

ARISTOLOCHIA SPP. (ARISTOLOCHIACEAE) POLLINATED BY FLIES BREEDING ON DECOMPOSING FLOWERS IN PANAMA¹

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This study presents breeding and pollination systems of *Aristolochia maxima* and *A. inflata* in a seasonal tropical forest of Panama. *Aristolochia* is the most diverse genus of Aristolochiaceae, with ~120 species distributed throughout the tropics and subtropics. All the *Aristolochia* species studied so far are pollinated by saprophagous flies of different families, which are presumably deceived by floral odor. Flowers of many species have trap-and-release mechanisms. The flowers attract and imprison pollinators during the female stage first day of flowering and release them after anther dehiscence. Pollination systems of *A. maxima* and *A. inflata* are different from those of other *Aristolochia* in lacking trap mechanisms. Furthermore, the pollinators oviposit in the flowers, and their larvae grow on the fallen, decaying flowers on the ground. Therefore, the plants have a mutualistic relationship with their pollinators. Self-compatible *A. inflata* is pollinated by *Megaselia sakaiae* (Phoridae, Diptera). The pollinator may be specialized to *Aristolochia* flowers, which is the only substrate for larval development. On the other hand, self-incompatible *A. maxima* is pollinated by *Drosophila* spp. (Drosophilidae, Diptera), which utilize *Aristolochia* flowers as a breeding site only occasionally. This pollination mutualism might have evolved from deceit pollination.

Key words: Diptera; Drosophilidae; flower-breeding pollinator; Panama; Phoridae; tropical forest.

In the angiosperms, amazingly diverse pollination mechanisms have evolved for a single function: transferring pollen from one plant to a stigma of another conspecific. In most pollination systems, insects are the principal pollinators, and this is thought to be related to the success of the angiosperms (Burger, 1981). Many insects primarily visit flowers for pollen and nectar, but some pollinators visit flowers for mating and oviposition.

Pollination systems involving pollinators breeding on the flowers or inflorescence of the plant have been found in different plant groups. The pollination systems can be subdivided into three categories. First of all, plants that offer ovules or developing seeds as a breeding site to pollinators are known only from limited plant genera, *Ficus* (Moraceae) (Janzen, 1979; Wiebes, 1979), *Yucca* (Agavaceae) (Baker, 1986), *Trollius* (Ranunculaceae) (Pellmyr, 1989), *Lithophragma* (Saxiflagaceae) (Pellmyr and Thompson, 1992), and possibly *Piper* (Ollerton, 1996), probably because of the high cost for plants to sacrifice part of their ovules for pollinator development. The second category includes plants pollinated by pollen feeders developing on living flowers, mostly thrips (Thysanoptera). Thrips, agricultural and horticultural pests, are often found in flowers of many wild plants and are thought to rarely contribute to pollination (Mound and Marullo, 1996; G. Francesco, the University of Milan, Italy and D. W. Roubik, Smithsonian Tropical Research Institute, Panama, unpublished data). They

are regarded as principal pollinators only in limited plant species of Annonaceae (Webber and Gottsberger, 1995; Momose, Nagamitsu, and Inoue, 1998), Moraceae (Sakai, 2001), Winteraceae (Thien, 1980; Pellmyr et al., 1990), Zamiaceae (Mound and Terry, 2001), and others. The third group involves pollinators that oviposit on floral parts other than ovules. Their larvae develop on plant reproductive organs such as male inflorescences and corollas after pollination. The pollinators, usually dipteran (see DISCUSSION) or coleopteran (e.g., Rattray, 1913; Henderson, 1986; Pellmyr and Thien, 1986; Norstog and Fawcett, 1989; Armstrong and Irvine, 1990) insects, may have evolved many times from nonpollinating herbivores feeding on living or dead plant reproductive organs. Our knowledge of these pollination systems, which involve most diverse plant and pollinator groups, is still fragmentary.

The present study reports pollination systems of *Aristolochia maxima* Jacq. and *A. inflata* H. B. & K., in which flower-breeding flies pollinate their host plants. *Aristolochia*, the most diverse genus of the family Aristolochiaceae, contains ~120 species distributed throughout the tropics and subtropics (Mabberley, 1995). Their zygomorphic flowers are diverse in size, shape, and color, but based on the same groundplan (Endress, 1994). The perianth of the flowers has only three sepals. The sepals are united into a tubular calyx, of which three parts can be distinguished. The basal part is 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.

In all *Aristolochia* species studied so far, flies of different families, including Anthomyiidae, Chloropidae, Milichiidae, Phoridae, Sarcophagidae, and Syrphidae, have been recorded as pollinators (Cammerloher, 1923; Petch, 1924; Brues, 1928; Lindner, 1928; Brantjes, 1980; Costa and Hime, 1983; Wolda and Sabrosky, 1986; Hall and Brown, 1993). Their flowers are strongly protogynous. On the day the flowers open, they attract flies primarily by odor, and trap the flies inside the utricle. On

¹ Manuscript received 4 May 2001; revision accepted 7 September 2001.

