

Pollination in Some New Guinea Palms

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During recent extensive field work in Papua New Guinea, I had the opportunity to make some observations on the phenology and pollination of three native palms. These observations were limited by time, logistics, and particularly by the infrequency of flowering in accessible specimens. They therefore are not as complete as might be desired, but they do suggest some interesting conclusions and point the way to further work by specialists in floral ecology.

Nypa fruticans Wurmb was observed in an extensive natural population in a brackish lagoon near Lae, Morobe District (vouchered by Galore NGF 41101, LAE, BH). *Hydriastele microspadix* (Becc.) Burret (cf. Essig LAE 55001, LAE, BH) and *Ptychosperma macarthurii* (H. Wendl.) Nichols (Essig LAE 55195, LAE, BH) were observed in the Botanic Garden at Lae. The former occurs there naturally, but the latter is cultivated there, some distance from its natural range in the Fly River area.

For each of the three species the sequence of flowering and related phenomena was noted, the morphology of the flowers described, and the insect visitors and their activities recorded. Specimens of the more common insects were collected for later identification.

Ptychosperma macarthurii

Morphology and phenology

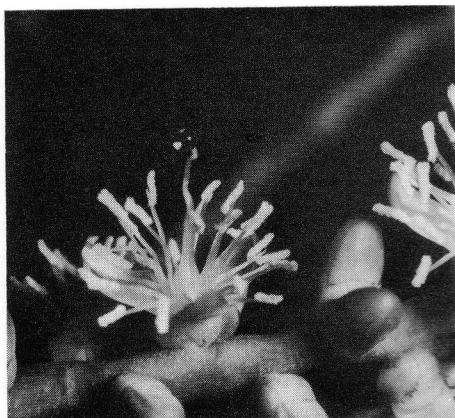
The inflorescence in *Ptychosperma* is an infrafoliar, short-pedunculate panicle, branched to two or three orders. The

flowers are unisexual and borne in spirally arranged triads consisting of a central female flower flanked laterally by two male flowers. The female flower, and sometimes one of the male flowers, are generally lacking in the more distal "triads."

The male flowers (Fig. 1) are cartridge-shaped in bud, i.e., cylindrical with a round-pointed apex. The petals are very hard, valvate, and tightly closed before anthesis. The sepals are broad, rounded, and imbricate, and one-fourth to one-third the length of the petals. The stamens are numerous (c. 30–40), with long, subulate filaments and versatile anthers that bear white, moderately sticky pollen. The center of the flower is occupied by a lageniform pistillode with an elongate neck and a slightly expanded and cleft apex, from which nectar is secreted.

The female flowers (Fig. 2) are conicovoid with three broad, rounded, imbricate sepals and three broad, imbricate, apically subvalvate petals. The four to nine staminodes are inconspicuous, dentiform, and appressed against the lower part of the pistil. The pistil is conicovoid with three essentially sessile stigmas that reflex at anthesis. Three nectaries are present near the top of the pistil, alternate with the three stigmas.

The flower buds are all initiated very early in the development of the inflorescence and subsequently mature uniformly. At the time that the two outer, enclosing bracts are shed, the flowers are all the same size and very small. They



1. A male flower of *Ptychosperma*. Note the globule of nectar at the tip of the pistillode.

continue to grow very slowly, fully exposed to the elements, for another three months, and only then are ready for anthesis. The very tough and tightly closed perianth protects the inner organs during this long period.

The inflorescence is protandrous, that is, all the male flowers open and shed their pollen before any of the female flowers become receptive to pollen. This effectively prevents pollination between flowers on the same inflorescence. The opening of the male flowers, though they are essentially equally mature, is staggered over a period of about two weeks. The flush of flowers that opens each day is apparently randomly distributed throughout the inflorescence, though the two male flowers in one triad seldom open at the same time. The flowers open just before dawn, and each lasts only one morning. By mid-morning the anthers are essentially empty of pollen, and by noon the open flowers have mostly fallen.

