Pollination of two species of *Zamia* in south Florida and its implication for the evolution of cycad strobili

PRISCILLA K.S. FAWCETT,* KNUT J. NORSTOG* AND ANDREW P. VOVIDES**

*Fairchild Tropical Garden, Miami FL, 33156 USA.
**Instituto de Ecologia, Xalapa, Veracruz, Mexico.

Abstract
The pollination biology of *Zamia* sheds new light on the general mode of pollination among most members of the Cycadales. A Mexican cycad, *Zamia furfuracea*, introduced into Florida many years ago, is effectively pollinated by a weevil, *Rhopalotria mollis*, inadvertently introduced along with the cycad. *Zamia pumila*, the native Florida cycad, displays a similar relationship with two beetles: the clavicorn beetle, *Pheresaonotha zonae* and *Rhopalotria slosani*, a snout weevil. *Pheresaonotha* is a destructive pollinator, laying eggs among the microsporangia of male cones. Both adults and larvae eat pollen but larvae also excavate male cone stalks, passing through about 20 workers in male cones, then drop out of the cone stalk, burrow into soil, pupate and complete metamorphosis. *Rhapalotria slosani* swarms on male cones, lays eggs in cone tissues and completes its life cycle within 30 days. It does not consume pollen but takes shelter in male cones, becomes dusted with pollen, visits female cones and pollinates the ovules.

Key words: *Rhopalotria mollis* - *Rhapalotria slosani* - *Zamia pumila* - *Zamia furfuracea* - *Pheresaonotha*.

Introduction
So entrenched is the concept of wind-pollination of cycads that even today it is not uncommon to read or hear that cycads are wind-pollinated plants, as are most other gymnosperms. Charles Chamberlain, the most highly respected student of cycads, declared in his book on gymnosperms (Chamberlain, 1935) that nothing in his experience had convinced him that cycads were anything but wind-pollinated. Yet, if one were asked to invent a strobilus which would be most unlikely to intercept airborne pollen, it is quite possible that one could not improve upon the strobilar design of females of all the genera and species of cycads with the exception of *Cycas*. *Cycas*, of course, does not possess a true, determinate strobilus and of all cycads seems to us to be somewhat compatible on a structural basis with a system of aerial pollen transport.

Fairchild Tropical Garden in Miami, Florida has an extensive collection of living cycads; all genera are represented and these include about 100 species. As one might suppose, a primary interest of the Garden is the propagation of these specimens and the dissemination of seeds, especially those of the more rare species. Unfortunately, most of the cycads in the collection do not reproduce themselves, even when male and female plants are very near each other. For example, the colorful female cones of *Encephalartos* ferox remain infertile even though male plants are producing pollen within a meter’s distance. Similar experiences also are encountered with other species of *Encephalartos*, as well as those of *Ceratozamia*, *Lepidozamia*, *Macrozamia* and *Microcycas*. *Dioon* and *Stangeria* sometimes exhibit low fertility in cultivation as do several species of *Cycas*. (We lack information on *Bowenia* and *Chigua* because of limited cone production.) It may be added that the low fertility in cultivated cycads is common in botanical gardens elsewhere; many specimens of *Encephalartos* in African gardens require artificial pollination if seeds are desired (Cynthia Giddy, personal communication). On the other hand, specimens of *Zamia* from throughout the Caribbean are always fertile in cultivation in Florida, as is the Mexican *Zamia furfuracea*.

Experiences such as these lead one to believe that agents other than air currents are responsible for the pollination of most, if not all, cycads. Indeed, when one examines immature female strobili of a cycad such as the Florida cycad *Zamia pumila* L., one is struck by the fact that from earliest inception, right up to pollen receptivity, the ovules are hidden behind a barrier of sporophyll endings ("shields"). Except for *Cycas*, this is the case with ovules and cones of all the genera. In these cycads, at the time of pollination, access to the cone’s interior is provided by slight separations of the mega-sporophylls, but even so, within the cone all of the ovules are oriented with their micropyles toward the cone axis—scarcely an arrangement one would envision as facilitating impact of wind-borne pollen grains upon micropyles, but one that is quite consistent with insect pollination.

