Notes on the Reproductive Biology of Asterogyne Martiana (Palmae).

II. Pollination by Syrphid Flies

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In 1870 Federico Delpino published part of his classic work on reproductive biology and indicated that "many palms" (p. 202) exemplify the motionless or "immobile" type of flower of anemophilous (wind-pollinated) angiosperms. Since then, a number of writers (e.g., Baker and Hurd, 1968; Drude, 1889; Eames, 1961; Good, 1956; Lepesme, 1947; Rendle, 1930; and staff and students in the Organization for Tropical Studies' Advanced Botany Course "Reproductive Biology" held in Central America in Summer, 1968) have assumed that palms are anemophilous, though exhibiting some entomophily (insect-pollination). Good (1956, p. 366), in fact, even considered the palms "in some ways [to be] functionally the counterparts of the Catkin-bearers in the Dicotyledons".

These conclusions have been re-enforced by the many features of the anemophilous syndrome that palms as a group show, namely: a certain gregariousness of individuals; production of many flowers; absence of showy parts and bright colors; a frequent lack of floral fragrance and/or nectar; a rather small perianth; prominent exposure of anthers and of the long, recurved stigmas; production of large amounts of often smooth, powdery pollen; and production of few ovules per flower (Faegri and van der Pijl, 1966; Menon and Pandalai, 1958).

The presence of entomophily in palms has been underrated, in part because many workers have concentrated on the predominantly anemophilous cultigens. Actually, the Palmae are both anemophilous and entomophilous, a fact adequately documented by Knuth (1904) and recognized by many other authors (e.g., Corner, 1966; Coulter and Chamberlain, 1903, and other works by Coulter; Kraus, 1896; Kugler, 1955; Strasburger *et al.*, 1898, and other editions; Wettstein, 1935, and other editions; Willis, 1966, and other editions). Coulter and Chamberlain (1903) and Eames (1961) considered palm pollination in transition from entomophily to anemophily.

Beetles (Coleoptera), flies (Diptera), moths (Lepidoptera), bees (Hymenoptera), and other insects visit palm flowers for pollen, nectar, floral tissue, and/or other objectives. Numerous insects are commonly observed on palm inflorescences (Knuth, 1904; Lepesme, 1947; Seemann, 1856; Wettstein, 1935; and in Costa Rica, stingless bees visiting *Elaeis guineensis*, personal observations, and *Scheelea rostrata*, G. Stiles, personal communication), particularly on the male flowers. Birds (Eames, 1961; Knuth, 1904, 1905; Porsch, 1926, 1930), bats (Corner, 1966; Porsch, 1935), and even snails (Knuth, 1904, pp. 60, 75) also visit palm flowers. Only detailed observations, however, will reveal whether

such visitations are indiscriminate, exploitative, or indeed effective for pollination. For example, it is doubtful if bats or snails effect pollination of palms (see Faegri and van der Pijl, 1966; van der Pijl, 1956).

Actually, very little is known about the pollination of wild palms. The information available is scanty, not only for the dwarf palms, but also for the large palms, the great size of which renders investigation difficult, even with the aid of binoculars. From the literature, but mainly from personal observations, Knuth (1904, 1905, 1909) compiled pollination data for 72 palm species distributed among 40 genera. The observations that Knuth (1904, pp. 55–82, 1905) made on 55 palm species (in 34 genera) at the Buitenzorg (now Bogor) Botanical Garden in Java (now Indonesia) from November 16, 1898, to March 20, 1899, are the most extensive to date, but in most cases these are merely lists of insect visitors to the palms. Knuth (1904, pp. 60–61) considered 21 palm species (in 17 genera) as entomophilous, although he had observed insects on most of the 55 palms he had studied. Knuth regarded most of the anemophilous palms as at least partly entomophilous.

Little work on pollination of palms seems to have been done since Knuth's 1904 compilation, which, incidentally, is often overlooked by later writers (e.g., Corner, 1966; Lepesme, 1947; Menon and Pandalai, 1958). Almost all the subsequent work has been on such economically important cultigens as *Cocos nucifera*, *Elaeis guineensis*, and *Phoenix dactylifera*. Even here, however, controversy persists about the entomophilous and/or anemophilous nature of coconut (see Menon and Pandalai, 1958, pp. 67–68), the pollination biology of which is among the most intensively investigated of all palms.

