees move for long distances by wind, and effectively pollinate emergent trees (*Shorea*, Dipterocarpaceae).

Castilla elastica (Moraceae), a deciduous tree pollinated by thrips, has an inflorescence structure adapted to thrips pollination (Sakai 2001). The species is androdioecious (bisexual and male individuals within a population). Interestingly, the staminate inflorescences of bisexual and male trees are strikingly different (Cook 1903). The staminate inflorescence of the male trees is bilabiate (see: Fig. 2 of Sakai 2001). The flat involucre of the inflorescence is folded, and the staminate flowers are attached onto the inner surface of the structure. As the anthers dehisce, the inflorescence opens slightly and the anthers become visible.

The staminate inflorescences of the bisexual trees are urceolate, and resemble the syconium of figs (see: Fig. 4 of Sakai 2001). The small entrance at the top of the inflorescence is covered with imbricate bracts, which loosen when the anthers open. In both types of staminate inflorescences, only small insects can gain access to pollen, and almost all the flower visitors are thrips (Sakai 2001). Such closed structures protect not only pollen grains from robbers, such as stingless bees and beetles, but also the pollinating thrips from predators (ants and spiders). Thrips are attracted to the pistillate and staminate flowers of *Castilla elastica* by a common floral odor.

Macaranga (Euphorbiaceae), a dioecious pioneer tree, presents an interesting exception in thrips pollination. The main reward is not pollen, but nectar secreted by trichomes on the adaxial base of the bracteoles. Thrips commence breeding in male flowers 2 weeks prior to the emergence of female flowers and thus carry large quantities of pollen to these newly emerged flowers (Moog et al. 2002). Although the plants not providing pollen to the pollinators cannot be identified, I tentatively place *Macaranga* in this category because thrips are the exclusive pollinator.

Group III. Postpollination larval development in decomposing flowers and inflorescences

In this group, pollinator larvae grow on floral parts or inflorescences (postpollination) that no longer play a role in attracting pollinators. In most cases, the flowers and inflorescences have abscissed from the plant body, and the larvae grow on the decomposing plant material on the forest floor. In this group, the pollinators are beetles (Curculionidae and Nitidulidae) and flies (Cecidomyiidae, Drosophilidae and Phoridae; Table 1).

In more than half of the plants in this group, larvae of pollinators breed on the staminate inflorescences. For example, pollinators of *Artocarpus integer*, two species of gall midges, visit and oviposit on the flowering staminate inflorescences (5–6 cm in length; Sakai et al. 2000). During oviposition, bodies of the midges are covered with pollen grains. The eggs hatch in a few days and the larvae feed on mycelia infecting the inflorescence during and after flowering. The larvae mature in about 2 weeks. The midges, attracted by odor, also visit pistillate inflorescences, and passively deposit pollen grains on the stigmas. However, they rarely oviposit on pistillate inflorescences and eggs deposited on pistillate inflorescence never grow, as mycelia of the fungi (food of the larvae) do not grow on pistillate inflorescences. The short generation time (about 2 weeks) of the midges dramatically increases population size during the flowering period of *Artocarpus* (about 3 months), which greatly increases pollination efficiency. The *Artocarpus*–gall midge pollination mutualism is unique in that the relation-

Table 1. Plants pollinated by insects breeding on decomposing flowers after pollination

Plant	Pollinator	Reference
Encephalartos (Zamiaceae)		Rattray (1913); Donaldson (1997)
Zamia (Zamiaceae)	Curculionidae, Nitidulidae (Coleoptera)	Tang (1987); Norstog and Fawcett (1989)
Eupomatia (Eupomatiaceae)		Armstrong and Irvine (1990)
Various palms (Palmae)		Henderson (1986)
Carludovicoideae (Cyclanthaceae)		Eriksson (1994)
Aristolochia (Aristolochiaceae)		Sakai (2002)
Alocasia (Araceae)	Cecidomyiidae, Drosophilidae, Phoridae (Diptera)	van der Pijl (1953); Yafuso (1993)
Siparuna (Siparunaceae)		Feil (1992)
Artocarpus (Moraceae)		Sakai et al. (2000)
Nypa (Palmae)		Essig (1973)

ship is mediated by fungi. It is unknown if the pollinators are restricted to the plant, or if they reproduce in other places, such as rotten fruits. Since the fungus on *Artocarpus* inflorescences is thought to be a generalist (Sakai et al. 2000), it is quite possible that the midge pollinator can also reproduce on plants of other species.