The author thanks David W. Roubik and S. Joseph Wright for invaluable support throughout the study at STRI; the Smithsonian Tropical Research Institute for the use of the canopy crane; Vibeke Horlyck for arrangement of my crane work; Carlos R. Vilela, R. Henry L. Disney, and Raymond J. Gagne for insect identification; and Makoto Kato, Hidetoshi Nagamasu, Jeff Ollerton, and an anonymous reviewer for comments on the manuscript. This study was supported by JSPS Postdoctoral Fellowships for Research Abroad and Young Scientists.

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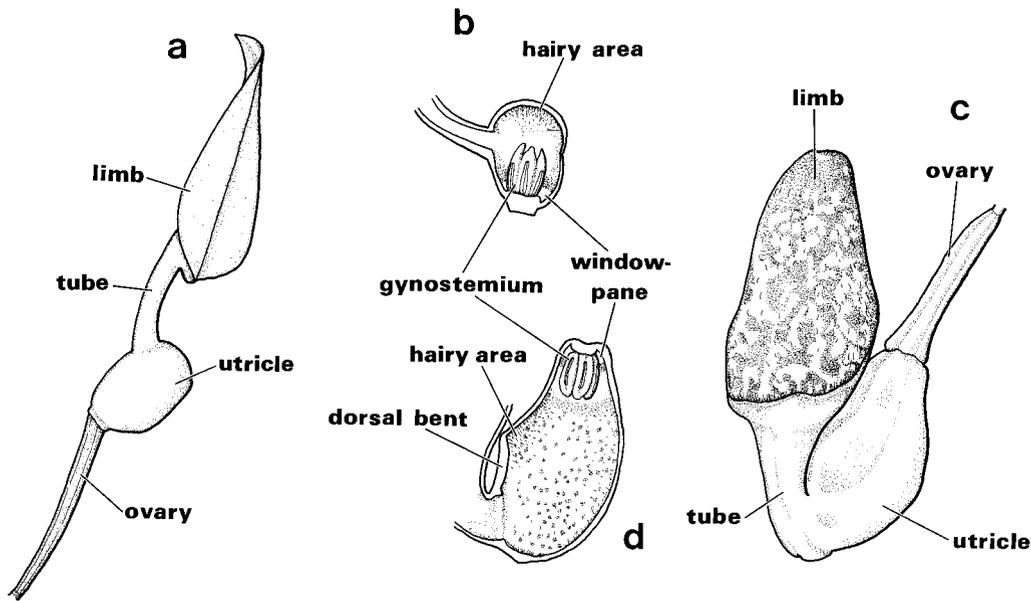


Fig. 1. *Aristolochia inflata* and *A. maxima* flowers. (a) Flower of *A. inflata*, natural size. (b) Longitudinal section of utricle of *A. inflata*, natural size. (c) Flower of *A. maxima*, natural size $\times 0.9$. (d) Longitudinal section of utricle of *A. maxima*, natural size $\times 0.9$.

the second day, the anthers dehisce and the flies are released with pollen load. Because the pollinators belong to saprophagus groups and it is unlikely that they depend on floral nectar and pollen of *Aristolochia*, the pollination system is regarded as deceptive. The pollination systems of *A. maxima* and *A. inflata* reported in this study are unique in the genus in that their pollinators oviposit and develop on the flowers. This paper shows that deceit pollination is not always the case with *Aristolochia* and suggests potential diversity of the plant–pollinator interactions in the genus.

MATERIALS AND METHODS

Study site and plant—The study was conducted in a seasonally dry forest in the Parque Natural Metropolitano near Panama City, Panama. Annual rainfall at the site is 1740 mm on average, most of which occurs during the rainy season (from May through December). The forest is ~80-yr-old second growth up to 40 m in height. The canopy layer is dominated by *Anacardium excelsum* (Anacardiaceae) and *Luehea seemannii* (Tiliaceae). I used a 42-m tall tower crane with a 51-m jib permanently installed in the park (Parker, Smith, and Hogan, 1992) to reach lianas growing on the forest canopy.

Aristolochia maxima and *A. inflata* are relatively common species in Central America (Pfeifer, 1966). Both are lianas that often grow in thickets and secondary forests. The former is distributed from southern Florida to Panama and the latter from southern Mexico to Panama. At the study site, most flowers of the both species opened in the canopy layer of the forest 10–30 m above the ground, while some of the flowers of *A. maxima* occurred on thick stems in the understory. Preliminary observation and insect collection were conducted in October to December 1999. In 2000, *Aristolochia maxima* and *A. inflata* flowered from mid-October to early December and from early November to late December, respectively. In this flowering season, three individuals (M1, M2, M3) of *A. maxima* and one (I1) individual of *A. inflata*, within reach of the crane (~1 ha) were studied. Specimens of the plants were deposited at the Smithsonian Tropical Research Institute (Summit Herbarium [SCZ]) and Panama University (PMA) (voucher specimens: *A. maxima*: S. Sakai 535; *A. inflata*: S. Sakai 551).

