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FLORAL BIOLOGY OF *MYRISTICA INSIPIDA* (MYRISTICACEAE), A DISTINCTIVE BEETLE POLLINATION SYNDROME¹

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ABSTRACT

The floral biology and pollination of *Myristica insipida* were studied in two different rain forest communities in Queensland. Floral morphology of *M. insipida* resembles that of *M. fragrans* in virtually all respects. The majority of female flowers were receptive 48–72 hr. Male flowers were shorter-lived, functional for 12–48 hr. Both male and female flowers opened daily between 1800 and 2200 hr, but the activity of floral visitors did not begin until the next morning. The inconspicuous, creamy-white to light-green flowers had a strong, pleasant “floral” fragrance. The male flowers only offered pollen as a reward, and female flowers, offering no reward, were judged to function by automimicry. A taxonomically diverse array of small, pollen-foraging beetles were the effective pollinators, although thrips and ants were common floral visitors. In almost all respects, the beetle pollination syndrome of *Myristica* differs from the cantharophily of most other primitive angiosperms.

WITHIN THE MAGNOLIALES there exists a diversity of floral forms and pollination syndromes, although beetle pollination, cantharophily, is common in many of these families (Gottsberger, 1974, 1977; Thien, 1974, 1980; Endress, 1986; Bernhardt and Thien, 1987). The small, inconspicuous, unisexual flowers of the Myristicaceae are not like the large, many-parted, spirally-arranged flowers usually associated with beetle pollination, and thought of as “primitive” and “typical” in the Magnoliales. *Myristica fragrans*, the nutmeg of commerce, has been reported to be pollinated by small insects, moths, or possibly wind (Deinum, 1949; McClroy, 1967; Purseglove, 1968; Cogley, 1976), but was found to be pollinated by a small beetle (Armstrong and Drummond, 1986).

Cantharophily is a diverse pollination syndrome and even among primitive angiosperms different aspects of beetle-plant interactions have been identified (Gottsberger, 1977; Thien, 1980). Several studies have demonstrated that the “primitive,” magnoliaceous flowers pollinated by the haphazard, “mess-and-soil” activities of beetles (*sensu* Faegri and Pijl, 1971),

represent a highly specialized pollination syndrome involving pollinator constancy and rewards of food, predator protection, breeding site, and brood substrates (Gottsberger, 1974, 1977; Thien, 1974, 1980; Beach, 1982; Pellmyr, 1984, 1985; Pellmyr and Thien, 1986; Tang, 1987).

A study of cultivated nutmeg indicated that the male flowers only offered pollen as a reward, that the female flowers offered little or no reward, functioning by automimicry (Armstrong and Drummond, 1986). The small, beetle pollinator did not engage in breeding activities or destructive feeding on floral parts. This is similar in many respects to the beetle pollination reported for *Drimys brasiliensis* and *Diospyros pentamera* (Gottsberger, 1977; Gottsberger, Silberbauer-Gottsberger, and Ehrendorfer, 1980; House, 1985). There is some chance that the flowers or flowering of cultivated nutmeg may have been altered through conscious or unconscious selection during their domestication. Further, in a plantation setting, pollinators and pollinator activity may differ from those in a natural, rain forest community. In order to corroborate and further document this unusual type of beetle pollination, we studied a species of *Myristica* in its natural rain forest communities.

Myristica insipida is a subcanopy tree that occurs in several different rain forest communities in Queensland. We studied the floral biology and pollination of this nutmeg species in two different rain forest communities, a lowland study site at Little Pine Creek (LPC) and an upland study site at Curtain Fig State Forest (CF), described in the preceding paper (Arm-

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strong and Irvine, 1989). Specifically, our studies were designed to answer the following questions about floral function and pollinators: 1) What are the flowering patterns and longevity of the male and female flowers? 2) What are the floral attractants and rewards? 3) What are the floral visitors and pollen vectors? The seasonal flowering, sex ratios, spacing, and reproduction were studied also and the results reported in the preceding paper.

METHODS—Floral longevity was determined by making daily observations of marked individual flowers on conveniently located and accessible trees. Observations of the frequency, duration, and diversity of floral visitors were made hourly over a 24-hr period on several occasions. Changes in floral appearance, odor, presence or quantity of secretions and pollen were noted. Visual changes in the female flowers were experimentally coordinated with stigma receptivity by pollinating flowers of known age and visual condition with a 200+ pollen load from distant intrapopulation donor trees. Floral visitors were captured and examined microscopically for pollen loads. Voucher specimens were sent to the CSIRO Division of Entomology in Canberra. Visited flowers were examined for evidence of damage or visitors' reproductive activities. Fresh, functional flowers were stained with 0.1% neutral red for twenty minutes and then rinsed with distilled water to identify any secretory tissues (Vogel, 1962).

