

# Meetings of the Royal Botanical Society of The Netherlands

## MEETING OF THE SECTION FOR PLANT SYSTEMATICS AND GEOGRAPHY ON 25 NOVEMBER 1988

### TOWARDS A CONSERVATION PROGRAMME FOR *GENTIANA* S. L. IN THE NETHERLANDS

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Recently research was started on the functioning and population dynamics of species that are endangered in the Netherlands. In the project we focus on the Dutch *Gentiana* and *Gentianella* species. The study was started with the perennial herb *Gentiana pneumonanthe*, and successively the other Dutch species were included: the very rare, perennial *G. cruciata* and the *Gentianella* species *amarella*, *campestris*, *germanica* (all behaving as annuals and/or biennials) and the extremely rare perennial *G. ciliata*.

If gene flow is limited or even absent so that variation decreases and inbreeding takes place, fitness is negatively influenced. This is the very problem many endangered species are presently facing.

Populations of *Gentiana pneumonanthe* are genetically not impoverished: several loci have heterozygosity levels around 50%. Without exception all polymorphic loci are bimodal sometimes with fixation for either allele (some populations are strongly differentiated). Low frequency alleles or private alleles (unique to one population) are essentially lacking. This hints at a bottleneck in the population from which all studied populations originated. Insufficient time has elapsed to build up new variation or recurrent bottlenecks have removed this (low frequency) recent variation.

*Gentiana pneumonanthe* is being studied now in nine localities (about 20 permanent plots), situated in the greater part of the Dutch distribution area, including the main habitat types, i.e. poor meadows and heath vegetations of *Erica* and *Molinea*. The first data indicated a striking lack of seedlings and juveniles in some of the sites. It also became obvious that many individuals of a population became dormant and remained underground for 1 (or more) years(s), thus forming a potential reserve of the population, comparable to the situation in many orchid species. Rabotnov diagrams and transition matrices will produce more insight in the population dynamics. Other aspects under study are: predation effects of *Maculiniaalcon* (*Lepidoptera, Lycaenidae*) and other ovary predators such as *Dasyneura* sp. (*Diptera, Cecidomyidae*), pollination biology and seed-setting ratios and (syn-)ecological relations.

*Gentianella campestris* and *G. amarella* plots were installed in the dune area and similar studies have been started; the same holds for *G. germanica* and *G. ciliata* in South Limburg.

This study may be the instigation of a broad and integrated program of conservation of *Gentiana* and *Gentianella* in the Netherlands.

## SPORE TYPES OF POLYPODIACEAE (FILICALES)

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A representative sample of spores taken from 240 species out of a total of c. 550, and representing all the genera of Polypodiaceae, was studied with light and scanning electron microscopy. Additionally, the spores of c. 55 species were studied with the transmission electron microscope (TEM).

The spore wall consists of two main layers, the exospore and the perispore which are easily distinguished using TEM. The exospore consists of a thin innermost layer with a well-developed outermost layer superimposed on it. It appears that the surprising morphological variation in outer surface ornamentation is dictated by properties of either the exospore or the perispore or both.

Within the Polypodiaceae four different types of exospore are recognized. The differences between the types relate to the composition and thickness of the walls, as well as to differences in types and distribution of submicroscopic channels and in the presence or absence of tangential bandings. The greater part of the species have an exospore that conforms with Lugardon's *Blechnum spicant* type of exospore. This type obviously represents the original condition in the family. The *Lepisorinae* have a *Belvisia* type of exospore. The exospore is rather thick and throughout provided with microchannels situated perpendicularly to the surface. The *Polypodium vulgare* type of exposure has a verrucate outer surface and shows, in cross-sections, microchannels near the aperture only. This type has been found in different natural groups; it obviously represents a parallel development. The *Microsorium membranaceum* type of exospore is a unique development within *Microsorium*.

A significant number of species have an indistinct or scarcely developed perispore. However, quite a number of markedly developed perispores were encountered. Within one genus the perispore might be either almost lacking or most complex. Also, a similar, intricately shaped perispore may occur in quite different monophyletic genera. Obviously the perispore is most liable to change.

## INVESTIGATIONS ON FRUITS AND SEEDS OF ANNONACEAE AND A COMPARISON WITH THE RESULTS OF FLOWER MORPHOLOGICAL RESEARCH

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Within the framework of the multidisciplinary project on Annonaceae, coordinated in Utrecht character analyses on flowers and on fruits and seeds of Annonaceae (world-wide) were carried out.

A first attempt to analyse fruit and seed characters resulted in several morphological series. An incomplete and simplified diagram of these series is presented. The highly variable genus *Polyalthia* is taken as a starting point of several series, a.o.: via apocarpous fruits with one basal seed to syncarpous fruits with rudimentary arils, with or without basal 'collar'; via several lateral seeds in one row towards many lateral seeds in two to several rows, partly with and partly without rudimentary arils; or via several lateral seeds in one row towards moniliform fruits with lateral seeds in one row.

