

MEETINGS OF THE ROYAL BOTANICAL SOCIETY OF THE NETHERLANDS

MEETING OF THE SECTION FOR PLANT TAXONOMY AND PHYTOGEOGRAPHY ON 18 OCTOBER 1985

THE MEETING WAS A WORKSHOP ON THE SYSTEMATICS OF THE POLYPODIACEAE (FILICALES).

E. HENNIPMAN (*Vakgroep Plantensystematiek en -geografie, Institute of Systematic Botany, Heidelberglaan 2, 3584 CS Utrecht*).

Posing the problems

1. Methods of phylogeny reconstruction. The central focus of the Polypodiaceae Project is understanding of the evolutionary history of this taxon. We are developing discussions about this much disputed issue as part of the process of establishing systematic relationships both between species of inferred monophyletic groups, and also between (groups of) genera.

P. Hovenkamp is dealing with an a priori approach to phylogenetic reconstruction of the genus *Pyrrosia* (51 species) whereas M.C. Roos is applying in cooperation with Dr. M. Zandee an a posteriori method in reconstructing the phylogeny of the drynarioids (31 species).

Under the joint supervision of Dr. P. Hogeweg, P. Veldhoen is showing the results of establishing relationships between (groups of) genera using several numerical methods.

2. Character analysis. Systematics of pteridophytes is hampered by the general lack of datamatrices of selected characters. At present, the search for new character sets showing distinct character states in Polypodiaceae is concentrating on characters from low integration levels, e.g. cells, ultrastructure of cells, and molecular data.

Electrophoretic analysis of isozymes and allozymes of Polypodiaceae started last summer in a joint project with Prof. Haufler, Kansas, who spent his sabbatical leave in Utrecht to help establish this kind of work in Utrecht.

Ultrastructural data on spores and sporogenesis are becoming available through a research grant given to G.A. van Uffelen, whereas Hennipman and Verduyn are finalizing an elaborate data matrix on the (ultra)structure of spores of ca. 250 species of Polypodiaceae. Freeze-breaking techniques are at present being applied on sporangia in close cooperation with research workers at the British Museum (Nat. Hist.), London and elsewhere.

Baayen is demonstrating the significance of comparative anatomical data on (cells of) indument of fronds (hairs, scales and paraphyses) using traditional microscopical techniques; T.E.M.-studies on glandular cells are in progress.

At present other workers are concentrating on ontogenetic studies of rhizome scales and venation patterns.

Vicariance phytogeography will be applied for the first time using the tracks of species of genera that have already been monographed. The results will be compared with those obtained using classical methods.

A great many workers in the Netherlands and elsewhere are working together toward solutions of the problems mentioned. See also HENNIPMAN (1985).

HENNIPMAN, E. (1985): Progress report of the Polypodiaceae Project. *Taxon* 34: 354.

While revising the genus *Pyrrosia* large variability in rhizome morphology was encountered. A general pattern could be recognized in which two rows of fronds alternate with two rows of lateral branch buds. Each bud seemed to be associated with the frond directly apical to it, and is not of axillary origin.

After study of a number of other Polypodiaceae cultivated in the botanical gardens of Leiden and Utrecht it was found that with few deviations this pattern is found in all Polypodiaceae. The relevance of the deviating structures could not be assessed.

Two aspects of this pattern were discussed: 1. How does the pattern develop? 2. Does it occur outside Polypodiaceae as well? A survey of available literature showed that two possible patterns of development have been proposed. According to one, all branching in ferns is due to lateral branching of a main axis (TROLL 1937); the other supposes all branching to be the result of apical dichotomies (BIERHORST 1977). The second view was adopted and used as a basis to discuss the views of NAYAR *et al.* (1985) about the rhizome morphology of the genus *Nistarika*. With regard to the generality of the pattern, the Polypodiaceae were compared to Davalliaceae on basis of two independent aspects: the spatial relation between branch and frond, and the numerical relation between (numbers of) branches and fronds. In Davalliaceae the numerical relation is similar to that in Polypodiaceae (1 : 1), the spatial relation, however, seems to be fundamentally different, with buds located just in front of the fronds instead of behind.

The preliminary conclusions reached were: 1. Modifications of a basic Polypodiaceous pattern may provide interesting characters within genera as well as a basis to compare different genera. 2. The numerical and spatial relations of branch initials and fronds may provide a basis for comparison of Polypodiaceae with other families of rhizomatous ferns. However, as yet an adequate theory of development that is able to explain the diversity in a unified way is still lacking.

BIERHORST, D.W. (1977): On the stem apex, leaf initiation and early leaf ontogeny in Filiclean ferns. *Amer. J. Bot.* **64**: 125–152.

NAYAR, B.K., P.V. MADHUSOODANAN & M.J. MOLLY (1985): *Nistarika*, a new genus of Polypodiaceae from Silent Valley, South India. *Fern Gazette* **13**: 33–42.

TROLL, W. (1937): *Vergleichende Morphologie der höheren Pflanzen I*. Borntraeger, Berlin.

G.A. VAN UFFELEN (*Rijksherbarium, Postbus 9514, 2300 RA Leiden*)
Sporogenesis in *Drynaria sparsisora* (Desv.) Moore (Polypodiaceae)

Spores of the Polypodiaceae are bilateral and monolete. The exospore may be smooth or variously sculptured. A perispore is present in all species and can be very thin and inconspicuous or thicker, with various kinds of ornamentation. The endospore is not present until germination.

I applied TEM to 14 species of Polypodiaceae. Not all stages of sporogenesis have been studied in all species. The species most extensively studied, with TEM and SEM, is *Drynaria sparsisora*, in which many different stages may be found in one sorus.

There are two main difficulties to be overcome in studying sporogenesis. First, it is very difficult to capture the dynamics of a process in the series of snapshots one gets while studying fixed, dead material, and, second, it may be difficult to place this series of snapshots in chronological order.

I distinguish six main stages in sporogenesis: presence of spore mother cells, meiosis, formation of: plasmalemma, inner exospore layer, outer exospore layer, perispore.