RESULTS—*Floral morphology*—The flowers of *Myristica insipida* are identical to those of *M. fragrans* in essentially all respects (see Wilson and Maculans, 1967; Armstrong and Drummond, 1986; Armstrong and Tucker, 1986, for details of floral morphology). Both male and female flowers are borne on axillary inflorescences (Fig. 2) and have a 3-merous, syntepalous perianth subtended by a minute bracteole (Fig. 3–6). Both male and female flowers are small, although differing slightly in size and shape. Female flowers were 4–5 mm tall and 3–4 mm in diameter with a vase shape that was widest at the bottom (Fig. 3, 4). Each flower has a single pistil containing a single ovule and bearing a sessile, bilobed stigma. Male flowers have a fairly uniform columnar shape 5–7 mm tall and 2–3 mm in diameter (Fig. 5, 6). Each flower has a columnar receptacle upon which there are 6–9 laterally sessile anthers.

Flowering phenology and longevity—The flowering of *Myristica insipida* follows a very regular daily pattern. On both male and female

trees, over 85% of each day's flowers open between 1800 and 2200 hr. The remaining flowers reach anthesis during the remainder of the night. No new flowers open from 400 to 1800 hr.

Male flowers are relatively short-lived and show visible signs of senescence after 12 hr with 40% abscising after 12–24 hr and the remaining 60% abscising between 24–48 hr (Table 1). Newly-opened male flowers have creamy-white to light-green perianths, and creamy-white, turgid androecia. After 12 hours the androecia start to shrivel and turn a pink to light-brown color. The pollen was viable and could successfully pollinate female flowers throughout the life of the male flowers. In many cases flowers still borne on a tree largely were depleted of pollen. Fresh male flowers produce a strong fragrance, which wanes as the flowers senesce. However, even senescent and abscised flowers produce some fragrance. We judged male flowers to be functional as long as they contained pollen and/or remained on the tree.

The female flowers are functional longer than male flowers with 69.5% lasting longer than 48 hr and a few lasting over 72 hr (Table 1). The perianths, pistils, and stigmas are colored a light-green to greenish-white to creamy-white while fresh. Fresh stigmas always appear moist but show no accumulation of liquid. The female flowers are very fragrant when fresh and they remain very fragrant until senescence begins. The stigma and tips of the tepal lobes of postpollinated and senescent flowers turn a dark, red-brown color (Fig. 4). The color change of the stigma was highly correlated with loss of receptivity. Light-colored stigmas are receptive continuously until the beginning of color changes that mark the onset of senescence. The stigmas of hand-pollinated flowers turned dark within 12–24 hr post-pollination.

Floral attractants and rewards—Both male and female flowers produce a similar fragrance that is a slightly heavy, sweet, pleasant, "floral" odor. Individual female flowers seemed to be more strongly scented than individual staminate flowers, but because of the larger number of flowers (Armstrong and Irvine, 1989), male trees were more fragrant than female trees and could often be smelled several meters away. We judge floral fragrance to be the primary attractant because the small, dull-colored flowers produce a very weak visual image (Fig. 1).

No nectar is produced by either male or female flowers. On several occasions receptive female flowers were found with a liquid filling the space between the pistil and the perianth,



Fig. 1-6. Flowering twigs, female flowers, and male flowers of *Myristica insipida*. 1. One of the authors (AKI) examining a male tree in full flower. This illustrates the visual impact of the inconspicuous flowers at a distance of 3 m. 2. Flowering twigs from a male tree showing several axillary inflorescences. Inflorescences on female trees are similar, but with fewer flowers. Bar = 1 cm. 3. Indeterminate axillary inflorescence showing one senescent (center) and two receptive, vase-shaped female flowers. Bar = 5 mm. 4. Apical view of receptive female flower showing stigma occupying the perianth opening. Stigma within senescent flower has turned a dark red-brown. Bar = 5 mm. 5. Indeterminate axillary inflorescence showing a functional, 12-hr-old male flower with androecial column exposed by the three recurved perianth lobes, and several columnar flower buds. Bar = 5 mm. 6. View into the perianth opening of a male flower showing the androecial column within. Bar = 5 mm.

but refractometer readings indicated no dissolved sugars. Open female flowers, no matter what their orientation, were found to take up water by capillary action when hit by drops of water from a pipette. Checks with weather data indicated that all observations of liquid in female flowers followed recent rainfalls. No accumulation of liquid was ever observed on a stigma.