Intrigued by the dearth of pollination data on palms, especially on wild palms, I spent five days in Summer, 1968, investigating the pollination biology of *Asterogyne Martiana*, a dwarf palm in the Geonomeae, at two sites in Costa Rica: near Rincón de Osa, Puntarenas Province, and at La Selva, near Puerto Viejo, Herédia Province. Methodology, exact locational information, and details of floral structure and phenological events are given in Schmid (1970). Unfortunately, lack of time prevented the accumulation of detailed behavioral information for most of the insect visitors.

OBSERVATIONS AND DISCUSSION

Although *Asterogyne Martiana* possesses some of the anemophilous features listed above, the following characteristics militate against an anemophilous nature for this palm: (1) occurrence in dense wet forest undergrowth, a habitat where several factors, including the extreme stillness of air, are unfavorable for anemophily (see Whitehead, 1969); (2) production of showy, white inflorescences, which are prominently silhouetted against the dark forest, particularly around sunrise; (3) production of fragrant flowers with copious amounts of nectar (Schmid, 1970); (4) production of stickly pollen that is shed in small clumps (Schmid, 1970); (5) no evidence of pollen on three vasoline-coated microscope slides that were suspended for five hours next to inflorescences bearing male flowers; and (6) visitation of both male and female flowers by numerous insects (Table 1, Fig. 1–7, and below), at least one group of which can be demonstrated to be the pollinating agent.

Insects visit *Asterogyne Martiana* for several purposes: a source of food

TABLE 1. *Insects visiting* Asterogyne Martiana *near Rincón de Osa (July 21, 1968) and at La Selva (August 3–6, 1968), Costa Rica. Determinations (sources given in brackets) were based on specimens, Kodachrome transparencies, and field identifications. Some groups are undoubtedly inadequately sampled; most probably occur at both sites. KEY: F = field identification(s); K = Kodachrome(s); O = insect(s) observed at Osa; S = observed at La Selva. Collection numbers in brackets.*

COLEOPTERA
- Cantharidae
  - Chauliognathus pallidus Waterhouse [det. P. Vaurie—#9: S]
  - other [det. H. Dietrich—K: S]
- Chrysomelidae
  - Alticinae
    - Centralaphthona robusta Jacoby [det. J. A. Wilcox—#42–47, K: O]
    - other (3 + species) [D. F. Veirs—F: S]
  - Galerucinae
    - Monolepta sp. near Luperodes humeralis Jacoby [det. J. A. Wilcox—#40–41, K: O]
  - other [D. F. Veirs, R. Schmid—F: S]
- Cucujidae [det. I. J. Cantrall—#39: O]
- Curculionidae
  - ?Baridinae [det. P. Vaurie—K: S]
  - Erirhininae
    - Celetes sp. or Phytotribus sp. [det. P. Vaurie—#10–13, plus ca 75 unnumbered specimens: S; #48–50: O] [also K: S, O]
  - other [det. I. J. Cantrall—K: S] [det. R. Schmid—F: S]
- Ptiliidae [det. D. F. Veirs—F: S]
- Staphylinidae
  - Aleocharinae [det. P. Vaurie—#8, 22: S]
  - Staphylininae [det. P. Vaurie—#23: S]
  - other [det. G. C. Eickwort—K: O]

DIPTERA
- Ceratopogonidae
  - Atrichopogon spp. [det. W. W. Wirth—#31–32: S]
  - other [det. L. L. Pechuman—K: S] [det. D. F. Veirs—F: S]
- Drosophilidae
  - Drosophila sp. [det. W. W. Wirth—#57–58: O] [det. D. F. Veirs—F: S] [R. Schmid—F: S; K: O]
- Empididae
  - Rhamphomyia sp. [det. L. V. Knutson—#60: O]
- Sphaeroceridae
  - Leptocera (Pterogramma) sp. nov. [det. G. Steyskal—#54–56, 59, 61–62, plus ca. 50 unnumbered specimens: O]
  - ?other [D. F. Veirs—F: S]