Some problems awaiting an answer are:

- Where do the exospore precursors originate? In the spore cytoplasm (haploid, gametophytic phase) or in the tapetum (diploid, sporophytic phase)?
- During formation of the outer exospore layer the differences between the species in Polypodiaceae start to show. In *Drynaria* almost all of the outer exospore layer is deposited in lumps and the exospore is not smooth until its formation is complete. In other species, there is a different succession of smooth and patterned stages in exospore formation. This may be of systematic significance in Polypodiaceae.
- It is not quite clear whether the increase in size during sporogenesis is caused by intercalary growth

or whether the exospore is supple enough to stretch. Such stretching may also account for some of the changes in surface patterning during exospore formation.

– What factors determine the surface structure of the exospore? A mucopolysaccharide coat, the ambient temperature, electro-magnetical forces, micro-tubules? It seems impossible that the disorganized periplasmoidal tapetum can contribute anything but simple precursors.

– After exospore formation is completed, the perispore, which originates from the tapetum, is formed. In Polypodiaceae an enormous variation in perispore morphology exists. It is difficult to realize that the often beautifully patterned perispore is organized by the tapetum, which is almost completely degenerated at this stage. The blobs that play a role in perispore formation seem to be found almost universally.

M.T.M. BOSMAN (*Rijksherbarium, Postbus 9514, 2300 RA Leiden*)

Preliminary results of monographic studies in *Microsorium*

Within the group of microsoroid ferns generic boundaries, especially of *Microsorium* (= *Microsorium* auct.), have never been satisfactorily defined. At present, the tropical fern genus of *Microsorium* is usually characterized by small, round, superficial and irregularly scattered sori, clathrate scales, and usually thin frond texture. These character states are neither exclusive for the genus nor cover all species, and this has led to the uncertain position of a considerable number of species.

Research on soral position in relation to venation patterns (partly based on HETTERSCHIED & HENNIPMAN (1984) has facilitated a provisional delimitation of *Microsorium* s.s. All of the 40–50 species of this genus now show small or medium sized superficial sori, which are round and sometimes confluent or slightly elongated and which are distributed either irregularly or more or less regularly in rows parallel to the secondary veins. In the latter case there are at least two sori on (or near to) most connectives between two adjacent secondary veins. This circumscription thus excludes the acrostichoid species (e.g. *Colysis* and *Leptochilus*) and those with rather large sori in single rows parallel to the secondary or primary veins (e.g. *Neolepisorus* and *Phymatosorus*).

On the species level the structure of rhizome scales appears to supply useful characters, with which at least some species in *Microsorium* s.s. can easily be recognized. For instance, in a group of three poorly understood species (*M. musifolium* (B1.) Copel., *M. congregatifolium* (v.A.v.R.) Holtt. and *M. neoguineense* (Copel.) Copel.) the very dissimilar scales are a welcome addition to other less obvious characters used in identification.

It is expected that an analysis of scale structure (including anatomy and ontogeny) as well as further study of venation patterns in relation to soral position, will contribute to a solution of taxonomic and phylogenetic problems concerning the microsoroids.

HETTERSCHIED, W.L.A. & E. HENNIPMAN (1984): Venation patterns, soral characteristics and shape of the fronds of the microsoroid Polypodiaceae. *Bot. Jahrb. Syst.* 105: 11–47.

E. HENNIPMAN (*Vakgroep Plantensystematiek en -geografie, Institute of Systematic Botany, Heidelberglaan 2, 3584 CS Utrecht*)

Preliminary results of studies on the ant-fern *Lecanopteris* s.l.

The Malasian ant-ferns are generally accommodated in the genus *Lecanopteris* sensu lato. This genus comprises two distinct elements that have been given generic rank by some authors (e.g. PICH SER-MOLLI 1977). These are *Lecanopteris* sensu stricto, characterized by rhizomes without scales and an intricate gallery system, and *Myrmecopteris* (syn.: *Myrmecophila*) with scaly rhizomes having only one central cavity.

Myrmecopteris, considered as a distinct genus, consists of four species. *Lecanopteris sarcopus* (de Vriese & Teijsm.) Copel. from Sulawesi and Luzon shares the inferred apomorphic character state of 16 spores per sporangium with its sister species *L. crustacea* Copel. from S. Thailand, Malacca, Sumatra and Borneo. These two species and *L. mirabilis* (C.Ch.) Copel. from Halmahera and New Guinea share a unique rhizome anatomy. The sistergroup relation of these three species is with *L. sinuosa* (Hook.) Copel., which occurs in Indo-China and throughout Malesia.

The genus *Lecanopteris* sensu stricto is easily divided into two taxonomic groups using the criteria of size of the sorus, shape of the frond, and the number of sori per lobe of the frond. The first

group, the *L. curtisii* group is still a taxonomic puzzle. It may either consist of only one species occurring throughout Malesia, or may include two or three different species. The second group, the *L. carnosa* group, is much more diversified. It may include a minimum of 8 species, with at least one confined to Sumatra, Malacca and Borneo, one endemic to the Philippines, and all others endemic to Sulawesi. Three endemic species of Sulawesi inhabit separate mountains in Central and Southern Sulawesi at ca. 2000 m. It now appears that several other endemics including *L. carnosa* (de Vriese & Teijsm.) Copel. occur at ca. 1000 m. The material at hand suggests that the resolution of species in Sulawesi of this particular group of *Lecanopteris* is unusually high and unsurpassed in ferns. This gives special significance to a detailed study of the phylogenetic relationships between the species. The phylogeny reconstruction, in turn, is a prerequisite for the study of the evolutionary significance of the association between ants and ferns and the phytogeography of the respective parts of Sulawesi using vicariance phytogeography.

PICHI SERMOLLI, R.E.G. (1977): Tentamen Pteridophytorum genera in taxonomicum ordinem redigendi. *Webbia* 31: 315–512.

C.H. HAUFLER (*Dept. of Botany, The University of Kansas, Lawrence, Kansas 66045, U.S.A.*)
Electrophoretic evidence for diploidy and outcrossing in homosporous pteridophytes

Ongoing studies indicate that the analysis of evidence from patterns of biochemical variability can be valuable in elucidating the generic structure and evolutionary processes of homosporous pteridophytes. A priori assumptions based on superficial observations have led to two common misconceptions about homosporous pteridophytes. First, species having high chromosome numbers have usually been considered highly polyploid. However, since the essence of polyploidy involves increases in the number of component genomes (sets of active genes) rather than just a numerical increase in chromosome number, this definition may be oversimplified. Second, the fact that homosporous pteridophytes have bisexual gametophytes has suggested that they could be primarily inbreeding and therefore genetically homozygous.

Electrophoretic analysis of enzyme variants is an ideal technique for generating evidence on the genetic consequences of polyploidy and breeding system differences. Recent work with seed plants has provided base line comparative data on isozyme numbers in diploids and polyploids: diploids have fewer isozymes than polyploids (GOTTLIEB 1982). New data obtained through electrophoretic analysis indicate that all species defined as 'diploid' by MANTON & VIDA (1968) have the number of isozymes considered typical for diploid seed plants. Species that have multiples of these base chromosome numbers do show increases in isozyme number. Thus, fern species at $n = 30, 42, 52$ or 69 that may be termed 'polyploid' based on chromosome number have proven to be genetically diploidized. These data indicate that ploidy level estimates in homosporous ferns have often been inflated.

Electrophoretic data also indicate that a majority of diploid (*sensu* MANTON & VIDA 1968) homosporous pteridophytes are outcrossing. Individual populations have an excess of heterozygotes and contain a majority of the total species variability. Thus, although the presence of bisexual gametophytes would seem to enhance intragametophytic selfing, other factors may be driving mechanisms for outcrossing. Among diploid homosporous fern species, inbreeding may, in fact, be a derived character state.

Considered in combination, these data may be used to propose a mode of origin of taxa with high chromosome numbers and diploid genetic systems. Outcrossing mechanisms would stimulate formation of interspecific hybrids. Chromosome doubling in these sterile plants would reestablish sexual reproductive competency. Chromosomal diploidization (regular bivalent formation during meiosis) appears to evolve rapidly in pteridophytes. This may be followed by genetic diploidization through gene silencing. Genetically diploid species with many chromosomes would result. These hypotheses are testable through karyological and molecular techniques.

GOTTLIEB, L.D. (1982): Conservation and duplication of isozymes in plants. *Science* 216: 373–380.

MANTON I. & G. VIDA (1968): Cytology of the fern flora of Tristan da Cunha. *Proc. Roy. Soc. London B* 170: 361–379.

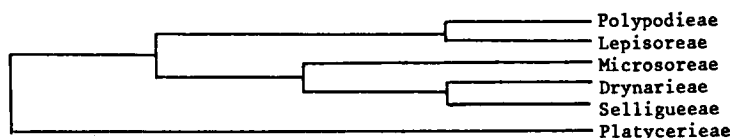
P. VELDHOEN (*Vakgroep Plantensystematiek en -geografie, Institute of Systematic Botany, Heidelberglaan 2, 3584 CS Utrecht*)

Numerical evolutionary research in Polypodiaceae

Using a number of different methods and datasets, we attempted to gain insight into the relationships between the genera of the Polypodiaceae. Eighty-one species of the Polypodiaceae were characterized by four different datasets following earlier character analyses and monographic research. The sets concerned are 1) venation patterns, shape and position of the sori (155 characters), 2) paraphyses and leaf indument (39 characters), 3) spores (27 characters), and 4) rhizome-scales (23 characters). The combination of these four comprised a dataset of 244 characters.

First, we investigated the four sets using agglomerative clustering with GROUP as a criterion. We found that the sets were not in agreement with each other and that not one genus stuck together in all the sets. Most of the six tribes, provisionally and intuitively distinguished by Hennipman & Veldhoen, were recognized by one set only. The three of the combined set showed that most of the genera were distinct and that the clusters coincided largely with the earlier mentioned tribes. The great exception was the Microsoreae, which was subdivided in three groups, each with members of *Microsorium* and *Colysis*. The Lepisoreae was subdivided into two groups which formed a cluster with one group of the Microsoreae.

The next step was to investigate the relationships between 9 clusters of the dendrogram of the combined set and between the six tribes, without imposing an equal rate of change on the analyses (as agglomerative clustering does). For this purpose two methods were used i.e. the present-day ancestor method of KLOTZ & BLANKEN (1981) and the branch and bound algorithm for minimal evolutionary trees of HENDY & PENNY (1982). These methods were applied on subtrees formed by agglomerative clustering of the tribes or clusters. Using the tribes, many minimal and nearby minimal trees were found. Many of these were similar to the tree shown in fig. 1 in the sense that the Polypodiaceae and Lepisoreae formed a group separate from the Microsoreae, Selliguaeae and Drynariaceae. This particular tree was also found twice with the present-day ancestor method. When the clusters were used, we achieved a similar result with one exception. A part of the Microsoreae (*Microsorium angustatum*, *M. samarense*, *Colysis minor* and *Lecanopteris carnosa*) was usually joined with clusters belonging to the Lepisoreae. The heterogeneity of the Microsoreae could be one of the reasons why so many minimal trees in the analysis of the tribes were found. It seems therefore, that the Microsoreae as a group in its present concept is heterogeneous. This conclusion seems to be in agreement with the provisional results of the monographic study of the Microsoreae presently executed by M.T.M. Bosman.



KLOTZ, L.C. & R.L. BLANKEN (1981): A practical method for calculating evolutionary trees from sequence data. *J. Theor. Biol.* 91: 261-272.

HENDY, M.D. & D. PENNY (1982): Branch and bound algorithms to determine minimal evolutionary trees. *Math. Biosc.* 95: 277-290.

P. HOVENKAMP (*Rijksherbarium, Postbus 9514, 2300 RA Leiden*)

The use of biological knowledge in phylogeny reconstruction

The general question that was considered is: at which stage during the reconstruction of phylogeny can we best apply biological knowledge (Roos 1985). With this question in mind, an analysis of the process of phylogeny reconstruction is presented which will be treated in detail elsewhere. The conclusion reached is that incorporation of biological knowledge is necessary, firstly, in order to code the data; secondly, to find an out-group; thirdly, to find the series of homologous characters

and lastly, to find the order in which the characters are to be combined into these series.

It is noted that the application of biological knowledge in the first and last of these steps is complementary: if series of ordered homologues are incorporated in the first step, it is not necessary to find them afterwards. If they are not used, they have to be reconstructed in a later step of the analysis. It is maintained that for this process no generally applicable solution has been found. Without incorporating this knowledge, however, we may be on the wrong track. If all attributes are treated as separate character-states, the resulting cladogram is likely to be incompletely resolved, as characters uniting large groups will be underrepresented. Because of this loss of information, the 'recovery' of transformation series will be even more difficult than it already is.

According to this analysis we are therefore faced with two options: either we state transformation series in advance, or we risk losing important information. If we specify transformation series in advance, cladistic analysis provides a method by which new conclusions may be derived from them. Ultimately, this process may lead to the formulation and testing of predictions. Conversely, if anything is tested with the aid of a cladogram, it can only be the initial set of assumptions about character transformation upon which it has been based.

Roos, M.C. (1985): *Phylogenetic systematics of the Drynarioideae*. Thesis, Utrecht.

M. C. ROOS (*Vakgroep Plantensystematiek en -geografie, Institute of Systematic Botany, Heidelberglaan 2, 3584 CS Utrecht*)

Cladistic analysis by means of group compatibility and parsimony

One of the main objectives of my Ph.D study on drynarioid Polypodiaceae (Roos 1985) was to outline and illustrate a method for phylogenetic systematic research of which the starting points and purposes are consistent with the main axiom of evolution, i.e. descent with modification. Reconstructing of the phylogeny was carried out using a method of cladistic analysis developed by ZANDÉE (1985). This is a four step analysis, which starts with the transformation of the data resulting from determining the distribution of character states among the taxa and the delimitation of terminal taxa into a binary data matrix (step 1). The presence or absence of each character state is indicated for each species without being concerned with polarity. Partially monothetic sets, defined by unique character states, are then read off from the data matrix (step 2). Apart from overlap, these sets show inclusion or exclusion relations. Sets that mutually include or exclude each other are called compatible. From within these sets, the largest cliques are sought (step 3). Cliques are defined here as sets of partially monothetic sets that are all mutually compatible (group compatibility). The maximum size for cliques is $2N-1$. N is the number of terminal taxa, and $N-1$ is the maximum number of inclusion relations. The largest cliques are transcribed into cladograms (step 4). These cladograms are judged according to their reflection of the data matrix, i.e. the amount of homoplasy (= contradiction) and fitting character states (= support). Also, the fitting character states are tested using outgroup comparison. Cladograms that show the lowest value for contradiction minus support and that are supported by potential synapomorphies, are evaluated further using biological criteria. This procedure has the following advantages: 1) transformation series are not a priori established, 2) an integration of compatibility and parsimony methods is achieved, 3) no data are discarded initially or weighted otherwise a priori, 4) all possible cladogenetic relationships are unambiguously defined and presented, 5) the sistergroup of the group under study is required for outgroup comparison at the basal node only, and 6) the systematicist gets the opportunity to evaluate all possible hypotheses according to auxiliary criteria.

Roos, M. C. (1985): *Phylogenetic systematics of the Drynarioideae (Polypodiaceae)*. Thesis, Utrecht.

ZANDÉE, M. (1985): C.A.F.C.A. - A collection of APL functions for cladistic analysis. Online C.A.F.-C.A. documentation (internal report ITB, in dutch).

E. O. WILEY (*Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045, U.S.A.*)

Comments on different approaches to phylogenetic systematics

Since the rise of phylogenetics in the 1960s, many attempts have been made to quantify its methods in the form of computer algorithms. To date, the only algorithm which has been shown to be logical equivalent to Hennig's methods is the Wagner algorithm (KLUGE & FARRIS 1969). It uses characters whose polarities have been determined a priori and it groups on the basis of parsimony. Both characteristics are shared by Hennigian argumentation methods where outgroup analysis is primarily used to determine character polarity and parsimony is embodied in Hennig's "auxiliary principle" (HENNIG 1966). The use of the parsimony principle has been most recently analyzed by SOBER (1983). It is important to understand that Wagner methods were developed in parallel to Hennigian methods and that the use of computers is not a response to a failure of classical Hennigian methods. Indeed, computer methods are judged, in part, by their ability to produce the same results as classical methods. It is also important to realize that many available programs fail to live up to this criterion, either because they do not mimic classical results or because they are not efficient in finding the shortest trees (the major strength of computer methods) when there is a lot of homoplasy in the data. The only programs I have found satisfactory are PAUP (developed by David Swofford, Univ. Illinois) and PHYSIS (developed by J. S. Farris and M. F. Micevich, SUNY, Stony Brook). Finally, it should be realized that computer programs are not substitutes for good data. "Rubbish in, rubbish out" remains true.

Today we are faced with another algorithm, the Zandee algorithm. It differs from both classical and Wagner methods. However, we do not know, at this time, whether its results mimic classical methods or whether there is any logical connection between the methods of this algorithm and Wagner methods. What is needed is a phase of comparison of the results of implementing the Zandee algorithm and the results derived from the other two methods.

HENNIG, W. (1966): *Phylogenetic Systematics*. University of Illinois Press, Urbana.

KLUGE, A. G. & J. S. FARRIS (1969): Quantitative phyletics and the evolution of anurans. *Syst Zool.* 18: 1-32.

SOBER, E. (1983): Parsimony in systematics: philosophical issues. *Ann. Rev. Ecol. Syst.* 14: 335-357.

A. C. JERMY (*British Museum, Natural History, Cromwell Road, London SW7 5BD, Great Britain*)

Some ecological aspects of Polypodiaceae

An illustrated talk was given in which the following three questions were discussed: 1. Which major habitats have been colonized by Polypodiaceae. 2. How have these plants adapted themselves (both structurally and physiologically) to exploit these habitats and radiate to colonize peripheral ones. 3. Are there basic (i.e. primitive) morphologies (or by extrapolation physiological systems) that will help us to elucidate how many lines of evolution there may have been and in which environments and geographical areas they may have evolved.

