BLUMEA 25 (1979) 107–113

MORPHOLOGY AT THE RIJKSHERBARIUM

W. A. VAN HEEL
Rijksherbarium, Leiden

In the following the role of morphology, anatomy and palynology in systematics at the Rijksherbarium will be discussed, as far as flowering plants are concerned. It will be demonstrated that most of the research in this field is rooted in the interest of individual workers, and that no planning was involved until recently. The scope of it varied, as it was done either for pure taxonomic purposes, or for systematic and phylogenetic reasons, or for its own merit. Chiefly, I think, the study of morphology s.l. originated because Suringar, Hallier, Lotsy, and especially Lam, were interested in achieving a more natural or evolutionary system of the Angiosperms. Lotsy and Lam extended their interest to the other Cormophytes as well.

In 1895 W. F. R. Suringar published a booklet which was intended as a summary of his lectures. His idea was that the tree of natural affinities could be a preparation and a guide to a real genealogical tree. He pictured this tree with a number of main branches, each of them bearing a number of ramification systems. He adorned this tree with a winding red line connecting groups of plants from different ramification systems. Formerly these groups had been arranged in a linear sequence of increasing complexity by A. P. de Candolle.

H. Hallier, who was at the Rijksherbarium from 1908 till 1922, published his ideas in 1912, and illustrated them by a – as he called it – phylogenetic tree. According to Hallier groups like Choripetalae, Gamopetalae, Apetalae, and Amentiferae cannot be used to subdivide the Dicotyledonae. It was his opinion that Apetalae and Amentiferae should be distributed over different phylogenetic branches. As a whole the Angiosperms would be monophyletic, originating from groups that have some affinity with the fossil *Bennettitales*. Hallier elaborated on these views by making use of morphological and anatomical characters, such as the form of the flowering axis, the form of the ovules, the reduction of the integuments, the structure of the embryo, the arrangement of the pollen tetrads and the number of colpi on the pollen, the position of the sclereid layer of the testa, as well as vegetative anatomical characters, such as the perforation type of the vessels and the pattern of vascular bundles in petioles, etc. He used these data for the discussion of affinities of plant groups. This was done in the fashion of Engler and Prantl's Pflanzenfamilien. Also some chemical characters were taken into account. I have the impression that Hallier mostly evaluated and used the available anatomical knowledge, but that he also added data from his own investigation (*Crypteroniaceae*).

Three publications by J. P. Lotsy (1904, 1906, 1907–1911) are of interest to the present subject. Lotsy worked on these publications while being reader of botany at Leiden university, and director of the Rijksherbarium for a short period. Lotsy recognized three phases in botanical science, firstly the descriptive phase, secondly

the comparative phase in which the affinities by descent are established, and thirdly the phylogenetic phase comprising genetics, evolution, and paleontology. The work Lotsy did during his stay at the Rijksherbarium falls in the second phase. His work follows that of Hofmeister. It is the study of Cryptogams and Phanerogams in their evolution from 'single to double beings' (W. A. Goddijn), which means the evolution of the alternation between haploid and diploid periods during the 'life cycles' of the organisms. Lotsy was especially interested in the comparison of gametogenesis, embryogenesis, pollination and fertilization processes, using cytological methods mainly. While being at Bogor he had published on the 'life history' of *Gnetum*. The expression 'Auxiliary Forces of Systematics' was coined by Lotsy, meaning anatomy, cytology, paleobotany, etc. Certainly Lotsy could not be called a strict systematic botanist, his interest lay far more in the course and processes of evolution. Later his work entered his 'third phase', and he became an experimental breeder of plants, trying to explain the genetical connections between successive generations. The last (fourth) volume of his 'Stammesgeschichte' was never finished. It is interesting to note that in his 'Stammesgeschichte' there is a chapter on the ontogeny of flowers, which deviates from the general line of the book. I am convinced that this chapter was accomplished with the aid of J. W. C. Goethart, who at that time was conservator at the Rijksherbarium. The chapter closely resembles Goethart's thesis on the development of the androecium of the *Malvaceae* (1890). However, Goethart never continued with this kind of work.

