ARTOCARPUS (MORACEAE)–GALL MIDGE POLLINATION MUTUALISM MEDIATED BY A MALE-FLOWER PARASITIC FUNGUS[1]

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A previously undescribed pollination system involving a monoecious tree species, *Artocarpus integer* (Moraceae), pollinator gall midges, and fungi is reported from a mixed dipterocarp forest in Sarawak, Borneo. The fungus *Choanephora* sp. (Choanephoraceae, Mucorales, Zygomycetes) infects male inflorescences of *A. integer,* and gall midges (*Contarinia* spp., Cecidomyiinae, Diptera) feed on the fungal mycelia and oviposit on the inflorescence. Their larvae also feed on the mycelia and pupate in the inflorescence. The gall midges are also attracted by female inflorescences lacking mycelia, probably due to a floral fragrance similar to that of male inflorescences. Because of the sticky pollen, dominance of *Contarinia* spp. in flower visitors, and pollen load observed on *Contarinia* spp. collected on both male and female inflorescences, *Artocarpus integer* is thought to be pollinated by the gall midges. Although several pathogenic fungi have been reported to have interactions with pollinators, this is the first report on a pollination mutualism in which a fungus plays an indispensable role. The pollination system described here suggests that we should be more aware of the roles fungi can play in pollinations.

Key words: Borneo; gall midge; Lambir; monoecy; Moraceae; Mucorales; pollination.

Animal-pollinated flowers have evolved various rewards and attractants to entice pollinators and thus promote pollen transport. Whereas nectar and pollen are the most common rewards, floral tissues may also be offered as brood sites for pollinators in some plant groups. Plants such as *Ficus* (Moraceae) (Janzen, 1979; Wiebes, 1979; Bronstein and McKey, 1989; Herre and West, 1997), *Yucca* (Agavaceae) (Baker, 1986), *Trollius* (Ranunculaceae) (Pellmyr, 1989), *Heuchera* (Saxflagaceae) (Pellmyr et al., 1996) sacrifice a portion of their ovules for brood sites of their pollinators. On the other hand, other plants have developed brood sites and nutrients for pollinators independent from ovules. Androecial parts of plants function as brood sites for pollinators in *Peltandra* (Araceae) (Patt et al., 1995), *Zamia* (Zamiaceae) (Tang, 1987; Norstog and Fawcett, 1989), and *Eupomatia* (Eupomatiaceae) (Armstrong and Irvine, 1990). In most of the cases, however, plants and pollinators directly exchange service and rewards, and participation of fungi in pollination has rarely been reported, although fungi may sometimes have great effects on the pollination success of their host or nonhost plants (Patt, 1992; Roy, 1994, 1996).

Here, we report on the pollination system of *Artocarpus integer* (Thunb.) Merr. (Moraceae) from Sarawak, Borneo. It appears that male inflorescences of *A. integer* on a tree are infected by the fungus *Choanephora* sp. (Choanephoraceae, Mucorales, Zygomycetes), and gall midges (*Contarinia* spp., Cecidomyiinae, Diptera) and their larvae feed on the fungal mycelia. The gall midges are attracted to both male and female inflorescences and thus pollen transport occurs. This is the first report on a pollination mutualism in which a fungus plays an indispensable role.

Moraceae are a family with 38 genera and 1100 species distributed mainly in tropical regions (Mabberley, 1997). Throughout the family, unisexual flowers of both sexes are produced on the same or separate plants and are often arranged in heads to form spadices. Animal pollination has been confirmed only in *Ficus* and a few other genera of the family (Bawa et al., 1985; Momose et al., 1998), whereas wind pollination seems to be common (Zapata and Arroyo, 1978; Bawa and Crisp, 1980; Williams and Adam, 1993; Bullock, 1994). The genus *Artocarpus* consists of 50 species including some cultivated species such as jack-fruits and is distributed throughout the Indomalesia region (Primack, 1983; Mabberley, 1997). Both animal-pollinated and wind-pollinated species are thought to occur in the genus (Corner, 1952; van der Pijl, 1953; Primack, 1983; Endress, 1994).

