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Towards an evolutionary basis for floral ecology: some methodological aspects

Fossil flowers cannot be studied directly, because of their extreme rarity in the fossil record. This study tries to relate the results of a statistical analysis of the recent insect-flower relationships with the phylogeny of the insect-taxa in which anthophily developed, dated by their relatively rich fossil record. A postulate is the principle that the length of the tongues of fossilized anthophilous insects of a certain period is some relative measure for the length of the corolla-tube of the flowers visited. On the basis of the stratigraphical appearance of the anthophilous insects it is, then, possible to state that flower taxa with longer corolla-tubes are more advanced than those with shorter tubes and with dish- to bowl-shaped flowers.

A statistical analysis is carried out on the world's least anecdotically compiled survey of insect visits to flowers, *viz.*, Knuth's "Blütenbiologie", as far as the Central European area is concerned. For inductions within the insect-flower relationships as a whole, and starting from a restricted area, the following presupposition is required: the processes within the insect-flower relationships in other areas follow the same course as those in the Central European area (horizontal uniformitarianism). Because the recent insect-flower relationships are to be correlated with the phylogeny and the fossil record of anthophilous insects, a second presupposition is necessary: the processes within the insect-flower relationships in the past did not run differently from those in recent insect-flower relationships (vertical uniformitarianism).

The correlation of the phylogeny of the anthophilous insects with the evolutionary developments in the Angiosperm flowers in the widest sense (including, *e.g.*, the development of insect vision and the biochemical evolution of flower pigments) requires a philosophical procedure, often indicated as "reciprocal illumination", which is a sort of spiral reasoning, necessary for founding a sound evolutionary basis for floral ecology.

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Nectar robbing of the flowers of the broad bean (Vicia faba L.), regarded from the viewpoint of fitness

The flowers of the Fabaceae can be distinguished in monadelphous and diadelphous types. The former type does not produce nectar, although there is a honey-guide present; visitors find a compensation in large quantities of pollen. Diadelphous flowers do produce nectar. The nectary is situated within the staminal sheath near the receptacle, and the nectar is accessible through two slits, next to the loose stamen, at the same height as the nectary. Thanks to these slits no damage is caused when nectar is collected.

Investigations have been made of the visitors of the broad bean, *Vicia faba* L. (diadelphous). Long-tongued bumble-bees (*Bombus agrorum*) are able to reach the nectar legally, by pressing down keel and wing, forcing the head into the opening of the corolla-tube and inserting the tongue into the tube. Short-tongued bumble-bees (*B. terrestris*) cannot do it the legitimate way, because of their short tongue and relative large head. They rob the flowers by biting holes through calyx and corolla,

mainly in the upper part of the flower, at such a distance of the nectary that this is within reach of their tongue. Our observations wholly confirmed that the robbing has no negative effects on the yield.

INOUYE (1983) distinguishes primary and secondary nectar robbers: the former bite the holes themselves, the latter use holes made by primary robbers. *B. terrestris* acts both ways. In the same publication, Inouye adds a new dimension to the phenomenon nectar robbing, by interpreting it from the viewpoint of fitness. In our case, it is evident that the way *B. agrorum* collects nectar, by entering the flower from the front, is less efficient than simply landing on the upper part of the flower, biting a hole (if necessary) and robbing the nectar, as *B. terrestris* does.

INOUYE, D. W. (1983): The Ecology of Nectar Robbing, in: B. BENTLEY and T. ELIAS (Ed.) *The Biology of Nectaries*, pp. 152–173. Columbia University Press.

RAOUL J. BINO (*Hugo de Vries-laboratorium, Plantage Middenlaan 2a, 1018 DD Amsterdam*)

Nectar secretion in the dioecious gymnosperm Ephedra aphylla Forsk.

Studies by Porsch (1910) have shown that *Ephedra campylopoda* C. A. Mey is frequently visited by insects which consume the sugary pollination droplets exuded by the ovules of functionally female plants and by the ovules of morphologically hermaphrodite but functionally male plants. The importance of such data in connection with the advent of entomophily was pointed out by MEEUSE (1978). During an investigation into the possible incidence of entomophily in the strictly dioecious *Ephedra aphylla*, this species appeared to produce a sugary exudate on the reproduction units of both sexes. The investigation was carried out by the present author, together with A. Dafni (University of Haifa, Israel) and A. D. J. Meeuse (University of Amsterdam).