During the period of male anthesis, the female flowers on the same inflorescence remain quiescent. After the last male flower has fallen, the female flowers begin to expand, mostly vertically, pushing the tip of the pistil up between the



2. Several female flowers of *Ptychosperma*. The two at the right are at anthesis and secreting nectar.

tips of the petals. After three to four days the stigmas reflex (also in the early morning) and nectar secretion begins. This process is not always uniform throughout the inflorescence and it may take two to three days for all the female flowers to become receptive. The exact duration of receptivity is not known. The stigmas only gradually become brown and withered over a period of about two days. Nectar secretion can usually still be seen on the second day.

Insect visitors

Insect visitors to *Ptychosperma macarthurii* in the botanic garden were quite varied. To what extent these reflect the range of visitors in a natural population remains to be determined, but judging from the generally heavy fruit set, they include effective pollinators. The most important visitors fall into three categories: (1) bees of the families Halictidae and Apidae, (2) medium flies of the families Syrphidae and Calliphoridae, and (3) small flies of the family Drosophilidae. (All identifications by G. C. Eickwort, Dept. of Entomology, Cornell University.)

The most prominent bees were identified as *Trigona* (*Tetragona*) sp. (Apidae: Apinae), *Nomia* (*Mellitidia*) sp. (Halictidae: Nomiinae), and *Homalictus* sp. (Halictidae: Halictinae). These were all seen collecting pollen from the male flowers, but none were seen collecting the nectar on the same flowers, nor were any seen visiting female flowers during the early morning hours. Only later, toward mid-morning were any bees seen on the female flowers, and then only *Nomia*. They were fairly abundant and moved methodically from flower to flower collecting nectar. Some of them carried heavy pollen loads on their hind legs and sometimes on the thorax between the front legs. The bees often landed upon or crawled across the tops of the flowers, undoubtedly losing some pollen to the sticky stigmas.

The syrphid flies were seen on the male flowers, where they ignored the nectar of the pistillode and apparently fed on pollen. They were also found on the female flowers feeding on nectar. Flies captured on the female flowers had very little pollen on their bodies. They were less numerous than the bees and their activities were less regular. They spent much time sitting motionless on unopened flower buds and in wandering apparently aimlessly on the inflorescence. Calliphorid flies were captured from the male flowers, but their feeding activities were not observed. They are not known to feed on pollen. On two isolated occasions a different and much larger kind of fly was observed, but not captured, that very methodically moved from one male flower to another siphoning off the drops of nectar at the tips of the pistillodes. This was the only insect seen to feed on the nectar of the male flowers, but it was never observed on a female flower.

Drosophilid flies were observed in large numbers around the nectaries of

both male and female flowers about mid-morning, after most other insect activity had ended. There was little pollen left in the flowers and the flies were small enough to land on the pistillodes without contacting the anthers. Consequently, little pollen was found on their bodies.

Conclusions

The spottiness of the data concerning insect visitors makes it difficult to arrive at very precise conclusions. The possible pollen vectors can however be narrowed down by the process of elimination.

Wind-pollination can be ruled out for two reasons. First, the pollen is too heavy and sticky to be carried an appreciable distance by the breeze. Pollen of wind-pollinated plants is very distinctive, being rather dry and powdery. Second, even in the relatively open habitat of the botanic garden, breezes were too infrequent, particularly during the early morning hours, to account for the consistently heavy fruit sets seen on the palms. Typically the air is perfectly still at the time the pollen is released. Fruit sets were equally heavy and breezes even rarer in the rainforest habitat of various species of *Ptychosperma* seen by me.

It is probably also unlikely that the drosophilid flies contribute to the pollination of *Ptychosperma*. Their small size and limited contact with pollen-bearing anthers makes them poor pollen carriers.

That leaves flies, mainly syrphids, and bees, particularly *Nomia*, as the most likely pollinators. The other flies and bees mentioned are generally too few in number or they fail to regularly contact both male and female flowers. Between the syrphids and *Nomia*, I would regard the latter as the most important pollinator at the time and

place that the study was made. They regularly carry much more pollen than the flies, both on their hind legs and also adhering to other parts of the body. In addition, their movements from flower to flower seem more methodical and their activities more intensive. I should emphasize however that more observations are needed, particularly from *Ptychosperma* growing in its natural habitat. The flies, the other bees, and conceivably other unobserved kinds of insects could play important roles in the pollination of this species.