The stigmas and tips of the tepal lobes in female flowers retained the neutral red stain indicating the location of secretory tissue. In male flowers only the tissues surrounding and

lining the pollen locules took up the stain. The apex of the androecium, the androecial column, and perianth remained unstained. In the absence of all other secretory functions, the stain-retaining tissues probably function as osmophores producing the floral fragrance.

With no evidence of feeding on other floral structures, pollen is the only apparent food reward offered to floral visitors of male flowers. There was no evidence that floral visitors used flowers as a protected breeding site or floral tissues as a brood substrate. Female flowers produce no perceivable reward. The perianths

TABLE 1. Longevity of male and female flowers

	Duration (hr)					Total
	12-24	24-48	48-60	60-72	72+	
Male flowers						
N	45	66	0	0	0	111
%	40.5	59.5	0	0	0	100
Female flowers						
N	9	23	46	23	4	105
%	8.6	21.9	43.8	21.9	3.8	100

of female flowers closely encircle the stigma (Fig. 4) and restrict entry of most floral visitors. There was no evidence of any feeding on stigmatic or perianth tissues. Some of the floral visitors probed the moist stigma, but did not remain long.

Floral visitors—Newly-opened flowers are functional all night, but remain unvisited until the following dawn when the activity of floral visitors commences. During the day several species of small beetles (2–3 mm in length) visit the flowers (Fig. 7; Table 2) with peak activity in the late morning. Although weevils (Curculionidae) were the most frequent Coleopteran floral visitor, beetles in Nitidulidae and Staphylinidae were also common floral visitors. There were no differences in visitation patterns, seasonal or daily, among the beetle floral visitors. Several different beetle species could be found visiting a tree simultaneously. The Coleopteran floral visitors were more taxonomically diverse at the upland Curtain Fig (CF) study site than at the coastal Little Pine Creek (LPC) study site (Table 2).

With the exception of the Staphylinid beetle, all of these Coleopteran floral visitors are strong, rapid flyers. Beetles' visits to flowers are solitary and relatively brief. Beetles visiting male flowers stayed 30 sec to several minutes, unless disturbed. They orient their ventral surface along the long axis of the androecial column parallel to the microsporangia placing their mouth parts in a position to feed on pollen grains. The weevils all have relatively short snouts (Fig. 7). Visits to female flowers were very brief, rarely lasting more than 10–15 sec. Beetle visitors to female flowers stand astride the stigma and probe the stigmatic cleft or the space between the perianth and the pistil before taking wing and leaving.

Most of the beetles were captured just before or after visiting male flowers. The beetles had an average pollen load of 5.4 grains (Table 2), which was carried mostly on their ventral side.

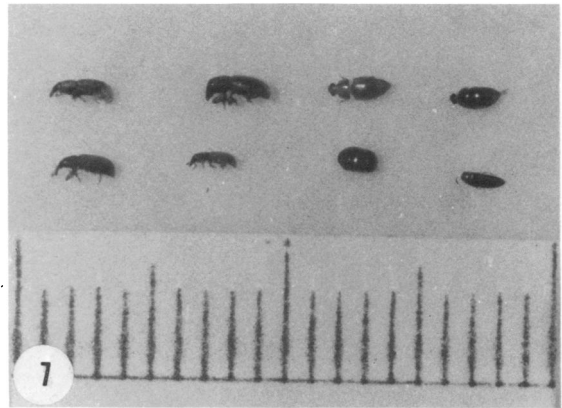


Fig. 7. Beetle visitors to flowers of *Myristica insipida*. From left to right; top row, Short-snouted, wide-eyed weevil; Larger, short-snouted weevil; Narrow-waisted Nitidulid beetle; Long-necked beetle; bottom row, Long-snouted, narrow-eyed weevil; Tortoise-shell weevil; Short, stubby Nitidulid beetle; Black Staphylinid beetle. Scale shows 1 mm divisions.

Only one species of floral visitor, the most common weevil (short-snouted, wide-eyed), was observed visiting a female flower with a pollen load ($N = 10$; Table 2).

Very small ants frequently were observed moving along branches to visit female flowers, but they were not observed visiting male flowers nor did they ever have pollen loads. Larger tree ants, black and green, were found on several nutmeg trees, and while they would defend their tree against invading botanists, they were not floral visitors.

Very small thrips were the most frequently observed floral visitors, particularly in male flowers, where they would spend considerable time within the flowers, often for the duration of the entire observational period lasting several hours. Other than the ever-present thrips, we observed no nocturnal visits to nutmeg flowers. Thrips removed from male flowers had an average pollen load of 2.1 grains, but thrips captured from female flowers ($N = 18$; Table 2) never had a pollen load. The thrips did not demonstrate any movements or behavior that would suggest that they are capable of regular inter-tree movements.

