

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. Researches in America, South Africa and Australia are all confirming the beetle involvement. Only few species seem to be actually only wind pollinated. It is evident that the role of insects with the Mesozoic related Bennettitales and Pteridospermae must have been also very important, but Bennettitales 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 myr). 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 go on speaking separately about Erotylidae and Languridae for practical reasons.

Cycad cones produce, during certain periods of the day (Tang, 1989; Tang et al., 1987; Terry et al., 2004), volatile components and various odors, resinous, fruity, mouldy, etc., certainly to attract pollinating insects. The cones are visited by more or less specific beetles, and the young fronds 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 by night or at dusk. It however remains to be adequately demonstrated for certain species of beetles and cycads, because female cones are often very tightly closed, and are often without any insects within them. That is why anemophily or dissemination by wind was, until mid-1980, supposed 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 the coleopterous fertilization have written about it (Norstog et al., 1992; Rattray, 1913; Tang, 1987a and b; Jones, 1993; Norstog and Nicholls, 1997). Crowson mainly (1981, 1989, 1991), in his remarkable study of the relationships beetles-cycads 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).

1.- 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 fronds is very short, and it sometimes happens during the night or at dusk (Windsor et al., 1999). The author observed them on the fronds (*Aulacoscelis*) during short visits at spring. The insects come to the plants one week after the strong spring rains, in May normally, and their visits stop totally one month later. They seem to survive as diapausing eggs and larval stages hidden somewhere, perhaps into the seeds. The appearance of the insects on the 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 fertilization, 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 radiculous life and probably the larvae of aulacoscelines are seed borers, as those of bruchids, but these probabilities remain to be confirmed or infirmed.

1.1.- Insects on cones.

Insects frequenting male cones and eventually female cones during the pollen production are not many. There are mainly Coleoptera. Oberprieler (2004a) has recently summarized our knowledge about the cycad-associated weevils.

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 cubic cm for *Cycas circinalis* cones. Actually, except for *Cycas*, the cones are firmly closed, and it seems difficult that wind alone can allow the pollen to enter into the micropyle, often situated several centimeters down inside the cone itself. With a few exceptions, often the entomophile solution, rarely observed, because very short, seems possible. Often weevils seem 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 first the male cones, then visit the female cones. Doing that they fertilize them. According to the same author, *Strangeria kaatzeri* would be, on the contrary, exclusively anemophilous, which should be the reason why the cones of that plant do not produce heat.

Zamia furfuracea L., in Mexico, is pollinated by the weevil *Rhopalotria mollis*. *Zamia pumila* L. in Cuba has two pollinators, and also *Zamia floridana* A.D.C. (= *integrifolia* L.), in Florida, the male cones of which are visited by *Rhopalotria slossoni* and by the Langurid, *Pharaxonota floridana* Casey. Larvae and adults of these beetles feed in the male cone tissues and get covered with pollen. These insects get attracted by the female cones, probably by the heat produced by the cones and their specific odour. In a recent paper (Norstog et al., 1992), pollination of various *Zamia* has been detailed. *Dioon califanoi* in Mexico (Vovides, 1991) is pollinated by various species of *Pharaxonota*. These langurid beetles (actually for some specialists Erotylidae) frequent equally the male and female cones of *Ceratozamia* in Mexico. In Costa-Rica, in La Selva, several *Pharaxonota* frequent the male cones of *Zamia skinneri* Warsz. There are also, sometimes, on *Zamia* cones, Lepidoptera eggs, larvae and pupae, including those of Lycaenidae (*Eumaeus* spp.), which feed normally on the fronds.