The pollination system of *Artocarpus* may have arisen from wind pollination, as wind-pollinated species occur in many species of Moraceae. The staminate inflorescences usually start rotting and become infected by fungi as soon as pollen has been dispersed (or earlier). It is not surprising therefore that midges oviposit eggs on inflorescences still flowering on the plant body. During oviposition, the midges inevitably become dusted with pollen grains. If pistillate inflorescences emit an odor similar to staminate structures, or if they flower near staminate inflorescences, midges may also visit pistillate ones. Oviposition on staminate inflorescences after pollination cost the plant little or no resources, and the interaction could easily lead to the evolution of a pollinator breeding on the flower.

Most members of this group are plants in tropical forests, and further studies may reveal many more plant species belonging to this group. Some plants of Piperaceae (Ollerton 1996), Sterculiaceae (Young 1984, 1985) and Poaceae (Soderstrom and Clederón 1971) may have similar pollination systems.

Pollinating and nonpollinating parasites of *Aristolochia* spp.

Sakai (2002) reported nonpollinating parasites of *Aristolochia* spp. coexist with pollinators in the flowers in the seasonal tropical forests of Panama. *Aristolochia* is the largest genus in Aristolochiaceae with approximately 120 species distributed throughout the tropics and subtropics. Their zygomorphic flowers ("Dutchman's pipe") are diverse in size, shape and color (Endress 1994). The perianth of the flower has only three sepals united to form a calyx tube. The basal part forms a chamber (utricle) around the fused styles, stigmas and anthers (collectively known as the gynostemium) (Fig. 1). The utricle is connected to a tube ending with an expanded limb, which is often colorful and thought to visually attract pollinators. This bizarre floral structure has for years attracted the attention of naturalists, with its flower biology being published (e.g., Cammerloher 1923; Petch 1924; Brues 1928; Linder 1928; Iwata 1975).

All species of *Aristolochia* are pollinated by flies representing various families, including Anthomyiidae, Chloropidae, Milichiidae, Phoridae, Sarcophagidae, and Syrphidae (Cammerloher 1923; Petch 1924; Brues 1928; Lindner 1928; Brantjes 1980; Costa and Hime 1983; Wolda and Sabrosky 1986; Hall and Brown 1993). The pollinators belong to saprophagous groups and the pollination system is regarded as brood-site deception (mimics of mammalian feces and carrion and decomposing plant materials). Nectar secreted by some species of *Aristolochia* (Cammerloher 1923; Petch 1924; Daumann 1959; Costa and Hime 1983), is apparently produced for the survival of pollinators inside the trap flower during captivity rather than as a reward for pollination (many flies are found dead in the flowers without nectar; Vogel 1998).

Sakai (2002) discovered that the larvae of flies that pollinate two species of *Aristolochia,* successfully reproduce on abscissed floral parts. The plants, *Aristolochia maxima* and *A. inflata*, are lianas in secondary forests, with flowers 10–30 m above the ground. Both species produce flowers that last for 2 days and are female on the 1st day of flowering and male on the 2nd day (protogynous); *A. inflata* has a yellow calyx tube about 7 cm in length (Fig. 1A). In the afternoon of the second day, the calyx tube abscisses and falls to the ground. Flowers of *A. inflata* are pollinated by a single species of female phorid fly (*Magaselia sakaiae*), which oviposits on and around the gynostemia, and sucks nectar secreted by sticky hairs on the inner surface of the utricle (Table 2). *A. maxima* has a larger calyx tube (Fig. 1B). Its glaring limb is dark purple dotted with yellow. The calyx tube of the species also falls in the afternoon of the 2nd day. Its pollinators, drosophila flies (*Drosophila* spp.), emerge from flowers in the male phase carrying a large pollen load

Table 2. A list of dipteran species found on *Aristolochia* flowers and their relationships with the flowers

Family Species	Breeding on flowers		Visits frequency to flowers		Contribution to pollination	
	A. maxima	*A. inflata*	*A. maxima*	*A. inflata*	*A. maxima*	*A. inflata*
Drosophilidae						
Drosophila spp.	++	+	+++		+++	
Zigothrica sp.		+++				
Phoridae						
Megaselia sakaiae	+++	+++	+++	+++		+++
M. metropolitanoensis	++					
Puliciphora pygmaea	++	++				
Cecidomyiidae						
Clinodiplosis sp.	++		+			

