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

I. Inflorescence and Floral Morphology; Phenology

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As a participant in the Organization for Tropical Studies' (OTS) Advanced Botany Course "Reproductive Biology in Tropical Plant Ecology" held in July–August, 1968, I had the opportunity to make detailed observations on the reproductive biology of *Asterogyne Martiana* (H. Wendl.) H. Wendl. ex Hemsley* (subfamily Arecoideae, tribe Geonomeae), a small showy palm native to Costa Rica and much of Central America.

Asterogyne, a genus of one to three species, depending upon taxonomic concepts, ranges from British Honduras to western Colombia (and perhaps also to northern Venezuela—see Wessels Boer, 1968). The most widely distributed species of the genus, *A. Martiana,* is a common undergrowth component of wet lowland forests (up to 500 m. elevation) (Fig. 1, see cover) of the Atlantic and Pacific coasts, ranging from British Honduras and Guatemala to western Colombia.

A dwarf palm, *Asterogyne Martiana* (Fig. 2) sometimes reaches 2 m. or more in height, and the unbranched, unarmed trunk becomes 3 to 5 cm. thick. The showy deep green leaves, up to 1.3 m. long and 25 cm. wide, are usually entire, though deeply bifid at the apex; they frequently become frayed with age. White, fragrant, unisexual flowers are produced on axillary inflorescences typically of 2 to 7 dull pale red rachillae (Fig. 3), 10 to 25 cm. long, which radiate from the end of an elongate, slender arching peduncle. The one-seeded, fleshy, smooth, ellipsoid-ovoid fruits are at first red but become purplish black at maturity.

METHODS

Asterogyne Martiana was studied at two different sites in Costa Rica. Preliminary observations were made on July 21, 1968, in an alluvial plain tropical wet forest near the Pacific road, about 12 km. (by road) southwest of the town of Rincón de Osa (8° 42′ N, 83° 29′ W), Osa Peninsula, Puntarenas Province. Detailed observations of the palm were made from August 1–6, 1968, in the tropical wet forest on Finca La Selva (Fig. 1), about 5 km. (by river) south of Puerto Viejo (10° 26′ N, 83° 59′ W), Herédia Province.

Using a census technique, I wandered in the forest, taking notes on the palms in flower and on their insect visitors. Plants were labelled and their sequence of flowering (phenology) was traced over a period of several days. Observations were generally possible only between 4:00 and 11:00 A.M. due to the torrential afternoon rains characteristic of the wet season. The most complete observations were made between 6:00 and 10:00 A.M. Flowers were examined in the field with a hand lens or dissecting