The sugary exudate is excreted on the so-called "perianth" in the male plants and on the "outer bracts" in the female ones. In addition, the female plants, like all other species of the genus, also exude a pollination droplet from the micropyle. Plants of both sexes are regulary visited by insects which consume the pollination droplets and the nectar excreted by the female reproductive units and also the nectar produced by the male ones.

In a preliminary paper (Bino et al., 1981) the incidence of entomophily in *Ephedra aphylla* was reported; for some generalities the reader is referred to the two earlier contributions.

BINO, R. J. & A. D. J. MEEUSE, (1981): Entomophily in a dioecious species of Ephedra: A preliminary report. *Acta Bot. Neerl.* **30**: 151–153. (1981).

MEEUSE, A. D. J. (1978): Why were the Angiosperms so successful? – A morphological, ecological and phylogenetic approach. *Proc. Kon. Ned. Akad. Wetensch. ser. C* **82**: 343–369.

PORSCH, O. (1910): Ephedra campylopoda, eine entomophile Gymnosperme. *Ber. deut. bot. Ges.* **28**: 404–412.

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Seed ferns and Angiosperms: relations

New discoveries and interpretations of both glossopterid and early angiosperm reproductive units lead RETALLACK & DILCHER (1981a, b) to the hypothesis of glossopterids being the likely ancestors of angiosperms. An early angiospermous female fructification is characterized by the joint occurrence of carpels and bitegmic ovules. It is likely that fructifications consisting of numerous follicles arranged helically on elongate axes (multifollicles) are ancestral in angiosperms. Each follicle is a fruit developed from a single conduplicate carpel; the fossil follicles of Mid-Cretaceous angiosperms are well cutinized and have numerous ovules attached submarginally to the inner surface and probably open adaxially. There is no evidence that phaneranthous bisexual flowers are more ancient than apetalous, unisexual reproductive units.

Glossopterid seed ferns were most abundant in the Permian Gondwanaland and became extinct in the Triassic. The female reproductive unit consists of numerous multiovulate structures, helically borne on a short shoot. Each ovule is surrounded by a single integument; they are scattered over the lower surface of a laminar structure which is typically adnate to an associated, sterile-like leaf.

One to several laminar structures per associated leaf occur. RETALLACK & DILCHER (1981a) consider the outer integument and the carpel of an angiosperm ovule homologous with the ovule bearing structure and associated leaf of glossopterids, respectively. Microsporangia, pollen, leaves, wood anatomy and age contradict a close relationship between glossopterid seed ferns and angiosperms.

At this time a more plausible hypothesis is that of a peltaspermaceous - gnetalean evolutionary lineage. KERP (1982) found peltaspermaceous female reproductive units in the Lower Permian. Since then, there exists a transition within a group of closely related female fructifications (*Autunia* to *Peltaspermum*) in subsequent time spans (Lower Permian to Upper Triassic). Parallel to this series there is a transition of associated pollen organs (*Pterispermostrobus* to *Antevsia*, respectively) and pollen (monosaccoid to bisaccoid to monosulcate, respectively). If one considers the peltate heads to be homologous with ovule-containing angiospermous carpels and the monosulcate pollen type to be derived from an alete bisaccoid condition, this lineage leads more conveniently to early angiospermous multifollicles and the characteristic, monocolpate pollen. Sulcate, gnetalean pollen types must then be closely related with or intermediate between peltaspermaceous seed ferns and angiosperms.

KERP, J. H. F. (1982): Aspects of Permian palaeobotany and palynology, II. On the presence of the ovuliferous organ Autunia milleryensis (Renault) Krasser (Peltaspermaceae) in the Lower Permian of the Nahe area (F.G.R.) and its relationship to Callipteris conferta (Sternberg) Broignart. *Acta Bot. Neerl.* **31**: 417–427.

RETALLACK, G. & D. L. DILCHER (1981a): Arguments for a glossopterid ancestry of angiosperms. *Palaeobiology* 7: 54–67.