TABLE 1. Continued

DIPTERA
- Syrphidae [*all* det. F. C. Thompson]
  - Baccha sp. [#37: O]
  - Ornidia obesa (Fabr.) [#38: O]
  - Copestylum (= Volucella) tympanitis (Fabr.) [#1, 18: S]
  - Copestylum (= Volucella) sp. nov. 1 [#2, 3, 19, 28, 33, K: S]
  - Copestylum (= Volucella) sp. nov. 2 [#6, 7, 21, 26, 30, 34, K: S; #36: O]
  - Copestylum (= Volucella) sp. nov. 3 [#4: S]
  - Copestylum (= Volucella) sp. nov. 4 [#5, 27, 29: S]
  - Copestylum (= Volucella) sp. nov. 5 (tricincta Bigot group) [#20: S]
- Tipulidae [det. R. Schmid, D. F. Veirs—F: S]

HYMENOPTERA
- Apidae: Meliponini
  - Melipona fasciata fasciata Latreille [det. G. C. Eickwort—#52: O]
  - Trigona (Partamona) ?cupira Smith [det. G. C. Eickwort—#24, 35: S]
  - Trigona (Partamona) ?testacea (Klug) subspecies [det. G. C. Eickwort—#14: S]
  - Trigona (Trigona) amalthea silvestriana Vachal [det. G. C. Eickwort—#15: S]
  - Trigona (Trigona) fulviventris Guérin [det. G. C. Eickwort—#51: O]
  - Trigona sp. [det. G. C. Eickwort—K: S] [det. R. Schmid, D. F. Veirs—F: S, O]
- Formicidae
  - Crematogaster sp. (orthocrema species group) [det. W. L. Brown, Jr.—#53: O]
  - Paraponera sp. [det. D. F. Veirs—K, F: S]
  - Pheidole sp. [det. W. L. Brown, Jr.—K: S]
  - other [det. R. Schmid—F: S]
- Halictidae [det. G. C. Eickwort]
  - Augochlorini
    - Neocorynura sp. [#25: S]
  - Halictini
    - Habralictus sp. [#16: S]
- parasitic Hymenoptera [D. F. Veirs—F: S]

LEPIDOPTERA
- ?Dioptidae [det. J. G. Franclemont—#17, K: S]
- Pyralidae
  - Desmia sp. [det. J. G. Franclemont—K: S]
- other Heterocera [det. R. Schmid—F: S]