Cycad Toxicity and Pollination
Because cycads are well-known for their content of compounds that are toxic to animals, we may
question how predatory animals, especially pollinators which receive nutritive rewards from cycads, achieve and maintain immunity to those poisons. The principle cycad poisons are several glycosides, commonly referred to as cycasin, neocycasin and macrozamin (Moretti et al., 1983; Rothschild et al., 1986), and a non-protein amino acid, B-N-methylamino-L-alanine, commonly known as BMAA (Vega & Bell, 1967; Spencer et al., 1987). Recently, we have found evidence that cycad poisons probably are sequestered in idioblasts of male- and female cone-parenchyma tissue and our studies show that idioblasts of Zamia contain BMAA. There also is indirect evidence that in addition they may contain macrozamin (Norstog et al., in review). There is some question whether or not beetles that pollinate Zamia are sensitive to cycad poisons but we have uncovered evidence that weevils involved in pollinating two species of Zamia avoid intoxication when they feed on cycad parenchyma by a voiding undigested idioblasts in their dung.

Pollination of Zamia furfuracea

For some years we have studied the pollination biology of the Mexican cycad, Zamia furfuracea L. fil. growing in considerable numbers at Fairchild Tropical Garden as well as elsewhere in southern Florida. As related above, this cycad is perfectly fertile in cultivation owing to a small snout weevil, Rhopalotria mollis Sharp (Fig. 1), which is not only an obligate pollinator of Z. furfuracea, but is itself completely dependent upon the cycad for food, a brood place, and for long-term dormancy (Norstog & and Stevenson, 1980; Norstog et al., 1986; Norstog & Fawcett, 1989). We suspect that similar though more complex insect-plant interactions occur in nature, and field studies of the pollination of Z. furfuracea now underway show that R. mollis, or a very similar species, is present also in wild plants in Veracruz, Mexico (Fig. 2). In addition, an undetermined species of Pharaonotha is also present (Fig. 2). We have no reason to doubt that they pollinate Z. furfuracea in nature in the same manner as we have described for specimens at Fairchild Tropical Garden.

In essence, weevils are attracted to male cones of Z. furfuracea at about the time microsporangia are mature and just before they begin to dehisce (Fig. 3). At about this time also both male and female cones become aromatic and warm, and a few of the sporophylls begin to loosen and separate. The process is general one among cycads and functions both to

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Fig. 1. Rhopalotria mollis, a pollinator of Zamia furfuracea. x8.0. a, egg and hatching larva. b, fully grown larva. c, adult male. d, adult female. e, male pupa. f, female pupa.

Fig. 2. Pollinators of Zamia furfuracea in Mexico. x8.0. a, female Rhopalotria sp. b, male Rhopalotria sp. c, Pharaonotha sp. d, ventral view of female Rhopalotria sp. e, ventral view of male Rhopalotria sp. f, ventral view of Pharaonotha sp.
open male and female cones and volatilise fragrances (Tang et al., 1987).

The weevils that start the annual breeding cycle on *Z. furfuracea* emerge from long-dormant larvae that "winter" in debris at the base of the cycads they later infest and appear at about the time male cones approach maturity. The first breeding cycle of the weevil is short, a week or so, and involves just a few individuals, but increasingly large number of offspring in succeeding generations soon follow.

Swarming weevils exhibit cone preferences, selecting only one or two cones from among as many as 15-20, and remaining upon the chosen cone 1-3 days before abandoning it (Fig. 3a). (Male cones of *Z. furfuracea* become mature sequentially; the cones upon which swarming occur are those in which sporophyll separation, which gives access to the cone's interior, will occur within about 24-48 hours.) We think that in these aspects, both *Z. pumila* and *Z. furfuracea* give evidence of evolution of morphological and physiological characters that enhance effective pollination by insects. In fact, presence on a single plant of numerous small pollen cones ripening sequentially, constitutes evidence that insect pollination is the mode of reproduction of both of these as well as other species.
Rhopalotria mollis is an excellent flyer and males and females are attracted to male cones where they mate and probe for food at the end of microsporophylls in which females lay eggs (Figs. 1: 3b, c). Within a day or so, the eggs hatch, producing larvae which eat their way inwardly from the tip of a microsporophyll (Fig. 3d). As is typical of weevils, the larvae are legless grubs (Fig. 1b), and are quite active.