Hydriastele microspadix

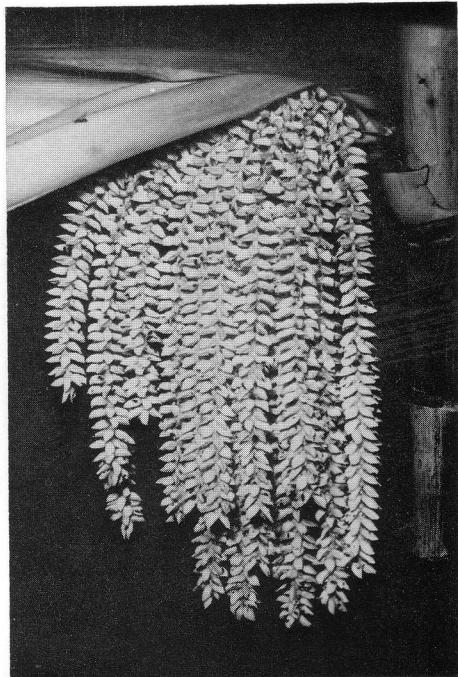
Morphology and phenology

The inflorescence of *Hydriastele* (Fig. 3) is an infrafoliar, short-pedunculate panicle branched to two orders. The flowers are unisexual and arranged in triads that are decussate (aligned in four vertical rows) on the elongate, drooping rachillae. The triads are complete even at the distal ends of the rachillae.

The male flowers (Fig. 4, 5) are asymmetric, with three very small, slightly imbricate sepals, and three large, soft, acute and slightly twisted petals that are only loosely valvate. There are six stamens with large, basifixated anthers and very short filaments. The pollen is white and moderately sticky. There is no nectary.

The female flowers (Fig. 4) are conic-ovoid and tightly enveloped by the more-or-less equal, broadly rounded and imbricate sepals and petals. The tip of the pistil protrudes through the top of the perianth, even in bud. The three stigmas are sessile, rounded, and slightly reflexed at anthesis. Again, no nectaries are present.

Development of the inflorescence is similar to that in *Ptychosperma* in that maturation of the flower buds is uniform after a very early stage of initiation.

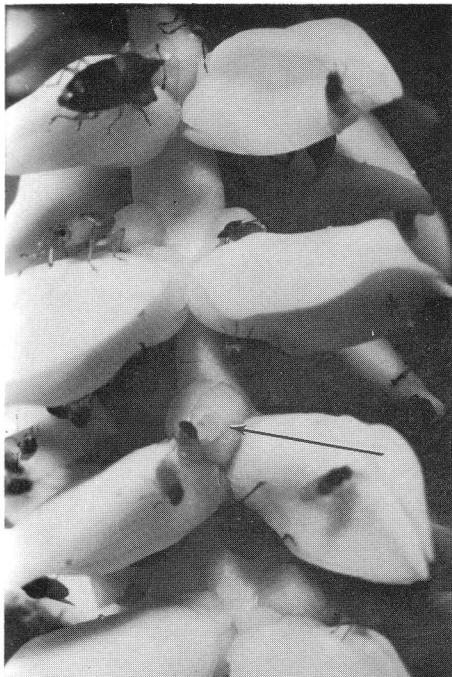


3. An inflorescence of *Hydriastele* just after emerging from its protective bracts.

Unlike *Ptychosperma*, however, the buds are completely mature before the two enclosing bracts open. Reproductive activity begins almost immediately upon exposure of the flowers.

The inflorescences are protogynous, i.e., the period of female receptivity precedes the period during which pollen is shed in the male flowers. The bracts open before dawn and the first light of day finds the female flowers with stigmas reflexed and slightly moistened. Anthesis is simultaneous for all the female flowers on the inflorescence and probably lasts only a few hours. In the afternoon the stigmas become noticeably withered.

