Symposia Biologica Hungarica 12

EVOLUTION IN PLANTS

Akadémiai Kiadó, Budapest

EVOLUTION IN PLANTS
12

EVOLUTION IN PLANTS

(*Symposia Biologica Hungarica 12*)

Edited by

G. VIDA

Most of the papers in this volume deal with the evolution of a well-defined taxonomic group, underlining the importance of specified factors such as introgression, polyploidy, ecological adaptation and geographical speciation. Some remarkable features of the evolution of cultivated plants are also presented. Methods and tools used for investigations of evolutionary processes include experimental hybridization, cytology and cytogenetics, the application of phytotron, cytophotometry and chromatography. Among evolutionary factors studied in general terms the role of extrachromosomal particles, the patterns of geographical distribution, and pesticides as promoters of evolution are discussed. — Botanists, geneticists and plant breeders interested in evolution will find this book stimulating and useful.

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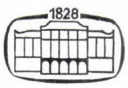

AKADÉMIAI KIADÓ, BUDAPEST 1972

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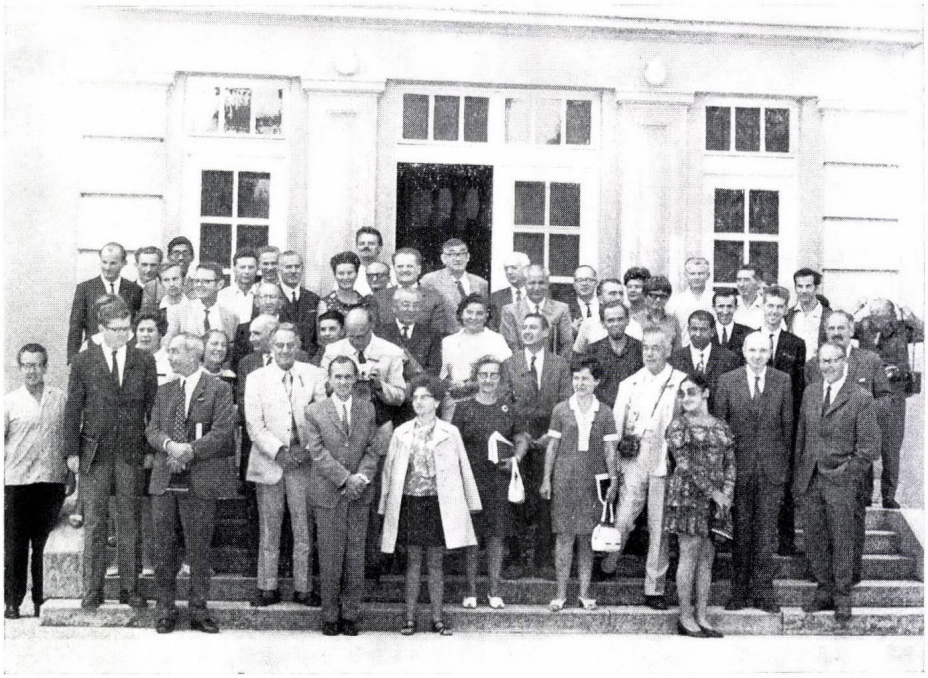

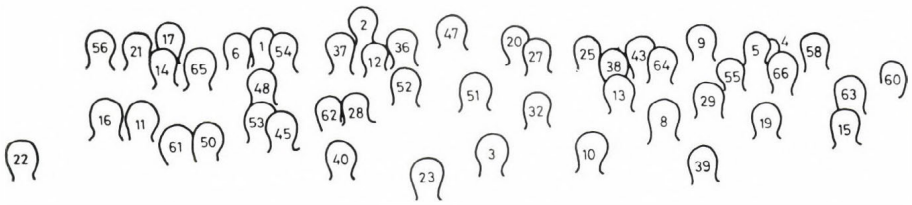
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PREFACE

by

G. Vida

SECRETARY OF THE ORGANIZING COMMITTEE OF THE SYMPOSIUM

The papers of this volume were presented at the Symposium on Evolution in Plants, sponsored by the Hungarian Academy of Sciences and held in the Institute of Biology, Tihany (Hungary), on 1–4 September 1970. The idea of this Symposium came from the late Professor B. Győrffy, then Director of the Institute of Genetics, Hungarian Academy of Sciences. He devoted a great deal of effort to making the meeting successful. His untimely death on 5th August, 1970, just four weeks before the Symposium, prevented him from seeing and enjoying the good results of his work. All the participants and the Organizing Committee wish to express their deep sorrow felt for his tragic death and their thanks for his work, by dedicating this volume to Professor Barna Győrffy.

The Symposium had three main purposes: (i) to make Hungarian botanists and geneticists acquainted with the present status of plant evolutionary studies in progress in different countries; (ii) to give an account of the Hungarian research in this field; (iii) to bring together biologists from all over the world so that they might exchange ideas and promote international co-operation based on personal contacts.

The Symposium was attended by scientists from fourteen countries, among them the President (Prof. H. Lewis), Past-President (Prof. T. W. Böcher) and Vice-President (Prof. D. H. Valentine) of the International Organization of Plant Biosystematists. After the welcome on behalf of the Hungarian Academy of Sciences by Professor J. Szentágothai and the introductory remarks by Professor L. Alföldi (representing the Hungarian Genetics Committee) 24 papers were delivered in seven sessions. The sessions were chaired by Professors D. H. Valentine, W. F. Grant, J. G. