Beetle pollination of two species of *Zamia* : evolutionary and ecological considerations

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Two species of cycads in Florida are invariably pollinated by beetles. The native Florida *Zamia pumila* L. is pollinated by a snout weevil, *Rhopalotria slossoni* Schaeffer, and a clavicorn beetle, *Pharaxonotha zamiae* Blake. An introduced cycad, *Z. furfuracea* L. fil., is pollinated by the snout weevil, *R. mollis* Sharp, apparently introduced from Mexico along with its host. Observations and experiments show that zamias are dependent upon pollinating beetles for their reproduction, and, in turn, the pollinating insects are dependent upon the cycads for brood places, food and shelter. The two cycads have evolved similar "rewards" which function as pollinator attractants. The importance of these coevolutionary inter-relationships for the ecology and conservation of these cycad species is unquestionable. Neither the insects nor the cycads are separately capable of long-term survival in nature, and unless both are protected and conserved, wild populations of *Zamia* are in jeopardy.

Key-words—Evolution, Ecology, Cycads, *Zamia*, Pollination.

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सारॉंश

ज़ेमिया की वो जातियों क्र भृंग परागण : वैकासिक एवं पारिस्थितिक महत्व

नुट जे० नॉर्सटॉग, प्रिसिला के० एस० फ़ॉसॅट एवं एन्ड्रिव पी० वोवाइड्स

फ्लोरिडा में साइकेडों की जातियों में भृंगुओं द्वारा परागण होता है। इनमें **ज़ेमिया प्यूमिला** एल० में प्रोथ घुन, **रोपेलोट्रिआ स्लॉसनी शैफ़र** एवं **फेरेक्सोनोथा ज़ेमी** ब्लेक नामक एक घुन द्वारा परागण होता है। मेक्सिको में पोषी के साथ-साथ अन्तर्वेशित **ज़े० फ़रफ़ुरेसिआ** एल० फ़िल० में **रो० मॉलिस** शार्प नामक प्रोथ घुन द्वारा परागण होता है। प्रेक्षणों एवं प्रयोगों से व्यक्त होता है कि **ज़ेमिया** अपने प्रजनन हेतु परागणी घुनों पर निर्भर करता है तथा परागणी कीट भी अपने अंडों के लिए स्थान एवं भोजन तथा आवास के लिए साइकेड पौधों पर आश्रित रहते हैं। उक्त दोनों साइकेडी पौधे एक ही प्रकार से विकसित हैं तथा परागण हेतु कीटों को अपनी ओर आकर्षित करते हैं। पारिस्थतिकी एवं संरक्षण हेतु इन दो साइकेडी जातियों के सहविकासीय अन्तरसम्बन्ध अत्याधिक महत्वपूर्ण हैं। एक दूसरे के बिना न तो ये कीट ही और न ये जातियाँ ही प्रकृति में अधिक समय तक जीवित रह सकते हैं और जब तक इन दोनों को उचित संरक्षण नहीं किया जाता, जंगली **ज़ेमिया** के पौधों का जीवन खतरे में है।

ALTHOUGH some early reports (Rattray, 1913; Baird, 1938) suggested the possibility that at least some cycads were pollinated by insects, it is only in recent years that this concept has gained any wide acceptance (Norstog, Stevenson & Niklas, 1986; Norstog, 1987; Tang, 1987; Norstog & Fawcett, 1989). Because cycads are well-known for their content of compounds that are toxic to animals, we may question how predatory animals, especially pollinators that receive nutritive rewards from cycads, achieve and maintain immunity to those poisons. The principle cycad toxins are several glycosides, commonly referred to as cycasin, neocycasin, and macrozamin (Moretti, Sabato & Siniscalco Gigliano, 1983; Rothschild, Nash & Bell, 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 toxins 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 they may in addition contain macrozamin (Vovides *et al.*, in Press). There is some question whether or not beetles that pollinate