Anthesis of the male flowers follows that of the females by 24 hours and is simultaneous throughout the inflorescence. Pollen is shed rather quickly between dawn and about 8:00 A.M. By



4. Part of a *Hydriastele* rachilla soon after emerging from the protective bracts. The arrow points to the slightly expanded stigma of one of the receptive female flowers. Insects present are curculionid beetles and drosophilid flies.

that time the flowers are beginning to loosen and fall.

Insect visitors

The insect visitors to *Hydriastele microspadix* fall into three categories: (1) bees—essentially the same as those listed for *Ptychosperma*, (2) small flies of the family Drosophilidae, and (3) small flower-feeding beetles of the family Curculionidae (weevils).

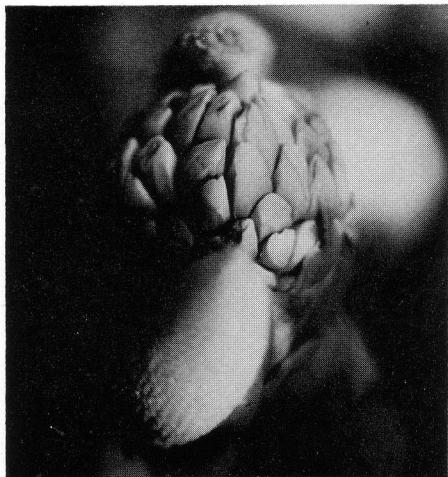
The bees (*Nomia*, *Homalictus*, *Trigona*) were abundant, collecting pollen from the open male flowers. None of them, however, visited inflorescences on which there were receptive female flowers, for these lack nectar as well as pollen.



5. Male flowers of *Hydriastele* at anthesis.

The drosophilid flies were found in some abundance on both male and female flowers. The exact nature of their feeding activity was not observed, though they were seen to move about, sometimes contacting the stigmas of the female flowers. Captured specimens from the male flowers sometimes carried a few pollen grains. Specimens from the female flowers seldom carried any pollen.

The activities of the weevils were similar to those of the drosophilids, though they were larger and carried much more pollen. They began appearing on the newly exposed inflorescences, where the female flowers were receptive, almost as soon as the enclosing bracts had opened. They are probably attracted by the musky odor of the inflorescence. The weevils apparently feed on and in the male flowers as long as they remain closed, but leave rather quickly when they open the next morn-

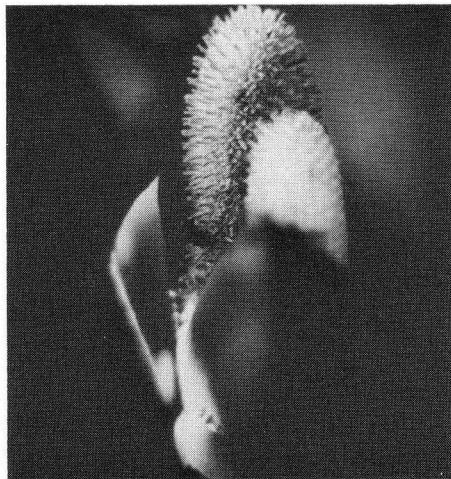


6. A head of female flowers of *Nypa*, with the two uppermost male spikes attached just below.

ing. In this way, the weevils migrate each morning from an inflorescence in which pollen is being shed to one in which the female flowers are receptive.

Conclusions

The possibility of wind-pollination in *Hydriastele* can be dismissed for the same reasons given in the case of *Ptychosperma*. The pollen is too sticky and breezes are too rare to make this an effective means of pollen dispersal. Bees must be considered unlikely pollinators of *Hydriastele* since they virtually never visit female flowers. The remaining two kinds of insects, drosophilid flies and curculionid beetles, both have the potential to pollinate *Hydriastele microspadix*. Of the two, however, the beetles appear to carry much more pollen, and are probably the main pollinating agent for the species. It should be noted that the morphology, phenology, and insect visitors described here for *Hydriastele* are remarkably similar to those of *Bactris* (Essig 1971), an unrelated genus from tropical America.