In Australia, the cycads *Macrozamia communis* and *Lepidozamia peroffskyana* are associated with the weevil *Tranes lyterioides*, a big nocturnal species, which develop inside male cones and eat the pollen. Many other beetles are associated with male cones of Cycadales, viz. 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 in Wilson Botanical Garden quantities of langurids, probably some *Pharaxonota*, invading the male cones of *Zamia fairchildiana* Gomez, devouring the starch. Those small brown beetles could be easily confounded with *Aulacoscelis melanocera* Stal or *A. costaricensis* Bechyne, if it was 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 met with 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* (Strangeriaceae) in Queensland. The pollination vectors are *Miltotrane*s weevils. Beetles however are not always fertilizing the cycads. Kato (2001), for instance, quotes the larvae of a Cerambycid in Japan on *Cycas 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 almond. *Antliarrhinus zamiae* digs with its rostrum through the sporophylls and ovae, and lays, with its telescopic ovipositor, its eggs inside the cones of *Encephalartos longifolius* and *E. altensteini*. *Antliarrhinus signatus* comes 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 in their mandibles cavities used to carry pollen grains. Others, such as the Allocorynidae and certain Curculionidae, have antennal cavities, perhaps for this purpose.

1.2.- Insects on fronds.

Crowson (1989) has mentioned on *Macrozamia* fronds, 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 fronds of *Macrozamia*. The relationships of these insects with cycads has not been fully elucidated. *Carpophagus* being an archaic sagrine, a Gondwanian relic, the relationships, if true, could be a very old one.

Really, there are many frond frequenting insects on the cycads, in tropical America as well as in South East Asia. Good observations in Africa and Madagascar are lacking. We must observe the time of appearance of these insects, which have only a short adult life, most of their life being in the larval stage.

In South East Asia, *Liliocercis*, normally a Liliaceae feeder, frequents also local cycads. In New Guinea, Szent-Ivany et al. (1956) have been the first to mention *Liliocercis clarki* (Baly) on the new fronds of *Cycas circinnalis*. Later on, Hawkeswood (1992) recorded *Liliocercis nigripes* (Fabricius) in Queensland on the forest dwelling species *Bowenia spectabilis* Hook, a Zamiaceae. There were similar captures in Vietnam, and Shepard (1997) has reported an undetermined species of *Liliocercis* on the fronds of *Cycas siamensis* Miquel in Thailand in a *Dipterocarpus* forest. Larvae were localized under leaflets, and were browsing the abaxial epidermis and a part of the mesophyll. These larvae, as also the adults, were red, very prominent over the dark green foliage. *Cycas circinnalis* Linné (= *C. celebica* Braun), the unique and rare cycad in New Caledonia, does not seem to harbour any criocerine, and the local members of this leaf beetle subfamily have been captured there on orchids only.

Aulacoscelis spp. (Chrysomelidae: Aulacoscelinae) also rasp young and new tender green fronds of several *Zamia* species, to suck up sap. They are mostly common in Central America and Mexico, after the spring rains. Adults migrate over the mountains of Panama (El Cope), probably looking for new plants. In Central America, they are often in company of the caterpillars of *Eumaeus minyas* and *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 for 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 fronds. 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 study, but no proof of the relationships has been really demonstrated.

It seems very probable that, during the Jurassic the Protoscelinae, were feeding on Cycadales or Bennettiales, 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 base. All first observations on aulacoscelines were done in Panama and Costa-Rica (Jolivet, 1998; Windsor and Jolivet, 1997; Windsor et al., 1999). There exist a dozen of species of *Aulacoscelis* in America and five species of *Janbechynea* from Mexico to Bolivia. When fed in laboratory, aulacoscelines accept fruit juices, like mangoes, which means that juice sucking is part of their normal diet. Very probably *Janbechynea* feeds on cycads in Bolivia.

2.- Toxicity.

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

Many lycaenids (Lepidoptera) are specialized for feeding on cycad fronds, 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 specially 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* in Miami botanical gardens.

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 macrozamine, a very efficient toxin. These seeds are often brightly coloured to attract local animals, naturally immune to the poison. The seeds are often red, scarlet, orange, or yellow and most of the time bright. Some cones are often orange, red or yellow (*Encephalartos*), sometimes even green, contrasting then with the seed colour.

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, the fronds and even the fruits are sometimes eaten in Malaysia. As for cassava, precautions should be taken by those, who want to get a taste of it for the first time, because the toxicity of the plant. *Zamia* extracts are sometimes also used as a poison, though they are edible only after a special treatment of the roots. It is the same in Africa with *Encephalartos*. *Aulacoscelis* when offered to chickens, kill them instantaneously. The chamorro aborigines in Guam eat flying foxes (*Pteropus marianus*), and the bats eat the seeds of cycas trees (*Cycas micronesia*). 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 the beetles, which feed on them are very toxic themselves, and thus are protected from predators. Weevils, which feed on the parenchymatic tissue, avoid partially the toxins by keeping clear of the epidermic trichomes.