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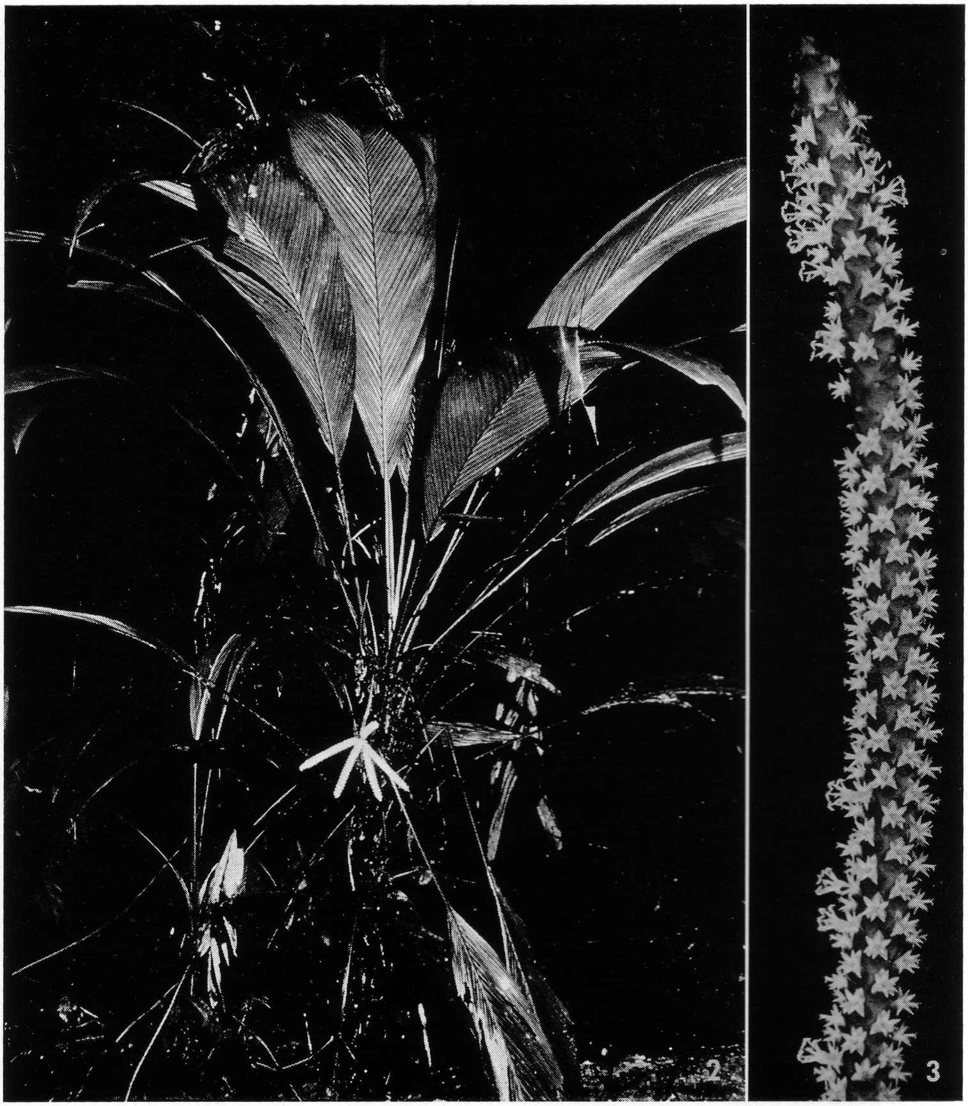
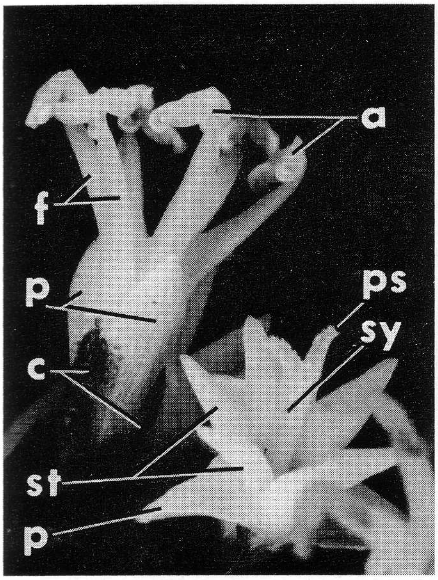
* Synonyms include *Geonoma Martiana* H. Wendl., *G. trifurcata* Oerst., and *Asterogyne minor* Burret.



2–3. *Asterogyne Martiana.* Fig. 2, habit. Fig. 3, inflorescence branch with 7 clockwise spiraling rows of female (and male) flowers, 12:02 P.M., ×0.9.

microscope, and throughout the morning were checked for nectar production, either visually or with a Bellingham and Standley Pocket Refractometer (distributed by Epic, Inc., 150 Nassau St., New York, N. Y. 10038). Insect collections and floral material preserved in FAA were also examined.

The photographs were originally taken on Kodak Kodachrome II Film; the close-ups of the insects and flowers were taken at initial magnifications of ×0.2 to ×1.65 with a Micro-Nikkor Auto 55mm. f/3.5 lens on a Nikon F Photomic TN camera. Illumination was by electronic flash ringlight (Honeywell



4. Male and female flower of *Asterogyne Martiana,* 12:07 P.M. ×8.9. Abbreviations: a, anthers; c, sepals; f, filaments, basally connate; p, petals; ps, papillate stigma; st, staminodes; sy, style.

Prox-O-Lite) operating off a Honeywell Strobonar P65C power pack. The accompanying black-and-white photographs were produced from Ansco (GAF) Versapan Negative Film or Kodak Plus-X Pan Film copy negatives (Schmid, 1969) of the Kodachrome II originals.