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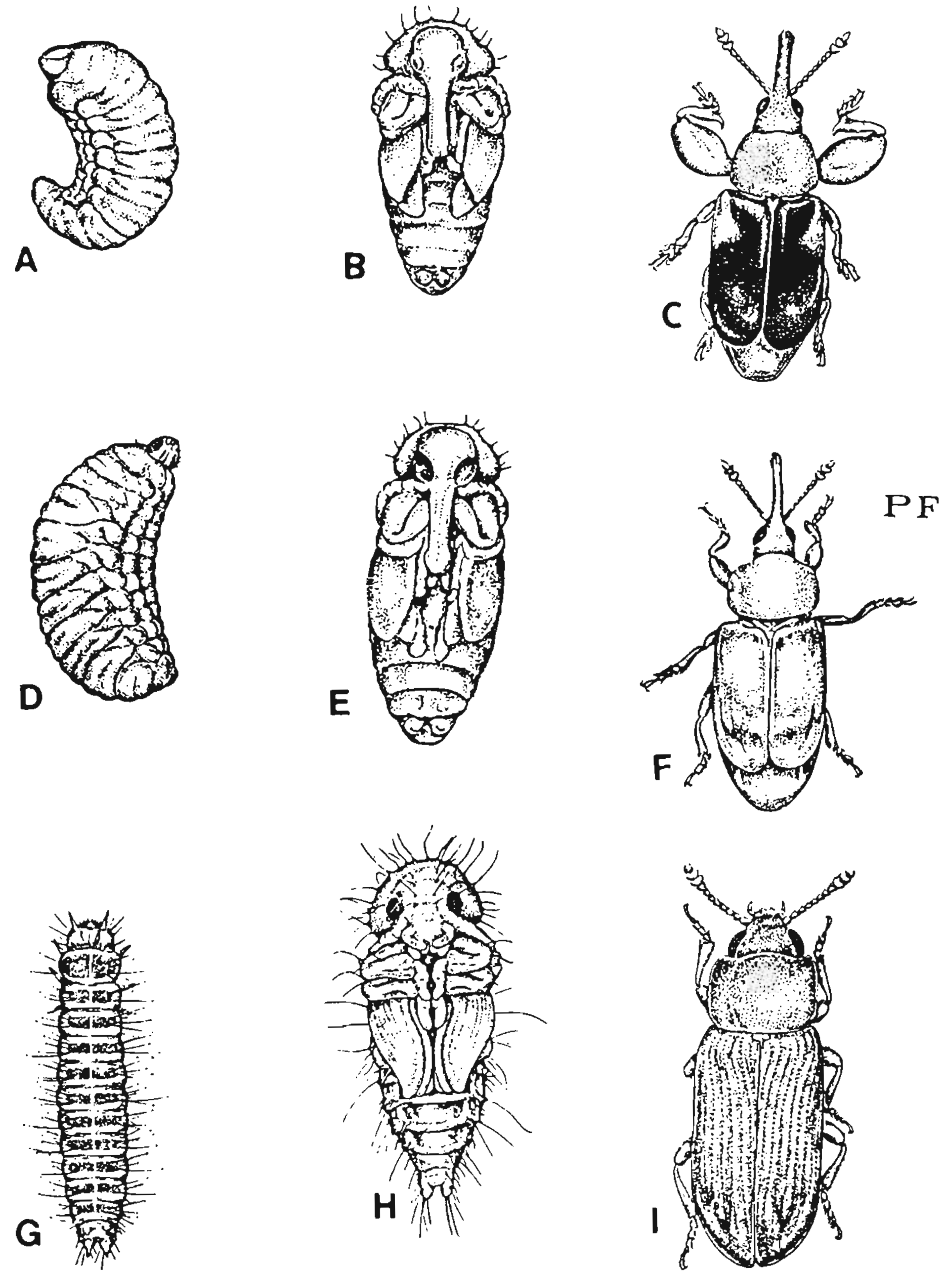


Text-figure 1—Beetle pollinators of *Zamia*. **A, B, C,** larva, pupa and adult male, respectively, of *Rhopalotria slossoni*, a pollinator of *Zamia pumila*, × 35. **D, E, F,** larva, pupa, adult female, respectively, of *R. mollis*, a pollinator of *Z. furfuracea*, × 35. **G, H, I,** larva, pupa, adult, respectively, of *Pharaxonotha zamiae*, a pollinator of *Z. pumila*, × 35.

Zamia are immune to cycad toxins but we have uncovered evidence that weevils involved in pollinating two species of *Zamia* avoid intoxication when they feed on cycad parenchyma by voiding undigested idioblasts in their dung.

The native Florida cycad, *Zamia pumila* L., is pollinated by two species of beetles (Text-figure 1 C, I). *Rhopalotria slossoni* Schaeffer, a snout weevil, and a clavicorn beetle, *Pharaxonotha zamiae* Blake. The former does not consume pollen but does shelter in male cones, becomes dusted with pollen, visits female cones and pollinates the ovules. *Pharaxonotha* is a destructive pollinator, laying eggs and feeding among the microsporangia of male cones, and in the process also becomes dusted with pollen which it transports to female cones. 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.

Zamia furfuracea L. fil., a cycad of Mexican origin, is pollinated by another host-specific weevil, *Rhopalotria mollis* Sharp (Text-figure 1F), which swarms upon male cones, where mating, feeding, and oviposition occur (Norstog & Fawcett, 1989).

POLLINATION OF *ZAMIA PUMILA*

Life cycle of *Rhopalotria slossoni*

The life cycle of *R. slossoni* is similar to that we have described for *R. mollis*, a snout weevil which is the pollinator of *Z. furfuracea* (Norstog & Fawcett, 1989). *Rhopalotria slossoni* conforms to this pattern rather closely, but it differs from *R. mollis* in that it is less active during the day. During its congregational invasion of male cones of *Z. pumila* the weevils mate, feed on the starchy sporophyll tissue, and lay their eggs in holes which they make when they feed. The front legs of most of the males have enlarged and muscular femurs with which they are able to fight off other males when mating (Text-figure 1C) 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! Females superficially resemble males but lack inflated forelegs and have longer snouts.