Dipteran larvae were found within several flowers of both sexes. Male flowers that contained these larvae were fluid-filled, generally devoid of pollen, and usually senesced in less than 24 hr. The female flowers were also fluid-filled, but there was no significant damage to the pistil and the stigma appeared receptive. The light trichome tomentum on the pistil was

TABLE 2. *Floral visitors captured at Curtain Fig (CF) and Little Pine Creek (LPC) study sites and their average pollen loads (APL)*

Visitors	Number captured			APL
	CF	LPC	Total	
Coleoptera				
Curculionidae				
Short-snouted, wide-eyed weevil	30	61 ^a	91	3.6
Larger, short-snouted weevil	11	—	11 ^c	21.8
Long-snouted, narrow-eyed weevil	8	7	15 ^c	12.2
Tortoise-shell weevil	8	—	8 ^c	9.7
Nitidulidae				
Narrow-waisted beetle	10	—	10 ^c	4.6
Short, stubby beetle	5	—	5 ^c	6.8
Staphylinidae				
Black beetle	8	23 ^b	31	2.4
Undetermined family				
Long-necked beetle	1	—	1 ^c	3.0
Totals	81	91	172	5.4
Hymenoptera				
Small ant	—	24	24 ^c	0.0
Thysanoptera				
Thrips ^d	15	27	42 ^c	2.1
	—	18	18 ^c	0.0

^a $N = 4$ captured from female flowers, APL = 1.0.

^b $N = 6$ captured from female flowers, APL = 0.0.

^c Captured from male flowers only.

^d Most frequent floral visitors, 50–70% of male flowers.

^e Captured from female flowers only.

usually gone and the pistil often showed shallow, superficial damage. The larvae fall to the ground within the senescent flowers. A small dipteran was observed atop mature flower buds, perhaps in the process of oviposition. We judged this dipteran to be a floral parasite.

Visitation rates—Over 95% of all recorded insect visits to the flowers of *M. insipida* were to male flowers. Based on observed diurnal visits per flower-hr (1 flower observed for 1 hr equals 1 flower-hr), beetles were over four times as likely to visit a male flower (0.056 visits/flower-hr) as a female flower (0.013 visits/flower-hr). Therefore, a female flower of average longevity (60 hr) would be expected to receive 0.39 visits during its functional life at the observed rate of diurnal visitation. A male flower of average longevity (36 hr) would be expected to receive one visit during its functional life.

DISCUSSION—Floral biology—The flowers of *Myristica insipida* attract ants, thrips, and a variety of beetles. While the most common and easily observed floral visitors are thrips, only the beetles possess the characteristics of an effective pollinator. Thrips and diverse small in-

sects have been reported as floral visitors of Neotropical Myristicaceae (Bawa et al., 1985), and while undoubtedly accurate, a similarly conducted survey would probably yield the same report for *Myristica fragrans* and *M. insipida*. The lack of pollinator diversity observed in a plantation of nutmeg in India (Armstrong and Drummond, 1986) could be the result of a loss of rain forest habitat to support a diverse population of pollen-foraging beetles.

In most respects the floral biology and pollination syndrome of *Myristica insipida* is identical to that of *M. fragrans* (Armstrong and Drummond, 1986). One significant difference is that *M. insipida* flowers nocturnally, exactly like *M. fragrans*, but has only diurnal floral visitors. The Anthicid beetle pollinator of *M. fragrans* is completely nocturnal. It seems that *M. insipida* has retained nocturnal flowering even though there is no nocturnal insect fauna in Queensland to act as pollinators. Both male and female flowers of *M. insipida* function somewhat longer than those of *M. fragrans*, which probably represents an adaptation to better accommodate the delayed diurnal activity of floral visitors. The physiological response necessary to produce a precise start of

anthesis can be considered relatively refractory to change in comparison to a gradual delay of senescence necessary to increase floral longevity. When plant-insect interactions in pollination systems routinely are represented as efficient products of natural selection, examples such as this serve as a reminder that evolutionary processes are only as efficient as necessary to assure the reproduction of the organisms involved.

The results of this study support the interpretation that the female flowers of *Myristica* provide no pollinator reward and function by automimicry. The perianth closely encircling the stigma excludes the beetles from the floral interior. During brief visits to female flowers, beetles may probe the stigmatic surface, but there is no evidence that they receive any substantial reward.