The Polypodiaceae are predominantly ferns of the everwet and seasonally wet tropics; some 80% of the species are epiphytes or occasionally lithophytes. Moisture, light and nutritional requirements are critical. On open mountain ridges epiphytes may descend to ground level on well-drained moss tussocks where cloud cover maintains a high humidity. Many genera have succulent rhizomes (e.g. *Drynarioid* spp.) or specialized water storage "nest" leaves (e.g. *Platyserium*). Leaves or pinnae may abscise in dry periods (e.g. *Drynaria rigidula*). Poikilohydrous species occur which in times of drought can lose all apparent moisture from their leaves without rupturing cell membranes so that when moisture again becomes available they can become turgid and continue to metabolize (e.g. *Belvisia* spp., *Pyrrosia* spp., *Loxogramme* spp.). Thick hypoderms in many high altitude epiphyte species protect leaves against fluctuating high temperatures resulting from insolation. Stomata though present, are frequently closed and in some species of *Pyrrosia* C.A.M.-type respiration has been shown to exist and most likely other succulent-leaved species (e.g. *Belvisia*, *Lemmaphyllum*, *Paragramma*) will be shown to have a similar metabolism to reduce day-time transpiration. More field observations are needed on the biochemistry, physiology and structure of these ferns and from

an analysis of the responses of plants under natural conditions we need to develop a strategy using where necessary controlled environment grown facilities to understand the adaptive characteristics of tropical ferns.

R. J. JOHNS (*L. J. Brass Memorial Herbarium, P.N.G. University of Technology, LAE, Papua New Guinea*)

The influence of rainforest instability on the pteridophytes of tropical rainforest communities in New Guinea

The traditional concept of the tropical rainforest as a stable ecosystem is questioned. Studies of rainforest cores from the Pleistocene have shown a lowering of vegetation zones at higher altitudes and a replacement, due to reduced rainfall, of lowland tropical forest by savannah communities at lower altitudes. Few researchers have accepted the continuing disturbance of rainforest communities since the Pleistocene.

In New Guinea a series of natural factors have lead to a continuous destruction of rainforest. The location of New Guinea to the north of the Australian Plate is reflected in the frequency of volcanic eruptions and earthquakes in the region. Volcanoes are common in New Guinea. The largest eruption studied is that of Long Island (circa 350 years ago) when extensive areas of rainforest would have been destroyed in northeast New Guinea. In the Torricelli, Finisterre and Bewani mountains severe earthquakes are common and have resulted in frequent landslides and widespread destruction of forests over large areas.

New Guinea rainforest has regularly been destroyed by droughts and cyclones associated with the El Nino effect. Intensive droughts and resultant fires in New Guinea rainforest are known from the 1880's, 1906, 1914, 1941, and 1972. In 1941 large areas of rainforest in the Madang and Sepik Provinces were destroyed by fires. Examination of forests dominated by *Araucaria*, *Intsia*, *Pometia*, and *Anisoptera* suggests that these are secondary in origin. At higher altitudes drought conditions cause considerable destructions of epiphytic communities in mid and upper montane rainforest, due to dessiccation and the effects of freezing temperatures. Destructive cyclonic winds are also common during these periods. Two cyclones destroyed large tracts of lowland rainforest in southeast Papua and the Northern Province in 1941. The rarity of rheophytic species in New Guinea is possibly explained by the frequency of landslides and flash floods following intense rainstorms. In coastal communities lightning strikes are probably responsible for a regular destruction of mangrove vegetation. On Woodlark Islands up to 9 epiphytic species of ferns grow in mangrove areas in protected limestone depressions. In comparison communities regularly destroyed by lightning support 2 to 3 epiphytic species.

Few rainforest areas in New Guinea are primary. Elsewhere in the tropics similar events probably occur. The destructive effects of man in tropical areas are also important. Vegetation destruction must be taken into account in any explanation of the distribution patterns of terrestrial and epiphytic ferns, and also when studying speciation in tropical environments. Local species diversity is probably both caused by, and results from rainforest instability.

MEETING OF THE SECTION FOR VEGETATION RESEARCH ON 26 OCTOBER 1984

J.H. PETERS (*KIWA, Postbus 1072, 3430 BB Nieuwegein*)

What do we know of borehole recharge?

Lagoon or open recharge of phreatic aquifers proved to be a valuable technique to turn surface water of unpredictable quantity and/or quality into a safe source for water supply. However in Holland recharge sites are not numerous and since this technique meets serious opposition because of its impact on environment, resort to deeper aquifers is planned. Increased storage possibility by displacing native water of poor quality is considered a spin-off advantage of borehole recharge, an alternative of promise.

The last decade a lot of research has been carried out by Dutch Waterworks. In the seventies attention was focused on clogging phenomena. Now other aspects are under study as well because an enterprise on operational scale requires a profound knowledge not only of pretreatment and feasibility but also of environmental impact, recovery efficiencies, protection facilities, flow and quality changes in the subsoil. The paper deals with these aspects that have to be studied when designing a full scale borehole recharge project. It also gives a review of the state of the art of borehole recharge in Holland.

H.W.J. VAN DIJK (*Centrum voor Milieukunde, Postbus 9518, 2301 RA Leiden*)

Chemical aspects concerning wet dune slack regeneration

Most wet dune slacks in the Dutch coastal dunes have been disturbed by activities related to public water supplies. This disturbance is the drying out caused by extraction of natural groundwater, or artificial recharge (infiltration) of eutrophic river water. Both types of drinking water production lead to the disappearance of many rare phreatophytic plant species. In the first case aphreatophytes have replaced the indigenous vegetation, in the second case nitrophilous species dominate the vegetation of wet biotopes.

Regeneration of desiccated dune slacks appears to be relatively easy. Wetting of dried dune biotopes is followed by a rather quick resettlement of the indigenous vegetation. Temporarily this resettlement is preceded or accompanied by an abundant cover of nitrophilous plant species. These species are promoted by an excessive supply of the macronutrients phosphate and nitrogen by intensified mineralization. Adequate management (e.g. stimulating of sand drift, removing of humus layers, mowing and grazing) may restrict this growth sufficiently.

The situation occurring as a result of artificial infiltration is more complex. In the examined dune areas, large loads of phosphorus (the most significant growth limiting macro-nutrient in wet dune biotopes) were found to be accumulated. This accumulation is different in pure dune sand and peat containing sub-soils. Phosphate accumulation is highest in banks of pools and ponds. The distribution of peat layers is known approximately only, therefore the phosphorus transport after return of the natural hydrological régime can hardly be predicted. At places with high phosphate accumulations mowing and grazing seem to be ineffective measurements to avoid prolonged abundant covers of nitrophilous tall hemicryptophytes and of leaching of phosphorus into other places. Here removing of thick soil layers seems to be necessary for the return of plant species adapted to nutrient poor circumstances.

