

## MEETINGS OF THE ROYAL BOTANICAL SOCIETY OF THE NETHERLANDS

MEETING OF THE SECTION FOR FLOWER BIOLOGY ON SEPTEMBER 14, 1979

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### Deceptive pollination syndromes in some Orchids in Israel

About 23 species out of the 28 Israeli orchids have no food reward and therefore, are candidates to have deceptive means to attract pollinators.

*Epipactis veratrifolia* (syn. *E. consimilis*) is pollinated mainly by the Syrphid fly *Ischionodon aegypticus* which oviposited on the flower which has aphid mimics, in addition to the nectar in the hypochyle, (IVRI & DAFNI 1977).

*Cephalanthera longifolius* has the same colour combination, in the human spectrum, as has *Cistus salviifolium*: yellow-white. The labellum of *C. longifolius* has a patch of yellow hairs of the same colour and of the same size as the pollen of *C. salviifolius*: ca. 50  $\mu\text{m}$ . The hairs serve as pollen mimic for a *Halictus* bee which pollinates both species. *C. longifolius* has a sweet fragrance which also can attract pollinators in the absence of *C. salviifolius*, but in that case the fruitset is less. We suggest to term this situation as a "facultative floral mimicry".

*Orchis israeliensis* mimics *Bellevia flexuosa* by its colours, and shares its pollinators, which are *Anthophora* bees and Bombilid and Syrphid flies.

#### REFERENCE

IVRI, Y. & A. DAFNI (1977): The pollination ecology of *Epipactis consimilis* Don (Orchidaceae) in Israel. *New Phytologist* 79: 173–177.

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### *Passiflora* and *Xylocopa*: economic and evolutionary considerations

The yellow passionfruit, *Passiflora edulis* f. *flavicarpa* Degener, is grown commercially in St. Vincent, West Indies, where the most frequent visitor to the flowers is the carpenter bee *Xylocopa* sp. nr. *mordax* Smith. Evidence for this bee's role in pollination comes from observations on its behaviour on the flowers; from the finding that pollen arrives on the stigmas at the time of day when stigmas are recurved and bees are visiting flowers; and from an exclusion experiment. Flowers were tagged, or tagged and bagged in muslin bags. Some were self-pollinated, some cross-pollinated and some left untreated. Fruit set was assessed after five days. The results demonstrated self-incompatibility, and showed that exposure to natural pollinators resulted in a percentage fruit set (27% on that day) that was higher than that of flowers from which pollinators were excluded (0%) but lower than that of hand-cross-pollinated flowers (73–77%). Studies of the bees' behaviour indicate that they probably spent much of their time seeking nest-sites, concentrating nectar by evaporating it on the tongue, or collecting pollen from *Gliricidia*. The bees' pollinating effectiveness might be improved by providing more dead wood for nest sites, and more flowers such as *Gliricidia* from which they can collect pollen.

This introduced plant seems not to be a perfect match for the native species of *Xylocopa* in some features of its floral biology. Consideration of these in relation to the pollination syndrome suggests another feature to be added to the list of nine characteristics of tropical *Xylocopa* flowers of Van der Pijl (1954): provision of pollen which, because it is unacceptable to the bee, is allowed to remain ungroomed on the back for long enough to participate in pollination. It is concluded that whether *P. edulis* is oligophilic or monophilic, it has probably had *Xylocopa* or a similar large bee as a major partner in its floral evolution.

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**Partitioning of the floral resources of *Justicia aurea* (Acanthaceae) amongst pollinators and nectar thieves.**

A study of competition and co-existence amongst foragers on the flowers of *Justicia* was carried out at La Selva, Costa Rica. The flowers are characteristically ornithophilous, secreting abundant nectar which was of fairly constant concentration but which varied considerably in volume, and hence in caloric reward, through the day, with maximum sugar availability in the early morning. This reward was utilised by a broad spectrum of visitors, each of which showed some diurnal patterning in their foraging behaviour. Two species of hummingbird (*Phaethornis superciliosus* and *Campylopterus hemileucrus*) visited the flowers early in the day, and apparently defended territories. These two species were the only legitimate visitors and potential pollinators. Another smaller hummingbird (*Phaethornis longuemareus*) also foraged for the floral nectar, but collected it illegitimately by piercing the base of the corollas. This hummingbird foraged in different parts of the *Justicia* patch continuously through the day, but was excluded from the territories of the larger birds in the morning.