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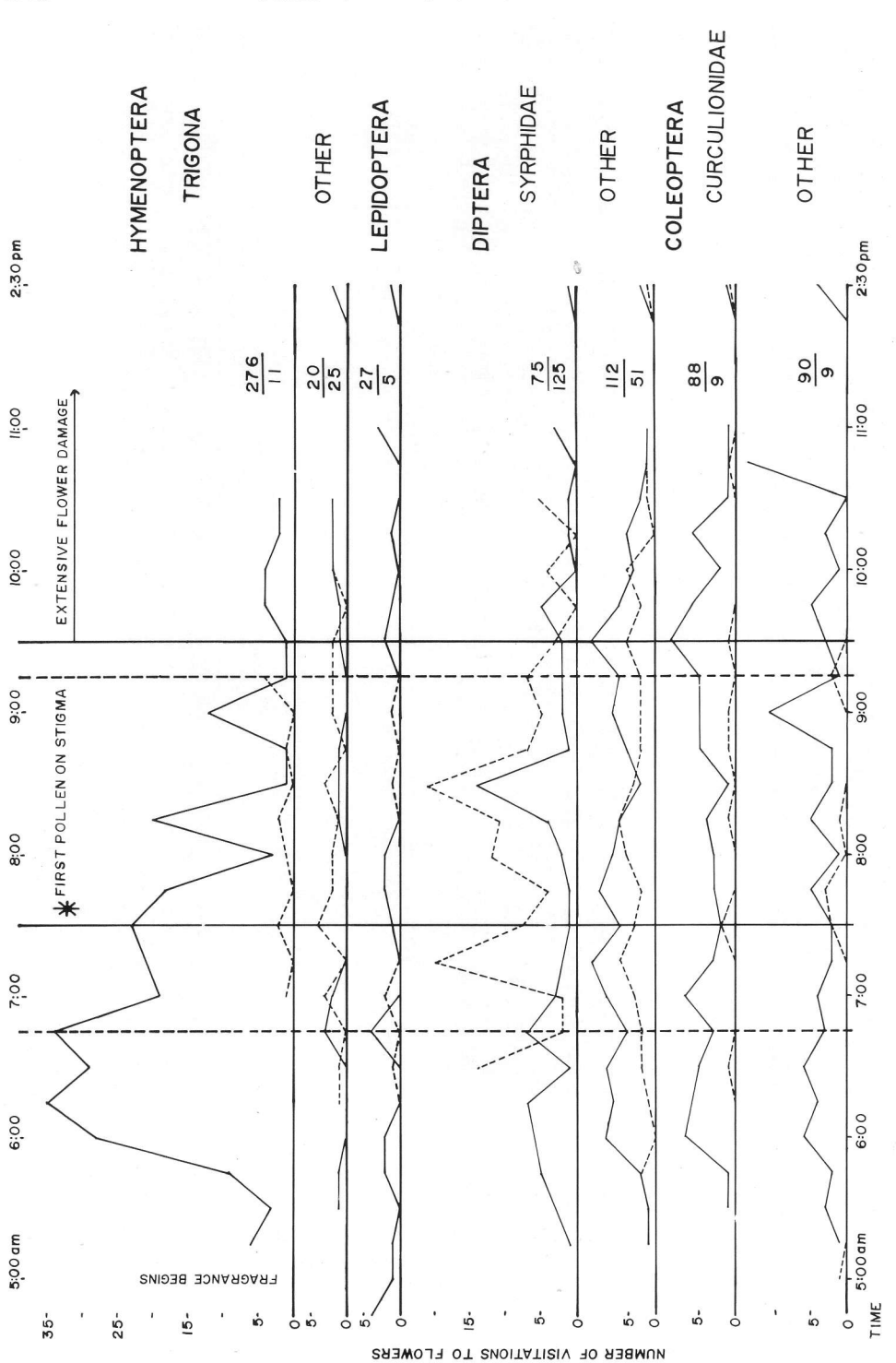
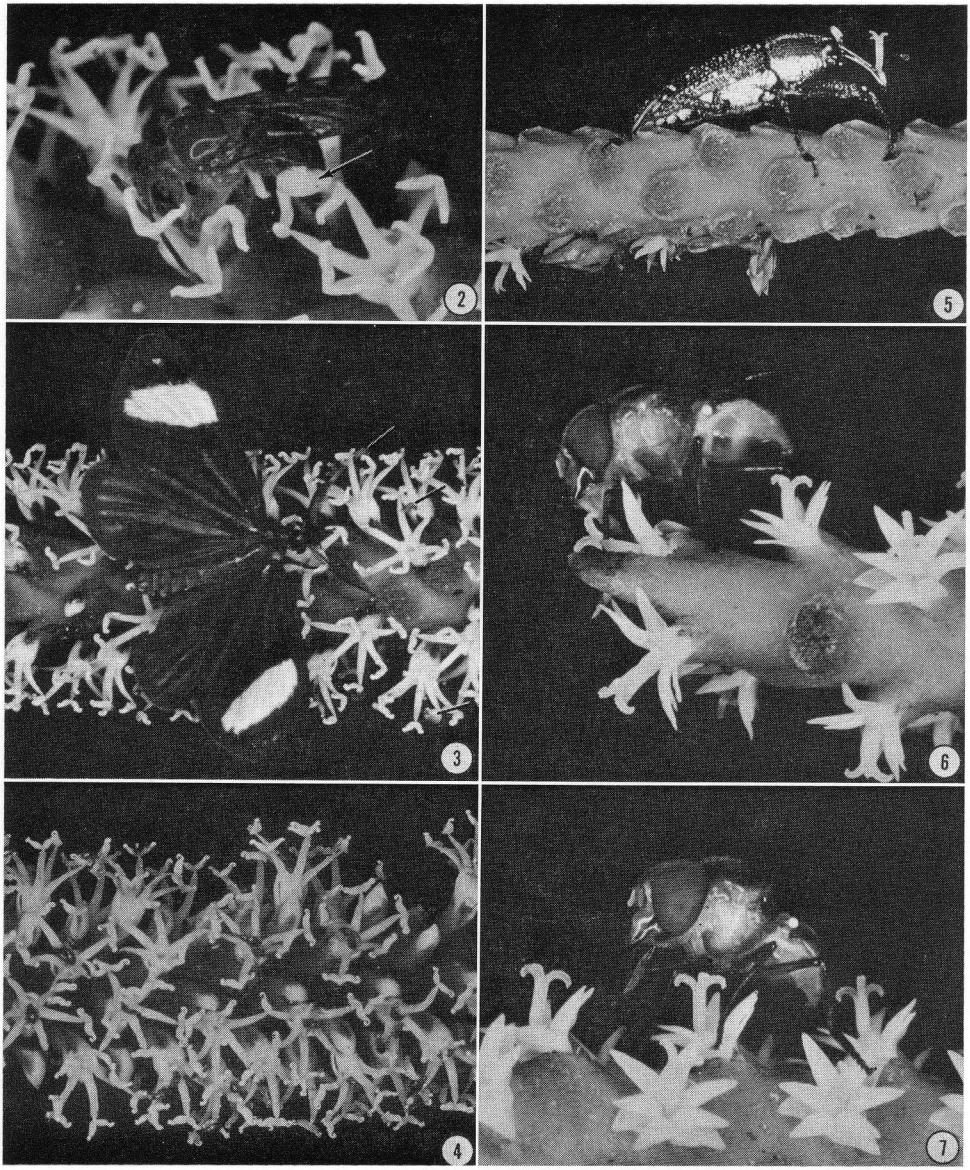
1. Visitation by main insect groups (see Table 1) to flowers of *Asterogyne Martiana*, and some phenological events (see Schmid, 1970) of the palm flowers, based on observations near Rincón de Osa (July 21, 1968) and at La Selva (August 3–6, 1968), Costa Rica. Data for insects represent the number of *individuals* detected on flowers, except for "Diptera—Other" and "Coleoptera—Curculionidae", for which data represent the number of occurrences of *groups* of insects detected on flowers. KEY: Fractions represent total recorded occurrences of insects (individuals or groups) on flowers: numerator = male flowers; denominator = female flowers. Insect visitation to flowers: solid lines = male flowers; dashed lines = female flowers. Limits of detectable nectar production: solid vertical lines = male flowers; dashed vertical lines = female flowers.