I cannot overemphasize the value of an adequate photographic record. Examination of the Kodachromes under a 25– and 50-power dissecting microscope not only substantiated many of my field observations, but also revealed much additional information.

INFLORESCENCE AND FLORAL MORPHOLOGY

The following description of the reproductive structures of *Asterogyne Martiana* will supplement previously published accounts (see Wessels Boer, 1968, and references therein). In general, *Asterogyne* resembles *Aristeyera* (Moore, 1966, 1967; Uhl, 1966), which Wessels Boer (1968) recently transferred to *Asterogyne.*

A sexually mature plant of *Asterogyne Martiana* may bear 1 to 6 inflorescences (average of 2.4 for 110 plants sampled) concurrently, each inflorescence consisting of 2 to 8 branches (average of 4.6 for 36 plants sampled). Inflorescences may also be spicate (Wessels Boer, 1968). Pits containing the flowers are arranged on the inflorescence branches (rachillae) in close-set, vertical, clockwise (Fig. 3) or counterclockwise spiraling rows. Most inflorescences (over 60%) bear floral pits in 7 longitudinal rows (Fig. 3). Less common are inflorescences with floral pits either 6-ranked or 8-ranked. Occasionally, the same inflorescence may bear rachillae with 6- and 7-ranked pits, 7- and 8-ranked pits, or 6- and 8-ranked pits; a comparable situation exists in *Aristeyera* (or *Asterogyne*) *ramosa* (Moore, 1967, p. 146).

Both male and female flowers are whitish, fragrant, and nectariferous. Flowers occur deeply sunken in pits in the fleshy inflorescence branches. As is typical for many palms, three flowers occur at a pit site, each triad consisting of an inner central female flower and two outer lateral male flowers. The pits at the tips of the inflorescence axes usually bear only male flowers. A fleshy, sunken pit-closing bract completely covers each floral pit, and a small bractlet subtends each flower. The male flowers of my Costa Rican material were 7.5 to 9 mm. in length, the female flowers 6.5 to 8 mm.

The male flowers (Figs. 4, 5, 7) have 3 distinct sepals, 3 basally connate petals, 6 stamens with the filaments basally united into a short tube that is weakly adnate to the petals, and a small, tripartite rudimentary pistil (or pistillode) about 2 mm. long. Initially slender, the bifid connectives of the inflexed anthers become greatly enlarged (to about twice their former diameter) shortly after the flowers open; this causes the separate pollen sacs to dehisce introrsely, become erect, and coil back upon themselves (Figs. 4, 5, 7). The large, ellipsoidal, monocolpate pollen (see Punt and Wessels Boer, 1966) is whitish and smooth-surfaced. It is rather sticky and is shed from the anthers in small clumps, which are frequently found on the ventral surfaces of insects and also on the inflorescence axes, littered among the flowers.

The female flowers (Figs. 4, 6, 7) have 3 distinct sepals, 3 basally united petals, 6 very prominent staminodes, basally connate and strongly adnate to the petals, and a short, trilocular, tri-ovulate ovary surmounted by 3 fused, elongate styles with 3 papillate stigmas that are recurved at anthesis. The lower halves of the styles display a warty, glandular appearance suggestive of the structure of nectaries. Both these translucent stylar protuberances and the fleshy staminodes readily exude fluid when slightly damaged; the fluid gave a reading of 22% in a pocket refractometer, a reading identical to that obtained for nectar concentration.

PHENOLOGY: FLORAL EVENTS OCCURRING OVER SEVERAL DAYS

Asterogyne Martiana is monoecious and markedly protandrous. The pit-closing bracts recurve and roll back (see Uhl, 1966) just before the flowers emerge. The flowers of an inflorescence then open in gradual daily succession, emerging one by one from each floral pit: first the two male flowers, then the female flower.