In addition, the nectar was collected illegally from perforations in the corollas by stingless bees of the genus *Trigona*, and by ponerine ants who patrolled the inflorescences, thus creating further competition for the limited floral resources. While these visitors also showed temporal patterning in their foraging, their periods of activity overlapped considerably with each other and with the hummingbird visitors. Further examples of aggressive interference between the most common ant species (*Ectatomma ruidum*) and three species of *Trigona* were observed; but if the foragers were only separated along a temporal axis, considerable exploitative competition would also be inevitable.

Consequently an analysis of the spatial distributions of foragers was required. Rather than using a conventional "geographical space" axis, the best correlations were obtained by considering foraging in relation to "microclimatic space", and in particular to the insolation of individual flowers. This effect could be partly explained by the direct effects of insolation on temperatures near the flowers, and hence on the relative energetic costs for foragers of different sizes; but sun and shade patterns also had consequences for the timing of nectar secretion in different areas of the patch. Hence each species of forager appeared to have definite preferences for shady or sunlit areas.

Thus by combining the visiting frequencies and distributions of each of the three species of birds, the three species of *Trigona* and the ponerine ants along temporal and microclimatic axes, it was possible to present a single scheme allowing for the co-existence of these diverse foragers. There were minimal overlaps in the resource utilisation, except in those situations where attempts at direct aggressive exclusion between species had been observed.

Nevertheless, the consequences for the plant appeared to be inadequate pollination, with less than three percent of the anthers receiving pollen as a result of the larger hummingbirds' activities, and with little or no fruit set. This may have resulted from the high incidence of nectar robbery; the "thieves" could reduce the overall profitability of the patch of flowers to the legal visitors during the crucial period of the day when the anthers had fully dehisced and stigmas were receptive. *Justicia* is probably not endemic at La Selva, and it may be experiencing climatic differences which have disturbed the normal timing and synchrony of anthesis and so resulted in this disruption of its pollination ecology.

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**Pollination mechanisms in Polygalaceae**

With their secondary pollen presentation on the style the Polygalaceae form an important family in the study of the evolution of pollen presentation mechanisms. The stigma gland produces a sticky fluid, which becomes smeared onto the pollinator and to which the pollen adheres. The four types of

pollen presentation that are recognised in the Fabaceae are also represented in the Polygalaceae. Type 1, *Astragalus*-type, with movable carina, in *Polygala vulgaris* L., *P. comosa* Schkuhr, *P. chamaebuxus* L.; Type 2, *Lotus*-type, with pump, in *P. klotzschii* Chodat; Type 3, *Vicia*-type, with style-hairbrush, in *P. monticola* HBK var. *brizoides* (St. Hill & Mg.) Steyerm. and *P. violacea* Vahl; Type 4, *Medicago*- or *Genista*-type, with explosive flowers in *P. myrtifolia* L., *P. bracteolata* L., *Muraltia* spp.

These 4 types correlate with several of the diverse style structures (Brantjes & Van der Pijl, in prep.) in the family.

A, (spoon in front of stigma), B, (hair-pencil), E, (shelf in front of stigma) are found in type 1. F, (stump style ending behind stigma) is associated with type 2. G, (hair-basket behind stigma) is associated with type 3. H, (hammer stigma above hole in style) is associated with type 4. The other style forms (C, D, I, J, K) remain to be analysed. Minor variants occur in the morphology of the lower petal (position of the hinge, or its absence, and the fingerlike appendices).

The precise localisation of pollen deposition on the insect results in reproductive isolation between the sympatric *P. monticola* var. *brizoides* and *P. monticola* in Brasil, which share the same set of bee-visitors (Brantjes, in prep.). Similar reproductive isolation by dimensional differences may occur between two European species which differ in the distance from the stigma to the nectary: *P. vulgaris*, 3.0 mm; *P. comosa*, 2.2 mm.

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#### Pollen in tertiary insects

This communication gives an interim survey of the first attempts of pollen analysis on insects enclosed in amber. Three attempts appeared to be successful.