Calyx tubes of *A. maxima* are coriaceous, creamy white tinged with purple, and totally glabrous outside. The utricle is $\sim 3.5 \times 2.0$ cm and is obovoid with a dorsal dent on the distal third (Fig. 1c, d). The inner surface is mostly

white with purple dots and covered with nectarial transparent hairs, especially on the dorsal surface and on the broad purple band above the gynostemium (Fig. 1d). The hairs are ~ 1.2 mm long, are very sticky, and cling to each other. At the bottom around the base of the gynostemium, the utricle has a clear translucent “windowpane” fringed by a thin purple band on the inner surface (Fig. 1d). The other end of the utricle is connected with a glabrous tube, which expands into a limb (Fig. 1c). The limb is purple with yellow patches and thick purple hairs on the inner surface. The limb is erect when the flower opens. In the late afternoon of the first day of flowering, it gradually bends inward over the entrance of the tube, and the hairs on the limb wither. Pollen is very sticky, usually forming large clumps in the utricle after anther dehiscence and on the bodies of pollinators. Pollen grains are spherical, ~ 30 μm in diameter.

Flowers of *A. inflata* are smaller and more delicate. The calyx is white and glabrous outside. The utricle is $\sim 1.3 \times 1.0$ cm and is ellipsoid (Fig. 1a). The flower also has a windowpane fringed by a reddish-brown band at the bottom of the utricle around the gynostemium (Fig. 1b). Inside the column of the gynostemium, transparent sticky liquid is secreted. The inner surface of the distal dome of the utricle is spongy, with suppressed hairs (Fig. 1b). The soft transparent hairs secrete nectar. The glabrous tube is connected with the glabrous limb, which is narrowly triangular, yellow inside, white outside. In this species, a calyx does not show clear changes in appearance from the outside in the course of flowering. Pollen is powdery. The inside of the utricle is sometimes dusted with pollen throughout after anther dehiscence. Pollen grains are spherical, ~ 20 μm in diameter.

Fruits of *A. maxima* and *A. inflata* matured in early March and late January, respectively. They dehisce acropetally, and seeds are dispersed by wind. Mature fruits of *A. maxima* are cylindrical and large, measuring $\sim 12 \times 5$ cm, with 520 ± 140 seeds ($N = 10$) (mean \pm SD, throughout the text), while that of *A. inflata* is narrow, cylindrical, and strongly six-ribbed, measuring $\sim 3.5 \times 1.0$ cm, with 140 ± 60 seeds ($N = 15$).

Pollination experiment—Pollination experiments were conducted on M1 in *A. maxima* and I1 in *A. inflata*. In both species, flowers for the experiments were enclosed in mesh bags before anthesis except flowers used for open-pollinated control. In *A. maxima*, geitonogamous pollen from second-day (male-stage) flowers on the same plant and cross pollen from M3 was applied to 13 and 12 first-day (female-stage) flowers, respectively, on 2 November at 0700 to 1100. Sixty-nine bagged flowers were left without hand-pollination

TABLE 1. Fruit set of the pollination experiments of *Aristolochia maxima* and *A. inflata* in 1999 and 2000 at the Pargue Natural Metropolitan, Panama.

Species Treatment	Fruit set (%)		N
	after 2 wk	after 8 wk	
<i>A. maxima</i>			
Cross-pollinated	66.7	66.7	12
Self-pollinated	0.0	0.0	13
Bagged	0.0	0.0	69
Open-pollinated control	2.4	2.4	164
<i>A. inflata</i>			
Self-pollinated	89.4	89.4	19
Bagged	2.9	2.9	35
Open-pollinated control	18.7	15.9	107

as the bagged treatment. As control, 164 open-pollinated flowers were tagged and their fruit set was monitored. In *A. inflata*, geitonogamous pollen was applied to in total 19 1-d flowers on 24 and 27 November at 0700 to 1000, and 31 bagged flowers were left without hand-pollination as the bagged treatment. As the control, 109 open-pollinated flowers were also observed. Fruit set of the flowers was monitored until fruit dispersal. Differences in fruit set 2 wk after flowering between treatments were statistically examined with Fisher's exact test (one-sided) using the SAS system (SAS, 1988).

Observation and collection of flower visitors—Insects in utricles were collected by sampling whole calyces. The insects were preserved in 50% alcohol or in dried state, and parts of them were stored at the Smithsonian Tropical Research Institute and Panama University. Some utricles with flies inside were brought to a laboratory, and behavior of the flies was observed through a hole made in the utricle.

To examine pollen loads of insects leaving flowers of *A. maxima* after anther dehiscence, first-day flowers of M1 were collected in the afternoon and placed in a mesh bag and kept overnight. The following morning, flies in the bag were sampled, and the numbers of pollen grains on their bodies were counted under a microscope. The numbers were compared among the following three insect groups: Coleoptera, Phoridae, and Drosophilidae. In *A. inflata*, insects were collected from second-day flowers on I1 at 0600 to 0700 to examine the pollen on their bodies.

Phorid and drosophilid flies were counted in flowers at different flowering

stages. For *A. maxima*, insects in first-day flowers were counted at 0600–0700 and 1030–1130 and second-day flowers at 0600–0700 (20 flowers each); for *A. inflata*, first-day and second-day flowers were examined at 0600–0700 and 1100–1200 (10 flowers each).

Rearing—Twenty-four flowers of each species collected directly from inflorescences were kept in plastic containers with wet sand for 1 mo or more to examine insect species that had oviposited on the flowers. Insects that emerged from the flowers were collected and kept in alcohol.