Often the entire inflorescence is covered with flowers (Fig. 2), two flushes of male flowers preceding a flush of female flowers. In other cases flowers emerge basipetally on the spikes, so that on the first day only the tips of the spikes have male flowers, on the second day the middle parts of the spikes are in flower, on the third day the bottom portions of the spikes are in flower, and on the fourth or fifth day the second set of male flowers or the set of female flowers may emerge, either in small groups or as a flush. Wendland (1856) reported that the female flowers of an inflorescence appear four to six days after the male flowers, but at La Selva the former generally appeared within a day or two of the latter. Thus, although it is possible for all the buds of an inflorescence to open completely within three days, five or more days are usually required.

Two flowers generally do not occur at one pit at the same time. Occasionally two male flowers may occur together at a pit site, but more commonly a male flower and an emerging bud occur side by side at one pit. Only very rarely do a male and female flower occur together at the same pit site (Figs. 3, 4, 7) or even at different sites on the same inflorescence. In addition, only one inflorescence of a plant is usually in flower at any one time, other inflorescences on the plant bearing only buds or fruits. Of

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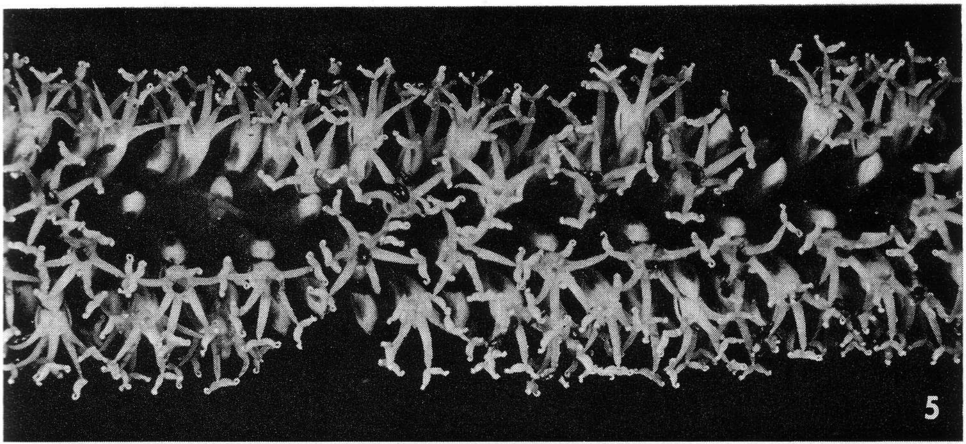
5–7. Portions of inflorescence branches of *Asterogyne Martiana*. Fig. 5, male flowers, 7:57 A.M. × 2.0. Fig. 6, female flowers, 8:15 A.M., × 2.0. Fig. 7, enlargement of Fig. 3, an atypical situation with both male and female flowers occurring together at the same pit sites, 12:10 P.M., × 3.9.



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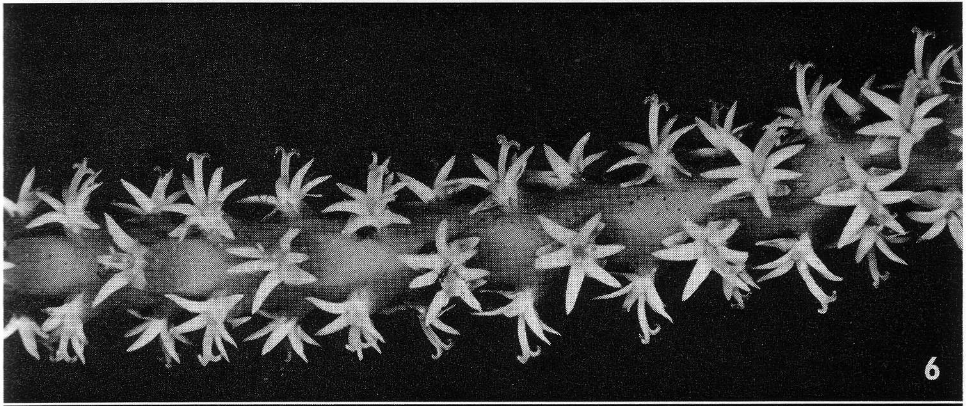

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some 50 plants observed in flower, only one bore two flowering inflorescences concurrently: on the first day both inflorescences bore only male flowers, on the second day one inflorescence had male and the other female flowers, and on the third day both inflorescences bore only female flowers.