Groups based on fruit and seed characters, however, do not always correspond with groups based on flower morphological characters. Examples both of congruence and divergence are given. Finally the position of *Monodora* and *Isolona*, two genera which are kept together as a separate subfamily of Annonaceae by most authors, is discussed. Neither flower morphology nor fruit and seed morphology supports the placing of these genera into a separate subfamily.

## ENTROPIC INDIVIDUALS

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Immediately after the rediscovery of Mendel's laws attempts were made to connect the generally accepted typological species concept with Genetic Theory and Darwin's Evolutionary Theory. The result was a number of species concepts, each emphasizing different aspects of species. Attempts to combine the aspects into one 'synthetic' species concept seem to obey Gödel's theorem thus far: the logically correct ones are incomplete.

Evolutionary Theory is the only available scientific theory explaining the diversity of living nature. A species concept, consistent with Evolutionary Theory is the most satisfactory one, but also implies a choice between relevant aspects. The ongoing debate whether natural species are to be regarded as sets (as structurally defined classes of objects) or as unique, cohesive individuals has clarified the implications of some alternative choices.

The attempts towards a unified theory of living and non-living nature, recently developed by Brooks and Wiley (*Evolution as Entropy*, 1988, 2nd edition. University of Chicago Press) provides fundamental concepts from physico-chemical and mathematical laws. Their major message is that the evolutionary process must be an entropic process. This theory resulted in the development of an optimal criterion for phylogenetic trees. Disjunct species (*Acacia koa/A. heterophylla* and *Rhynchosia rothii*), chaotic supraspecific evolution (tribe *Millettieae*), sympatric uniparental (*Indigofera*), and parapatric (*Millettia* sect. *Fragiliflorae*) speciation, are demonstrated to show some applications of these theoretical considerations.

## MEETING OF THE SECTION FOR THE RELATION BETWEEN PLANTS AND ANIMALS, 19 NOVEMBER 1988

THE SYSTEMATICS OF THE MALAYSIAN ANT-FERN GENUS *LECANOPTERIS* (POLYPODIACEAE) AND ITS INHABITING ANTS

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The Malaysian ant-ferns are provisionally accommodated in one genus *Lecanopteris* (Polypodiaceae; Filicales). All the species are epiphytes and live in association with ants which inhabit the variously swollen hollow or otherwise deviating rhizomes. The genus is divided into two inferred monophyletic groups. The *Myrmecophila* group (with four species) is characterized by its scaly rhizome that is devoid of hairs, and a simple branching pattern of the rhizome. Cladistic analysis has revealed that *Lecanopteris sarcopus* (Teijsm. & Binn.) Copel. (Sulawesi, Luzon) and *L. crustacea* Copel. (West Malaysia) are taxonomically strongly linked species, and that their closest relative, *L. mirabilis* (C. Chr.) Ching, is endemic to the Eastern Moluccas and New Guinea. *L. sinuosa* (Hook.) Copel. is widespread in Malaysia. The nine species of the *Lecanopteris* group have a rhizome which

is covered with hairs, at least when young, and a complex system of galleries. Six species of this group are endemic to Sulawesi. The relationships within this group have not been fully resolved yet.

In order to establish the nature of the inferred mutualism between the ant-fern and the ant, a taxonomic study of the ants living in association with the ant-ferns was executed by R.V. Hensen. From a large amount of preserved ant-fern collections only 54 were found with preserved ants. They represent 11 ant-fern species belonging to six different genera from four different subfamilies of the Formicidae. Ants are not uniquely associated with ant-ferns and vice versa. For instance, in different plants of *L. sinuosa*, seven different species of ants from three different subfamilies were found. On the other hand, the ant *Crematogaster difformis* Smith was found in the rhizomes of five different *Lecanopteris* species. Widespread ant species occurred in ant-fern species with a limited distribution and vice versa. These data suggest a low specificity of the two partners.

An anatomical study of the rhizomes confirmed the idea put forward by earlier authors that the cavities in the rhizome result from the breakdown of water storage tissue present in the rhizome apices where the fronds develop. Consequently, the cavities present in the older parts of the rhizome are interpreted as waste, which at the same time provides a nesting facility for ants. The nature of the inferred mutual relationship between an ant-fern and its ant species needs further study.

#### MYRMECOCHORY IN *POLYGALA VULGARIS*, *LUZULA CAMPESTRIS* AND *VIOLA CURTISII* IN A PRIMARY DUNE VALLEY ON THE ISLAND OF TERSCHELLING

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Myrmecochory, or dispersal of seeds by ants, is considered to be a mutual relationship from which both plants and ants benefit.

For the ants, the lipids, sugars, and sometimes also proteins and vitamins in the seed appendages are all useful supplements to their normal diet. The benefits for the plants, however, are often not so clear. We therefore attempted to study the relationship between ants and three myrmecochorous plant species that all occur in a primary dune valley on Terschelling.

It was found that fresh seeds of all three species were readily taken by the ants into their nests. The most active dispersing species was *Lasius niger*, which is very abundant in young dune valleys. It appeared that *Lasius niger* had a distinct preference for the seeds of *Polygala*, which is a specialized myrmecochore, as compared with *Luzula* and *Viola*, both diplochore with a relatively smaller food-body.

