Cycads and Beetles: Recent Views on Pollination

Pierre Jolivet

Cycads are very primitive plants and survivors of the Jurassic and the Cretaceous. Their association with insects is known for a long time, but the insect role in pollination has been discovered only recently. Those plants were supposed before to be all only wind pollinated. Research in North America, South Africa and Australia all confirm beetle involvment. Only a few species seem to be only wind pollinated. It is evident that the role of insects with the Mesozoic related Benettitales and Pteridospermae must have been also very important, but Benettitales had bisexual cones, surrounded with petaliform bracts, showing some kind of bisexual flowers. Beetles at that time frequenting them were probably mostly borers.

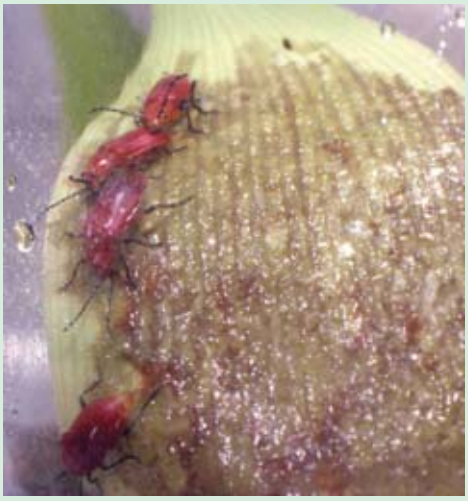
Cycads probably originated from the Permian, together with the beetles, and they flourished during the Mesozoic (-206 to -65 mya). That was also the period of the great diversification of the beetles. We know that cycads are essentially tropical, with the exception of some species in China, Japan and Florida. Some specialized beetle families feeding on cycads are either neotropical or Southern Gondwanian in distribution, but some are cosmopolitan. There is a Coleoptera Languriidae on *Zamia floridana, Pharaxonotha floridana* Casey and rather abundant around Gainesville, who was reclassified so one day by our friend John Kingsolver (1973). Now Richard Leschen (2003), from the far away New Zealand, by the magics of cladistics, has placed the languriids among the erotylids. Here we will continue to keep the Erotylidae and Languridae separate for practical reasons.

During certain periods of the day cycad cones produce volatile components and various odors - resinous, fruity, mouldy, etc. - likely to attract pollinating insects, (Tang, 1989; Tang et al., 1987; Terry et al., 2004). The cones are visited by more or less specific beetles, and the young leaves by Lepidoptera, mostly lycaenids, and many beetles. We suppose that the beetles attracted by male cones and their nutritive sources, go later on to female cones by "mistake," and in doing so pollinate them. It has been very rarely observed, the fertilization often done at dusk or during the night. It remains to be adequately demonstrated, however, for certain species of beetles and cycads, because female cones are often very tightly closed, and are often lack insects within them. That is why anemophily or dissemination by wind was, until mid-1980, thought to be the only fertilizing mechanism for the cycads. Beetle intervention is now fully proven, namely for the Australian cycad, *Lepidozamia peroffskyana* (Zamiaceae) which is pollinated exclusively by *Tranes* weevils (Hall *et al.*, 2004). Many supporters of coleopterous fertilization have written about it (Norstog *et al.* 1992; Rattray 1913; Tang 1987a,b; Jones 1993; Norstog and Nicholls 1997). Crowson (1981, 1989, 1991), in his remarkable studies of beetle-cycad relationships, has strongly insisted on the pollinating role of the beetles. Some *Macrozamia* in Australia are pollinated only by species of *Thrips* (Terry *et al.*, 2004).

Insects and beetles frequenting cycads.

It is always difficult to see cycad beetles on these plants, because their appearance period on the cones and also on leaves is very short, and it sometimes happens during the night or at dusk (Windsor *et al.* 1999). The author observed them on the leaves (*Aulacoscelis*) during short visits in spring. The insects come to the plants one week after the strong spring rains, normally in May, and one month later their visits totally cease. They seem to survive as diapausing eggs and larval stages, perhaps hidden in the seeds. The appearance of the insects on male cones is linked with the latter's maturity and can be autumnal, as in Florida. Some Aulacoscelinae (Chrysomelidae) appear on leaves in spring in Central America and in December in Bolivia, for instance. As mentioned by Crowson (1989), the beetles frequenting cycads are found mostly on the male cones and on the leaves, and rarely on the trunks (only some weevils). A few have been observed on female cones, where they help fertiliza-

1. Aulacoscelis melanocera *(Coleoptera, Chrysomelidae) on fronds of* Zamia elegantissima *(June 97, Panama).*



2. Aulacoscelis melanocera *scraping* Zamia *leaves.*

Aulacoscelis melanocera *on leaves of* Zamia elegantissima.

tion, often in the evening, probably connected with the volatiles emitted. None has yet been found on the roots, but that is probably due to lack of careful search. Some larvae are certainly adapted to radicolous life and the larvae of aulacoscelines are probably seed borers, as are those of bruchids, but these probabilities remain to be confirmed.