RESULTS

Pollination experiments—In *A. maxima*, flowers pollinated with self-pollen did not set fruits. Fruit set in cross-pollination treatment was 66.7% 2 wk after pollination (Table 1) and significantly higher than that of self-pollination and open-pollinated control ($P = 0.0005$ and $P < 0.0001$, respectively; Fisher's exact test, one-sided). All the fruits remaining 2 wk after flowering grew into mature fruits (Table 1).

In *A. inflata*, 89% of self-pollinated flowers had grown into immature fruits 2 wk after pollination and were retained until fruit dispersal, while only 1 flower out of 35 set a fruit in the bagged treatment (Table 1). Difference between the treatments was significant ($P < 0.0001$; Fisher's exact test, one-sided). Fruit set of open-pollinated controls (18.7%) was significantly lower than that of self-pollinated flowers, but higher than that of the bagged treatment ($P < 0.0001$ and $P = 0.014$, respectively; Fisher's exact test, one-sided). Among the 20 fruits retained 2 wk after flowering in the open-pollinated control, 17 fruits matured in January (Table 1).

Flower visitors—The most abundant insect families among flower visitors in *A. maxima* ($N = 921$) were Phoridae (53%), Drosophilidae (19%) (Diptera), and Staphylinidae (18%) (Coleoptera) (Table 2). All the flies of Phoridae except two belonged to a single species, *Megaselia sakaiae*. Most of them (99.7%, $N = 376$) were female. All ($N = 177$) of the drosophilid flies were various species of *Drosophila*, including *D. aff. bromeliae*, *D. aff. florum*, *D. neocardini*, *D. malerkotliana*, *D. mesostigma*, *D. equinoxialis*, and *D. latifasciaeformis*. Fif-

TABLE 2. The numbers of insects collected from utricles of three individual of *Aristolochia maxima* and one individual of *A. inflata*, respectively, in 1999 and 2000.

Order Family Species	<i>A. maxima</i>						<i>A. inflata</i>		
	1999	2000				Total	1999	2000	Total
		M1	M2	M3	Total				
Coleoptera									
Staphylinidae	8	115	22	21	158			166	
Chrysomelidae		4	5	2	11			11	
Others	2	30	4	8	42			44	
Diptera									
Phoridae									
<i>Megaselia sakaiae</i>	132	165	2	192	359	491	20	190	210
Others		1		1	2	2			
Drosophilidae									
<i>Drosophila</i> spp.	9	140	8	20	168	177			
Others		18	4	2	24	24			
Hymenoptera		3	1		4	4			
Psocoptera		1			1	1			
Total	151	477	46	246	769	920	20	190	210

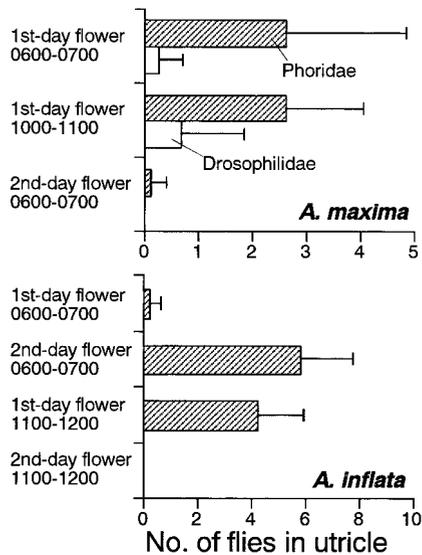


Fig. 2. The average numbers of phorid and drosophilid flies in a single flower of *A. maxima* and *A. inflata* at different stages (± 1 SD) ($N = 20$ flowers/stage in *A. maxima*; $N = 10$ flowers/stage in *A. inflata*).

ty-eight percent of *Drosophila* spp. ($N = 69$) were female. *Megaselia* flies were observed licking nectar secreted from hairs inside the utricles of *A. maxima* and *A. inflata*. I could not observe behavior of *Drosophila* in a utricle, because cutting the utricle disturbed flies and most of the flies left it immediately.

Most of the insects collected from second-day flowers of *A. maxima* had only <10 pollen grains on their body (55% of Drosophilidae, $N = 58$; 99% of Phoridae, $N = 83$; and 82% of Coleoptera, $N = 89$). All of the visitors that carried 100 or more pollen grains were Drosophilidae (37% of Drosophilidae, $N = 58$).

All 210 insects found in utricles of *A. inflata* were *Megaselia sakaiae*. All of the individuals examined were female ($N = 108$). An individual of *M. sakaiae* from a second-day flower carried 66 ± 78 pollen grains, and 81% of the flies had 10 or more pollen grains on the body.

In *A. maxima*, utricles of most second-day flowers were already empty at 0600–0700, and 2.6 ± 2.2 phorid and 0.25 ± 0.43 drosophilid flies were found in first-day flowers. The number of drosophilid flies increased thereafter and was 0.65 ± 1.19 at 1030–1130 (Fig. 2). On the other hand, first-day flowers were almost empty, and 4.2 ± 1.7 phorid flies were still found in second-day flowers in *A. inflata*. There were 5.8 ± 1.9 phorids in first-day flowers at 1100–1200, and second-day flowers were empty (Fig. 2).