The vivid interest H. J. Lam (director from 1933 – 1962) took in extensive floral morphological investigations is evidenced by his contributions to the flora of the Malay Archipelago, especially those on the *Burseraceae-Canarieae* and the *Sapotaceae-Madhuceae* (published from 1931 – 1938). Lam thought that meiomery and pleiomery could not be explained by differences between floral sectors only, but that differences in the supply of nutrients to the whorls of floral organs should play a part as well. Features of obdiplostemony Lam adduced to 'contractive reduction' of centripetal and centrifugal androecia, as did Čelakovsky (Lam was always keen on conveying his ideas in apt new terms). Apart from floral morphology, the stipules had Lam's interest, and that led to the concept of 'metastipules', being stipules that would have evolved from pseudostipules. This led to further study by P. W. Leenhouts and the co-operation on the subject with F. Weberling in recent times. Lam also investigated the composition of the vascular bundles in leaf-petioles and in flowers. Lam used his morphological results to assess evolutionary advance of the 'taxa' he recognized, defining a 'specialization index'. At first he thought that this index had no taxonomic or phylogenetic value, but later under the influence of W. Zimmermann he changed his mind to the contrary. In *Burseraceae*, as well as in *Sapotaceae*, he found correlations between groups of species in remote parts of the area with certain derived characters. In diagrams he plotted the evolution of these groups against geographical distribution. He realized that 'features can travel independently through space and time'. As a continuation he set himself to construct phylogenetic trees of Cormophytes, which were three-dimensional representations, using perspective drawing-techniques (1936, 1938).

Deeply impressed by the 'new morphology' of H. H. Thomas, Lam (1948) published his theory of phyllospory and stachyospory. This theory was an extension of a division of the Gymnospermae into Phyllospermae and Stachyospermae by the paleobotanist Sahni. Lam extended the theory to all Cormophytes, including the Angiospermae. As a result there was no need any longer to explain the Angiosper-

mous flowers either by the euanthium theory or the pseudanthium theory, because the Angiosperms were biphyletic from groups of Pteridosperms. Fossil remains from the lower Cretaceous were adduced in favour. With the new morphology a confrontation between idealistic and realistic methods in floral morphology started. It was Lam's constant concern to find out in how far 'typological' considerations could be translated in phylogenetic terms. And also in how far morphological-anatomical arguments could be valid in rejecting or corroborating the deductions from paleobotany in the understanding of the reproductive structures of higher plants. Especially on the last issue Lam's attitude has been ambiguous, often he advocated more precise morphological research (s.l.), and at the same time he argued that morphological facts (alone) cannot prove a phylogenetic development (1954, 1959). Lam's theory has met with strong opposition, even abuse. Two considerations pleaded very much against it, firstly the very special process of the double fertilization present in all Angiosperms is strongly in favour of a monoreithry of the Angiosperms, and secondly the fact that some groups, like *Cycadeoidea* and some Angiospermous groups, were stachyosporous in the female sex, and phyllosporous in the male, which seems to be evolutionarily impossible. Furthermore the integuments of the ovules could find their place in the theory only with difficulty. Later Lam thought that organs of a nature intermediate between axes and leaves may exist. He also added some views on the evolution of the leaf-axillary axes units in the Cormophytes, which he extended to the Angiospermous flowers. On balance I think that the fate of the theory of stachyo- and phyllospory was that it was rooted in the concept of idealistic morphology and its irreducable categories of leaves and stems. Lam's work shows on every page a struggle between the old idealistic morphology and a new realistic one. Without comment Lam considered the male scales of Conifers phyllosporous for the reason that they are arranged in spirals! Secondly I think it was the fate of his theory that it could not be based on 'sound morphological facts', as these were claimed by his traditional opponents.

Some time after World War II the diversification of the Rijksherbarium started as a result of Lam's wide interests. It was his idea to transform the Herbarium into an Institute for Systematic Botany in a wide sense. Later this line was pursued by C. G. G. J. van Steenis. In some of his students Lam aroused a strong interest for morphology. Many taxonomic works were preceded by ample morphological notes, some are even richly provided with them, for instance W. Vink's studies of the *Winteraceae*. Also C. Kalkman's 'Mossen en Vaatplanten', being a thorough student-handbook on the structure of Cormophytes, has been characterized as 'Lamian' in outlook (F. Jonker).