Insects on cones

Not many insects frequent male cones (and eventually, female cones) during pollen production, and those are mainly Coleoptera. Oberprieler (2004a) has recently summarized our knowledge about weevils associated with cycads.

The idea of anemophilous pollination of cycads comes mainly due to an analogy with Coniferae. A male cone can produce enormous quantities of pollen, up to 100 cm^3 for *Cycas rumphii* cones. Actually, except for *Cycas*, the cones are tightly closed, and it seems difficult for wind alone to transport pollen to the micropyle, often situated several centimeters deep inside the cone. With few exceptions, the entomophilous solution seems possible, though rarely observed because it is so short. Weevils often seem to be involved in this, as mentioned by Rattray (1913), in South Africa in case of *Encephalartos altensteini* Lehm. and *E. villosus* Lehm. Species of the genus *Phlaephagus* visit male cones first, then female cones, fertilizing them in the process. According to the same author, *Stangeria eriopus* would be, on the contrary, exclusively anemophilous, which should be the reason why the cones of that plant do not produce heat.

The Mexican species *Zamia furfuracea* L.f. is pollinated by the weevil *Rhopalotria mollis*. *Zamia pumila* L. in Cuba and Z. floridana A.DC. in Florida (=*integrifolia* L.) each have two pollinators, male cones of which are visited by *Rhopalotria slossoni* and by the Langurid, *Pharaxanotha floridana* Casey. Larvae and adults of these beetles feed on male cone tissue and get covered with pollen. These insects are attracted by the female cones, probably by the odor resulting from heat produced by the cones. Norstog *et al.*(1992) detailed the pollination of various *Zamia* spp. *Dioon califanoi* in Mexico (Vovides, 1991) is pollinated by various species of *Pharaxanotha*. These langurid beetles (Erotylidae according to some specialists) frequent male and female cones equally in Mexican *Ceratozamia*. At La Selva in Costa Rica, several *Pharaxanotha* frequent male cones of *Zamia skinneri* Warsz. Lepidoptera eggs, larvae and pupae, including those of Lycaenidae (*Eumaeus* spp.), which routinely feed on the leaves, are sometimes found on *Zamia* cones. In Australia, the cycads *Macrozamia communis* and *Lepidozamia peroffskyana* are associated with the weevil *Tranes lyterioides*, a big nocturnal species, which develops inside male cones and eats the pollen. Many other beetles are associated with male cones of Cycadales, such as Tenebrionidae, Rhizophagidae, Languridae, Anthribiidae, Boganiidae, and Nitidulidae. Other insects frequent male cones of cycads, like *Trigona* bees, a genus known from the Cretaceous, suggesting a very ancient association.

In Costa Rica, Gomez has observed and photographed quantities of langurids in Wilson Botanical Garden, probably some *Pharaxonotha*, invading the male cones of *Zamia fairchildiana* Gomez, devouring the starch. Those small brown beetles could be easily counfounded with *Aulacoscelis melanocera* Stal or *A. costaricensis* Bechyne, if it were not for their much smaller size.

Crowson (1981, 1989, 1991) has pointed out that certain beetles frequent specially the cycad cones, namely the Boganiidae, dating from the lower Cretaceous and linked with Australia and Africa, then still loosely connected, as suggested by the Gondwana hypothesis. In South Africa, it is a boganiid, *Metacucujus encephalarti*, which pollinates *Encephalartos lunatus*, and, in Australia, *Paracucujus rostratus*, which is found on the male cones of *Macrozamia riedlei* (Endrody-Younga and Crowson, 1986). Wilson (2002) confirmed records of entomophilic pollination in cycads in both species of *Bowenia* (Boweniaceae) in Queensland. The pollination vectors are *Miltotranes* weevils. Beetles, however, are not always fertilizing the cycads. Kato (2001), for instance, quotes the larvae of a Cerambycid in Japan on *Cycas*

Zamia elegantissima *leaves scraped by* Aulacoscelis melanocera *and* Nomotus sp. (Languridae).