Larval stages: Although up to six eggs may be laid in one microsporophyll, subsequently each sporophyll will contain only one large larva and, later on, a single pupa or a recently metamorphosed adult (Fig. 3d, e). As the larvae eat away the sporophyll tissue, they meet, and one eats the other. With the possible exception of cannibalism, larvae feed almost exclusively on parenchyma; the larval gut is packed with material which stains lightly for starch with I₂ KI but intensely with periodic acid Schiff reagent (PAS), possibly indicating the presence of partially digested carbohydrate material. Also included are particles which stain heavily with ninhydrin-Schiff reagent, suggesting presence of amino acids, possibly BMAA.

About 3-4 days after hatching, a larva constructs a chamber in a microsporophyll stalk within which it pupates (Fig. 3e, f), its head oriented toward the outer end of the microsporophyll. The pupal case is constructed of fecal matter so the larva and later pupa are housed within a tough, cylindrical capsule. The adult emerges after metamorphosis, usually by boring out through the tip of the sporophyll (Fig. 3g); the entire process is completed in 7-9 days, and it is possible that during the season several generations of weevils may result from an initial mating.

Pollination: As described for Z. pumila, weevils in Z. furfuracea become covered with pollen while sheltering and feeding in male cones, but do not feed on pollen. A single cone at this stage may contain more than 100 weevils. At this stage visitation to female cones takes place (Fig. 3k). However, female cones are not fed upon, although interior surfaces sometimes exhibit healed scars of superficial wounds which may have been made by weevils. Weevil pollination of this cycad is very efficient and cone fertility may approach 100% (Norstog et al., 1986; Norstog & Fawcett, 1989).

Dormancy: A physiological change in microsporophylls and at least some larvae occurs toward the end of the breeding season. Microsporophyll edges become chlorophyllous and full of idioblasts; later instar larvae develop thick, opaque cuticles, become fat and waxy and build very thick-walled pupal cases in which they go into diapause until the next season (Fig. 3h-j). Diapause, which is a type of dormancy consisting in an arrested state of development, can last for two or more years. This, we believe, accounts for the long-term efficiency of this relationship between the cycad and its insect pollinator.

Because weevils feed on parenchyma tissue which contains toxin-containing idioblasts, and because idioblasts and their toxins pass undigested through the weevil's digestive tract and are excreted in the dung, the pupal cases, which are composed largely of dung, probably contain a high proportion of idioblast toxins, among them BMAA and macrozamin (Norstog et al., in press). Both compounds have been found in weevils of all stages of metamorphosis (Vovides et al., in review).

Pollination of Zamia pumila

In South Florida, the cones of Zamia pumila L. often harbour two species of beetles which have been

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Fig. 4. Rhopalotria siossoni, the pollinator of Zamia pumila. x8.0.

a, egg; b, hatching larva; c, nearly full-grown larva; d, female pupa; e, male pupa; f, female adult; g, male adult.
Fig. 5. Basic life cycle of *Rhopalostria slossonae* in *Zamia pumila* (diagrammatic). a, adult weevils visit an attractive male cone. b, they feed on the tissue at the ends of the sporophylls, mate and lay their eggs, then go inside the cones to continue feeding at the base of the sporophylls until another male cone is ready for visits. c, the eggs hatch and the larvae eat their way towards the base of the sporophyll, and when they meet, one of them eats the other. d, only one larva generally survives to build a pupal case from fecal matter. e, after 2-3 days, the larva metamorphoses into a pupa. f, next day, the mature *Rhopalostria* chews its way out of the pupal case and through the end of the sporophyll, then flies to an attractive male cone (a) to feed and breed. g, pollination takes place when some individuals or leaving a male cone in search of a new feeding and feeding site, enter a receptive female cone. There they try to feed, but find no food or egg-laying site. Some become trapped inside the cone, but probably many escape. h-j, alternate, late-season route. h, weevils avoid chlorophyllous areas in ends of microsporophylls, feeding, laying eggs and pupating in its sides and base. i, cone deteriorates, freeing dormant larva in thick-walled pupal case. j, pupal case containing larva in diapause, as present in soil at base of male plant.
shown to effectively pollinate female cones of the species (Tang, 1987). Male cones provide an egg laying site, as well as food for both the adults and the larvae of Rhopalotria slossoni Schaeffer, a weevil, and Pharaonotha zamiæ Blake, a pollen-eating clavicorn beetle (Figs. 4-6). Both beetles are able to live only in the male cones of the native Florida Z. pumila or closely related Caribbean forms of this species.