The higher visitation rates to male trees can be attributed to their greater attractiveness. Male trees produced 2.14 times as many flowers as female trees (Armstrong and Irvine, 1989), but the visitation rate to male flowers was over four times greater than for female flowers. Larger floral displays have been demonstrated to increase the removal of pollen and contribute to a directional pollinator movement (Willson and Rathcke, 1974; Willson and Price, 1977; Queller, 1983). Even though beetles are more frequent visitors at male trees, the frequency of intertree movements of these small beetles is unknown. Although the pollen loads observed on floral visitors were low, the results of pollination manipulations suggest that if half of the average pollen load carried by floral visitors was deposited on the stigma during a visitation, the observed 1% fruit production of open-pollinated flowers could be accounted for (Armstrong and Irvine, 1989). Given the pollinator activity we observed, three out of every five female flowers will never be visited. We interpreted the reproduction of *Myristica insipida* to be pollination limited (Armstrong and Irvine, 1989).

Dioecy and floral function—Unisexual flowers separate male and female functions. The separation of sexual functions allows male and female flowers to have different floral longevity, and female flowers generally last longer than male flowers (Primack, 1985). The intersexual difference in floral longevity of nutmeg can be attributed to their different functions. Once a male flower is depleted of pollen, its functional role is completed. The only other possible function would be in contributing to the overall attractiveness of the plant. If too many pollen-depleted flowers are used as part

of the tree's display, the reward quality of the individual would decrease and cause reward-sensitive floral visitors to seek a more rewarding tree. Female flowers must last long enough to reasonably assure fertilization, and in this species female flowers function about twice as long as male flowers.

There may be additional advantages to separating male and female functions in unisexual flowers. Male nutmegs flower and produce pollen earlier and in greater quantity without the cost of producing excess pistils and ovules (Armstrong and Irvine, 1989). In flowers of *Myristica* the larger perianth opening of male flowers allows small floral visitors access and provides an enclosure while they forage for pollen (Fig. 6). The smaller perianth opening of female flowers tightly encircles the stigma (Fig. 4). Only the smallest floral visitors (ants and thrips) could enter the female flowers, but these were not judged to be effective pollen vectors. The beetle visitors attempting entry to the female flowers are accurately positioned atop the stigma. When flowers function by deceit, the reduced duration of visits requires such a mechanism to efficiently transfer pollen to the stigma (Little, 1983). Unisexual flowers may have evolved partly because of the greater efficiency and effectiveness of separating such "conflicting" male and female functions (Lloyd, 1982).

Cantharophily, the beetle pollination syndrome—Beetle-pollinated flowers of primitive angiosperms can be grouped into three types (Thien, 1980), but all three groups possess similar features including large, flattened stamens and staminodes that can best be interpreted as specializations for beetle pollination (Carlquist, 1969; Endress, 1984b). These flowers are generally large with numerous, spirally-arranged parts that often form an enclosure. If the flowers are small, they are aggregated into large inflorescences that function like a many-parted flower. The rewards offered typical beetle pollinators include food, protection from predators while within the flower (or inflorescence), a location for mating activities, and, in many cases, a brood substrate (Grant, 1950; Faegri and Pijl, 1971; Thien, 1974, 1980; Gottsberger, 1977; Beach, 1982; Endress, 1984a, b, 1986). Beetles often congregate in considerable numbers within such flowers or inflorescences. Members of Palmae and Zamiaceae also have beetle pollination with many of the same characteristics (Norstog and Stevenson, 1980; Henderson, 1986; Norstog, Stevenson, and Niklas, 1986; Barfod, Henderson, and Balslev, 1987; Tang, 1987).

The phytophagy of beetles involved in cantharophily is often called "destructive" because various floral parts are partly or wholly consumed. Many beetle-pollinated flowers show specializations for this type of pollination with some combination of numerous parts, fleshy perianth parts, fleshy anthers, stamnodes, or some other specialized structures to provide the food reward (Endress, 1984a, b). Such feeding is not necessarily destructive in the sense of detrimental. However, in some cases the distinction between beetles that function as floral pollinators and beetles that are floral predators may be difficult (Armstrong, 1979; Crowson, 1981).

The beetle pollination syndrome of *Myristica* is similar to only two other species, *Drimys brasiliensis* (Gottsberger, 1977; Gottsberger et al., 1980) and *Diospyros pentamera* (House, 1985). The flowers of *Myristica*, *Drimys brasiliensis*, and *Diospyros pentamera* are small, inconspicuous, numerous, but not aggregated into large inflorescences, with few, exposed floral parts, and little or no post-opening movement of floral parts. The floral odors are absolute rather than deceptive (sensu Faegri and Pijl, 1971). The beetle pollinators do not feed on floral parts, but forage specifically on pollen. In *Myristica* male flowers alone provide a food reward of pollen to floral visitors, while female flowers function by automimicry. However, we do not suggest that unisexual flowers or automimicry necessarily are features to be associated with this pollination syndrome. A female reward of a stigmatic exudate was reported in *Drimys brasiliensis* (Gottsberger et al., 1980), and as we envision this syndrome, stigmatic or glandular exudates would be the primary reward of female or female-phase flowers.