Zamia elegantissima *male cone, Chagres Park, Panama.*

Zamia fairchildiana *male cone, Wilson botanical Garden, Costa Rica.*

Zamia elegantissima, *Chagres Park, Panama (June 1997).*

Don Windsor looking at Zamia elegantissima, *Chagres, Panama (June 1997).*

revoluta, mining the megasporophylls, but not contributing to pollination. Brentids of the genus *Antliarrhinus* breed inside the ovules of *Encephalartos* in Africa, and feed on the seed kernel. *Antliarrhinus zamiae* digs with its rostrum through the sporophylls and ovae, and lays its eggs inside the cones of *Encephalartos longifolius* and *E. altensteinii* with its telescopic ovipositor. *Antliarrhinus signatus* goes directly inside the cone to lay its eggs (Oberprieler 2004b). Crowson (1989) mentions many other curculionids attacking cycad male cones, namely the genera *Porthetes* and *Amorphocerus* (both Cossoninae) in Southern Africa. According to Crowson, many beetles, supposed to be cycad pollinators, possess cavities used to carry pollen grains in their mandibles. Others have antennal cavities, perhaps for this purpose, such as the Allocorynidae and certain Curculionidae.

Chagres Park, Panama.

Larvae of Eumaeus atala (Lycaenidae) *on* Zamia fairchildiana *leaves, Wilson Botanical Garden*

Don Windsor with the author in front of Gunnera *sp., El Cope, Panama.*

Insects on leaves

Crowson (1989) has mentioned on *Macrozamia* leaves, in Australia, buprestids, such as *Xyroscelis crocata* and *X. bumanna*. The sagrine, *Carpophagus banksiae*, which looks like a big bruchid, has been also found on the leaves of *Macrozamia*. The relationships of these insects with cycads has not been fully elucidated. *Carpophagus*, is an archaic sagrine, a Gondwanian relic; the relationships, if true, could be very old. There are many leaf-frequenting insects on cycads in tropical America as well as in Southeast Asia. Good observations in Africa and Madagascar are lacking. We must observe the timing of these insects' appearance; they only have a short adult life, most of it in the larval stage.

In Southeast Asia, *Lilioceris*, normally a Liliaceae feeder, also frequents local cycads. In New Guinea, Szent-Ivany *et al*. (1956) were the first to mention *Lilioceris clarki* (Baly) on new leaves of *Cycas circinalis*. Hawkeswood later (1992) documented *Lilioceris nigripes* (Fabricius) in Queensland on the forest-dwelling species *Bowenia spectabilis* Hook. There were similar captures in Vietnam, and Shepard (1997) has reported an undetermined species of *Lilioceris* on the leaves of *Cycas siamensis* Miq. in Thailand in a *Dipterocarpus* forest. Larvae were localized under leaflets, and were browsing the abaxial epidermis and a part of the mesophyll. The red larvae and adults were very visible on the dark green foliage. The *Cycas* species in New Caledonia (see my article in the June 2005 TCS Newsletter), does not seem to harbour any criocerine, and the local members of this leaf beetle subfamily have been captured there only on orchids.

Don Windsor looking at Aucascelis melanocera *on* Zamia elegantissima, *Cerro Azul, Panama (June 1997)*

Aulacoscelis melanocera *on new leaf of* Zamia elegantissima.

Aulacoscelis spp. (Chrysomelidae: Aulacoscelinae) also rasp young and new tender green leaves of several *Zamia* species to suck up sap. They are mostly common after the spring rains in Central America and Mexico. Adults migrate over the mountains of Panama (El Cope), probably looking for new plants. In Central America, they are often in company of caterpillars of *Eumaeus minyas, E. godarti* (Lycaenidae) and the langurid *Nomotus lateralis*. Langurids and *Aulacoscelis* seem to rasp the leaves, partly for pharmacophagy, as toxicity of the cycads protect them against predators. Being very toxic, they are never attacked by ants, birds or lizards. *Nomotus* is black and *Aulacoscelis* is orange-red and both are aposematic over the green leaves. The *Eumaeus*, in contrast to many lycaenids, are not assisted with ants. That is probably why they are aposematic with bright colors. Their own acquired toxicity protects them very well. The larva of *Aulacoscelis* have been recently described by Cox and Windsor (1999). Its biology is unknown (Jolivet, 1998; Windsor and Jolivet, 1997; Windsor *et al*., 1999), but with what we know at present of *Janbechynea*, a big aulacosceline, we could suspect a development inside the seeds and the cones. This aspect is actually under

Pollinators of Zamia floridana. left: Pharonoxotha floridana (Languriidae); right, Rhopalotria mollis (Curculionidae)

study, but no proof of the realtionships has been really demonstrated.