Thus, allogamy (cross-pollination) is the rule, usually consisting of xenogamy (pollen transfer between flowers of different plants). Geitonogamy (pollen transfer between two flowers on the *same* plant) is extremely unlikely; only rarely do male and female flowers occur *at the same time* on the same inflorescence or on different inflorescences on the same plant. The unisexual nature of the flowers, of course, prevents autogamy (self-pollination).

According to Allen (1956), in Costa Rica flowers of *Asterogyne* normally appear in late January or early February, followed in March by the small fruits. At Osa in late July and at La Selva in early August all reproductive stages were present, from newly emergent inflorescences with flower buds to old inflorescences bearing mature fruits. It would be interesting to determine if there is greater flowering in the dry season (see Janzen, 1967). I suspect, however, that flowering is more or less continuous throughout the year.

Since each plant produces twice as many male as female flowers, each lasting one day, one might expect a census of plants in flower to reveal this ratio, especially if the census were taken over an extended period of time. However, a census of plants in flower at La Selva on August 1–6 yielded 61 plants bearing male flowers and 20 plants bearing female flowers. Presumably this variance from the expected 2:1 ratio is because it takes two to six days or longer for *all* the male flowers of an inflorescence to emerge from the floral pits, whereas the female flowers of the inflorescence require only one day, at most two, to emerge. That is, flowering in the male condition is prolonged, accentuating the protandry and thus ensuring a longer period of time in which pollen will be available for transport to the female flowers.

PHENOLOGY: FLORAL EVENTS OCCURRING IN ONE DAY

Most male and female flower buds start opening around dawn (5:00 A.M.). Some buds open as early as 4:40 A.M. (but never before 4:30), whereas a few open only by 5:30 or later. Initially both male and female flowers are closely appressed against the spikes, but within an hour or so of anthesis the flowers reflex abaxially about 60° so that their exserted axes are nearly perpendicular to the spike axes (Figs. 3–7).

By 6:00 A.M. most anthers have completely dehisced, in the manner described above. Stingless bees (Apidae: *Trigona* spp.) were observed collecting pollen as early as 5:20 A.M. Pollen is copiously produced. Gravity and the action of insects scatter much pollen onto the spike axes, around the male flowers. By 9:15 A.M. most anthers have lost nearly all their pollen.

The flowers of both sexes have a strong, sweetish fragrance reminiscent of honeysuckle or gardenia. The scent is noticeable from dawn on, although its strength is somewhat variable throughout the morning.

Nectar production in the male flowers seemed to begin about 7:30 A.M. Nectar is abundantly produced from 8:00 to 9:00 A.M., so much, in fact, that it frequently fills the staminal tube. Traces of nectar were evident in flowers collected as late as 9:30 A.M.

Nectar production in the female flowers begins somewhat earlier and is less abundant than in the male flowers.

Traces of nectar were evident in flowers examined as early as 6:45 and as late as 9:25 A.M. Nectar from both male and female flowers gave a reading of 22% in a pocket refractometer.

Pollen was first observed on stigmas of flowers collected at 7:36 A.M. Fewer than five pollen grains of the palm were generally present on the stigmas of a flower, but this small quantity is more than adequate to effect fertilization since only one of the three ovules in an ovary develops.

Insect damage to the flowers increases as the day progresses. By 9:30 A.M. damage from chewing insects (mainly Coleoptera) was often considerable. The petals and stamens of the male flowers and the fleshy staminodes of the female flowers are especially susceptible to insect mutilation.

Both male and female flowers last one day. Male flowers, unfertilized female flowers, or the upper withered portions of fertilized female flowers (see Burret, 1930, p. 141) begin to fall from the inflorescences by noon; some male flowers were dropping from the spikes as early as 11:05 A.M. By 4:30 P.M. the spikes had lost most of their flowers. After flowering is completed, the pit-closing bracts reflex adaxially to reseal the floral pits, later rolling back to allow the exsertion of the enlarging fruits. Spent flowers which may happen to remain on the spikes the following day evoke almost no attention from insects, and then only from Coleoptera. Afternoon wind and rain probably accelerate the shedding of the flowers from the inflorescences.

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