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G. LONDO (*Rijksinstituut voor Natuurbeheer, Postbus 46, 3956 ZR Leersum*)

Dune slack vegetation, its habitats and the related management practices

R.A.M. STEVERS (*Centrum voor Milieukunde, Rapenburg 127, 2311 GG Leiden*)

Restoration of wet dune slack ecosystems in the heavily affected dune areas of Meijndel and Berkheide

The coastal dune areas in The Netherlands are intensively used for public water supply purposes. This is especially true for Meijndel and Berkheide, two dune areas lying in the province of South-Holland, with a total area of 2800 ha. The water supply function has had a great impact on the natural ecosystems. Outside the dune slacks, there have been extensive digging activities over some 200 ha, replacing rich oligotrophic vegetation with marrain monocultures. In the dune slacks the direct effects are: inundation of many dune valleys with eutrophic riverwater, dessication of many others: irregular fluctuations of the water table and introduction of large amounts of nutrients in the original oligotrophic environment. As a consequence of these changes in the abiotic environment, most of the authentic plant species, among which a large number of rare species, have been outcompeted by eutrophic newcomers.

A recently completed study on the South-Holland water supply has shown that it is preferable to switch away from the current practice of riverwater infiltration in the dunes. This creates possibilities to restore the wet dune slack ecosystems in their pre-infiltration richness. This paper will focus on the prospects of this restoration in Meijndel and Berkheide.

Restoration of the wet dune slack ecosystems has to start with restoration of the relief. This can be achieved passively, using the natural relief forming proces, i.e. dispersion of sand by the wind, or actively, using machines to displace sand. Active sand displacement is fast and effective, and almost a necessity at places where deep canals have been cut. The machine work may be carried out roughly so that the wind may finish the job. For Meijndel and Berkheide active restoration of the relief means that an area of 120 ha heavily affected dunes has to be reshaped, implying a sand displacement of about one million m³.

The second aspect to be restored is the hydrological system. In Meijndel, termination of the current water production activities will not result in groundwater tables returning to the original level, i.e. the level during the genesis of the dune slacks. The cause of this phenomenon is that polder waterlevels outside the dunes have been lowered in course of time. In Berkheide there is a clay layer in the subsoil, which almost completely excludes influences outside the dunes. This results in an almost completely restored water table. The total area to become wet or moist will be about 5–10% in Meijndel and 10–20% in Berkheide.

The third important factor to restore is the nutrient level, especially the level of phosphate. To remove the accumulated excess of phosphate the topsoil of bottom and banks of all infiltration ponds and some seepage pools have to be removed (cf. Van Dijk's paper, this Meeting, p. 123). Some of the phosphate, accumulated farther away from the infiltration ponds may be washed out by pumping very clear water through the system for some years.

When the abiotic conditions of the dune slack ecosystem are restored and an adequate nature management practice (mowing and grazing) is introduced to remove remaining excess nutrients, good chances exist for the return of the wet dune slack communities, which are one of the most diverse communities in the Netherlands.

It is concluded that basic conditions for a successful restoration of wet dune slacks are favourable. In order to design the most efficient restoration strategy it is desirable to start a field experiment testing different restoration measures and tactics in different types of initial conditions.

CH. VAN SCHAİK (*Stichting Duinbehoud, Postbus 11059, 2301 EB Leiden*)

Increasing chances for the ground water level in South-Kennemerland?

The dune area between Zandvoort and IJmuiden is dried up. Main cause is the water catchment for the making of drinking water for the inhabitants of this area. Last century there were still many dune marshes with their characteristic vegetation and fauna. Now there is only vegetation on dry soil, which means a strong devaluation of the natural values of this area.

However, one can restore these values to their original conditions by deminishing the ground water catchment. The environmental Report for the Water Catchment in South-Kennemerland shows that ending the water catchment means the return of the dune marshes in nearly all areas

in which they could be seen last century. At the same time this return is neither impeded by high levels of phosphate (as the result of big infiltration works) nor by deep canals (compare the Luchterduinen). The relief is hardly effected, so that quite a natural situation will come to exist.

The latest plans in the policy of the drinking water industry are: halving the ground water catchment by the 'Haarlem' water company, which would mean a limitation of c. 25% for the whole region.

However, this limitation will not lead to the return of the wet dune valleys, because the rise of the ground water level is not sufficient to influence the valley soil. There will be nearly as much water pumped up as will be replenished by rain. One can make up from the research model in which the hydrological situation is calculated in the present situation and after ending the water catchment, that only a considerable limitation of the ground water catchment can lead to the return of the rare and characteristic dune marsh vegetation.

There are two alternative ways to make drinking water for the inhabitants of the Zandvoort-IJmuiden region. First, the Water Company of Amsterdam, which can supply Haarlem and surroundings by means of their over-capacity in the Loosdrechtse Plassen area. Secondly, borehole recharge (see the paper by J.H. Peters, this Meeting, p. 123) – provided that it is selectively used – might give a solution to the devaluation of nature by ground water catchment.

C.L.G. GROEN (*Centrum voor Milieukunde, Rapenburg 127, 2311 GG Leiden*)

Restoration of the Luchterduinen and the presence of two different ground water levels

After the start of the ground water catchment for the drinking water delivery of Amsterdam in 1859, the Luchterduinen – a dune area of 1300 ha between the Langevelderslag and the border between North- and South-Holland – are dried up to a high degree. Then, 30% of the vegetation was influenced by the ground water, which is now less than 1%. Many plant species that are bound to a moist and nutrient-poor environment, have disappeared from the Luchterduinen.

After 1957 the quantitative part of the Luchterduinen in the entire water delivery of Amsterdam became relatively small.

Between 1982 and 1984 research was done to find out if ending the ground water catchment, together with adaptation of the relief in and near the water canals and an adequate nature management, could lead to the return of a moist and nutrient-poor dune environment, despite other factors that lowered the ground water level, such as digging down the inner dunes and the reclamation of the Haarlemmermeer.