**Life cycle of Rhopalotria slossoni**

The life cycle of *R. slossoni* closely resembles that of *R. mollis*, the pollinator of *Z. furfuracea* (Norstog & Fawcett, 1989), but *R. slossoni* differs from *R. mollis* in that it is less active during the day. During their congregational invasion of male cones of *Z. pumila* the weevils mate, feed on the starchy microsporophyll tissue, and lay their eggs in holes which they make when they feed (Fig. 5a, b). The front legs of the males have enlarged muscular femurs with which they are able to fight off other males when mating (Fig. 4). The smaller males lack these powerful front legs, but manage to mate by moving in quickly, often when two larger males are distracted by fighting with each other!

**Feeding behaviour** : After feeding and mating on the outside of the cone, both sexes go inside, entering between the loose scales at the base, and continue feeding on the bases of the sporophylls while waiting until another male cone is ready. Meanwhile, the eggs hatch and the larvae feed on the sporophyll tissue making their way towards the stalk (Fig. 5c). When the larvae meet, one of them eats the other. In *R. slossoni* up to four eggs can be laid in a sporophyll but only one larva survives to build a pupal case from fecal material (Fig. 5d, e). The pupal cases contain a high proportion of undigested storage cells or idioblasts (Norstog et al., in press), and probably include a neurotoxin (BMAA) (Spencer et al., 1987), as well as cycasin a demonstrated mutagen for Droso phila (Teas & Dyson, 1967). After about a day spent as a pupa the weevil emerges as a young adult and escapes by chewing through the end of the microsporophyll without damaging any of the microsporangia (Fig. 5i). The entire life cycle is completed in 7-9 days.

As was the case in pollination of *Z. furfuracea*, some of the weevils go to the female cones (Fig. 5g), which also become warm and aromatic when they are ready for pollination. The tissue of the female cone has almost no starch, and contains idioblast cells that have released their contents (toxins?) into the cone tissue. We find no evidence of feeding by weevils, although there are nibble marks where they have tried to feed. We think this may be the result of diffusion of poison throughout the female cone tissues making them unpalatable to predatory insects including the two pollinating species. A weevil that has been waiting inside a male cone picks up a lot of pollen, particularly if *Pharaonotha* is also present as is discussed later on in this account. The female cone of *Z. pumila* opens along irregular cracks, so that once inside a weevil has to find its way out again in order to escape. It may be pointed out here that female-cone opening in *Z. furfuracea* seems more highly specialized for insect pollination than does that of *Z. pumila*. In *Z. furfuracea* the cone opening is generally a single vertical crack between adjacent rows of cone scales (Fig. 3k), and it is possible that this species is more highly adapted for insect pollination than *Z. pumila*.

**Dormancy** : At the end of the cycad’s reproductive season there is a change in both the behaviour of the weevils and in the nature of the sporophyll tissue of the male cone, as also occurs in *Z. furfuracea* (Fig. 3). The tissue at the ends of the sporophylls becomes greenish and acquires a preponderance of idioblast cells, as well as far less starch. The green tissue is to some extent avoided by feeding and egg-laying weevils (Fig. 5, h), only very few eggs are laid at the ends of the sporophylls; then, for want of an egg-laying site, weevils begin to lay in the sides and bases of sporophylls. The larvae eat their way through the sporophyll tissue as before, but some larvae become fat and waxy and build very thick pupal cases in which they go into diapause until the next season (Fig. 5i, j). Others go rapidly through metamorphosis and emerge as adults in a few days. Diapause, a type of dormancy consisting in an arrested state of development, may last for two or more years.

At the end of the reproductive season of *Z. pumila*, its male cones containing larvae in diapause become fragmented, mostly because the sporophylls and cone axes have been completely eaten away by larvae of both *R. slossoni* and a second pollinator, *Pharaonotha zamiæ*. Eventually the sporophylls rot away completely, so that only the pupal cases containing larvae in diapause remain in the soil, looking like little nearly black, cylindrical boxes (Fig. 5i). We think that the year-to-year continuity of successful pollination of *Z. pumila* depends largely on the wellbeing of these dormant pupae.
Life cycle of *Pharaxonotha zamiae*

We are not sure where the individuals of *Pharaxonotha zamiae* Blake that first invade the cones of *Z. pumila* come from. We suspect they overwinter in soil at the base of plants of *Z. pumila*. However, when male cones begin to become mature, *P. zamiae* goes to them when the pollen is mature. There they feed and lay eggs between the microsporangia, and sometimes inside a dehisced sporangium. We do not know where these beetles mate. It is possible that they mate underground, but we assume that they mate in the male cones when they go there to feed and lay their eggs.