HYMENOPTERA
TRIGONA
OTHER
LEPIDOPTERA
DIPTERA
SYRPHIDAE
OTHER
COLEOPTERA
CURCULIONIDAE
OTHER
276/11
20/25
27/5
75/125
112/51
88/9
90/9
EXTENSIVE FLOWER DAMAGE
FIRST POLLEN ON STIGMA
FRAGRANCE BEGINS
5:00 am
6:00
7:00
8:00
9:00
10:00
11:00
2:30 pm
TIME
NUMBER OF VISITATIONS TO FLOWERS
35
25
15
5
0



2–7. Insect visitors to male (Fig. 2–4) and female (Fig. 5–7) flowers of *Asterogyne Martiana*. Fig. 2, *Trigona* sp. (Apidae) probing for nectar; note corbicular pollen load (arrow); 6:24 A.M., × 4.7. Fig. 3, moth (?Dioptidae) obtaining nectar, and small Diptera (Ceratopogonidae) perched on anthers (arrows); 7:42 A.M., × 2.0. Fig. 4, weevils (Curculionidae: Erirhininae: *Celetes* sp. or *Phytotribus* sp.), especially at tips of staminal tubes and on anthers; eating, ovipositing, or copulating; 7:57 A.M., × 1.9. Fig. 5, weevil (?Baridinae); 2:30 P.M., × 2.0. Fig. 6, *Copestylum* sp. 2 (Syrphidae) probing for nectar; 7:32 A.M., × 4.0. Fig. 7, *Copestylum* sp. 2 with ventrum of thorax positioned over stigmas; 7:31 A.M., × 4.1.