MATERIALS AND METHODS

Study site and plant—The study site was a primary lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°20′ N, 113°50′ E, altitude 100–200 m). In August 1992, a Canopy Biology Plot (CBP) was demarcated for long-term monitoring of plant phenology and for the observation of plant-animal interactions, by the Canopy Biology Program of Kyoto University and Sarawak Forest Department. The CBP covered an area of 8 ha (200 × 400 m) and had a canopy observation system that consisted of tree towers and aerial walkways (Inoue et al., 1995).

Artocarpus integer, called ''chempedak'' by local people and often cultivated for edible fruits, is a monoecious tree up to 30 m in height with a widespread distribution in primary and secondary dipterocarp

forests in Sarawak. We observed six individuals of the species: three trees of ~20 cm dbh (diameter at breast height) at the forest edge near the headquarters of the National Park (K1, K2, K3) and three trees of 30–45 cm dbh in CBP (B187, B188, and B274).

Observation and collection of flower visitors—The midges on the marked male and female inflorescences on K1, K2 and K3 were counted at 0600, 1200, 1800, 2000, 2200, and 2400 on 30 April 1998 (four male and four female inflorescences) and 11 May (14 male and three female). Data at 2400 on 30 April were not collected because of heavy rain. At each collection, behaviors of midges on inflorescences were observed for 10–60 min. In addition, 92 male inflorescences of various stages from the six trees were collected and examined under a binocular.

Flower visitors on male and female inflorescences of the six trees were collected with suction bottles from the tree crowns up to 2 m high except B274. Collection on B274, the largest tree, was made using a walkway at the height of 20 m. Some of the sampled midges were used to examine pollen load under a stereoscopic microscope and an electron microscope. In addition, insect parasites inhabiting inflorescences were investigated by incubating inflorescences in plastic containers at our field laboratory.

RESULTS

Flowering of *Artocarpus integer* usually occurs once in several years in mature forests, and its flowering seems to be associated with general flowering as well as other *Artocarpus* species in the park, while more frequent reproduction was found in cultivated plants (Sakai et al., 1999; Sakai, personal observation). We started to monitor the largest tree, B274, in April 1993 (Sakai et al., 1999) and observed flowering for the first time in May 1998 except for minor flowering in July 1996.

Although *A. integer* is monoecious, the production of female inflorescence varied among trees irrespective of tree size. Among the six trees we observed, K3 and B188 produced more female inflorescences (~30) than the others, and K1 and B 187 rarely did. On the other hand, male inflorescences were found in all trees. Trees flowered for ~2 mo.

Male inflorescences are cylindrical, measuring 10 × 50 mm (Fig. 1), and are produced both on branches of various sizes or on the trunk of the tree. While they are flowering, the protrusion of stamens followed by anther dehiscence occurs continuously for 3–5 d. Pollen is spherical with a rough surface and measures 11 μm in diameter. It is barely dispersed by winds. As male flowers age, their color changes from greenish yellow to brown, and they gradually become covered with mycelia of *Choanephora* sp. (Choanephoraceae, Mucorales, Zygomycetes) (Fig. 2). Between days 4 and 6, *Choanephora* on the inflorescence produces sporangia and releases spores (Fig. 3). The fungal spores are ellipsoid, 18 μm long × 10 μm in diameter, and are not sticky. The inflorescences are then shed between days 5 and 9.

Female inflorescences are cauliflorous and ellipsoid, measuring 15 × 50 mm, and are green with white thread-like pistils of 1.5 mm in length (Fig. 4). The flowering period of a single female inflorescence lasts for ~10 d. After the receptive stage of the stigma, the stigma turns brown and withers. Almost all female inflorescences grow into fruits, which measure 30 × 18 cm. No mycelia or sporangia were observed on female inflorescences. Both male and female inflorescences release a scent similar to ripe watermelon between 1800 and 2000 while flowering.

The predominant flower visitors were two species of gall midges (*Contarinia* spp., Cecidomyiidae, Diptera) (Figs. 1, 2, 4), among which 92% were *Contarinia* sp. 1 (Table 1). The proportion of female midges on male inflorescences was significantly higher than that on female inflorescences ($P < 0.001$, χ^2 test; Table 1). Pollen grains were not found in their stomachs. Most of the midges collected on both male (85%, $N = 48$) and female inflorescences (84%, $N = 25$) carried pollen, but no fungal spores were found on the midges (Figs. 5, 6). Rare visits by cockroaches and beetles were also recorded (Table 1).