Feeding behaviour—After feeding and mating on the outside of the male cone, both sexes go inside, entering between the loose scales at the base, and continue feeding on the bases of the microsporophylls while waiting until another male cone is ready (Text-figure 2a-d). Microscopically, it can be observed that microsporophyll tissues (parenchyma and epidermis) include a type of storage cell, or idioblast. Meanwhile, the eggs hatch and the larvae (Text-figure 1A) feed on the sporophyll tissue making their way towards the stalk (Text-figure 2e, f). 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 pupa case from dung (Text-figure 2g). The pupa case is built from the inside, starting at the bottom. The larva then becomes a pupa (Text-figure 1A, B) which completes metamorphosis and then leaves the pupa case by chewing it's way out, emerging through the tip of the sporophyll (Text-figure 2h, i).

Pollination—Some of the weevils go to the female cones (Text-figure 2c), which become warm and aromatic when they are ready for pollination. The tissues of the female cone have little 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 postulate that diffusion of poison throughout the female cone tissues makes them unpalatable or even poisonous to predatory insects including the two pollinating species.

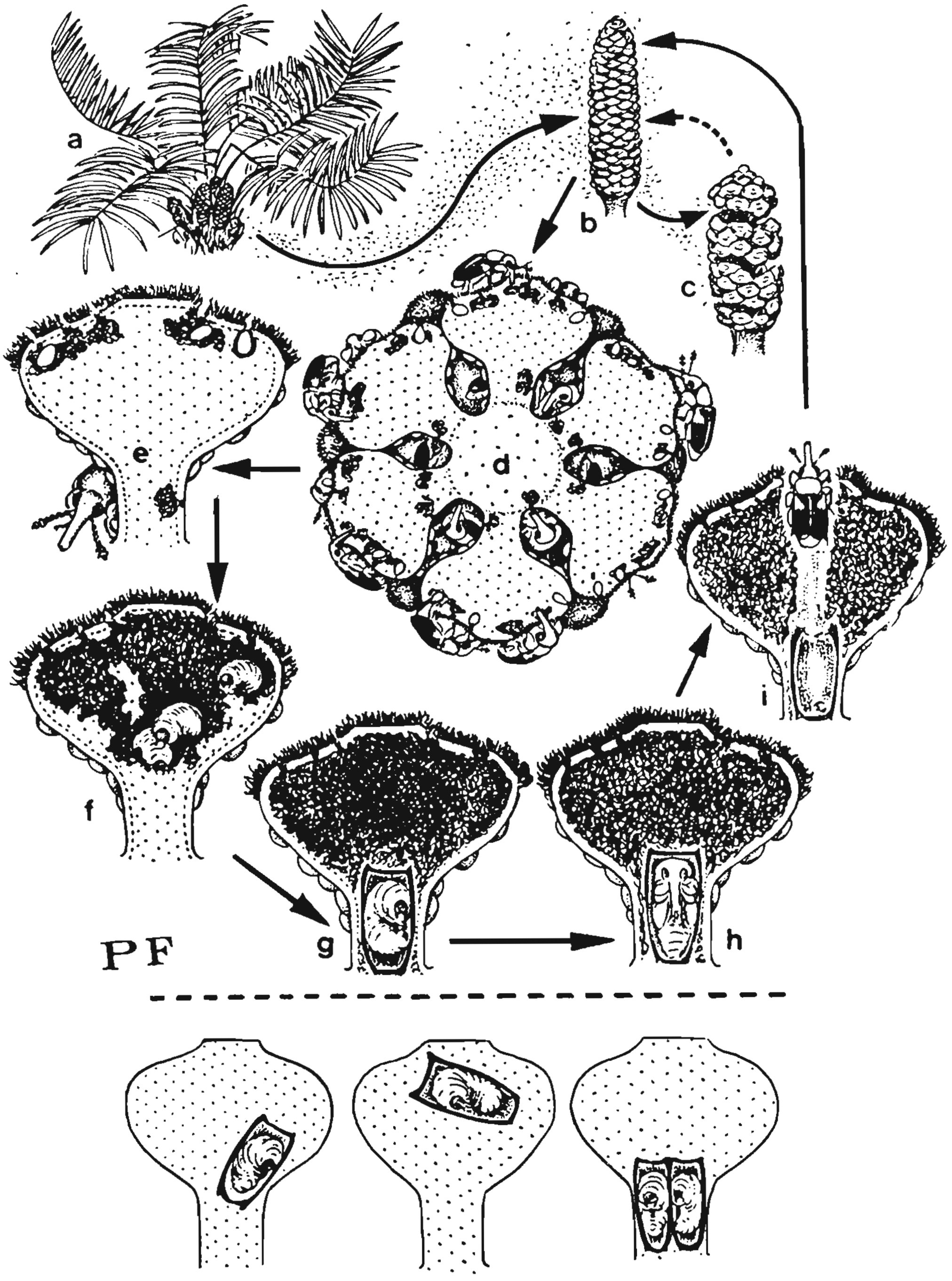
A weevil that has been waiting inside a male cone picks up a lot of pollen, particularly if *Pharaxonotha* is also present as we will discuss later. The female cone of *Z. pumila* opens along irregular cracks, so that once inside a weevil has to find it's way out again in order to escape (Text-figure 2c). 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 megasporophylls (Norstog & Fawcett, 1989) and it is possible that this species is better adapted to insect pollination that is *Z. pumila*.