It seems very probable that during the Jurassic, the Protoscelinae were feeding on Cycadales or Benettitales, their monoecious counterparts. The remains of those plants are contemporaries of these insects in the geological layers of Siberia. Those ideas have been attacked recently without any serious basis. All first observations on aulacoscelines were done in Panama and Costa-Rica (Jolivet, 1998; Windsor and Jolivet, 1997; Windsor et al., 1999). There are a dozen species of *Aulacoscelis* in America and five *Janbechynea* spp. from Mexico to Bolivia. When fed in laboratory, aulacoscelines accept fruit juices, like mangos, which means that juice sucking is part of their normal diet. Very probably *Janbechynea* feeds on cycads in Bolivia.

Toxicity

Most of the insects feeding on leaves or cones of Cycads are aposematic. The toxicity of the plant, cones and seeds is very high, and though many reptiles, birds and mammals seem to eat their cones and their contents with impunity, livestock in New Guinea, Australia and South Africa are gravely poisoned when feeding on the cones. We have often seen the cows sick after having eaten young cones in New Guinea. They spin around in circles and flop around like mad cows before dying. Cycad toxins are numerous, cycasine, neocycasin, macrozamine and methylamino-L-alanine and are probably sequestred in specialized cells, the idioblasts, in cones and leaf tissue (Schneider *et al.*, 2002; Norstog *et al.*, 1992).

Many lycaenids (Lepidoptera) are specialized for feeding on cycad leaves, such as *Catochrysops pandava* Horsfield in Indonesia or *Chilades cleotas kaiphas* Frühstorfer in New Guinea, various species of *Eumaeus* in Florida, Central America, etc. Those butterflies borrow their toxicity from their host plant. Myriam Rothschild (Rothschild, 1992; Rothschild *et al.*, 1986) has studied *Eumaeus atala* and its gregarious caterpillars, brightly coloured and containing cycasin, a violent poison. The lycaenid, despite its toxicity, seemed once endangered in Florida, but we saw plenty of them on *Zamia* at Fairchild Botanical Garden.

Some seeds from coastal species of cycads contain a spongy tissue and they float. The sarcotesta or external envelop of *Macrozamia* seeds contain a high concentration of macrozamin, a very efficient toxin. These seeds are often brightly coloured to attract local animals, naturally immune to the poison. The seeds are often brightly colored in red, scarlet, orange, or yellow. Some cones are often orange, red or yellow (*Encephalartos*), sometimes even green, contrasting with the seed color.

It may be noted that some *Cycas* seeds, after cooking, are eaten by Australian aborigines. The stem of other species is a minor source of sago in the Philippines, and the leaves and even the fruits are sometimes eaten in Malaysia. As for stem starch, precautions should be taken by those who want to taste it because of the plant's extreme toxicity. *Zamia* extracts are sometimes also used as a poison, though they may be edible after special treatment of the roots. It is the same in Africa with *Encephalartos*. *Aulacoscelis* when offered to chickens, kills them instantaneously. The chamorro aborigines in Guam eat flying foxes (*Pterotus marianus*), and the bats eat *Cycas* seeds (*C. micronesica*). That causes a degenerative brain disease among humans. At least it is one of the current interpretations (Cox et al., 2003). Toxicity of the cycads could be due to cyanobacteria with the roots.

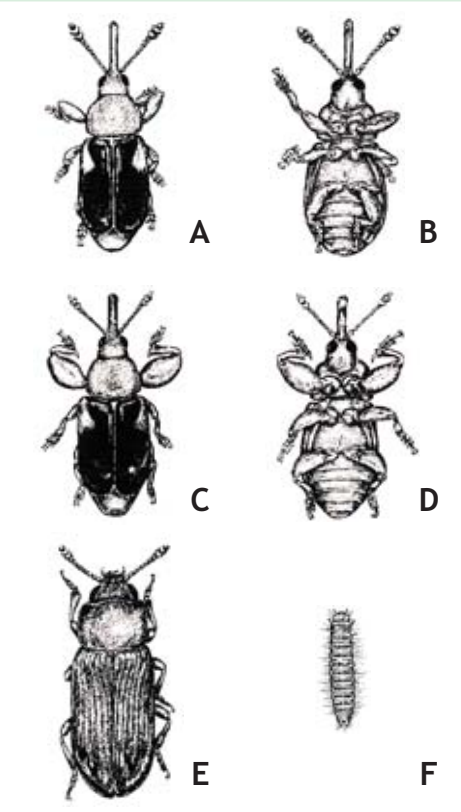
The toxicity of the leaves and of the fruits is so strong that beetles, which feed on them are very toxic themselves, and thus are protected from predators. Weevils, which feed on the parenchymatic tissue, partially avoid the toxins by keeping clear of the epidermal trichomes.