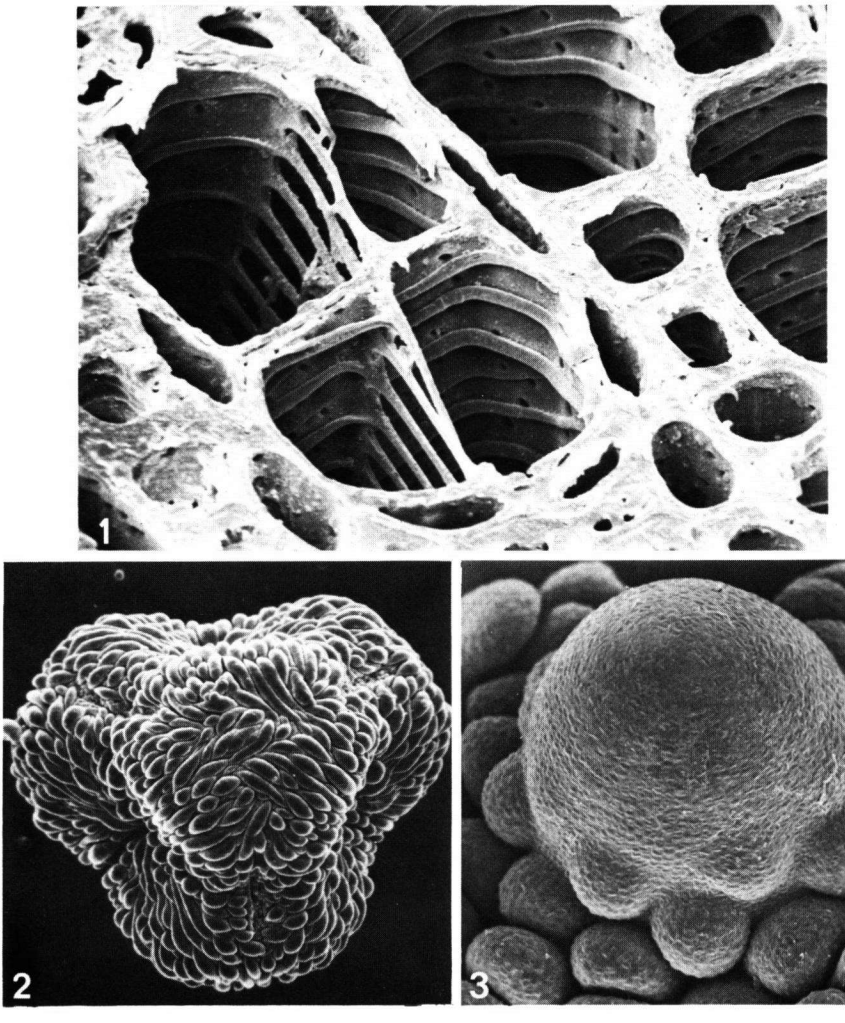
With the appointment of W. A. van Heel, J. Muller, and P. Baas as staff-members, study of the morphology of the Angiosperms was added to the research-program of the Rijksherbarium. The subject of Van Heel is floral morphology. A study on the androecium of the *Malvales* was published in 1966. This was a study of comparative development and the pattern of vascular bundles, and it was followed by a second, theoretical, paper. Lam had always shown a great interest in dichotomy. His pupil L. van der Hammen had written on 'ancient traces of dichotomy' (1948). Another paper on dichotomy, connected with the funicles of *Adansonia*, contained general viewpoints (Van Heel, 1974). The problem of dichotomy is considered to be intimately related to the structure of the stamens. Subsequently the large flat stamens in the *Nymphaeaceae* were anatomically in-

vestigated. According to the idealistic morphology they are homologous with foliage leaves, and from such stamens the commonly terete stamens of all Angiosperms must be derived. The outcome of the studies was that there is no reason to translate the classical concepts in a phylogenetic sense. The large flat stamens must be regarded as a specialization for their groups, they may even have evolved from terete microsporangiophores themselves. The two consistent pairs of pollen sacs are evidence of a double dichotomy. In the *Malvales* stamens occur which are three times dichotomous, partly in three dimensions, or partly flattened. Sterile ramifications occur on the dichotomous stamens of *Ricinus* and *Durio*. Dichotomy is thought to persist through continuous evolution in a few cases, and to become expressed anew in certain other cases in connection with special conditions of life.

As regards gynoecium morphology, a start was made to make visible the complicated primary development of the floral apex and the pistil, by the use of ultropak photography and scanning electron microscopy. It is thought that concepts of 'fusion' have to be formulated as developmental processes which must be compared with each other.

Finally the discovery of distal subdivisions of integuments should be recorded. This may represent a relic form of Pteridospermous stock. Among others it was found in *Scyphostegia borneensis* (1967) and in *Scaphocalyx spathacea* (1973), both possibly ancient monotypes.