Mapping studies demonstrate that the dispersal of the seeds by ants has a marked effect on the distribution of the established plants of *Polygala* and *Viola*. A large proportion of the adults is found on or in the direct vicinity of active ant nests, while the juveniles and seedlings are clearly clustered on the nest mounds. In this light it may be important that it was found that the nests of two of the seed dispersing ant species, namely, *Lasius niger* and *Tetramorium caespitum*, are richer in some essential plant macronutrients, e.g. potassium, phosphorus and nitrate.

Myrmecochores that grow on ant nests may therefore have a considerable advantage in competition in nutrient-poor environments, e.g. primary dune valleys. However, observations indicate that other factors, like escape from seed predation by rabbits by burial inside nests, and development away from competition with other plant species, may also be important for a successful relationship between the plants and ants.

EFFECTS OF THE PHYSICAL ENVIRONMENT ON THE FORAGING BEHAVIOUR OF THREE BUMBLEBEE SPECIES VISITING FRESH AND SENESCENT INFLORESCENCES OF *LUPINUS POLYPHYLLUS* LINDLEY

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From 1984 onwards, the foraging behaviour of bumblebees on *Lupinus polyphyllus* was studied. An increasing force and pollen gradient along the inflorescence was observed. Bumblebees forage in an upward direction, but leave prematurely, probably because the bee is incapable of activating the pollination mechanism above a certain tier. Our study of the relation between environmental conditions and the foraging behaviour revealed that: (i) with an increasing relative humidity (*RH*) and a decreasing temperature (*t*), *Bombus terrestris* leaves the inflorescences at lower tiers; (ii) the mean tier with the most within-flight movements (*WF*) is situated lower at a higher *RH* and lower *t*. These relations between *RH* and *t* can be explained by (a) the turgor pressure in the flower-cells changes and, thus the force required to free the pollen; or (b) the behaviour of *B. terrestris* changes itself. In 1987, a presumed positive correlation between the ability to gather pollen (tiers with *WF*) and the weight of bumblebees was studied. We observed *B. terrestris* (mean weight 0.208 g), *B. lapidarius* (0.156 g) and *B. agrorum* (0.151 g) on 4 days: 25-vi (*RH*: 62–65%, *t*: 17–21°C); 2-vii (*RH*: 60–70%, *t*: 18–27°C); 7-vii (*RH*: 50–64%, *t*: 27–33°C); 8-vii (*RH*: 66–98%, *t*: 17–26°C). The following results were obtained. 25-vi; *WF* equally spread over the tiers within the flight-range of *B. terrestris* (other bees were rarely foraging), 2-vii; *B. terrestris*, *WF* on tiers 2, 3, 4, *B. lapidarius*, the same, *B. agrorum*, *WF* on tier 2, 7-vii; all species, *WF* on tier 1 (the first tier with open flowers), 8-vii; all species, *WF* on tier 1–2 (somewhat lower than on 7-vii). There were no differences between the bee species in their preference for tiers due to weight, but it appeared that each bumblebee species used its own technique in relation to its size to manipulate the pollen-release mechanism. All bees select for senescent over fresh inflorescences and take advantage of senescence in being able to forage at higher tiers and in gathering pollen out of the (almost open) keel of withering flowers more easily. The differences between the results over the last 2 days can be explained by the differences between relative humidity and temperature.

POLLINATION OF THE DICHO-GAMOUS, PROTANDROUS AND 5-MEROUS FLOWER OF *THEVETIA PERUVIANA* (K) PERS. SCHUM. AND ITS MONOTROPIC POLLINATOR *XYLOCOPA LATIPES* F.

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Like other tropical apocynaceous flowers, *T. peruviana* has corolla scales. These long, hairy scales are connected to each other to form a plate. The basal part of the flower tube occurs first and is the nectar-room. It is separated from the upper part of the tube by an extension. The second room contains the five stamens and the disc. The third room is the wide open ante-room. Part of the disc is the stigma; represented by an annular ring of specific cells. Anthers dehisce in open flowers, with free and dry pollen.

After *Xylocopa* has alighted with some difficulty on the flower, it is confronted by the above mentioned plate, which bars the entrance to the nectar-room. According to its innate behaviour, the

*Xylocopa* gains entrance to the nectar by biting holes in the tight hairy pattern. In search of the nectar the bee moves over the surface of the disc with its tongue and thus contacts the dry pollen, but, because of its dryness, the pollen does not adhere to the tongue. Before the tongue can transfer pollen to the stigma, it is necessary for the fertile stigma to exude a sticky fluid. It is at this stage that the bee drinks and alternately flicks its tongue in and out of the nectar-room, the dry pollen then comes into contact with the sticky exudate. By these means the exudate enables the pollen to attach itself to the tongue of the bee. The tongue is then able to transfer pollen to the stigma. Cross-pollination can take place when the bee leaves the flower to visit another one. After having alighted on another flower the bee repeats its performance and in so doing establishes cross-pollination.