A piece of Baltic amber containing a specimen of *Scraptia pseudofuscula* Ermisch was divided into two parts: one with the beetle and one of pure amber (matrix). The two fragments of 0.15 and 0.25 gram respectively were dissolved in concentrated sulphuric acid and following acetolysis for a short period microscopic slides were made.

From the sample with *Scraptia pseudofuscula* 90 pollen grains could be extracted (*Pinus* 12, *Quercus* 38, Urticaceae 8, *Betula*-type 7, Gramineae 10 and single grains of *Rumex*-type, Cruciferae, *Zelkova*, *Aesculus*, *Acer*-type and Chenopodiaceae, and 9 grains indet.) and from the sample of pure amber (matrix) only 4 (*Artemisia*-type 2, and single grains of *Pinus* and *Betula*-type). Here it should be mentioned that the technique was not yet optimal. If proper equipment will be available the amounts of pollen found will certainly rise and may approximate those found in recent resins by LANGENHEIM & BARTLETT (1971).

The presence of *Aesculus* in the sample indicates Pliocene as time of origin. The results indicate that the specimen of *Scraptia pseudofuscula* visited the flowers of *Quercus* to feed on pollen (all grains were more or less damaged which indicate some gnawing by the mandibles during intake) before it got stuck to the resin. The composition of the pollen types (except those of *Betula*, see below) indicate a period in the year corresponding with the Western European month of May in recent times. The *Betula* grains cannot be taken into account because at the time of acetolysis and preparation of the microscopic slides (10th of February 1978) several *Betula* trees near the laboratory were flowering, so they could easily represent an impurity in the preparation.

The recent *Scraptia fuscula* Müll., which is the closest relative of *S. pseudofuscula*, is indeed found on flowering trees and shrubs along the borders of forests and recent flowers of *Quercus* are frequently visited by the beetles to eat pollen.

In the same way a mordellid beetle from Baltic amber (because of the quality of the amber the identification below family level of the beetle was not possible) was examined and it appeared that it visited a flower of a species with tricolporate, rather coarsely reticulate pollen. This pollen type is not yet identified, but it almost certainly means that the flower which produced it was entomophilous. This is in contrast with the situation in *Scraptia fuscula* which visited the anemophilous flowers of *Quercus* (it is hard to believe that temperate *Quercus* was entomophilous in the Pliocene).

The third attempt concerns a meliponine bee (Apidae-Meliponini) from Dominican amber

(Oligocene-Miocene). It appeared that the bee visited the flowers of *Hymenaea* (Leguminosae) to collect pollen before it got stuck in the resin, or got *Hymenaea* pollen on the body in the nest before it visited a tree of the same genus (*Hymenaea* produced the Dominican amber) to collect resin (as recent Meliponini do to form the propolis) which became fatal for the specimen. The *Hymenaea* pollen represents entomophilous flowers and is new for the Central American Tertiary.

It appeared that fossil pollen which represents entomophilous flowers can be demonstrated in fossil anthophilous insects. In this way new fossil pollen types can be described, because in stratigraphical pollen analysis mostly pollen is found which represents anemophilous flowers. Pollen analysis on fossil insects on a larger scale can provide knowledge on the palaeo-flower ecology. It may be possible to describe spectra of pollen types from amber corresponding with areas of the geological time scale.

#### REFERENCE

LANGENHEIM, J. H. & A. BARTLETT: (1971). Interpretation of pollen in amber from a study of pollen in present-day coniferous resin. *Bull. Torrey bot. Club* **98** (3): 127–139.

#### MEETING OF THE SECTION FOR PLANT MORPHOLOGY AND ANATOMY, AUGUST 26–30, 1979.

The section for Plant Morphology and Anatomy participated in the International Wood Anatomy Congress, organized by the International Association of Wood Anatomists and co-sponsored by the Wood Quality Subject Group of Division V of the International Union of Forestry Research Organizations.

Abstracts and titles of the 44 papers presented, covering the fields of comparative wood anatomy, ontogeny, morphogenesis, ultrastructure, wood quality as well as bark and bamboo anatomy have been published in *IAWA Bulletin* 1979/2&3: 34–43.