Midges on male inflorescences were observed eating exudate of the mycelia. Frequent oviposition by female midges and numerous larvae and pupae of the gall midges (69 ± 34 larvae and pupae per inflorescence, $N = 6$) were observed on male inflorescences (Fig. 7). Eggs and larvae of gall midges and fungal mycelia were found on most male inflorescences except for young ones just starting to flower (98%, $N = 92$). The midge larvae on a male inflorescence attached to the mycelia and sucked liquid from them. A larva remained on a single male inflorescence and pupated inside the spadix, which had become soft and rotten because of the fungus. Both species of *Contarinia* emerged from male inflorescences. Female midges did not have mature eggs upon emergence. The period required to grow from an egg to an adult midge was estimated to be 8 d. Only a few eggs were found on female inflorescences, and the eggs on female inflorescences did not develop, as evidenced by the lack of larvae and emerging adults from female inflorescences.

Although the gall midges remained on inflorescences throughout the day, density of gall midges on male inflorescences fluctuated considerably. They flew among the inflorescences most actively from 1800 to 2000, and recorded the highest density from 2000 to 0600 on the following day (Fig. 8). In contrast, density on female inflorescences was maintained at a lower level than that on male inflorescences (Fig. 8).

DISCUSSION

Although we did not perform exclusion experiments to confirm the contribution of the gall midges to pollination, sticky pollen, which is not easily dispersed by wind, dominance of two species of *Contarinia* in flower visitors, and pollen load observed on most *Contarinia* spp. collected on inflorescences of both sexes, indicate that *Artocarpus integer* is pollinated by gall midges, *Contarinia* spp. The midges are attracted to both male and female inflorescences by a fruit-like, somewhat unpleasant smell. On the male inflorescences, which are infected by the fungus *Choanephora,* female midges ingest nutrition from the mycelia for ovary maturation and oviposit, whereas they seem to leave a female inflorescence lacking mycelia soon after arriving (Fig. 9). Male gall midges possibly visit inflorescences for mating, while we could not observe mating behavior of gall midges. Male midges may not feed on mycelia as eagerly as the females and remain on a female inflorescence longer. The difference in their behavior can explain the higher ratio of female