7. A male spike of *Nypa* with the flowers at anthesis. Note the exserted staminal columns.

Nypa fruticans

Morphology and phenology

The morphology of the *Nypa* inflorescence has recently been described in detail by Uhl (1972). Flowers are unisexual, with male and female flowers segregated onto different parts of the interfoliar and much-branched inflorescence. The female flowers (Fig. 6) are borne in a dense globose head that terminates the main inflorescence axis, while the male flowers (Fig. 7) are borne on dense spikes that terminate the several orders of lateral branching.

The male flowers are bright orange and are composed of three separate, linear sepals, a similar whorl of three petals, and three stamens that are connate by the filaments and connectives into a single column. The pollen is also bright orange and very sticky. No nectar is produced.

The female flowers are very unusual. The perianth is essentially the same as in the male flowers but obscured at maturity by the three separate and greatly enlarged carpels. Each carpel terminates in an elongate, narrow slit,

the margins and inner surface of which are stigmatic, and which opens to the locular canal below. Uhl (1972) found a gelatinous substance in the openings of some of the carpels of preserved flowers, which she considered an unusual stigmatic secretion. This was not observed in the field.

The inflorescence is protogynous, with the female head emerging first, followed closely by one or two of the uppermost male spikes. The lower male spikes follow, staggered over an apparently long time. The flowers are mature when they emerge from the bracts, and reproductive activity begins within a few days. The timing and duration of female receptivity is not known; there seems not to be any external indication of the receptive state. Anthesis of the male flowers occurs in midmorning. After about 9:30 A.M. the staminal column elongates, pushing the anthers beyond the perianth (Fig. 7), and the pollen is released.

Insect visitors

Only two kinds of insects were found in significant numbers on the flowers of this particular population of *Nypa*: (1) bees of the genus *Trigona*, (2) small flies of the family Drosophilidae. The bees were numerous on the male flowers, but very rare on the female flowers. The flies, however, were numerous on the male flowers and also were frequently seen on the female flowers. Flies captured from the male flowers carried significant amounts of pollen stuck to various parts of the body.

Insect larvae were found burrowing among the closely packed male flowers where there was conspicuous, but not extensive damage. Some larvae were also found beneath the bracts of the female heads, but no damage from feeding could be found there. A few of the larvae were coleopterans, but most were of one species of the dipteran suborder Cyclorrhapha, to which the drosoph-

philids and many other common families of flies belong. They were of a new and unusual type, unlike any known drosophilid larvae, but identification as such was not completely ruled out. (Larvae were examined by C. O. Berg, Cornell University.) The connection with the adult drosophilids is logical, if not demonstrated, and it appears likely that the flies carry out their life cycle in the flowers of *Nypa*.

Conclusions

Wind-pollination is most conclusively eliminated as a possibility in *Nypa* by the nature of the pollen. It is very sticky and falls from the anthers in large, heavy clumps. Pollination by bees can also be considered as rather unlikely on the basis of these observations, since bees were rarely seen on the female flowers. Some selfing may occur since the uppermost male spikes sometimes emerge and flower rather soon after the female head emerges. This depends, however, on how long the female flowers remain receptive, which, unfortunately, has not yet been determined.

One logical hypothesis emerges from the data presented here: that pollination in *Nypa* is accomplished by drosophilid flies as they move about, feeding and breeding in both male and female portions of the inflorescence. Though in my all-too-brief visit to the *Nypa* swamp I failed to capture a fly bearing pollen on a female flower, two facts are clear: (1) drosophilid flies were definitely seen on both male and female flowers, and (2) the flies carry significant amounts of pollen—a marked contrast with all previously known instances of drosophilid-palm flower association. The validity of the hypothesis is partly dependent on the proper identification of the larvae found in the flowers, but the adult drosophilids seem to be good pollen carriers in any case.

Summary

Among the palms for which careful observations have been made, there appear to be four general types of pollination strategy. The first is wind-pollination, which has long been known for the date palms (*Phoenix* spp.), and which has recently been demonstrated for the coryphoid genus *Thrinax* (Read 1967). It has also been frequently suggested for the coconut palm (*Cocos nucifera*), though there is considerable controversy about this (Menon and Pandalai 1958, p. 67). Some good evidence has also been presented for wind-pollination in the betel nut, *Areca catechu* (Murthy and Bavappa 1961), and the oil palm, *Elaeis guineensis* (Hartley 1967).