Conclusion.-

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 the *Araucaria* (Coniferae), 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 one, and thus the fertilization is helped by beetles. However, many are the beetles, which only frequent the fronds 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; if the larvae develop into the seeds. This is just a hypothesis. The Bennettitales cones, during the Mesozoic, were bisexual and pollinated probably by borers, probably beetles, as suggested by fossil traces. They were of a protofloral type, probably protandrous, that is male organs maturing earlier, while the actual cycads have separated 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 a driver of diversification also in cycads. It is a point of view since cycads needed pollinators also during the Mesozoic and beetles were there to perform the task.

References.

- Cox, M.L. and Windsor, D.M. 1999. The first instar larva of *Aulacoscelis appendiculata* n. sp. (Coleoptera: Chrysomelidae: Aulacoscelinae) and its value in the placement of the Aulacoscelinae. *Journal of Natural History* 33: 1049-1087.
- Cox, P.A., Banack, S.A., and Murch, S.J. 2003. Biomagnification and Chamorro neurodegenerative disease. *Proceedings of the National Academy of Sciences* 100: 13380-13383.
- Crowson, R.A. 1981. *The Biology of Coleoptera*. Academic Press, London: 802 pp.
- Crowson, R.A. 1989. Relations of beetles to Cycads. *International Congress on Coleoptera C.A.C., Barcelona*: 13-15.
- Crowson, R.A. 1991. The Relations of Coleoptera to Cycadales. in Zunino et al. (eds.) *Advances in Coleopterology*: 13-28.

- Delevoryas, T. 1971. Biotic provinces and the Jurassic-Cretaceous floral transition. Proceedings of the North American Paleontological Convention 1: 1660-1674.
- Endrody-Younga, S. 1991. Boganiidae (Coleoptera: Cucujoidea) associated with cycads in South Africa: two new species and a new synonym. Annals of the Transvaal Museum 35(20): 285-293.
- Endrody-Younga, S. and Crowson, R.A. 1986. Boganiidae, a new family for African Fauna (Col. Cucujoidea). Ann. Transvaal Museum 34 (12): 253-273.
- Hall, J.A., Walter, G.H., Bergstrom, D.M and Machin, P. 2004. Pollination ecology of the Australian cycad *Lepidozamia peroffskyana* (Zamiaceae). Australian Journal of Botany. 52 (3): 333-343.
- Hawkeswood, T.J. 1992. Notes on the biology and host-plants of the Australian leaf-beetle, *Lilioceris (Crioceris) nigripes* (F.) (Col. Chrys.). Entomology 111: 210-212.
- Jolivet, P. 1991. Curiosités Entomologiques. Raymond Chabeau publ., Paris : 170 pp.
- Jolivet, P. 1998. Jurassic Park ou les Coléoptères des Cycadales., Le Coléoptériste, Paris 33 : 77-85.
- Jolivet, P. and Verma, K.K. 2005. Fascinating Insects. Pensoft publ. Sofia and Moscow, in print.
- Jones, D.L. 1993. Cycads of the World. Smithsonian Institution Press, Washington, D.C., USA: 312 pp.
- Kato, M. 2001. Insect fauna associated with *Cycas revoluta* (Cycadaceae) with a discovery of a cerambycid Megasporophyll miner. Spec. Publ. Japan Coleopt. Soc. Osaka 1: 73-78.
- Kato, M., Inoue, T. and Nagamitsu, T. 1995. Pollination biology of *Gnetum* (Gnetaceae) in a lowland mixed dipterocarp forest in Sarawak. American Journal of Botany 82 (7): 862-868.
- Kingsolver, J.M. 1973. New synonymy in Languriidae (Coleoptera). Proceedings of the Entomological Society Washington 75 (2): 247.
- Leschen, R. 2003. Erotylidae (Insecta: Coleoptera: Cucujoidea): phylogeny and review. Fauna of New Zealand. 47: 108 pp.
- Norstog, K.J. and Fawcett, P.K.S. 1989. Insect-cycad symbiosis and its relation to the pollination of *Zamia furfuracea* (Zamiaceae) by *Rhopalotria mollis* (Curculionidae). American Journal of Botany 76: 1380-1394.
- Norstog, K.J., Fawcett, P.K.S. and Vovides, A.P. 1992. Beetle pollination of two species of *Zamia*: evolutionary and ecological considerations. Paleobotanist 41: 149-158.
- Norstog, K.J. and Nicholls, T.J. 1997. The Biology of Cycads. Cornell University Press, Ithaca, USA: 363 pp.