Rearing—*Megaselia sakaiae* and *Drosophila* spp. (Drosophilidae) were bred from flowers of *A. maxima* (Table 3). Eggs of *M. sakaiae* on the flower were found throughout the inner surface of the utricle and limb. In *A. inflata*, *Zigotricha* sp. and *D. aff. bromeliae* (Drosophilidae) were bred mostly from floral limbs, while *M. sakaiae* was bred from utricles. Eggs of *M. sakaiae* were mostly found on and around the gynostemium. Eggs of Drosophilidae could not be located, probably because they lay eggs not on the surface but within floral tissue.

Larvae of *M. sakaiae* emerged from the eggs within a couple of days after oviposition. They fed on the inner surface of

TABLE 3. Flies that emerged from flowers of *Aristolochia maxima* and *A. inflata*. Flowers for rearing were directly collected from the plants. Flowers of *A. inflata* were cut into upper limb and lower utricle and reared separately to examine developing site differentiation among fly species.

Family	Species	Sex ^a	<i>A. maxima</i>	<i>A. inflata</i>	
				Limb	Utricle
Drosophilidae					
<i>Drosophila</i> spp.	M	7	2	0	
	F	8	0	0	
<i>Zigotricha</i> sp.	M	0	10	0	
	F	0	18	1	
Phoridae					
<i>Megaselia sakaiae</i>	M	99	0	66	
	F	99	0	127	
Cecidomyiidae					
<i>Clinodiplosis</i> sp.		10	0	0	

^a M: male, F: female

the calyx and gynostemium, which gradually changed from creamy yellow to black. Under the rearing conditions, they pupated 1 wk after oviposition, often on the wall of the plastic container or less frequently, on rotten flowers. Larvae of Drosophilidae were observed feeding on the inner surface of the calyx. From flowers of both species, adults of Phoridae and Drosophilidae emerged ~ 15 d after flowering.

DISCUSSION

Breeding and pollination systems of Aristolochia spp.

The failure to set fruit in self-pollinated flowers and the extremely high fruit set in cross-pollinated flowers of *Aristolochia maxima* suggest that the species is self-incompatible. Although self-incompatibility is suggested in some species of the genus (e.g., *A. gigas* [= *A. grandiflora*] and *A. ridicula*; Petch, 1924), it has rarely been demonstrated by hand-pollination. On the other hand, *A. inflata* is self-compatible because flowers pollinated with self-pollen showed high fruit set. The difference in self-compatibility may explain much higher fruit set of *A. inflata* (18.7%) than that of *A. maxima* (2.4%) in open-pollinated controls (Table 1).

Self-compatibility seems to be more common in the genus (Petch, 1924; Razzak, Ali, and Ali, 1992). Self-pollinated flowers set fruits in *A. elegans* [= *A. littoralis*] (Petch, 1924). Fruit set of bagged flowers was not significantly different from that of open-pollinated flowers in *A. bracteolata* (Razzak, Ali, and Ali, 1992). Cleistogamy is suspected in *A. serpentaria* (Pfeifer, 1966). A single fruit from a bagged, untreated flower indicates that autogamy can occur in *A. inflata*, but pollinators are essential for successful fertilization even in this self-compatible plant, considering the fact that bagged flowers had lower fruit set than the open-pollinated controls (Table 1). Furthermore, cross-pollinated flowers of *A. maxima* and self-pollinated flowers of *A. inflata* had much higher fruit set than the open-pollinated controls of each species, suggesting that limitation of compatible pollen is an important proximate factor in determining fruit set in the two species (Table 1).

Megaselia sakaiae, the exclusive flower visitor to *A. inflata*, is the primary pollinator of *A. inflata* (Table 4). Visitation frequency of the flies (5.8 ± 1.9 flies/flower) and the number of pollen grains on the flies (66 ± 78 pollen grains/fly) were high enough to explain fruit set of 18.7% and 140 ± 60 seeds in

TABLE 4. Dipteran species found on *Aristolochia* flowers and their relationships with the flowers (+++: much, ++: some; +: little).

Family Species	Breeding on flowers		Flower visit frequency		Contribution to pollination	
	<i>A. maxima</i>	<i>A. inflata</i>	<i>A. maxima</i>	<i>A. inflata</i>	<i>A. maxima</i>	<i>A. inflata</i>
Drosophilidae						
<i>Drosophila</i> spp.	++	+	+++		+++	
<i>Zigothrica</i> sp.		+++				
Phoridae						
<i>Megaselia sakaiae</i>	+++	+++	+++	+++		+++
<i>M. metropolitanaensis</i>	++					
<i>Puliciphora pygmaea</i>	++	++				
Cecidomyiidae						
<i>Clinodiplosis</i> sp.	++		+			

a fruit in self-compatible *A. inflata*. Most eggs of the fly in *A. inflata* were found on and around a gynostemium, which had sticky exudate inside. Probably the exudate sticks to the flies when they partially put their bodies into the gynostemium to oviposit, and functions as glue to attach powdery pollen grains to the pollinator. The other flies reared in *A. inflata*, *Zigothrica* sp. and *Drosophila* aff. *bromeliae*, are thought to oviposit from outside of the flower, as most of them were reared not in the utricles but in the limbs (Table 3). Besides, *Zigothrica* sp. was frequently observed on a limb of *A. inflata* (personal observation), but never in a utricle. The thin tube of the calyx may exclude larger visitors than phorids.