This research has shown that an extensive, intact bog layer exists in the Luchterduinen, right underneath the surface; on this bog layer a 'secondary' ground water level was found. This secondary level has no contact with the primary ground water level in deeper layers.

The ground water level was therefore much less lowered than one thought, based on measuring the primary ground water levels. Return of the moist environment means that the former contact between the primary and the secondary ground water level should be restored: ending the ground water catchment is sufficient to achieve this, although the area, especially in the eastern part, will moisten to a less high extent than in earlier days. Ten percent of the vegetation will again be influenced by the ground water, provided that the two canals are filled up till their soil-circumstances are moist. For this, one will need 570.000 m³ of sand. However, one cannot displace 240.000 m³ of this sand without affecting the landscape. It may be worth considering to get this sand from the infiltration area in the Brederodes Duinen, in which restoration is hardly possible.

A management of impoverishing the soil after ending the water catchment can minimise the negative effects of a rising ground water level on the vegetation and increases the chances of resettlement of the species originally found in the Luchterduinen.

MEETING OF THE SECTION FOR THE RELATION BETWEEN PLANTS AND ANIMALS ON 8 JUNE 1985

J.M.M. VAN DAMME (*Instituut voor Oecologisch Onderzoek, afd. Duinonderzoek, "Weevers' Duin", Duinzoom 20a, 3233 EG Oostvoorne*)

The influence of the mode of pollination on several reproductive characteristics in *Plantago lanceolata*

Reproductive characteristics related to sexuality, pollination and seed formation vary among and within *Plantago* species. Two cases of interaction of these aspects of sexual reproduction in *Plantago lanceolata* are presented: the mode of pollination (wind *versus* insect) appears to influence 1) the occurrence of sterile males in gynodioecious populations and 2) the distribution of seeds over capsules.

As insects visit plantains only for the pollen (plantains produce no nectar), they can be expected to visit male sterile plants less frequently than hermaphrodite ones. Therefore, in insect-pollinated populations, where pollination limits seed set, it should be relatively difficult for male sterile plants to compensate for the disadvantage that they do not reproduce as males (VAN DAMME 1984). Sex counts in sheltered and non-sheltered populations seem to support this hypothesis, as the frequency of male steriles was significantly lower in the former. These populations can be considered to be insect-pollinated.

In *Plantago lanceolata* there are two ovules per flower and, therefore, capsules may contain zero, one or two seeds. The distribution of seeds over capsules does not appear to be at random. These deviations from random distribution relate to pollination conditions. A model of resource allocation within an inflorescence is used to explain the observations (VAN DAMME 1985). Whether a capsule will contain one or two seeds depends on the difference in timing of pollination between the two ovules. When the two ovules in a flower are fertilised at the same time, they may both develop into seeds, whereas only one will, if the difference in pollination time between the ovules is sufficiently large. Furthermore, the fraction of all ovules of an inflorescence that develop into seeds depends on the capacity of the vascular system of the scape. The model explains the existence of seedless capsules in spite of adequate pollination as well as the observed distribution of seeds over capsules. The data of STELLEMAN (1982) are also in accordance with the model and demonstrate the effect of wind *versus* insect pollination on the seed distribution: the pollen in insect-pollinated populations is distributed in larger aggregates than in a wind-pollinated population. Therefore, confirming Stelleman's findings, this leads to the expectation that in the former there will be relatively more two-seeded capsules.

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A.H. DE MEIJER and S.M. WELLINGA (*Hugo de Vries-Laboratorium, Plantage Mid-denlaan 2a, 1018 DD Amsterdam*)

Further anthecological studies of *Ephedra aphylla* Forsk.

Previous studies by BINO et al. (1981, 1984) strongly suggest that the dioecious species *Ephedra aphylla* is at least partly entomophilous, which is of phylogenetic interest. How far it depends on biotic pollen transfer remained unsettled, however, so that populations were studied to the N. of Haifa, Israel, to establish the ratio entomophily/anemophily and the possible adaptations to wind and to insect pollination, respectively.

The contribution of visiting insects was assessed by caging in parts of female plants, other parts of the same individual being used as the reference. In addition, insects were caught on female plants and examined for the quantities of *Ephedra* pollen they carried on their bodies. By means of sprin-

klings images according to Knoll (STELLEMAN 1982) and of pollen traps, an insight could be gained into the adhesive capacity and the aerial dispersal of the pollen. No significant difference in seed set between caged-in branches and the controls was observed at the site studied where male and female plants grow together and are often entangled.

This does not mean that no insect pollination took place, because the pollen traps indicated a pollen rain at some distance from the male plants of only $\bar{n} = 2.4$ grains per cm^2 . Assuming that aggregates of ten or more pollen grains cannot be displaced by air currents to any appreciable extent, the result of the sprinkling image tests suggested that about 90% of a pollen biomass of 170,765 grains did not participate in wind pollination.

Taking the singular growing pattern of *E. aphylla* into account, it is easily demonstrable that the bulk of the pollen is not necessarily lost for the pollination as such: where male and female plants grow together, the male ones tend to climb beyond the female ones to form the crowns of the densely entangled *Ephedra* stands, thus raining pollen straight down onto the female plants below them. It appears that the greater part of the pollen is shed in large aggregates that drop down almost vertically unless they come into contact with a solid obstacle.

Such a pollen rain is brought about by the shaking following gusts of wind or by the activities of insects involved in pollination. The visitors, principally certain Calliphoridae, Muscidae and Sarcophagidae (Diptera), do not discriminate between male or female reproductive units, as can be deduced from the quantities of pollen transported by specimens caught when consuming nectar on female plants, the more so since the bulk of the pollen (85% of a cumulative total of 5,359 grains) is found on body parts that can easily come in contact with the micropyles (and pollination droplets): certain dorsal and ventral parts of body and legs.

It follows that the pollination biology of *E. aphylla* is a rather complex one and varies according to the local conditions (social as against isolated occurrence, shelter, exposition, availability of pollinators, etc.).