The beetles are very small, less than 3–4 mm long, and are pollen-foragers. Their visits to flowers are largely solitary, nondestructive (no feeding on floral parts), and do not involve mating or reproductive activities. In general, these small beetles appeared to be active and agile fliers. We interpret their relationship with the plants to be general rather than specific. Their brood substrates remain unknown, and it is possible that each species reproductively specializes on some visited plant species, while opportunistically foraging on other species in flower throughout the year. A similar situation was reported where a beetle pollinator of *Actaea* used a later-flowering species of *Geum* as its only brood substrate (Pellmyr, 1984).

Members of Myristicaceae are found in the forests of all major tropical areas. Their similar floral morphologies suggest the possibility of pollination syndromes similar to *Myristica*'s.

The successful cultivation of *Myristica fragrans* in other tropical areas, including the neotropics, indicates that pollen-foraging beetles are common to tropical forests and emphasizes the generalist nature of this pollination syndrome. Given the prevalence of small, inconspicuous flowers in tropical forests, it is not unreasonable to expect that *Myristica*-type beetle pollination will be discovered in other species.

Microcantharophily—The cantharophily of *Myristica*, *Drimys brasiliensis*, and *Diospyros pentamera* is clearly distinctive, differing from "typical" cantharophily in almost all respects (Table 3). To distinguish this beetle pollination syndrome from typical cantharophily, we propose referring to the beetle pollination of *Myristica*, *Drimys brasiliensis*, and *Diospyros pentamera* as "microcantharophily." The consistently small size of the pollen-foraging beetles prompted the selection of the descriptive prefix "micro-," although we recognize that small beetles can be involved in typical cantharophily as well. We regard the suggestion that "it may soon be necessary to distinguish between different syndromes of beetle pollination" (Bernhardt and Thien, 1987) as very prophetic.

The evolution of "deceptive" floral fragrances from compounds functioning in herbivore deterrence, and an accompanying shift from phytophagy to feeding/reproductive activities resulting in high species constancy (Pellmyr, 1985; Pellmyr and Thien, 1986) is a very attractive hypothesis to account for the origin of cantharophily. The evolution of microcantharophily cannot be so easily attributed to the same scenario because so many essential elements of the beetle/plant interactions are missing. It is equally difficult to derive microcantharophily from cantharophily, which would involve a major shift in both floral function and beetle behavior, eliminating all of those aspects (reproductive activities, use of floral parts as a brood substrate) that insure pollinator constancy.

The simpler beetle/plant interactions of microcantharophily were the basis for regarding the beetle pollination of *Drimys brasiliensis* as a primitive form of cantharophily (Gottsberger, 1977; Gottsberger et al., 1980). The complex beetle/plant interactions of cantharophily have been interpreted as a derived condition (Bernhardt and Thien, 1987), and most of the beetles involved in these complex interactions are more modern groups, some of which have specializations for floral feeding and pollen digestion (Crowson, 1981). An exception to

TABLE 3. Comparison of flower and beetle characteristics associated with cantharophily and microcantharophily

	Cantharophily	Microcantharophily
Plant characteristics		
Flower size	Generally large (> 1 cm) ^a	Generally small (< 1 cm)
Flower number	Few ^a	Numerous, not aggregated
Floral appearance	Conspicuous	Inconspicuous
Floral parts	Numerous, movement, specialized structures ^b	Few, no movement
Floral shape	Trap or enclosure	Enclosure or exposed
Landing area	Large	Small
Odor	Deceptive	Absolute
Rewards	Food: floral parts, pollen, ovules; protection; breeding place; brood substrate	Food: pollen, stigmatic exudates, nectar (?)
Beetle characteristics		
Size	Generally large	Generally small (< 4 mm)
Flying ability	Limited, clumsy	Active, agile
Visiting behavior	Accumulate in numbers	Largely solitary
Visit duration	Prolonged visits	Brief visits
Feeding behavior	General floral phytophagy ^c	Specialized pollen and/or nectar foraging
Mating behavior	Takes place within flowers	Mating elsewhere
Brood substrate	May use floral parts	Not known to use floral parts
Relationship to plant	Often specialized, high visitor constancy	Generalist, diversity of visitors

^a When small aggregated into large inflorescences that function similar to large, solitary flowers with numerous parts.

^b Broad, leaf-like stamens and staminodes.