- Oberprieler, R.G. 2004a. "Evil weevils"- the key to cycad survival and diversification in Lindstrom, J.A (ed.). The Biology, Structure and Systematics of the Cycadales. Proceedings of the Sixth International Conference on Cycad Biology, Thailand: 170-194.
- Oberprieler, R.G. 2004b. Antliarhininae Schoenherr, 1823 (Coleoptera, Curculionoidea). in Lindstrom, J. A. (ed.) The Biology, Structure and Systematics of the Cycadales. Proceedings of the Sixth International Conference on Cycad Biology, Thailand: 829-852.
- Rattray, G. 1913. Notes on the pollination of some South African Cycads. Transactions of the Royal Society of South Africa 3: 259-271.
- Rothschild, G. 1992. Egg protection by the Atala horstreak butterfly (*Eumaeus atala florida*). Phytochemistry 31(6): 1959-1960.
- Rothschild, M., Nash, R.J. and Bell, E.A. 1986. Cycasin in the endangered butterfly; *Eumaeus atala florida*. Phytochemistry 25 (8): 1853-1854.
- Schneider, D., Wink, M., Sporer, F. Ad Lounibos, P. 2002. Cycads: their evolution, toxins, herbivores and insect pollinators. Naturwissenschaften 89: 281-294.
- Schutzman, B. 1987. Mesoamerican Zamais. Fairchild Prop. Garden Bulletin July: 16-20.
- Shepard, W.D. 1997. *Lilioceris* sp. (Coleoptera: Chrysomelidae) herbivory on *Cycas siamensis* Miguel. Pan Pacific Entomologist 73 (1): 36-39.
- Szent-Ivany, J.J.H., Womersley, J.S. and Ardley, J.H.1956. Some insects of *Cycas* in New Guinea. Papua New Guinea Agriculture 11 (2): 53-56.
- Tang, W. 1987a. Heat production in Cycad cones. Bot. Gaz. 148 (3): 165-174.
- Tang, W. 1987b. Insect pollination in the Cycad *Zamia pumila* (Zamiaceae). American Journal of Botany 74 (1):90-99.
- Tang, W. 1989. In the heat of the night: notes on *Cycas* sex. The Cycas Newsletter 12 (1): 11-12.
- Tang, W., Sternberg, L. and Price, D. 1987. Metabolic aspects of thermogenesis in male cones of five Cycad species. American Journal of Botany 74 (10): 1555-1559.
- Terry, I., Moore, C.J., Walter, G.H., Forster, P.I., Roemer, R.B., Donaldson, J.D. and Machin, P.J. 2004. Association of cone thermogenesis and volatiles with pollinator specificity in *Macrozamia* cycads. Plant Systematics and Evolution, on line: 15 pp.
- Vovides, A.P. 1991. Insect symbionts of some Mexican cycads in their natural habitat . Biotropica 23: 102-104.
- Wilson, G.W. 2002. Insect pollination in the cycad genus *Bowenia* Hook. Ex Hook. F. (Strangeriaceae). Biotropica 34 (3): 438-441.
- Windsor, D. and Jolivet, P. 1997. Cycad feeding by an ancient beetle, *Aulacoscelis*, in Panama. Chrysomela 34: 5.

Windsor, D., Ness, J., Gomez, L. D. and Jolivet, P. 1999. Species of *Aulacoscelis* Duponchel and Chevrolat (Chrysomelidae) and *Nomotus* Gorham (Languridae) feed on fronds of Central American Cycads. *Coleopterist Bulletin* 53 (3): 217-231.