Pupation—Microsporophylls of *Z. pumila* are a little smaller than those of *Z. furfuracea*, and can accommodate fewer eggs (*ca* 4-6). While *R. slossoni* generally pupates at the base of the microsporophylls like *R. mollis*, some larvae pupate crosswise in the ends of the sporophylls. Occasionally one can find two pupae side by side in the base of a microsporophyll (Text-figure 2). This behaviour has not been observed in *Z. furfuracea*, and even in *Z. pumila* it is quite rare.

Dormancy—At the end of the reproductive season of *Z. pumila*, male cones containing larvae in diapause fall apart because many of the sporophylls and cone axes have been completely eaten away by larvae of both *R. slossoni* and *P. zamiae*. Eventually the microsporophylls rot away completely, so that only the pupa cases of *R. slossoni* containing larvae in diapause remain in the soil, looking like little, nearly black, cylindrical boxes. We think that the year-to-year continuity of successful pollination of *Z. pumila* depends largely on the well-being of these dormant pupae. However, many larvae in diapause become infected with fungus, and, although they generally undergo metamorphosis, they frequently die in the pupa case, surrounded by fungal fruiting bodies. Those infected adults which survive are unable to breed because their abdomens contain only fungal fruiting bodie's, which by defecation they scatter through any maturing pollen cone they happen to visit. Because of this high mortality, a larger number of larvae must go into diapause than would be the case if fungal infection were absent. We suspect that there is a complicated system of "checks and balances" between cycad weevils and their infective agents and predators.