(nectar, pollen, and floral tissue), a site for mating, and a site for oviposition and breeding. Table 1 lists the insects that were observed visiting flowers of the palm. Figure 1 summarizes the frequency of visitation of the main insect groups to both male and female flowers.

HYMENOPTERA: APIDAE—Several species of stingless bees (*Trigona* spp., Table 1) were common on male flowers throughout the morning, but especially early in the day when the supply of pollen was greatest (Fig. 1). At La Selva the orange species of stingless bee (including *T. ?testacea*) were much more numerous and more active than the black species (including *T. amalthea silvestriana* and *T. ?cupira*). In five mornings of observations only eleven *Trigona* were detected on female flowers of the palm (Fig. 1).

The stingless bees visited the male flowers to gather pollen soon after the flowers opened (and as early as 5:20 A.M.). While crawling over the male flowers, the worker bees picked up abundant pollen and brushed it back to the corbiculae on their hind legs, where the pollen collected as balls a millimeter or more in diameter (Fig. 2, arrow). Fragments of the anthers of the palm sometimes also accumulated on the corbiculae. By 9:30 A.M. pollen remaining on the anthers occurred mainly at the extremities of the pollen sacs; pollen removal by the bees was more difficult, and their activity and numbers on the palm were greatly reduced (Fig. 1). The bees were also observed taking nectar from the flowers (Fig. 2).

At Osa a species of *Melipona* (Table 1), active only on male flowers, collected pollen, which was transferred to its corbiculae. Pollen collecting was accompanied by a buzzing sound audible at a distance of twelve feet. This bee was not observed at La Selva.

Microscopic examination of the corbicular pollen loads of the *Melipona* species from Osa and of three specimens of *Trigona* (#14, 24, 35, Table 1) from La Selva revealed only pollen of *Asterogyne Martiana*. In addition, all specimens of Apidae (Table 1) bore only *Asterogyne* pollen on other parts of their bodies.

OTHER HYMENOPTERA—Other Hymenoptera (Table 1), notably ants (Formicidae), visited the palm in very limited numbers (Fig. 1), chiefly to obtain nectar. The Halictidae and Formicidae (Table 1) bore very sparse amounts of pollen.

LEPIDOPTERA—Throughout the morning small numbers (Fig. 1) of several species of moths (Table 1) sporadically visited the palm flowers, particularly the male flowers. The moths systematically worked over the inflorescences for nectar, generally probing each flower only once (Fig. 3). Although the abdomens of the moths repeatedly contacted the anthers or stigmas of the flowers, the one dioptid moth examined bore no pollen. The dioptids visited both male and female flowers.

COLEOPTERA: CURCULIONIDAE—Small weevils of the subfamily Erirhininae (Table 1; Fig. 4; also Fig. 5–6 in Schmid, 1970) were extremely abundant on the inflorescences, especially on male flowers (Fig. 1). Many members of the Erirhininae breed in palms; for example, larvae of *Celetes* and *Phytotribus* develop in the interior of the spathes of palms whereas the adults feed on pollen and the epidermal tissue of reproductive structures of newly opened spathes (Lepesme, 1947). On *Asterogyne* these weevils were typically oriented at the tips of the staminal or staminodial tubes (Fig. 4). Less frequently the weevils were perched on the anthers (Fig. 4); they were rarely seen on stigmas. The

weevils sought nectar and chewed floral tissue, including pollen. Copulating weevils (Fig. 4) were common on flowers and inflorescence axes. Oviposition was also prevalent and was usually into the staminal (or staminodial) tubes. The weevils generally seemed restricted to one plant, quickly returning to an inflorescence if it was disturbed by vigorous shaking. Many weevils were examined microscopically; several bore a few pollen grains, which belonged exclusively to *Asterogyne Martiana.*

Small numbers of medium- and large-size weevils (including the Baridinae) also visited the palm (Fig. 5).