+++ much, ++some, + little
From Sakai (2002)

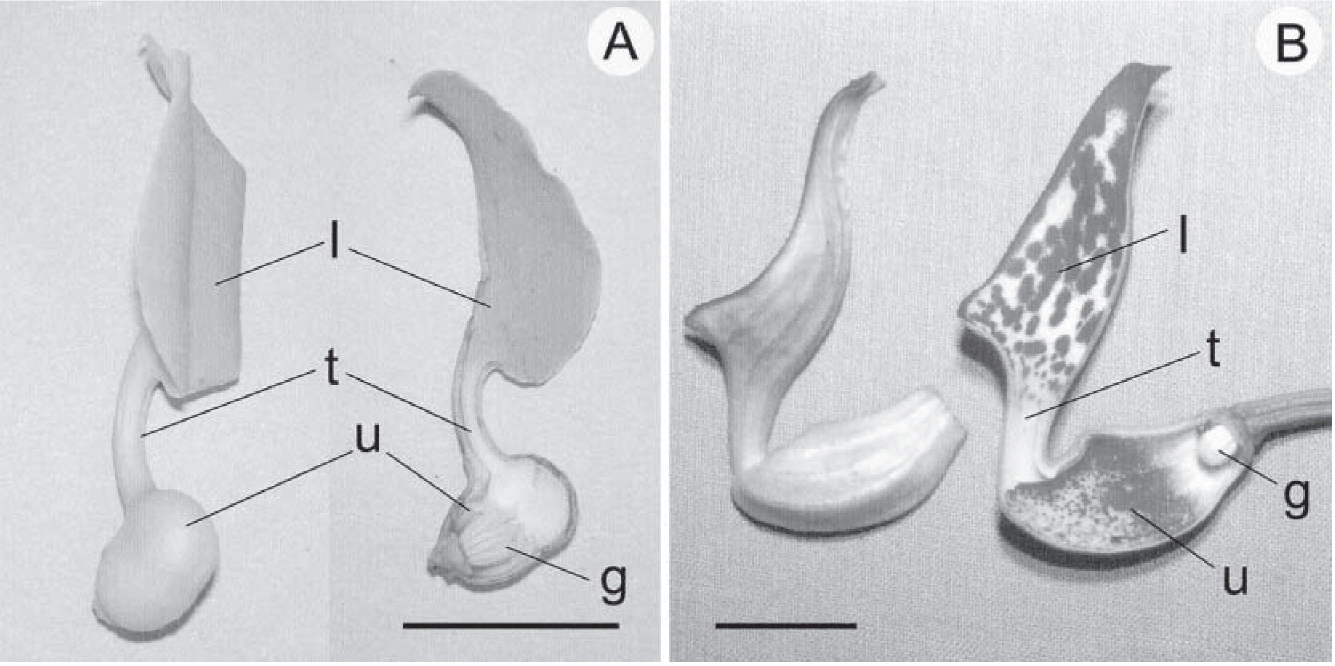

Fig. 1. **A** intact calyx tube (*left*) and dissected calyx tube with gynostemium (*right*) of *Aristolochia inflata* (Aristolochiaceae) (*g*, gynostemium; *l*, limb; *t*, tube; *u*, utricle). **B** Dissected flower of *A. maxima*. *Bar* 2 cm

on their dorsal bodies (Table 2). The flowers are visited by phorid flies, also pollinators of *A. inflata*, but are inefficient pollinators because they carry small pollen loads (Table 2).

Sakai (2002) studied insects breeding in the corollas of *Aristolochia* spp. by incubating the flowers collected from the canopy and forest floor. The experiments showed that many nonpollinating insects, mostly flies, were also breeding on the corollas. The important conclusion is that pollinators of each species can breed on both *Aristolochia* species (Table 2). *Megaselia sakaiae* (pollinator of *A. inflata*), and *Drosophila* spp. (pollinators of *A. maxima*), can both grow on the calyx tubes of *A. inflata* and *A. maxima*. Other *Drosophila* spp. also oviposit on the outside of the calyx tube of *A. maxima*, but never pollinate the flowers. On the other hand, due to its small body size, *Megaselia* can not pollinate *A. maxima*, even though they enter the corollas.