^c Feeding on floral parts.

this is the association of the primitive beetle family Nitidulidae with cantharophily and microcantharophily (Table 2) (Crowson, 1981; Gazit, Galon, and Podoler, 1982). While microcantharophily is simpler than cantharophily, involving fewer plant/beetle interactions, the same type of difficulties exist in constructing a scenario deriving cantharophily from microcantharophily. Thus, it is probably pointless to use designations of "primitive" and "specialized" for two beetle pollination syndromes that do not necessarily have a phyletic relationship.

Endress (1987) has proposed that among primitive angiosperms the unelaborated, "open" construction of flowers may have allowed the relatively easy transition between large, many-parted, spiral flowers and small, few-parted, cyclic flowers. This suggests that the flowers typical of cantharophily and microcantharophily can have a common origin, and, perhaps, can be found within the same taxon, e.g., Winteraceae. The flowers of *Myristica*, which presently show no structural evidence of a former bisexual or many-parted condition (Wilson and Maculans, 1967; Armstrong and Tucker, 1986), and other Myristicaceae, may represent an archaic adaptation to microcantharophily. Interactions with the generalist beetle pollinators could have led to an early evolution of dioecy in this family. Monoecy with simple 3-merous flowers is reported to still exist in neotropical *Iryanthera* (Myristi-

caceae) (Smith, 1937). This interpretation is consistent with the hypothesized phylogeographic history of the nutmegs (Raven and Axelrod, 1974; Thorne, 1974). The systematic relationships and similarities between Annonaceae, Canellaceae, and Myristicaceae (Thorne, 1974; Cronquist, 1981) are more evident when the differences in floral morphology are viewed in the preceding perspective.

Generalist entomophily, involving beetles, thrips, micropterigid moths, stoneflies, and possibly ancestors of Dipterans and Hymenoptera has been hypothesized for insect-pollinated protoangiosperms and ancestral Magnoliidae (Bernhardt and Thien, 1987). Microcantharophily might have arisen from such a general entomophily among protoangiosperms or early angiosperms. Perhaps, as we suggest, microcantharophily is best regarded as a distinctive, relatively archaic, perhaps relic, pollination syndrome.

LITERATURE CITED

- ARMSTRONG, J. A. 1979. Biotic pollination mechanisms in the Australian flora—a review. *New Zealand J. Bot.* 17: 467–508.
- ARMSTRONG, J. E., AND B. A. DRUMMOND III. 1986. Floral biology of *Myristica fragrans* Houtt. (Myristicaceae), the nutmeg of commerce. *Biotropica* 18: 32–38.
- , AND A. K. IRVINE. 1989. Flowering, sex ratios, pollen-ovule ratios, fruit set, and reproductive effort of a dioecious tree, *Myristica insipida* R. Br. (Myris-