Life cycle of *Pharaxonotha zamiae*

Pharaxonotha zamiae (Text-figure 1I) goes to

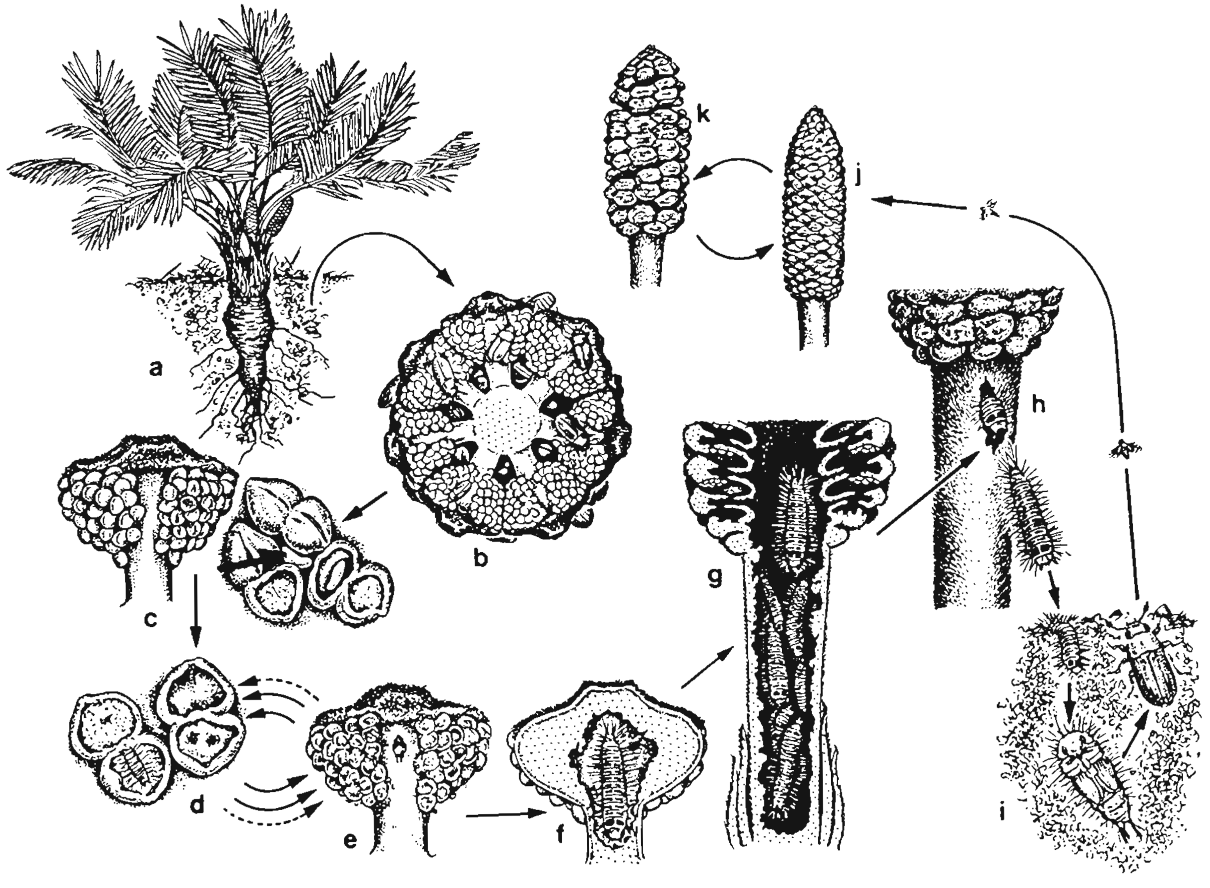


Text-figure 2—Life cycle of *Rhopalotria slossoni.* **a,** adult weevils leave the cones in which they were sheltering, and visit an attractive male cone (**b**). **c,** pollination takes place when some individuals on leaving a male cone in search of a new feeding and breeding site, enter a receptive female cone; there they try to feed, but find no food or egg-laying sites. Some become trapped inside the cone, but probably many escape. **d, e,** they feed on the tissue at the ends of the microsporophylls, 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 visitation. **f,** 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. **g,** only one larva generally survives to build a pupa case from fecal matter. **h,** after 2-3 days, the larva metamorphoses into a pupa. **i,** next day, the mature *Rhopalotria* chews its way out of the pupa case and through the end of the sporophyll, then flies to an attractive male cone (b) to feed and breed. At bottom, some larvae do not pupate at the base of the sporophylls but near its distal end; occasionally two larvae pupate at the base of the same sporophyll, but this is rare.

the male cones of *Z. pumila* when the microsporangia are about to dehisce, to feed and lay eggs between microsporangia, and sometimes within them after they have dehisced (Text-figure 3a, b). The eggs are comparatively large in proportion to the dimensions of the female, which may carry up to six eggs at a time. We are not sure where *P. zamiae* mates. 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 adults feed only on pollen, and when they are present, pollen is scattered everywhere in the male cone, so that all of the insects which happen to be in the cone, including *R. slossoni*, become covered with it. Otherwise, unless the microsporangia of *Z. pumila* are disturbed, the pollen tends to remain in the pollen sacs in little sticky clumps.

Larval stages—The oval eggs are greyish white and translucent, and about twice as long as they are wide. The red compound eyes of the larvae can soon be seen through the membrane of the egg. The larvae eat their way out of the egg and begin feeding on pollen (Text-figure 3c, d). Newly hatched larvae are almost white. All of the larval instars look very similar. Each segment has a pair of light brown patches on the dorsal side, so that the larvae appear transversely striped (Text-figure 1G). 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.



Text-figure 3—Life cycle of *Pharaxonotha zamiae*. **a,** young adults leave the soil and visit male cones of plants of *Z. pumila* in which the microsporangia are beginning to dehisce. **b,** beetles forage in the male cone. **c,** microsporophyll of male cone; in the cone the beetles feed on the pollen and lay their eggs between the sporangia (arrow) and sometimes in sporangia from which the pollen has been eaten. **d,** 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. **e,** when the larvae are ready to moult, they eat a little hole in the sporophyll into which they go to moult. When they emerge in the next instar they go back to feeding on pollen. Only the early instars feed on pollen, and by the third instar, there is not much pollen left. **f,** subsequent larval instars eat only tissue. They enter the main axis through a sporophyll and eat their way towards the cone stem. **g,** instars continue feeding until the cone stem is hollow, but they do not eat into the stem tuber. **h,** when the larvae are ready to metamorphose, they eat a hole in the stem, and drop to the ground. **i,** larvae burrow into the soil, pupate and after 4-7 days become mature beetles. **j,** adult beetles leave the soil in search of a cone to feed and breed in. **k,** pollination takes place when some individuals enter a female cone, instead of a male cone.

It is only the first instars that eat pollen, and in fact there is very little pollen left in the cone after the first two instars. A larva that is ready to moult eats a hole in the adaxial surface of one of the sporophylls and crawls inside, later emerging as the next instar (Text-figure 3e, f). The later instars eat only cone tissue, entering the cone axis via a microsporophyll, and eating their way down through the cone into the pedicel, which eventually becomes completely hollow (Text-figure 3g). They do not tunnel beyond the pedicel, hence do not damage the stem of the host. Because all feeding instars of *R. slossoni*, and the later larval instars of *P. zamiae* eat sporophyll and stem tissue, both must also have a way of avoiding the toxins. Both adults and early instars of *P. zamiae* eat pollen, but at present we have no information on the possible toxicity of pollen. When larvae have finished feeding and are ready to leave the cone, they eat a little hole in the cone pedicel and drop down to the ground where they burrow into the soil (Text-figure 3h, i).

Pupation—Larval *P. zamiae* pupate after several days and remain in this stage for about 4-7 days (Text-figure 1H). There is no pupa case or coccoon. No doubt earlier in the season some emerging adults visit ripening male cones, but we made these observations late in the season, when there were scarcely any new cones to visit. Upon emerging, young adults burrow into the soil instead of flying away to repeat the breeding cycle. When they were dug up, they seemed to have no inclination to leave, but only to hide. It is also possible that they needed a few days to harden their exoskeletons before emerging from the soil, and that what we saw was normal behaviour for a new adult.

Pollination—We have found *Pharaxonotha* in female cones of *Z. pumila* in South Florida, and we assume their visits are casual since they do not feed on female-cone tissues (Text-figure 3j, k). This is also the case with *R. slossoni*. Nevertheless, these visits accomplish pollination of ovules by both species of beetles (Tang, 1987). In North Florida a different species of *Pharaxonotha* appears to be the only pollinator of *Zamia* (Bart Schutzman, personal communication). *Rhopalotria* may have been there originally, but could have become extinct as a result of the "coontie" industry, coontie being the Seminole 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.