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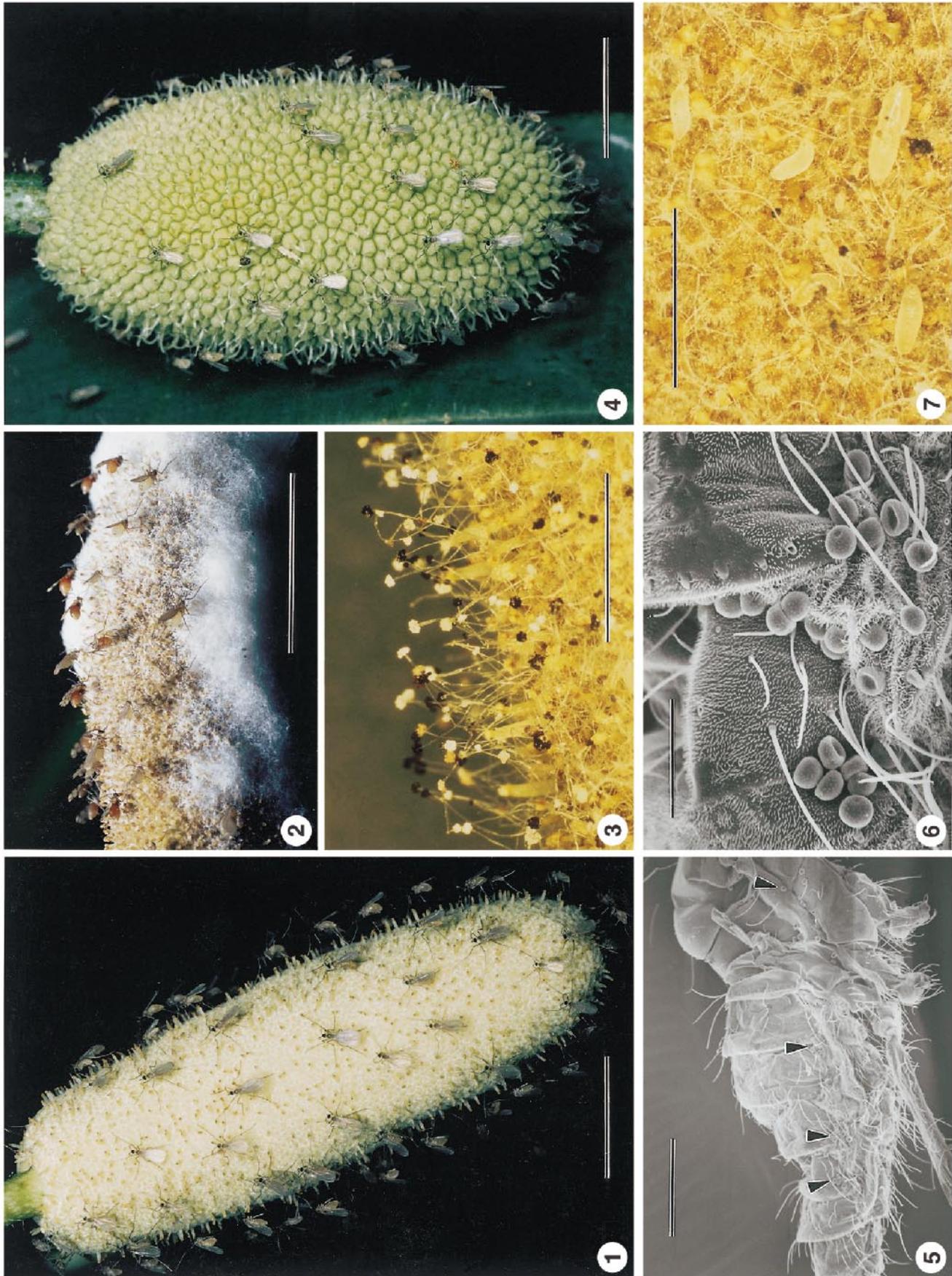
Figs. 1–7. *Artocarpus integer* (Moraceae)–gall midge (*Contarinia* spp., Cecidomyiinae, Diptera) pollination mutualism mediated by parasitic fungi (*Choanephora* sp., Choanephoraceae, Mucorales). **1.** Flowering male inflorescence visited by gall midges (bar = 1 cm). **2.** Gall midges on a male inflorescence heavily infected by the fungus (bar = 1 cm). **3.** Sporangia of the fungus on a male inflorescence visited by many gall midges (bar = 0.5 mm). **4.** Female inflorescence visited by a gall midge with pollen (arrows) attached (5, bar = 0.25 mm; 6, bar = 50 μm; bar = 0.5 mm). **5, 6.** Scanning electron micrographs of a gall midge on a male inflorescence (bar = 0.5 mm). **7.** Larvae of the gall midge feeding on mycelium on a male inflorescence (bar = 0.5 mm).

TABLE 1. The numbers of gall midges collected on inflorescences of six *Artocarpus* trees.

| | Male inflorescence | | | | | Female inflorescence | | | | |
| | *Contarinia* sp. 1 | | *Contarinia* sp. 2 | | | *Contarinia* sp. 1 | | *Contarinia* sp. 2 | | |
Tree ID	Male	Female	Male	Female	Others	Male	Female	Male	Female	Others
B187	2	15								
B188						17	22			
B274		16		1						
K1	2	32		2	1					
K2		8			1	3	7		4	
K3	14	37	1	7						
Total	18	108	1	10	2[a]	20	29	0	4	0

[a] Coleoptera (1) and Blattodea (1).

midges on a male inflorescence compared to those found on female inflorescences (Table 1).

Midge larvae also grow up feeding on the mycelia and subsequently emerge from the inflorescence (Fig. 9). During the relatively long flowering period of a tree (2 mo), gall midges can increase their population dramatically. Although female inflorescences are not infected by the fungus and therefore do not function as a brooding place for gall midges, the midges are sometimes deceived by its odor and on occasions oviposit even on a female inflorescence. Many myophilous flowers work by imitating oviposition substrate, and olfactory cue is thought to be important in these systems (Dafni, 1984; Roy and Raguso, 1997). This mimicry system, however, may seldom disadvantage the pollinators, because female inflorescences occur much less frequently than male inflorescences, and male inflorescences are easily found nearby on the same tree. No floral secretion was found in the species in a natural forest, while a secretion containing protein was reported in female inflorescences of cultivated *A. integer* (Momose et al., 1998). Genetic differences between wild plants and plants under cultivation remain to be studied.