The eggs are very large in proportion to the size of the female, which carries up to six eggs at various stages of maturity at a time. The adults feed only on pollen, and when present in numbers, there is pollen everywhere, so that all of the insects, including *R. slossoni*, which happen to be in the cone become covered with it. Otherwise, unless the sporangia of *Z. pumila* are disturbed, the pollen tends to remain in the microsporangia in little sticky clumps.

*Larval stages*: The oval eggs are greyish white and translucent, and about twice as long as they are wide and hatch within hours (Figs. 6a, b; 7b). The larvae eat their way out of the eggs and begin feeding on pollen. All of the larval instars look much alike; each body segment has a pair of light-brown patches on the dorsal side, so that the larvae seem to be striped (Fig. 6c). They have long stiff hairs all over their bodies, and all larval instars have simple compound eyes consisting of five ommatidia, and three pairs of soft legs, which are quite well developed and functional.

*Feeding behaviour*: It is only the first larval instars that eat pollen, and in fact there is very little pollen left in the cone after the first two instars (Fig. 7c). A larva that in ready to moult eats a hole in the back of one of the sporophylls and crawls inside, later emerging in the next instar (Fig. 7d, e). The later instars eat only tissue, entering the cone axis through a microsporophyll, and eating their way down through the cone into the stalk, which eventually becomes completely hollow (Fig. 7f). They do not tunnel into the stem of the plant. As both *R. slossoni* in all feeding instars, and the later larval instars of *P. zamiae* eat only toxin-containing cone parenchyma, the latter must also have a way of avoiding the toxins. At present, we have no information on the possible toxicity of *Zamia* pollen, but that of *Cycas circinalis* contains both BMAA and cycasin (Leonard Kurland, personal communication). When they have finished feeding and are ready to leave the cone, they eat a little hole in the stalk and drop down to the ground where they burrow into the soil (Fig. 7g).

*Pupation*: After several days, larvae become pupae and remain in this stage for about 4-7 days (Fig. 7h). There is no pupal case or cocoon. Our observations were made late in the season, when there were few new cones present. At this time the young adults instead of flying away to repeat the breeding cycle, burrowed down into the soil, and when dug up, seemed to have no inclination to leave, but only to hide (Fig. 7i). It is possible that late-season adults remain in the soil until the following season, but evidence is lacking.

*Pollination*: We have found *Pharaxonotha* in female cones of *Z. pumila* in southern Florida, and we assume they blunder into them in error as appears to be the case with *Rhopalotria* (Fig. 7j). In northern Florida
Fig. 7. Life cycle of *Pharaxonetha zamiiae* in *Zamia pumila* (diagrammatic). a, young adults leave the soil, and older adults leave spent male cones of *Zamia pumila* in search of a male cone in which the sporangia are beginning to dehisce. b, in the cone the beetles feed on the pollen and lay their eggs (arrows) between the sporangia and sometimes in sporangia from which the pollen has been eaten. c, the eggs hatch and the larvae feed on pollen. Often little holes in the clumps of pollen can be seen where a larva is feeding. d, when the larvae are ready to moult, they eat a little hole in the sporophyll into which they go back to feeding on pollen. Only the early instars feed on pollen, and by the third instar, there isn’t much pollen left. e, the later larval instars eat only tissue. They enter the main axis through a sporophyll and eat their way throughout the axis into the cone stalk. f, they continue feeding until the cone axis and stalk are hollowed out, but they do not eat into the stem tuber. g, when the larvae are ready to metamorphose, they eat a hole in the stalk and drop to the ground. h, the larvae burrow into the soil and pupate. i, after 4-7 days the mature beetles leave the soil in search of a cone to feed and breed in. j, pollination takes place when some individuals enter a female cone, instead of a male cone, as is the case with *Rhopalotria*. 
the other species of Phalaxonotha appears to be the only pollinator of Zamia. Rhopalotria may have been there originally, but could have become extinct as a result of the "coontie" industry, coontie being the Indian name for the Florida Zamia. At the turn of the century, white pioneers harvested coontie stem-tubers, from which they extracted the starch, exporting it to the north under the name of "arrowroot." We have seen references to a blue and orange Rhopalotria which may be extinct, but this could also be a R. slossoni preserved in some unorthodox substance.