— & — (1981b): Early angiosperm reproduction: Prisca reynoldsii gen. et spec. nov. from Mid-Cretaceous coastal deposits in Kansas, U.S.A. *Palaeontographica* (B) **197**: 103–137.

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Different effects of biotic pollination on the reproduction of Plantago lanceolata

In more or less humid environments the inflorescences of *P. lanceolata* are habitually visited by syrphids of the *Melanostoma-Platycheirus* assembly, which flies also act as pollen vectors. The effect of biotic pollination on the reproduction of this reputedly anemophilous species was investigated by caging in spikes during their flowering period within a gauze bag, thus rendering the inflorescences inaccessable to the hover flies but freely allowing pollination by air currents. After fructification the rate of fruit set was compared with that of uncovered control spikes. In open, wind-exposed areas, which make up the typical habitat of the ribwort plantain, fruit set of the caged-in spikes attained on the average 89% of the number of florets present originally. The reproductive effect of syrphid pollination appeared to be of only minor importance. On the other hand, in small, forest-enclosed meadows in S. Luxemburg with but little wind action the mean rate of fruit set of caged-in spikes turned out to be relatively low, *viz.*, 39%, whereas the reproductively effective contribution of the syrphids, *viz.*, 36% was considerable. An ensuing examination of seed set proper revealed that in open habitats 31%, and in the forest meadows 59%, of the capsules was two seeded (the ovary of this species normally contains two ovules). The latter reproductive result consequently must be attributed in particular to the effect of pollen transfer by the syrphids.

As had been assessed previously, the pollen of the plants from the forest meadows possesses an appreciably stronger adhesive capacity than that of populations from open areas. In the light of the information mentioned above this phenomenon may be interpreted as an adaptation to insect pollination under the locally prevailing conditions.

STELLEMAN, P. (1983): The significance of biotic pollination in a nominally anemophilous plant: Plantago lanceolata. *Proc. Kon. Ned. Akad. Wetensch.* ser. C (in press).

A. D. J. MEEUSE (*Hugo de Vries-laboratorium, Plantage Middenlaan 2A, 1018 DD Amsterdam*)

Angiosperm evolution and pollination strategies

The question whether the oldest Flowering Plants were entomophilous and bore ambisexual

"flowers" or anemophilous with unisexual ones is an essential and moot point in reconstructions of the evolutionary history of this group. If it is postulated that angiospermous seed plants are the descendants of advanced gymnospermous forms, the clear prevalence of dicliny among nearly all fossil and living Gymnosperms requires an at least one-time change of the sex distribution to account for the monocliny of many recent Angiosperms. This inevitable prerequisite is substantiated by conditions among most of the recent gnetate forms which often tend to be morphologically ambisexual but have remained functionally unisexual. The pollination droplets, also produced by the sterile ovules borne on male individuals, provide food for insects which accordingly pay attention to both male and female plants and become effective pollinators. A cumulative progression towards a complete state of monocliny could gradually develop out of this primary situation, mechanisms precluding autogamy becoming perfected concomitantly.

There is, however, an alternative pathway towards entomophily, *viz.*, the persistence of dicliny coupled with the advent of nectarial secretion in the immediate vicinity of the reproductive organs of the male and of the female individuals (as discovered by Bino; compare the report of his lecture). Such plants could thus retain the advantages of outbreeding and combine these with an effective animal pollination. Most probably certain angiospermous taxa inherited and retained this syndrome and never had monoclinous progenitors (*e.g.*, Myristicaceae, Cucurbitaceae, some or all Dioscoreaceae and Euphorbiaceae).

Such an explanation of the origin of plant-pollinator interactions have a considerable bearing upon the above-mentioned question concerning the ancientry of entomophily or of anemophily and indirectly also on the problem of a strictly mono- or a more pleiophyletic form of evolution of the recent Magnoliophyta and must be taken into account in all discussions concerning angiosperm phylogeny.

Lit.: MEEUSE, A. D. J. (1982): Evolution of the Magnoliophyta: Current and dissident viewpoints. *Ann. Rev. Pl. Sci.* **2**: 393–442. New Delhi.