- ticaceae), in two different rain forest communities. *Amer. J. Bot.* 76: 74–85.
- , AND S. C. TUCKER. 1986. Floral development in *Myristica* (Myristicaceae). *Amer. J. Bot.* 73: 1131–1143.
- BARFOD, A., A. HENDERSON, AND H. BALSLEV. 1987. A note on the pollination of *Phytalephas microcarpa* (Palmae). *Biotropica* 19: 191–192.
- BAWA, K. S., S. H. BULLOCK, D. R. PERRY, R. E. COVILLE, AND M. H. GRAYUM. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *Amer. J. Bot.* 72: 346–356.
- BEACH, J. H. 1982. Beetle pollination of *Cyclanthus bipartitus* (Cyclanthaceae). *Amer. J. Bot.* 69: 1074–1081.
- BERNHARDT, P., AND L. B. THIEN. 1987. Self-isolation and insect pollination in the primitive angiosperms: new evaluations of older hypotheses. *Pl. Syst. Evol.* 156: 159–176.
- CARLQUIST, S. 1969. Toward acceptable evolutionary interpretations of floral anatomy. *Phytomorphology* 19: 332–362.
- COBLEY, L. S. 1976. Introduction to the botany of tropical crops. 2d ed. Longman, London.
- CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York.
- CROWSON, R. A. 1981. The biology of the Coleoptera. Academic Press, New York.
- DEINUM, H. 1949. Nootmuskaat en foelie. *Landbouw Ind. Arch.* 2(b): 655–683.
- ENDRESS, P. K. 1984a. The flowering process in the Eupomatiaceae (Magnoliales). *Bot. Jahrb. Syst.* 104: 297–319.
- . 1984b. The role of inner staminodes in the floral display of some relic Magnoliales. *Pl. Syst. Evol.* 146: 269–282.
- . 1986. Reproductive structures and phylogenetic significance of extant primitive angiosperms. *Pl. Syst. Evol.* 152: 1–28.
- . 1987. Floral phyllotaxis and floral evolution. *Bot. Jahrb. Syst.* 108: 417–438.
- FAEGRI, K., AND L. VAN DER PIJL. 1971. The principles of pollination ecology. Pergamon, New York.
- GAZIT, S., I. GALON, AND H. PODOLER. 1982. The role of nitidulid beetles in natural pollination of *Annona* in Israel. *J. Amer. Soc. Hort. Sci.* 107: 849–852.
- GOTTSBERGER, G. 1974. The structure and function of the primitive angiosperm flower—a discussion. *Acta Bot. Neerl.* 23: 461–471.
- . 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Pl. Syst. Evol. Suppl.* 1: 211–226.
- , I. SILBERBAUER-GOTTSBERGER, AND F. EHRENDORFER. 1980. Reproductive biology in the primitive relic angiosperm *Drimys brasiliensis* (Winteraceae). *Pl. Syst. Evol.* 135: 11–39.
- GRANT, V. 1950. The pollination of *Calycanthus occidentalis*. *Amer. J. Bot.* 37: 294–297.
- HENDERSON, A. 1986. A review of pollination studies in the Palmae. *Bot. Rev.* 52: 221–259.
- HOUSE, S. M. 1985. Relationships between breeding and spatial pattern in some dioecious tropical rain-forest trees. Ph.D. dissertation, Australian National University, Canberra.
- LITTLE, R. J. 1983. A review of floral food deception mimics with comments on floral mutualism. In C. E. Jones and R. J. Little [eds.], *Handbook of experimental pollination biology*, 294–309. Van Nostrand Reinhold, New York.
- LLOYD, D. G. 1982. Selection of combined versus separate sexes in seed plants. *Amer. Naturalist* 120: 571–585.
- MCILROY, R. J. 1967. An introduction to tropical cash crops. Ibadan University Press, Ibadan, Nigeria.
- NORSTOG, K. J., AND D. W. STEVENSON. 1980. Wind? Or insects? The pollination of cycads. *Fairchild Trop. Garden Bull.* 35: 28–30.
- , ———, AND K. J. NIKLAS. 1986. The role of beetles in the pollination of *Zamia furfuracea* L. fil. (Zamiaceae). *Biotropica* 18: 300–306.
- PELLMYR, O. 1984. The pollination ecology of *Actaea spicata* (Ranunculaceae). *Nord. J. Bot.* 4: 443–456.
- . 1985. Pollination adaptations in the Cimicifugae and the evolutionary origin of pollinator-plant mutualism, 1–34. *Acta Univ. Upsaliensis* 2. Uppsala, Sweden.
- , AND L. B. THIEN. 1986. Insect reproduction and floral fragrances: keys to the evolution of the angiosperms? *Taxon* 35: 76–85.
- PRIMACK, R. B. 1985. Longevity of individual flowers. *Annual Rev. Ecol. Syst.* 16: 15–37.
- PURSEGLOVE, J. W. 1968. Tropical crops: dicotyledons 2. J. Wiley, New York.
- QUELLER, D. C. 1983. Sexual selection in a hermaphroditic plant. *Nature* 305: 706–707.
- RAVEN, P. H., AND D. I. AXELROD. 1974. Angiosperm biogeography and past continental movement. *Ann. Missouri Bot. Gard.* 61: 539–673.
- SMITH, A. C. 1937 (1938). The American species of Myristicaceae. *Brittonia* 2: 393–510.
- TANG, W. 1987. Insect pollination in the cycad *Zamia pumila* (Zamiaceae). *Amer. J. Bot.* 74: 90–99.
- THIEN, L. B. 1974. Floral Biology of *Magnolia*. *Amer. J. Bot.* 61: 1037–1045.
- . 1980. Patterns of pollination in the primitive angiosperms. *Biotropica* 12: 1–13.
- THORNE, R. F. 1974. A phylogenetic classification of the Annoniflorae. *Aliso* 8: 147–209.
- VOGEL, S. 1962. Duftdrüsen im Dienst der Bestäubung über Bau und Funktion der Osmophoren. *Akad. Wiss. Abh. Math.-Naturwiss. Kl.* 10: 598–763.
- WILLSON, M. F., AND P. W. PRICE. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31: 495–511.
- , AND B. J. RATHCKE. 1974. Adaptive design of the floral display in *Asclepias syriaca* L. *Amer. Midl. Naturalist* 92: 47–57.
- WILSON, T. K., AND L. MACULANS. 1967. The morphology of the Myristicaceae. I. Flowers of *Myristica fragrans* and *M. malabarica*. *Amer. J. Bot.* 54: 214–220.