As regards the palynological research, which was started by J. Muller in 1967, the relationship with taxonomic projects was most important. The study of the *Ochnaceae*, *Sapindaceae*, *Dipterocarpaceae*, and *Crypteroniaceae* (already studied by Hallier in 1910) should be mentioned in the first place. Furthermore Muller studied the pollen morphology in *Icacinaceae*, *Anacardiaceae*, and *Lecythidaceae*. Mostly this was done in co-operation with students or foreign guest-workers (a.o. S. K. Baksi, D. Lobreau-Callen). A question of general interest is the degree of correlation that may exist between pollenmorphological characters and other characters, or with the accepted taxonomic subdivision of the group under consideration. In *Ochnaceae* there proved to be a partial correspondence on the level of tribes and subtribes of the family. In *Lepisanthes* (1970) there is a correspondence on the level of four subgenera; and there is also correspondence with the migration scheme of the genus, isolation and endemism giving deviating pollen types. Witin the *Dipterocarpaceae* the pollen characters agree with the data from wood anatomy as regards the distinctness of taxa, but not as regards their level of advancement. By this kind of work the Rijksherbarium has been enriched with a large collection of pollen slides. In recent years the use of the scanning electron microscope has considerably extended the results obtained with the light microscope. Transmission electron microscopy has also been introduced and provides important details on the ultrastructure of the exine. Before he came to the Rijksherbarium Muller had gathered knowledge of fossil pollen of the tropical Cretaceous and Tertiary, and he used these data for a reconstruction of the history of the vegetation and the understanding of the present phytogeography. Muller (1970) published a paper that became well-known on the palynological evidence for the evolution of the Angiosperms. From his knowledge he could evaluate and compile the relevant data. The Angiosperm pollen is in the first place characterized by the evolution of columellae. He concluded that a slow single major radiation gave rise to the Angiosperms in the lower Cretaceous. The possibility remains that the Angiosperms started earlier, namely in the upper Jurassic by the *Magnoliales*. By the end of the Cretaceous all major



Scanning electron micrographs of three objects studied at the Rijksherbarium. 1. Vessels in the wood of *Ilex aquifolium*, showing scalariform perforations, spiral wall thickenings, and pits. 2. Pollen tetrad of *Magonia glabrata* (*Sapindaceae*), with rugulate tectum. 3. Stamen primordia on floral apex of *Magnolia stellata*.

groups were present. The herbaceous life form appears to be of Tertiary origin.

P. Baas entered the Rijksherbarium in 1969. His task was the study of vegetative anatomy. Interest in vegetative anatomy at the Rijksherbarium is not new. As early as 1875 J. G. Boerlage had earned his doctor's degree with a thesis entitled 'Bijdrage tot de kennis der houtanatomie' (Contribution towards the knowledge of wood anatomy) supervised by Suringar. This thesis in Dutch gives a very comprehensive history of the microscopical study of wood structure and includes many relevant data ignored by biohistorians (e.g. it gives credit to Nathan Henshaw for observing xylem elements for the first time in 1661). In another section of his thesis Boerlage reported on original wood anatomical studies of the *Artocarpeae* (*Moraceae*). The critical and careful conclusions of relevance for systematic anatomy in general that he derived from this study are still valid.

In a short time Baas made important contributions to the taxonomic work of the institute, often in co-operation with students or with foreign guest workers (W. C. Dickison, C. T. Johnson). His main work, until now, was on *Ilex* and putative relatives (thesis, 1975). Another large study on the wood of the *Myrtales* was recently carried out by G. J. C. M. van Vliet. The question of the correlation of vegetative anatomical characters with other characters must be answered differently for different plant groups. The leaf anatomy of *Ilex* did not agree with the old taxonomic subdivisions, which may, however, be obsolete. In the *Icacinaceae* three levels of specialization in wood and pollen coincide, but leaf characters behave differently and partly agree more with traditional taxonomic subdivisions. In the *Rhizophoraceae* the recognition of three distinct groups and a fourth heterogeneous assembly is corroborated by wood anatomy. In general, wood anatomy seems to correlate less with flower characters than pollen does. The anatomical work on genera of doubtful affinity ('incertae sedis') has formed an important part of the anatomical work (*Hua* and *Afrostyrax; Sphenostemon, Oncotheca* and *Phelline; Paracryphia* etc.) and in fact prompted the large-scale study on *Ilex*. In *Ilex* positive correlations were found between several wood anatomical characters and latitude and altitude of provenance of the species involved. These results, in combination with current ideas on evolutionary trends in xylem anatomy induced further studies centred on the inseparable problems of ecological, functional and phylogenetic anatomy. Baas (1976) thinks that there may be 'patio ludens' in the evolutionary diversification of wood characters, but that at the same time selection pressure by the physical environment may have been considerable. As with pollen morphology, the use of the scanning electron microscope became increasingly important, especially in connection with the study of vestured pit morphology in the *Myrtales*, but also for the study of intriguing alveolar material of cutinaceous nature overlying the cuticle proper and occluding the stomata in the *Winteraceae* and *Myristicaceae*. The comparative anatomical work at the Rijksherbarium has stimulated the fast growth of the wood slide collection indispensable to the systematic anatomist.