Although *M. sakaiae* was the most abundant flower visitor to *A. maxima*, this species is unlikely to be the principal pollinator of the plant (Table 4). Most *M. sakaiae* (99%) from male-stage flowers of *A. maxima* had less than ten pollen grains on their bodies, which was much less than the amount of pollen grains on *M. sakaiae* from flowers of *M. inflata*. It may be partly due to different behavior of *M. sakaiae* in flowers of *A. inflata* and *A. maxima*. Eggs of *M. sakaiae* were found only on and around a gynostemium in *A. inflata*, while those in *A. maxima* were found throughout the inner surface of the utricle and limb.

Considering the amount of body pollen on different flower visitors, *Drosophila* spp. are the primary pollinators of *A. maxima*. To fertilize a single flower of *A. maxima*, hundreds of cross-pollen grains are needed, since the species is self-incompatible, and a fruit contains as many as 520 ± 140 seeds. Thus a single visit of a pollinator with a large pollen load from another conspecific plant may be more important than visits of many insects with small pollen loads, most of which are from flowers on the same plant. Among insects that emerged from second-day flowers, only drosophilid flies had >100 pollen grains on their bodies. However, one cannot conclude that *Drosophila* flies are the exclusive pollinators. Beetles, mostly Staphylinidae, were as abundant as *Drosophila* flies on *A. maxima* flowers, although 82% of the beetles collected on second-day flowers carried <10 pollen grains. Besides, the visit frequency of Phoridae is up to 8.8 times as high as that of Drosophilidae (Table 2), although they likewise had little body pollen. The beetles and phorids may also play a role in pollination of *A. maxima*.

Why do pollinator flies visit flowers of *A. maxima* and *A. inflata*? Probably odor and, to a less extent, floral color function as proximate attractants for pollinators as suggested in other species (Vogel, 1990). What, then, prevents the flies in the utricle from leaving until the following day? Except for the limb in *A. maxima*, the calyx tube does not change in shape or position during flowering, and the limb does not keep flies

from flying away. Actually, flies can leave the flower, as they were observed to leave first-day flowers when the flower was disturbed. However, most flies leave the flower only after anther dehiscence. One of the rewards the plants offer to the pollinators is a breeding site. It was confirmed that the pollinators, *M. sakaiae* and *Drosophila* spp., breed on flowers of *A. inflata* and *A. maxima*, respectively. Apparently, this is the first report of the pollinators breeding on *Aristolochia* flowers, although it was suggested as early as 1839 by Graham. While Hime and Costa (1985) have already described *Megaselia* breeding on *Aristolochia* flowers, the contribution of the flies to pollination is unknown. The other reward for the pollinators is nectar secreted from the inner surface of the utricle. It must also be important especially in *A. maxima*, in which oviposition of the pollinators occurs less frequently than in *A. inflata* (Table 3). Thus, the pollination system can be regarded as a mix of nectar reward and decaying tissue as breeding sites.

Most studies on pollination systems of *Aristolochia* explain that the pollinator flies visit flowers because they are deceived by floral odor that mimics carrion, feces, fungi, etc. (Proctor, Yeo, and Lack, 1996). Flowers of some species have been documented to have elaborate trap-and-release mechanisms, such as the hairs on the tube of *A. grandiflora*. The hairs allow flies to enter the utricle but not to exit and wither when the flower switches its sex from female to male so that the flies can leave the flower with pollen loads (Cammerloher, 1923). Many *Aristolochia* species are known to have nectaries on the inner wall of the utricle (Cammerloher, 1923; Petch, 1924; Daumann, 1959; Costa and Hime, 1983), but the nectar is regarded as food to ensure survival of the imprisoned pollinators during captivity rather than a reward (Vogel, 1998). Petch (1924) observed many dead flies in flowers of *A. gigas* [= *A. grandiflora*], a species that does not provide any food to imprisoned flies. In a few *Aristolochia* species, nectar secreted at the floral entrance takes part in pollinator attraction (Daumann, 1959; Vogel, 1998).

The pollination system of *A. maxima* and *A. inflata* is different from the other *Aristolochia* species studied so far in that the plant does not deceive the pollinators but provides a breeding site for them. The nectar secreted from the inner surface of the utricle of *A. maxima* and *A. inflata* may also have more than a supplemental role. *Megaselia sakaiae* has been found only on *Aristolochia* flowers (Disney and Sakai, 2001). It is possible that the nectar is essential for their ovule development and oviposition. In contrast with *M. sakaiae*, which has a high female ratio among flower visitors (99.7%), the proportion of females in *Drosophila* spp. was much lower (58%). There were far fewer *Drosophila* flies reared in flowers than *M. sakaiae*. The *Drosophila* flies might visit flowers not only to ovi-

posit, but also to copulate and/or feed on the nectar. Lack of trap-and-release mechanism in both plants may reflect more mutualistic relationships of the plants with their pollinators than those of deceptive *Aristolochia* species.

The diversity within the Phoridae (2500 species) is high (Disney, 1994). Adult flies are found in damp places, on or near many kinds of decomposing plants and animal matter, on flowers and fungi, and in rodent burrows, ant and termite nests, and caves. In addition to those habitats, larvae are known from seed capsules, feces, and many kinds of gastropods and insects (Peterson, 1987; Disney, 1994), but phorids ovipositing and breeding on living flowers are only known from a single plant host in Liliaceae other than *Aristolochia* (Disney, 1994). Baumann (1978) reported that 77 species of phorid flies have been recorded visiting 60 species of flowers, although they have rarely been recorded pollinating plants other than *Aristolochia* (but see Young, 1984; Singer and Cocucci, 1999).