Interaction of Rhopalotria and Phalaxonotha: Both P. zamiae, and R. slossoni are often found together in the same male cone; however, there is no conflict because Rhopalotria prefers the sporophylls at the base of the cone while Phalaxonotha larvae generally prefer the sporophylls at the tip of the cone. The larvae of Phalaxonotha are not in any danger of being cannibalized by those of Rhopalotria because of their stout bristles and their three pairs of active legs. Furthermore, the eggs of Phalaxonotha are laid about a day after those of Rhopalotria, so that the larvae are already starting to pupate by the time that the Phalaxonotha larvae are ready to moult and begin the second instar.

Cycad pollination: Evolutionary implications

Although we think that insects are the primary agents of pollination in the two species of Zamia described above, allegations of wind transport of cycad pollen are so common that we cannot ignore the possibility that it occurs in at least some species.

Niklas & Norstog (1984) tested the "aerodynamics" of cycad cones by placing them in a wind tunnel and blowing cycad pollen past them. The results of these experiments suggested that pollen flow around certain cones is such that pollen tends to be preferentially deposited upon parts of the cone, and, depending upon the cone's orientation, a vis a vis direction of pollen flow, impacted upon certain receptive areas of the cone (Fig. 3k). However, it was not shown that airborne pollen impacted directly upon ovules. The female cone of Z. furfuracea becomes pollen receptive by means of a vertical crack between adjacent orthostichies of megasporophylls (Fig. 3k), and air currents in the wind tunnel tended to convey pollen toward this opening when the opposite side of the cone faced into the direction from which pollen came. Even so, the number of pollen grains impacting on ovules was very low. In Cycas rumphii, pollen tended to impact upon the lamina of megasporophylls and it was suggested that rain or even heavy dew could carry pollen in the direction of the ovules.

During the course of our studies of pollination in Z. furfuracea and Z. pumila, attempts were made to capture wind-borne pollen upon greased microscope slides attached near receptive female cones. Preliminary experiments with Z. furfuracea suggested that if every pollen grain had impacted directly upon a micropyle (a highly unlikely occurrence), fertility still would not have exceeded 22%. Actually, fertility approached 100% (Norstog, unpubl. observ.) In 1988, we made a similar study in a semi-natural (disturbed) pine-palmetto habitat in which Z. pumila was present. Again, greased microscope slides were placed adjacent to pollen-receptive female cones. The greased surface of each slide faced the nearest pollen-producing male plant and slides were monitored for 15-30 days (somewhat longer than the receptive period of female cones). The results, presented in Table 1, show that deposition of cycad pollen was minimal in comparison with pine pollen and that of other plants. Probably in sheltered locations very little pollen is carried to female cones of Zamia by air currents.

### Table 1. Aerial pollen on the vicinity of female cones of Zamia pumila

<table>
<thead>
<tr>
<th>Site</th>
<th>Days</th>
<th>Distance</th>
<th>Pollen per 4 cm² of greased slide</th>
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<tr>
<td>Cycad</td>
<td>Pine</td>
<td>Other</td>
<td></td>
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<tr>
<td>3</td>
<td>15</td>
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</tr>
<tr>
<td>12</td>
<td>36</td>
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</table>

1 Number of days slide was exposed to ambient conditions.

Some years ago, the then superintendent of Fairchild Garden, Mr. Stanley Keim, asked us for help with pollination of Dioon edule and D. spinulosum. He was unable to determine the period of pollen receptivity of female cones. Unlike cones of other cycads in which the megasporophylls separate slightly at pollination, nothing like this was observed in Dioon. Other cycads, Microcycas for example, could be manually pollinated by inserting the mouth of a small bellows between the slightly separated megasporophylls and thereby blowing pollen into the cone. But in Dioon we saw no natural opening into the cone and so we suggested cutting off its top and
blowing pollen through the new opening. It proved to be quite successful. Then, several years later, we saw that the female cones of *Dioon* were, in fact, briefly open at the time of pollination. A whorl of sterile mega-sporophylls at the base of the cone become reflexed and provide the sole access to the cone’s interior (Fig. 8).