Asterogyne martiana (Schmid 1970a, b) and *Ptychosperma macarthurii* can be placed together in a second category, in which the flowers are pollinated by insects (flies or bees) that are alternately attracted to male and female flowers by nectar in both and by pollen in the male flowers. In these two palms considerable maturation of the flower buds takes place after the inflorescence emerges from its enclosing bracts. The buds are protected in *Ptychosperma* by the tough perianths, and in *Asterogyne* by being recessed in covered pits. The genus *Archontophoenix* (Skutch 1932) fits into this category with respect to the sequence of flowering, the presence of nectar, and the types of insect visitors. It differs, however, in that the flowers are mature and ready for anthesis when the enclosing bracts fall. All three genera are protandrous, with flowering staggered over many days.

The third category is represented by *Bactris* (Essig 1971) and *Hydriastele microspadix*. Here neither male nor female flowers produce nectar. The latter, in fact, are small and inconspicuous, seemingly without any inherent attraction for insects at all. The pollinating insects

(small beetles) are attracted instead to the soft, odoriferous male flowers, which stand unopened beside the receptive female flowers, and upon which they feed. Pollination occurs as the beetles move from an old male-flowering inflorescence to a new female-flowering one. The palms in this category are protogynous, with the female flowers simultaneously receptive as soon as the inflorescence emerges from the enclosing bracts, and the male flowers opening simultaneously 24 hours later.

A fourth type of pollination strategy is that suggested herein for *Nypa fruticans*. The thick flowering axes of the inflorescence serve as burrowing-feeding sites for immature insects (in this case, small flies). The emerging adults become covered with pollen, and some of them, in search of a new site for oviposition, carry the sticky pollen to a new inflorescence in which the female head is emerging.

The striking coordination and intricate timing involved in the phenology of some of these palms is dependent upon the specialized way in which their inflorescences develop. Development can be thought of in terms of three phases: initiation, maturation, and anthesis. In many simple racemes or panicles, such as found in many orchids, lilies, and such dicotyledons as lupines and delphiniums, the three phases occur sequentially along an axis. Flowers at the base of the axis may be past anthesis and forming fruit, while at the apex new flower buds are still being initiated.

In many palms, however, including all those described here, initiation of all the flowers on the inflorescence is completed very early and subsequent maturation of the buds is uniform. The flowers all reach full size and readiness for anthesis more or less at the same time. The pattern of male and female anthesis that follows this nearly simul-

taneous maturation of the buds is thus independent of the sequence of initiation and maturation that might dictate the sequence of anthesis in other sorts of inflorescences.

The implications of this for pollination biology are great, for this flexibility, especially when combined with the monoecious habit, has allowed the palms to develop a variety of flowering patterns in response to various potential pollinating agents. For example, suppression of the male flowers until after female receptivity results in protogyny, while suppression of the female flowers until after male anthesis results in protandry. The flowers of one sex may all open simultaneously, or they may be staggered over many days. Flowers may open randomly throughout the inflorescence, or they may progress in some orderly fashion.

Much interesting work remains to be done on the pollination of palms. Aside from *Thrinax*, little has been done with the mostly bisexual flowered Coryphoid group, though Dransfield (1972) has suggested "mess and soil" pollination for *Johannesteijsmannia*. We have no pollination information from lepidocaryoid, borassoid or phytelphantoid palms, other than the superficial observations of some early botanists. Some work has been done on palms of the arecoid line, but this vast group has really only barely been tapped.

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Addendum

The small curculionid beetles thought to pollinate *Hydriastele* have now been identified to the genus *Nodocnemus* Marshall (Erirhininae, Derelomini). This genus and the other members of the Derelomini are said to occur almost exclusively in palm flowers and are pantropical in distribution. This instance of apparent close co-evolution between palm flowers and a particular group of insects should provide the substance for very interesting further investigation.

I am grateful to R. T. Thompson of the British Museum of Natural History for providing the identification and ecological notes, and once again to G. C. Eickwort of Cornell University for assistance in getting the specimens identified.