Interactions of *Rhopalotria* and *Pharaxonotha*

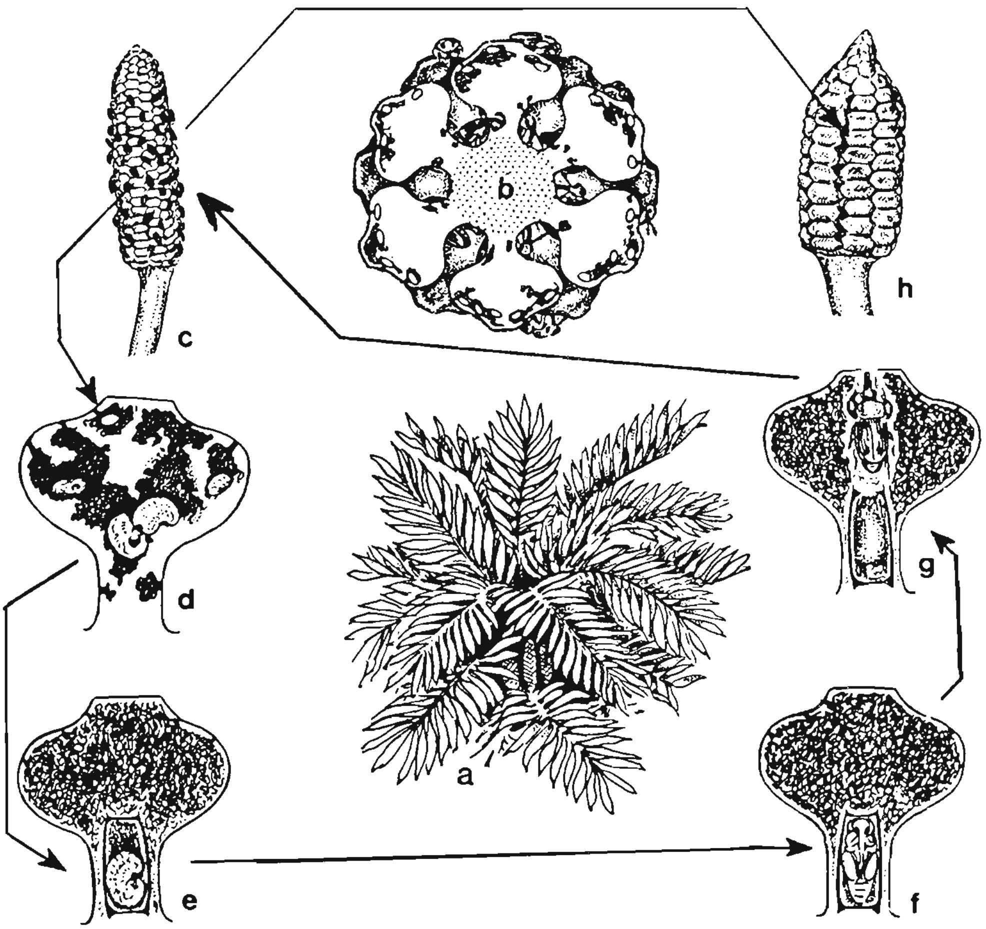
Both *P. zamiae*, and *R. slossoni* are often found together in the same male cone, however, there is no conflict because *Rhopalotria* prefers the sporophylls at the base of the cone while *Pharaxonotha* larvae generally prefer the sporophylls at the tip of the cone. The larvae of *Pharaxonotha* are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

Pollination of *Zamia furfuracea*

During the past decade we have obtained both circumstantial and experimental evidence, that one species of cycad, *Zamia furfuracea* L. fil., is in cultivation effectively pollinated by a small snout weevil, *Rhopalotria mollis* (Text-figure 1F), which completes at least one phase of its life cycle in pollen cones of that cycad. We have described various aspects of this relationship in previous papers (Norstog & Stevenson, 1980; Norstog, Stevenson & Niklas, 1986). These reports are based on observations of the cycad and its pollinating weevil in cultivation and may not necessarily reflect activities occurring in nature. However, we suspect they are similar though more complex, and field studies of the pollination of *Z. furfuracea* now underway show that *R. mollis* (or a very similar species) is present in wild plants in Veracruz, Mexico. The weevil parasitizes male cones of this cycad in much the same way as related here. In addition, an undetermined species of *Pharaxonotha* also is present (Andrew Vovides, unpublished data). 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 (Text-figure 4). 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, which occurs by starch and lipid-fueled metabolism (thermogenesis), is a general one among cycads and is considered as functioning both to open male and female cones and also produce fragrances (Tang, Sternberg & Price, 1987).