The introduction of the study of morphology, anatomy, and palynology has strongly augmented the contacts with colleagues in the Netherlands and all over the world, especially in connection with the International Association of Wood Anatomists and the International Commission for Palynology.

Since in 1979 the Rijksherbarium has put into use its own scanning electron microscope which will serve as a technical means of prime importance in the near future, a plate is added to the present contribution, which shows some photographs relevant to the subjects discussed.

REFERENCES

BAAS, P. 1975. Comparative anatomy of Ilex, Nemopanthus, Sphenostemon, Phelline, and Oncotheca. Thesis Leiden.
—— 1976. Some functional and adaptive aspects of vessel member morphology. Leiden Botanical Series 3: 157–181.
GOETHART, J. 1890. Beitraege zur Kenntniss des Malvaceen-Androeceums. Inaug. Diss. Göttingen.
HALLIER, H. 1912. L'origine et le système phylétique des Angiospermes exposés à l'aide de leur arbre généalogique. Arch. néerl. Sc. Exactes et Nat. Serie III B, I: 146–234.
HAMMEN, L. VAN DER. 1948. Traces of ancient dichotomies in Angiosperms. Blumea 6: 290–299.
HEEL, W. A. VAN. 1966. Morphology of the androecium in Malvales. Thesis Leiden.
—— 1967. Anatomical and ontogenetic investigations on the morphology of the flowers and the fruits of Scyphostegia borneensis Stapf (Scyphostegiaceae). Blumea 15: 107–125.
—— 1973. Flowers and fruits in Flacourtiaceae I. Scaphocalyx spathacea Ridl. Blumea 21: 259–279.
—— 1974. On dichotomy, w.sp.ref. to the funicles of the ovules of Adansonia. Proc. Kon. Ned. Akad. Wet. Series C, 77, 4: 321–337.
LAM, H. J. 1936. Phylogenetic symbols, past and present (being an apology for genealogical trees). Acta Biotheoretica, Ser. A., II, 3.
—— 1938. Studies in Phylogeny. I. On the relation of Taxonomy, Phylogeny and Biogeography II. On the phylogeny of the Malaysian Burseraceae – Canarieae in general and of Haplolobus in particular. Blumea 3: 114–158.
—— 1948. Classification and the New Morphology. Acta Biotheoretica VIII, IV: 107–154.
—— 1954. Again: The New Morphology – elucidated by the most likely phylogeny of the female Coniferous cone. Svensk Bot. Tidskr. 48, 2: 347–360.
—— 1959. Some fundamental considerations on the New Morphology. Trans. bot. soc. Edinb. 38: 100–134.
LOTSY, J. P. 1904. Wat is systematiek? Openbare les, Leiden.
—— 1906. Ueber den Einfluss der Cytologie auf die Systematik. Internat. Bot. Congres Wien, 1905.
—— 1907–1911. Vorträge über Botanische Stammesgeschichte. Jena.
MULLER, J. 1970. Pollen Morphology of the genus Lepisanthes (Sapindaceae) in relation to its taxonomy. Blumea 18: 507–561.
—— 1970. Palynological evidence on early differentiation of Angiosperms. Biol. Rev. 45: 417–450.
SURINGAR, W. F. R. 1895. Het Plantenrijk. Phylogenetische schets. 16 pp.

Title-page of one of the Rijksherbarium's treasures, the 16the century Rauwolf herbarium. The herbarium consists of four books and was collected by the physician Leonhard Rauwolf (c. 1540–1596), mainly in the Near East and the Mediterranean. Only the fourth volume has a beautiful, coloured title-page. Photo C. Marks, Rijksherbarium.