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R. VINKENOOG (*Hugo de Vries-laboratorium, Universiteit van Amsterdam, Plantage Middenlaan 2a, 1018 DD Amsterdam*)

Anthecological observations of *Euphorbia*

The most important potential pollinators of the two native species *Euphorbia esula* and *Euphorbia palustris* were recorded. Both spurges are characterised by a so-called cyathium, a condensed protogynous inflorescence consisting of one female floret and several male ones. The florets are surrounded by an involucre bearing four extrafloral nectar-glands. The pollination syndromes and visitor spectra of both species are very similar. They are probably self-compatible. The scent and colouration of the cyathia, in combination with their easily accessible pollen and nectar, attract a large number of insect visitors belonging to different orders:

	<i>E. esula</i>	<i>E. palustris</i>
Diptera	35 spp.	16 spp.
Hymenoptera	13 spp.	5 spp.
Coleoptera	9 spp.	6 spp.
Lepidoptera	4 spp.	2 spp.
Total:	61 spp.	29 spp.

Lepidoptera only occasionally pay a short visit to *Euphorbia* inflorescences, and, therefore, do not play any significant role in their pollination. Among the Coleoptera, representatives of the Cantharidae and the Mordellidae are more or less permanent inhabitants of the plants and sometimes stay at a plant for several days. They consume both nectar and pollen, and probably also gnaw at the young ovaria. Apart from the damage they cause in this way, they can only play a role in – perhaps ineffective – self-pollination.

In some populations of *Euphorbia esula* Cerambycidae are frequent visitors.

They fly from cyathium to cyathium, searching for pollen and nectar. All Cerambycidae examined carried *Euphorbia* pollen on their bodies.

Representatives of the Apoidea very rarely visit the inflorescences, which may be attributable to the nectar composition of *Euphorbia*, which contains equal amounts of fructose and glucose, while the social Apoidea prefer nectar with high amounts of sucrose.

Ichneumonid wasps and Tenthredinidae were frequently visiting both *Euphorbia* species. These Hymenoptera only collect nectar but carry an appreciable quantity of pollen with them, especially on head and thorax (upon the average 150 pollen grains per individual).

Some plants in *Euphorbia esula* populations are visited by ants. Probably the same ants keep returning to the same plants, as reported by FOWLER (1983). The ants only carry few pollen grains with them (about 5 per individual).

The most frequent visitors, both as regards the number of species and the number of visits, are Diptera. Sarcophagidae, Stratiomyidae and Calliphoridae were rather frequently recorded as visitors of *Euphorbia*. Large numbers of *Scatophaga stercoraria* are often found on the inflorescences. These flies may carry many pollen grains on their hairy bodies (upon the average 260 grains per individual), but because *Scatophaga stercoraria* is a rather inactive fly, and seems to use the *Euphorbia* plants mostly as a resting-place, it cannot be an effective pollinator.

The most important pollinators of *Euphorbia* belong to the Syrphidae. These very active flies, several species often consuming both pollen and nectar, often visit the inflorescences in large numbers. Because of their high mobility, their frequent visiting and the often high numbers of pollen grains they may carry, particularly *Eristalis* sp. (an average of 11 visits per 100 plants and of 500 pollen grains per individual), *Helophilus pendulus* (about 11 visits on 100 plants and about 50 pollen grains per individual) and in some *Euphorbia esula* populations, *Volucella pellucens* (about 5 visits per 100 plants and some 30 pollen grains per individual) were by far the most effective pollinators of *Euphorbia* in the biotopes studied.

J.T. WIEBES (*Rijksmuseum van Natuurlijke Historie & Geologie en Mineralogie, Postbus 9517, 2300 RA Leiden*)

New developments in fig- and figwasp-research

In the sycones of *Ficus ottoniifolia* (Miq.) Miq. in Gabon, two species of fig wasp were found, either together or separately (MICHALOU et al. 1985). In the rain-forest, the relative abundance of one, *Courtella camerunensis* (Wiebes), is higher than that of the other (*C. gabonensis* Wiebes); in the open habitat, *C. gabonensis* is dominant almost to the exclusion of *C. camerunensis*; at the rain-forest edge an intermediate situation occurs. When colonizing the sycones, *C. camerunensis* tends to be mainly gregarious, with about three colonizing females per sycone as an average in the full forest, whereas *C. gabonensis* mainly is solitary. The two do not seem to recognize each other, as neither is influenced in its colonizing number by the other, although of course they do compete for oviposition sites.

In the savannah of Ivory Coast, *C. gabonensis* appears to be gregarious (with three colonizing females per sycone as an average) and exclusive in colonizing the sycones of a fig representing another subspecies of *F. ottoniifolia*.

The new data were discussed and illustrated by a film (MICHALOU 1982).

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W. VERKERKE (*Hugo de Vries-Laboratorium, Plantage Middenlaan 2a, 1018 DD Amsterdam*)
 Syconium morphology and its relation to fig wasp pollination in *Ficus ottoniifolia*

The syconium of the monoecious *Ficus ottoniifolia* (Miq.) Miq. contains three types of flowers, viz., long-styled female flowers ('destined' to produce seeds), short-styled and pedicellate female flowers ('destined' to receive eggs of the pollinating wasp), and male flowers. Until fertilization the seed flowers and wasp flowers differ only in the length of the pedicel and the form of the style. The seed flowers have long, slender styles; the wasp flowers have shorter, thicker styles with a branched stigma. These differences suggest that style length is at least not the only factor inhibiting oviposition in seed flowers. Both types of flowers contain a functional ovule, and this enables also wasp flowers to develop seeds in case the oviposition might fail to come.

After fertilization or oviposition, major differences in shape and construction appear between the seed flowers and the wasp flowers. The wasp that develops in a wasp flower is surrounded by a thin endocarp and a thin mesocarp. The embryo that develops in a seed flower is eventually surrounded by a thin seed coat; mechanical protection is offered by the hard and thick endocarp and the inner mesocarp. The outer mesocarp develops a mucilaginous layer which eventually bursts out of the tanniniferous exocarp. The mucilage which surrounds the endocarp body ('seed') offers the possibility of exozoochoric dispersal in addition to the normal endozoochoric dispersal.

G. VAN DER VELDE (*Laboratorium voor Aquatische Oecologie, Katholieke Universiteit, Toernooiveld, 6525 ED Nijmegen*)

Developmental stages in the floral biology s.l. of Dutch Nymphaeaceae (*Nymphaea alba* L., *Nymphaea candida* Presl, *Nuphar lutea* (L.) Sm.)

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