We are not sure where weevils come from to



Text-figure 4—Life cycle of *Rhopalotria mollis* in *Zamia furfuracea*. **a,** in mid-June, male cones begin to mature and those near dehiscence attract swarms of adult weevil. **b,** weevils feed, copulate and females lay eggs in feeding holes. **c, d,** eggs hatch and one or more larvae feed upon parenchyma tissues, working their way toward the base of the microsporophyll. Usually only one larva survives. **e,** during early to mid-season, larva builds a thin-walled pupa case. **f,** within 2-3 days larva pupates. **g, h,** metamorphosis is rapidly completed and adult emerges, visiting both male and female cones and accomplished pollination. Late-season pollen cones have greenish microsporophylls and feeding, pupation, and subsequent dormancy closely resembles that shown in Text-figure 4.

start the annual breeding cycle on *R. mollis* but suspect they emerge from long-dormant larvae that "winter" in debris at the base of the cycads they later infest. The first breeding cycle of the weevil is short, a week or so, and involves just a few individuals, but increasingly large numbers 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 2-3 days before abandoning it (Text-figure 4c). 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 seems to us *prima facie* evidence that insect pollination is the mode of reproduction of that species.

Rhopalotria mollis is an excellent flyer and during the early part of the reproductive season of *Z. furfuracea*, males and females are attracted to male cones where they feed upon sporophyll tissue by making small holes in the ends of the sporophylls through which they probe for food and in which females lay eggs (Text-figures 4b, c, d). The diameter of the egg is slightly less than that of the snout of the female weevil. Ends of microsporophylls often become rather hollowed out and as many as six eggs can be present in one sporophyll.

Larval stages—Within a day or so, the eggs hatch, producing larvae which eat their way inwardly from the tip of a microsporophyll (Text-figure 4d). As is typical of weevils, the larvae are legless grubs (Text-figure 1D) and are quite active.

Although up to six eggs may be laid in one microsporophyll, and as many hatchling larvae may be present (Text-figure 4d), subsequently each sporophyll will contain only one large larva and, later on, a single pupa or a recently metamorphosed adult (Text-figure 4e, f). As the larvae eat away the sporophyll tissue, they meet, and one eats the other. This occurs also, as noted earlier, in the development of *R. slossoni* in *Z. pumila*. We have observed larvae eating each other, but we have not observed the entire process of cannibalism.

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 I_2KI 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.

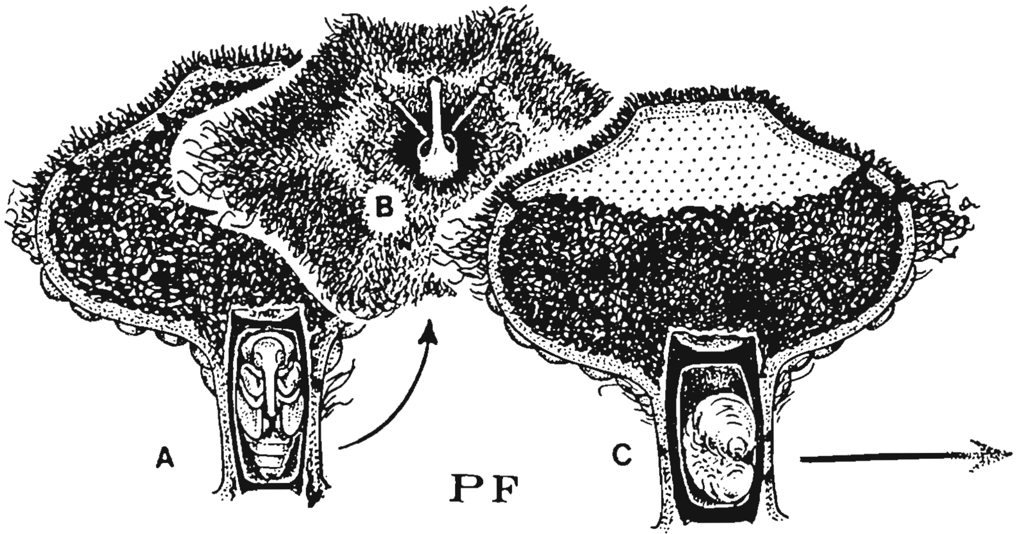
Pupation—Larvae of *R. mollis* grow rapidly, eventually hollowing out most of the sporophyll end and stalk, but the epidermis of the sporophyll together with the microsporangia remains intact. About 3-4 days after hatching, a larva constructs a chamber in a microsporophyll stalk within which it pupates (Text-figure 4e, f), its head oriented toward the outer end of the microsporophyll. The pupa case is constructed of fecal matter and a clear liquid secreted by the larva, so the larva and later pupa are housed within a tough, cylindrical capsule (Text-figures 4e, f; 5).

The adult emerges after metamorphosis, usually by boring out through the tip of the sporophyll (Text-figures 4g; 5B); 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* while sheltering and feeding in male cones become covered with pollen, but do not feed on pollen. A single cone at this stage may contain more than 100 weevils, and it is at this stage that visitation to female cones takes place (Text-figure 4h). However, female cones are not fed upon, although interior surfaces sometimes exhibit healed scars of superficial, punctate wounds which may have been made by weevils.

We have shown experimentally that pollination of this cycad by weevils is very effective and cone fertility as a result may approach 100 per cent (Norstog *et al.*, 1986; Norstog & Fawcett, 1989).