OTHER COLEOPTERA—An assortment of other beetles in at least five families (Table 1), but most notably the Chrysomelidae, was found on the palm flowers. Species diversity and number of beetles on the palm increased toward the end of the morning (Fig. 1). The beetles used the palm as a mating site (particularly the Chrysomelidae) and as a food source, chewing floral tissue, including pollen, and possibly also obtaining nectar. The beetles usually gnawed on the fleshy parts of the palm flowers (see Schmid, 1970). These Coleoptera, including the weevils discussed above, seemed responsible for most of the damage to the palm flowers, which by 9:30 A.M. was usually quite extensive. All insect specimens bore very little pollen.

DIPTERA: EXCEPT SYRPHIDAE—Small flies (Table 1), chiefly Ceratopogonidae (Fig. 3, arrows) and Sphaeroceridae, were present in large numbers on both male and female flowers of the palm (Fig. 1). These flies usually sat on or moved about the anthers (Fig. 3) and stigmas, which generally served as landing platforms, although the staminodes and perianth parts were also used for this purpose. Several flies were often active on one anther.

Drosophilidae were abundant on the female flowers (including the stigmas) but rarely visited the male flowers. Empididae and nectar-sucking Tipulidae (crane flies) were very infrequent visitors to the palm.

Many of these Diptera (Table 1) tended to be restricted to one plant for long periods of time. Nectar (and possibly pollen) seemed the main attractant. Only a few of the approximately 60 dipteran specimens (Table 1, DIPTERA, except Syrphidae) examined bore pollen, and then only one to several grains of *Asterogyne Martiana.*

For a variety of reasons none of the insect groups discussed so far can be considered effective pollinators of *Asterogyne Martiana* (see Table 1, Fig. 1):

(1) inability to carry much pollen: Hymenoptera—except Apoidea; Lepidoptera; all Coleoptera; Diptera—except Syrphidae.

(2) small numbers on both male and female flowers: Hymenoptera—except Apidae; Lepidoptera; Diptera—Empididae, Tipulidae.

(3) infrequent occurrence on male flowers: Diptera—Drosophilidae.

(4) infrequent occurrence on female flowers: Hymenoptera—Apidae; Lepidoptera; all Coleoptera.

(5) failure to contact stigmas of female flowers: Coleoptera—especially Curculionidae.

(6) sedentary nature of the insects (coupled with the tendency of palms bearing male or female flowers to be separated by some distance): Hymenoptera—Formicidae; Coleoptera—Curculionidae; Diptera—except Syrphidae.

DIPTERA: SYRPHIDAE—None of the above characteristics apply to the Syrphidae. There is strong evidence that syrphid or hover flies are the effective pollinators of *Asterogyne Martiana.*

The Syrphidae, which are specially

adapted to live on floral nourishment, visit the flowers of many plants (see systematic lists in Knuth, 1905, pp. 383–390, and 1909, pp. 567–579) to obtain pollen (see Baker and Hurd, 1968; Faegri and van der Pijl, 1966; Knuth, 1906, especially pp. 174–177; Kugler, 1955; Percival, 1965) and nectar. In Europe the Syrphidae contribute more to the pollination biology of flowers than all the other Diptera combined (Knuth, 1906). At Java Knuth (1904) observed syrphids on flowers of the palms *Phoenix "hybrida"* and *Latania Loddigesii.*

At least eight species of both male and female Syrphidae (Table 1) visited flowers of *Asterogyne* throughout the morning (Fig. 1), as many as thirteen syrphids active on an inflorescence at one time. The flies were initially much more abundant on the male flowers but became numerous on the female flowers when the latter began producing nectar around 7:00 A.M. (Fig. 1). Significantly, this activity correlates with the first record of pollen on stigmas at 7:36 A.M.

The syrphids systematically foraged both male and female flowers for nectar (Fig. 6). The flies also visited male flowers to eat pollen as a protein source or perhaps to squeeze the pollen to extract juices. Abundant pollen was evident not only on the heads and mouth parts of many of the syrphids collected, but also within the labellae, the lobes of tissue at the tip of the proboscis. Although syrphids foraged male flowers for nectar very early in the morning, it is questionable whether they obtained any liquid since I could detect no nectar in male flowers before 7:30 A.M. (Schmid, 1970).