In the wind-tunnel experiments discussed above, most interesting results were obtained when a female cone of *Dioon edule* was mounted in the wind tunnel. The female cones of *Dioon* are completely clothed by a dense blanket of hair throughout the pollination period (Fig. 8). This layer prevents entry of airborne pollen throughout the period when ovules are pollen receptive. When a receptive cone of *D. edule* was placed in a wind tunnel and a stream of pollen blown past it, the air currents around the cone were such as to "dump" pollen on the surfaces of these sterile sporophylls (Niklas & Norstog, 1984). They differ from fertile megasporophylls in having glabrous, bright yellow-green upper surfaces. Because it seemed unlikely that pollen would migrate up into the cone of itself, a combination of wind and insect pollen transport was hypothesised for pollination of *Dioon* in nature (op. cit.).

If one dissects a female cone of *Dioon*, one is struck by its resemblance to an old-fashioned fly trap in which a funnel of wire screening is inverted over an attractive bait. After feeding, flies and other insects tend to move upward, entering the funnel and, unable to find the open end, remain and die in the trap.

At the time of pollination, cones of most cycads become warm and fragrant (Tang et al., 1987). To us, *Dioon* cones seem to emit a fragrance resembling that of butyric acid. It was suggested by Niklas & Norstog (1984) that in some way the sterile sporophylls of *Dioon* acted as a kind of "landing platform" for pollinating insects and that these would wander into the interior of the cone, brushing pollen against ovules as they attempted to find an exit. Probably a fragrance attracts pollinating insects to both male and female *Dioon* cones. Entering the female cone via the basal sporophylls, insects move upward within the cone (Fig. 8). The covering of feathery hairs has two functions: to protect the cone’s interior and to impede the departure of polleniferous insects that have entered the cone at the bottom. Another function may be that it permits penetration of diffuse light—it is well known that insects move toward a unidirectional light source. The probable consequence is that insects wander upwardly within the cone, brushing off pollen on its inner surfaces, including those of ovules, and eventually emerge by parting a loose aggregation of sterile but piliferous sporophylls at the top (Fig. 8). Although the details of the *Dioon* pollination system have not been worked out completely, cones of *D. califanoi* are known to harbour a species of snout weevil, *Rhopalotria*

![Fig. 8. Longitudinal section of a female cone of *Dioon edule* at the time of pollination (diagrammatic). Pollen is deposited upon a basal whorl of sterile sporophylls by air currents. Visiting insects (probably a species of *Rhopalotria*) are attracted to the cone by fragrances, landing on the basal sporophylls, picking up pollen (or bringing it with them), and moving upward in the cone. As they wander around in a generally upward direction, they rub off pollen on ovules. Eventually, attracted toward dim light penetrating the rather dense outer layers of feathery epidermal trichomes, they escape. Note that the sporophylls at the top of the cone are sterile, as are those at the bottom. Some license was taken in making the drawing; the cone actually is totally blanketed by a matted covering of hairs, which airborne pollen cannot penetrate. (At Fairchild Tropical Garden, *Dioon* cones are manually pollinated by cutting out the topmost, sterile sporophylls and injecting pollen via the new opening. The remaining, fertile sporophylls soon close the gap and the ovules remain protected as they develop.) The scheme is quite hypothetical but seems consistent with what now is known about the morphology and ecology of the cycad and its probable pollinators.]
biclor, and these are thought to be pollen vectors for this and possibly other species of Dioon (Vovides, 1990). The slight fertility of Dioon in the Garden could have resulted from random insect visits—ants, possibly and their further transport of pollen within the cone.

Not much is known about the structural details of female cones of fossil cycads. The Cycas-like megasporophylls of a Lower Permian cycad, Crozozamia chinensis, apparently were borne loosely on a determinate strobilus (Gao Zhifeng & Thomas, 1989). The arrangement probably facilitated wind pollination. Beania gracilis and B. mamayii, of Jurassic age, had female cones equipped with Zamia-like megasporophylls (Harris, in Pant, 1973). These however, seem to have been more loosely arranged and widely spaced than those of modern zamias. Their petaloid megasporophylls bore adaxially oriented ovules much like those of Zamia and in that respect they seem less likely to have been efficiently wind pollinated. They may actually represent evolution of a morphology in transition from wind pollination to insect pollination. (It may or may not be relevant that when a "pickled" cone of Zamia accidentally became dried out, it resembled a Beania cone, with rather widely separated megasporophylls [Dennis Stevenson, personal communication]). We think it quite likely that "closed" cones of the Zamia type, and indeed of most species of cycads, probably have had a long coevolutionary history in association with insect pollinators. Certainly the highly specialized female cone of Dioon must have had such a history.

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References