Dormancy—A physiological change in at least some larvae occurs toward the end of the breeding season. "Early-season," but late-instar larvae are covered with thin cuticles through which internal



Text-figure 5—Pupation of *Rhopalotria mollis*. **A,** early season pupa; the microsporophyll parenchyma is entirely consumed by larvae; the pupa case is thin-walled. **B,** the adult emerges from pupation by boring through the tip of the microsporophyll. **C,** microsporophyll of late-season cone has a green area at tip, which is low in starch and high in idioblast cells. Weevils tend to avoid the green tissue when feeding and egg laying, and the weevil population is larger at end of the season, so there is a shortage of suitable space for feeding and breeding. At this time after feeding, mating and egg laying in non-green parts of sporophylls, the surviving larva which is yellowish and waxy looking builds a very thick pupa case. Subsequently the cone becomes fragmented and sporophylls begin to rot in the ground. Eventually only pupa cases remain, still housing unmetamorphosed larvae which will not complete their metamorphosis until the next season.

structures are visible; "late-season," late-instar larvae have thick, opaque cuticles, become fat and waxy and build very thick-walled pupa cases in which they go into diapause until the next season (Text-figure 5C). 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 pupa cases, which are composed largely of dung, probably contain a high proportion of idioblast toxins, among them BMAA and macrozamin (Norstog *et al.*, in review). Both substances have been found in weevils of all stages of metamorphosis (Vovides *et al.*, in Press).

An observation of feeding behaviour on the part of both *R. mollis* and *R. slossoni* may indicate direct rather than passive avoidance of cycad toxins. Adults of both species, when beginning to feed upon the surfaces of microsporophylls, use their mandibles to tear out epidermal trichomes, which then are discarded. Dennis Stevenson (personal communication) has evidence that the trichomes contain ninhydrin-positive substances, perhaps including BMAA. If the trichomes contain toxins, one can explain this remarkable behaviour as further exemplifying toxin avoidance by a direct behavioural response.

OTHER POLLINATORS OF AMERICAN CYCADS

Bart Schutzmann (personal communication) has found different fragrances in receptive cones in different populations of *Z. pumila* in North Florida, and one of the fragrances, methyl salycylate, draws the appropriate *Pharaxonotha* species in baited McPhail traps, which may indicate that there could be either different ecotypes, or different species of *Zamia* in Florida.

A snout weevil, *Rhopalotria bicolor*, is associated with a similarly bicoloured *Pharaxonotha* species in male cones of *Dioon califanoi* (Vovides, 1991), and a *Pharaxonotha* species is associated with *R. mollis* in male cones of *Z. furfuracea* as noted earlier, as well as a *Pharaxonotha*-like beetle in male cones of a *Ceratozamia* species (Vovides, unpublished data). Deborah and David Clark who are working on pollination in *Z. skinneri* at La Selva in Costa Rica have also found the probable pollinator to be a *Pharaxonotha* species (Deborah Clark, personal communication).

OTHER INSECTS IN *ZAMIA* CONES

In addition to the two pollinating species, a number of other insects can be found in the cones of *Zamia pumila*. These include the eggs, larvae and pupae of two moths, which live on debris in the old cones, and the eggs of the *Eumaeus* butterfly, the larvae of which devastate the leaves. Scale and other small insects are often present also.

IMPLICATIONS FOR CYCAD CONSERVATION

At Fairchild Tropical Garden cultivated cycads have been sprayed with insecticides to control predatory insects, and the Garden's wild population of *Z. pumila* has been reduced by collecting, fire, and habitat conversion to other purposes. As a result numbers of pollinators have also declined.

When a large *Zamia* is dug up, frequently small pieces of stem tuber remain to regenerate, and the extent of this regeneration can be remarkable. However, it takes several years for a regenerated plant to become big enough to cone. Without a series of cones to breed in, a weevil population cannot build up sufficiently to provide an adequate number of larvae in diapause for populational continuity of pollinators in subsequent years. Even under normal conditions, many larvae in diapause die and if the pollinators become extinct, the regenerating remnants of these cycads will cease to be fertile. We have seen evidence of much the same situation at Everglades National Park, in areas of pine-palmetto habitat where a practice of controlled burning every three years has been in effect. Here populations of *Z. pumila* consist of small and weak plants apparently regenerated from fire-damaged specimens. Such fires not only destroy the tops of the stem tubers, and male cones where both pollinators breed, but also the top layers of humus in which the dormant insects remain from one season to the next. We have observed similar destruction of cycads and their habitats in frequently burned forests and scrublands in Mexico, in which cycads once flourished but now are much reduced in numbers.

All cycads have recently become popular world wide, including the far north where the smaller species can be grown in glasshouses. We have seen evidence of indiscriminate collection in several populations, and this combined with the practice of "slash and burn" agriculture in both the sophisticated "first world" version, and the unsophisticated "third world" version, could very well result in the slow elimination of many cycad species because of the demise of pollinating beetles. Later attempts to re-establish these species in the wild would also require the re-establishment in the wild of appropriate pollinators, without which they cannot survive and reproduce. There can be no permanent survival without sexual reproduction!

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