The syrphids probed for nectar at the bases of the ovaries (pistillodes or pistils) of both male and female flowers (Fig. 6), typically probing one to three times per flower. Flies usually obtained both nectar and pollen from the same flower. In foraging, the flies dragged their ventral surfaces, especially their abdomens, over the anthers or the stigmas (Fig. 7). Thus pollen could be readily picked up from the anthers or deposited onto the papillate stigmatic surfaces (Fig. 7).

The syrphids carried abundant pollen, all of which seemed to belong to *Asterogyne Martiana.* For example, four flies (specimens #27–30) collected from female flowers between 8:45 and 8:50 A.M. bore an estimated total of 600 pollen grains, about 75 to 300 grains apiece. Pollen, frequently adhering in clumps, accumulated on or especially between hairs on all parts of the body, but particularly on the legs and on the posterior ventral surface of the abdomen. At least 100 pollen grains alone were restricted to the ventral abdominal region of one specimen (#38).

CONCLUSIONS

My studies on *Asterogyne Martiana* strongly suggest entomophily, specifically myophily (fly-pollination), for this plant. Anemophily can be definitely excluded. The evidence presented for the Syrphidae, in conjunction with the extensive evidence disqualifying the other insect groups as pollinating agents (see p. 46), necessitates the conclusion that the Syrphidae are the effective pollinators of *Asterogyne Martiana* in the areas studied.

From the moment the conspicuous white inflorescences are silhouetted against the dark forest by the dawn light, *Asterogyne* is very attractive to a wide array of insects. Apoidea, particularly stingless bees, forage on the male flowers for nectar and pollen, but rarely visit the female flowers. Other Hymenoptera

are very infrequent visitors to the palm. Lepidoptera, notable in their paucity, shift from inflorescence to inflorescence, draining the flowers of their nectar. Numerous Coleoptera gorge themselves on nectar or on floral tissue, mutilating the flowers in the process. Visiting first the male flowers for pollen and/or nectar and then, later in the morning, the female flowers for nectar, syrphid flies are responsible for almost all the pollen transfer. Large numbers of other Diptera visit both male and female flowers (including anthers and stigmas), but their significance as pollinators remains largely unknown. Their contribution is probably small, however, as these Diptera tended to be restricted to one plant for long periods of time and carried little pollen.

On the basis of such anemophilous characters as the exserted stamens, the long, recurved papillate stigmas, and the absence of nectaries, Wessels Boer (1968, p. 36) thought the small flowers of the geonomoid palms to be unattractive to insects and, hence, wind-pollinated. Spruce (1869, p. 96), however, more accurately suggested that *Geonoma* is pollinated by insects. Ule (1900, p. 130) observed various flies (unidentified) sucking secretions of both male and female flowers of a *Geonoma* in Brazil. *Asterogyne Martiana* is clearly insect-pollinated. In view of the rather similar, specialized floral structures of the other geonomoid palms, and their occurrence in dense, wet, generally tropical and montane rain forests (Wessels Boer, 1968), insect-pollination seems the prevailing situation in the tribe.

The frequently expressed notion that palms are predominately or exclusively wind-pollinated is also suspect. Palms cannot *a priori* be considered anemophilous. Rather the family exhibits a number of features of both the entomophilous and anemophilous syndromes. Detailed observations, for the most part lacking to date, are required for each taxon.

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ADDENDUM: Like so many other authors apparently unaware of Knuth's work [see R. Schmid and M. J. Schmid, 1970. Knuth's often overlooked "Handbuch der Blütenbiologie, III. Band." Ecology 51 (2): (In press.)], T. S. Mahabalé [1965. Evolutionary trends in the Palmae with special reference to fossil palms. The Palaeobotanist 14 (1–3): 214–222.] in his recent review erroneously assumes that the palms are mainly anemophilous; L. Emberger [1960. Traité de Botanique. Systématique. T. II. Les Végétaux Vasculaires. Fasc. II. Paris: Masson et C^ie^ Éditeurs.] also perpetuates the myth.