The Phoridae is one of the dipteran families frequently found visiting *Aristolochia* flowers (Carr, 1924; Brues, 1928; Iwata, 1975; Baumann, 1978; Hime and Costa, 1985; Hall and Brown, 1993). Some of the flies were reported to oviposit (Petch, 1924) and reproduce on *Aristolochia* flowers (Hime and Costa, 1985). Although some phorid species recorded from *Aristolochia* flowers were also found from fungi, ant and wasp nests, feces, insect larvae and pupa, etc. (Robinson, 1971), *M. sakaiiae* is thought to be specialized to *Aristolochia* flowers (Disney and Sakai, 2001). *Megaselia sakaiiae* and *M. aristolochiae*, a close relative of *M. sakaiiae* breeding on *Aristolochia labiata* flowers, have not been found in other places (Hime and Costa, 1985; Disney and Sakai, 2001).

Interestingly, two other species of Phoridae were found to breed on fallen *Aristolochia* flowers at the study site (Disney and Sakai, 2001). Wingless females of *Puliciphora pygmaea* (Phoridae) were frequently observed on fallen flowers of *A. maxima* and *A. inflata*, and adults of both sexes were reared from the flowers (Table 4; Disney and Sakai, 2001). The other species reared in fallen flowers of *A. maxima* was *M. metropolitanoensis*, a close relative of *M. sakaiiae* and *M. aristolochiae* (Disney and Sakai, 2001). Although adults have not been observed in the field, females of the species are thought to oviposit on fallen flowers of *A. maxima* because the species was not bred from flowers collected directly from the plant (Disney and Sakai, 2001). *Puliciphora pygmaea* and *M. metropolitanoensis* could also be specific to *Aristolochia* flowers, as breeding sites other than fallen *Aristolochia* flowers are not known in both species. The pollinator of *A. inflata* might arise from phorid flies breeding on fallen *Aristolochia* flowers. A mutualism similar to that of *A. inflata* and *M. sakaiiae* may also have evolved in a neotropical grass: Soderstrom and Calderón (1971) suggested that two species of phorid flies visited and bred on *Pariana* (Gramineae) and perhaps were responsible for its pollination as well.

In contrast with Phoridae, Drosophilidae have rarely been reported as the predominant visitors or pollinators of *Aristolochia* flowers. The family is large with 3000 described species, and more than half of these belong to the genus *Drosophila* (Weeler, 1987). Breeding sites and specificity for the sites in *Drosophila* are diverse. Their breeding sites include decomposing fruits and flowers and other plant materials, living leaves (mining in leaf tissue) and fungi (Carson, 1971). Many *Drosophila* species are known to oviposit exclusively or occasionally on flowers and flower buds (Pipkin, Rodríguez,

and León, 1966; Brncic, 1986; Vilela and Pereira, 1992). The host flowers are usually bulky and fleshy. *Drosophila* flies may lay eggs within the floral tissue with a sharp ovipositor. Oviposition in the floral tissue rather than on a surface may be the reason why eggs of *Drosophila* could not be found in *Aristolochia* flowers.

The extent to which *Drosophila* flies depend on flowers as a breeding site and their host specificity vary greatly among species. For example, cosmopolitan species mostly associated with fallen fruits and garbage, including *Drosophila melanogaster*, *D. ananassae*, and *D. busckii*, occasionally breed on living flowers (Carson, 1971; Brncic, 1986). Other *Drosophila* species in the *flavopilosa* group are only known from flowers of one plant species, and they depend on flowers for both adult food and breeding site (Pipkin, Rodríguez, and León, 1966; Vilela and Pereira, 1992). In general terms, however, the species associated with flowers are seldom specialized to a single host species (Brncic, 1986).

In contrast to *A. inflata*, which is pollinated by flies of a single species specialized to *Aristolochia*, *A. maxima* is pollinated by diverse species of *Drosophila*. *Drosophila* aff. *bromeliae* and *D. aff. florum* collected from *A. maxima* flowers belong to groups *bromeliae* and *florum*, respectively, that are "generalist flower-breeders," which breed on flowers of variety of species including *Datura* (Solanaceae) and *Ipomea* (Convolvulaceae) (Patterson and Stone, 1952; Carson, 1971). *Drosophila latifasciiformis* visiting *A. maxima* were also bred from *Borassus* flowers (Palmae) (Brncic, 1986). Other *Drosophila* flies are opportunistic flower breeders. *Drosophila cardinoides* visiting and bred from *A. maxima* flowers has been reared from flowers of Araceae, Heliconiaceae, Solanaceae, Zingiberaceae, as well as fruit of Annonaceae and Clusiaceae, and mushrooms (Pipkin, 1965; Brncic, 1986). *Drosophila malerkotliana* and *D. equinoxialis* are common flies often reared from fallen fruits (Sevenster and Alphen, 1996). Apparently *A. maxima* flowers are not the exclusive breeding site for the pollinator *Drosophila* species.