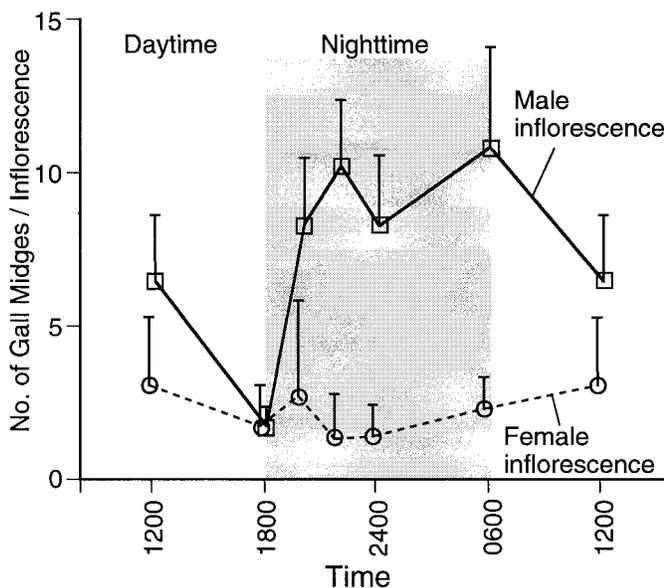The fungus *Choanephora* sp. belongs to the family Choanephoraceae, in which all members appear to be restricted to the tropics. They are soil fungi, which can be facultative flower/fruit parasites on a wide range of host plants (Issac et al., 1993). The genus *Choanephora* includes the well-known pathogen *C. cucurbitarum,* which infects floral parts of many plants after fertilization and invades the fruits causing soft and wet rot in a number of vegetable crops (Agrios, 1988). *Choanephora* sp. found on inflorescences of *A. integer* may also be more or less generalist parasites on plant reproductive organs. While some plant diseases are transmitted by pollinators of their host plants (Alexander, 1987, 1990; Roy, 1994), we could not find fungal spores from limited samples examined by scanning electron microscope. The spores may be predominantly dispersed by wind as those of many Mucolares are thought to be.

Contarinia is a large genus in the gall-midge family Cecidomyiidae with numerous species displaying a variety of living habits. In addition to gall-making forms, from which the common name gall midges arises, the family contains many species that are phytophagous on

Fig. 8. Changes in the mean number of *Contarinia* spp. on male and female inflorescences. Values are means ± 1 SE.
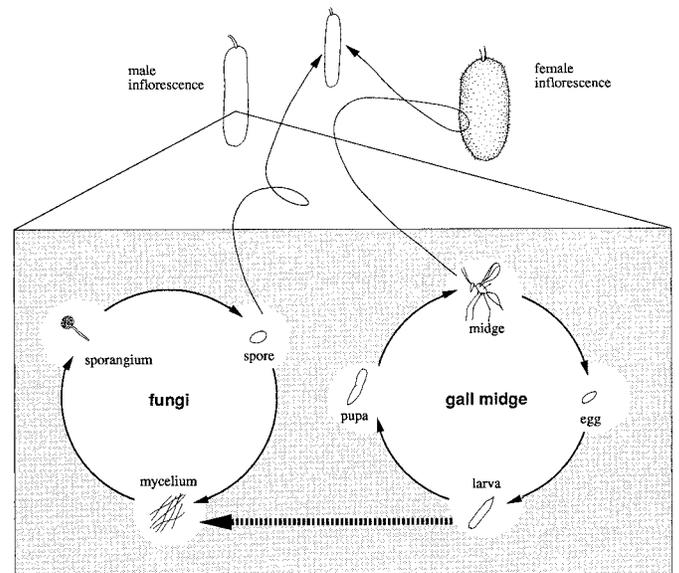