The other point is that in addition to pollinator flies, related or unrelated insects can also reproduce on the flowers. Two species of Phoridae, *Megaselia metropolitanoensis*, a close relative of *M. sakaiae* (Disney and Sakai 2001), and *Puliciphora pygmaea* (unrelated), use the flowers as breeding sites. They oviposit on the flowers after abscission from the plant and therefore do not contribute to pollination. The same is true for *Zigothrica*, which oviposits on the outside of the flowers, and thus cannot serve as a pollinator (Table 2).

Pollination of *Aristolochia inflata* and *A. maxima* differ in specificity of pollinators. *A. inflata* is pollinated by a

Table 3. Comparison of three groups pollinated by insects breeding on flowers

	Group 1	Group 2	Group 3
Larval food	Ovule	Pollen	Decomposing flowers
Insect order	Hymenoptera, Lepidoptera, Diptera	Thysanoptera	Coleoptera, Diptera
Plant lineages	5	Many	Many
Specialization of pollinators to host	Very high	~Low	Low-high
Specialization of plants to pollinators	High to very high	High?	~High
Parasites	Close relatives of pollinators	Coleoptera, bees etc.	Related or unrelated to pollinators
Shift of pollinators	Rarely occur only between related insect species	?	Can occur between unrelated insect species
Origin of relationship	Nonpollinating ovule parasite	Nonpollinating pollen feeder	Deceit pollination, insects breeding on flowers after pollination

single species of fly, *Megaselia sakaiae*, which can reproduce only on *Aristolochia* flowers (Disney and Sakai 2001). On the other hand, more than ten species of drosophila flies pollinate *A. maxima*, and *Aristolochia* flowers are one of many breeding sites for these pollinators. *Drosophila* spp. collected on *A. maxima* have been recorded on the flowers or rotten fruits of other plants; none of the *Drosophila* spp. are specialists of *Aristolochia* flowers (Sakai 2002).

How have these pollination systems evolved? One scenario is that some of the flies were originally attracted and deceived by *Aristolochia* flowers via the odor of decomposing organic matter. Phorid flies are often attracted to the flowers of *Aristolochia*. It is not unlikely that some species of flies used decomposing flowers as a breeding site, i.e., *Megaselia metropolitanoensis* and *Puliciphora pygmaea*, and eventually oviposited on fresh flowers rather than on fallen flowers on the forest floor. It is interesting to note that both deceit pollination and pollination involving insects breeding on inflorescences after pollination have been recorded in the Araceae (Yafuso 1993; Endress 1994; Protocor et al. 1996, Bown 1988).

Did the plant-pollinator relationships in *Aristolochia inflata* and *A. maxima*, which are very similar, evolve independently? Considering that each of the pollinators can breed on both flowers, the pollination system may have a single origin. Pollinator species might have changed in the course of speciation. Once the mutual relationships are established, quality of floral parts as food for pollinator larvae becomes an important factor in population growth of the pollinators. The high numbers of insects produced would lead to a greater number of pollinations and therefore increase the seed set of the plants. Subsequently other insects might use the resource-rich flowers as a breeding site (exploitation), but without rendering pollination. Changes in floral structure or fragrance may cause switches from parasitic visitors to pollinators and vice versa, with accompanying speciation of plants and insect pollinators.

Characteristics of pollinators breeding on flowers

One of the characters of this type of pollination system is that it evolved numerous times in various lineages of plants (Table 3). The evolutionary pathways may vary, and the pollinators may have evolved not only from parasitic insects breeding on flowers but also from other plant reproductive organs (Table 3). Pollinators may form highly specialized relationships with a host plant, but some are generalists in terms of breeding sites like *Drosophila* spp. pollinating *Aristolochia maxima*. Second, nonpollinating insects breeding on flowers of a group can be related or unrelated to the pollinator species. This situation is in contrast to pollination of ovule parasites, where nonpollinating ovule parasites are usually close relatives of the pollinators. Differences in the costs of ovules (seeds) versus floral parts (useless for plants after pollination) may cause specificity of plant–pollinator interactions. As mentioned above, our knowledge on pollination systems in this group is still fragmentary. Further studies may reveal dynamic relationships among plants, pollinators, parasites, and herbivores.

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