Plants pollinated by drosophilid flies breeding on reproductive organs of the plants have been reported only in a few taxonomic groups such as *Alocasia* spp. (Araceae) (van der Pijl, 1953; Yafuso, 1993) and *Nypa fruticans* (Palmae) (Essig, 1973). The pollination system of *A. maxima* is quite different from that of *Alocasia* and *Nypa* in that the pollinators include many species and that the flowers are not the major breeding site of the pollinator flies. In *A. maxima*, nectar may play a more important role than oviposition sites in keeping the flies in the utricle. It may be related to a lack of specialization of the plant and pollinators.

Interaction between *A. maxima* and *A. inflata*—Since flowering periods and flower visitors of *A. maxima* and *A. inflata* considerably overlap, they have the potential to affect each other positively or negatively through flower visitors and pollinators. The flowering period of *A. maxima* precedes that of *A. inflata* by ~2 wk, and *M. sakaiiae*, pollinators of *A. inflata*, breeds on flowers of *A. maxima* as well as those of *A. inflata*. Flowering of *A. maxima* may contribute to population growth of the pollinators and have a positive effect on pollination of *A. inflata*. In contrast, the frequent visits of *M. sakaiiae* to *A. maxima* may reduce the pollination success of *A. inflata* through interspecific pollen transfer and may decrease pollinator visits. Different timing of pollinator release and attraction (Fig. 2) is a possible mechanism for reducing inter-

specific pollinator movement, but the effect of a decrease in pollinator visits is unknown. In contrast, pollination success of *A. maxima* is unlikely to be affected by *A. inflata*. *Aristolochia inflata* flowers are thought to have little importance as breeding sites for the pollinators of *A. maxima*, because of the low host specificity of the pollinators and the rarity of *Drosophila* flies bred in *A. inflata*. Flowering of *A. inflata* may hardly reduce visit frequency of the pollinators to *A. maxima*, as the pollinators of *A. maxima* rarely visit flowers of *A. inflata*.

Dipteran pollinators breeding on flowers—Although not many plants have been reported to be pollinated by flies breeding on the flowers or inflorescences, it is clear that the pollination by flower-breeding insects has evolved more than once in different plant groups. Among myophilous plants, *Trollius europaeus* (Ranunculaceae) is unique in that developing seeds are the main reward for pollinators. The plant is pollinated by four anthomyiid species (Anthomyiidae, Diptera), which feed on pollen and nectar, mate in the flowers, and complete larval development in the seeds (Pellmyr, 1989). In the other dipteran pollinators breeding on the flower, larval development occurs mostly on decomposing flowers or inflorescences after pollination. Tropical aroids, *Alocasia* spp. (Araceae), are pollinated by *Colocasiomyia* spp. breeding on inflorescences of the plants (Drosophilidae) (van der Pijl, 1953; Yafuso, 1993). Feil (1992) observed that gall midges (Cecidomyiidae) pollinated flowers of *Siparuna* spp. (Monimiaceae) and that larvae of the midges develop on the flowers. Gall midges are also pollinators of *Artocarpus interger* (Moraceae), a species in which larvae of the midge grow by feeding on fungus mycelia on male inflorescences (Sakai, Kato, and Nagamasu, 2000). Similar plant-gall midge mutualism might occur in *Pariana* (Gramineae) (Soderstrom and Calederon, 1971), *Theobroma* and *Herrania* (Sterculiaceae) (Young, 1985, 1986), and *Piper* (Piperaceae) (Ollerton, 1996).

The present study is the first report of pollination mutualism of plants and flower-breeding pollinators in *Aristolochia*, in which scaptomyiophily by deceit is thought to be dominant (Endress, 1994). Future studies may reveal more *Aristolochia* species pollinated by flies breeding on the flowers, because only a limited number of species in this large genus have been studied in detail in a natural habitat. Fly larvae on flowers have been observed in other species (*A. saccata*, Graham, 1839; *A. elegans* [= *A. littoralis*], Petch, 1924; *A. labiata*, Hime and Costa, 1985; *A. gigantea*, S. Sakai, personal observation). In most tropical *Aristolochia* species, the calyx and gynostemium are shed immediately after flowering and rapidly decompose (Pfeifer, 1966). These floral characteristics might be a preadaptation for the pollination mutualism.

Origin of the apparent mutualism awaits further studies on pollination of more *Aristolochia* species and their phylogenetic relationships. It is possible that the pollinators breeding on *Aristolochia* flowers evolved either from pollinators deceived by flowers or from flies breeding on flowers without pollinating them. It is interesting that plants pollinated by flies breeding on inflorescences after pollination are also found in Araceae, in which many species are deceptive sapromyophily (Endress, 1994; Proctor, Yeo, and Lack, 1996). It is also uncertain whether the supposed mutualisms in *A. inflata* and *A. maxima* have evolved independently in *Aristolochia* or whether shifts of pollinators occurred during the course of evolution. Considering that the pollinators of *A. inflata* can also repro-

duce on flowers of *A. maxima* and vice versa, a two-way shift between nonpollinating floral herbivores and pollinators could occur. Coevolution of *Aristolochia* and their pollinators may involve dynamic pollinator shifts between unrelated insects and differ markedly from that of the plants pollinated by ovule parasites, in which pollinator shifts rarely occur and even then only between closely related insect species (Machado et al., 2001).

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