Conclusions

We are indebted to Crowson (1991), who made an extensive study of beetles associated with cycads. The observations, made and recorded in Panama and elsewhere in Central America, have provided further information. Pollination among aberrant gymnosperms, like Gnetales, is done by Lepidoptera and Diptera (Kato *et al.*, 1995). It is not the same for cycads, on which caterpillars feed only on the leaves, but the adults are not involved. Entomophily seems predominant among the cycads, but it is not the exclusive mode of pollination. It seems that entomophily is mainly due to the odour produced by the strobili, which also produce nectar. Among *Araucaria* (Araucariaceae), Palophaginae (Chrysomelidae) and Nemonychidae (Curculionoidea) live within the male cones, but do not seem to visit the female strobili, and they don't help in fertilization. What happens among the cycad cones? It seems that there is often passage from male strobilus to the female ones, and thus fertilization is helped by beetles. However, many beetles only frequent the leaves and never visit male or female cones, such as *Lilioceris* and probably many langurids. It is possible that some of them, like the aulacoscelines, visit the female cones only to lay eggs there; larvae may then develop in the seeds, but this is just a hypothesis. The Benettitales cones during the Mesozoic were bisexual and probably pollinated by borers, most likely beetles, as suggested by fossil traces. They were of a protofloral type, probably protandrous, i.e., male organs maturing earlier, while the actual cycads have separate sexes which makes fertilization more difficult.

The actual associations of cycads with aulacoscelines, Boganiidae and some weevils, are very ancient, but not entirely linked with pollination. The obligate entomophilous nature of pollination among some species of cycads explains why fertilization rates of plants in collections, even those in close proximity, are extremely low (Wilson, 2002).

For Oberprieler (2004), entomophily in cycads is a recent rather than an ancestral phenomenon and that was also a driver of diversification in cycads. Our views differ on this, since cycads also needed pollinators during the Mesozoic, and beetles were there to perform the task.



Pollinators of Zamia floridana.
A-D) Rhopalotria mollis: *A,B) female; C,D) male; E,F)* Pharaxonotha zamiae.

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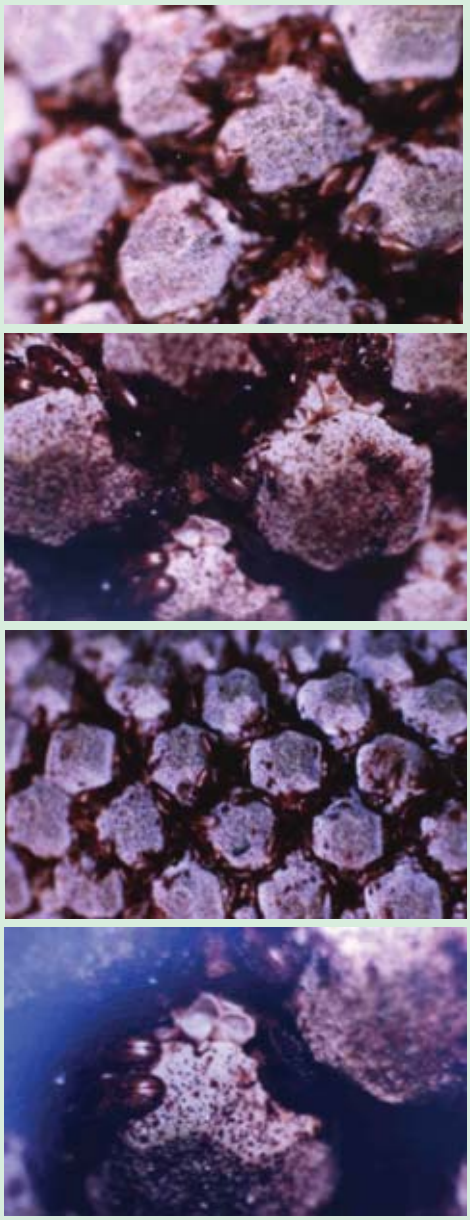

Male cones of Zamia fairchildiana *(Wilson botanical garden) invaded by* Pharaxonotha sp. *(Languridae). Photos by L.D. Gomez.*

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