Fig. 9. Diagram illustrating *Artocarpus integer*–gall midge (*Contarinia* spp.) pollination mutualism mediated by parasitic fungi (*Choanephora* sp.). The fungi grow on male inflorescences of *A. integer,* and the midges are parasites on the parasitic fungus. *Artocarpus* and the midges are mutualistic since the midges serve *Artocarpus* as pollination agents.

flower heads or stems without making galls; still others are found to be mycophagous, predaceous, or parasitoid (Skuhhrava, Skuhhravy, and Brewer, 1984). While gall midges are often observed visiting and laying eggs in flowers of different plants (Proctor and Yeo, 1973), pollination by gall midges is only known from *Siparuna* spp. (Monimiaceae) (Feil, 1992). In the case of *Siparuna,* gall midge eggs are laid within flowers and the larvae grow up in the flower probably feeding on floral tissues, whereas the emergence of adult gall midges has not been confirmed. The *Contarinia* species found in *A. integer* flowers are the first cecidomyiid midges that parasitize and pollinate the flowers.

Pollination mutualism in which a fungus plays an essential and indispensable role has never been reported. It is quite interesting that both the pollinator of *A. integer* and the fungus are originally flower parasites. In this system, however, the midges are parasites on the parasitic fungus, and *Artocarpus* and the midges are mutualistic since the midges serve *Artocarpus* as pollination agents (Fig. 9). Several other pathogenic fungi have interactions with pollinators (Batra and Batra, 1985; Alexander, 1987, 1990; Roy, 1994). In Moraceae, for example, the pathogen *Fusarium,* transmitted by the fig wasp and causing endosepsis (endo, inner; sepsis, rotting) of figs, is known to damage cultivated figs (Carter, 1973). However, only two other systems have been described that are very similar to the system reported here. *Peltandra virginica* is pollinated by a fly that breeds in the inflorescences and feeds on a rust fungus, which it also transmits (Patt, 1992; Patt et al., 1995). The other pollinator fungus mutualism involves the pollination of *Epichloe* fungi by flies. The flies feed on hyphae and transport spermatia of their host fungi, *Epichloe* (Bultman et al., 1995). However, in the former example the fungus does not seem to be essential for pollination, and pollination of a plant is not directly involved in the latter case.

There are some examples in which androecial parts of plants function as a brood site for pollinators. *Peltandra virginica* (Araceae) is pollinated by chrolophid flies. The adult flies feed on pollen and their larvae complete their development within the floral chamber (Patt et al., 1995). The flies are thought to breed only on inflorescences of *P. virginia.* Pollinators of *Zamia furfuracea* (Zamiaceae) are host-specific weevils, which feed and reproduce on male cones of the plant (Norstog and Fawcett, 1989). Pollination mutualism of weevil beetles and *Eupomatia* (Eupomatiaceae) also seems to be species specific. In these cases, the pollinators are adapted for flowering phenology of host plants and may be inactive during the nonflowering season (Armstrong and Irvine, 1990).

We do not have definite information on host specificity of *Choanephora* sp. or *Contarinia* spp. Rather low host specificity reported in other *Choanephora* species (Issac et al., 1993) suggests that the *Contarinia* sp. found on *A. integer* is also a more or less generalist species. Considering the irregular and supra-annual flowering of *Artocarpus* and the aseasonal climate of the forest, it is unlikely that *Contarinia* spp. are inactive or dormant during the nonflowering season. It is possible that *Choanephora* sp. use fruits of various plants as substrates and that *Contarinia* spp. usually feed and breed on fruits infected by *Choanephora* sp. or other fungi. When irregular flowering of *A. integer* starts, the fungi infect male inflorescences and the inflorescences are visited by *Contarinia* spp. A large population of *Contarinia* bred by male inflorescences could supply enough pollination service, although flowering of *A. integer* occurs at long and irregular intervals.

The pollination system of the genus *Artocarpus* still needs study. There are only brief reports on drosophilid fly pollination in *A. heterophyllus* (van der Pijl, 1953), moth pollination in *A. odoratissimus* (Momose et al., 1998), and wind pollination of the other species (Corner, 1952; Primack, 1983; Endress, 1994). The pollination system described here suggests that the evolution of pollination mutualisms in the Moraceae may be more widespread than just the fig-fig-wasp mutualism and that we should be more aware of the roles fungi can play in pollination.

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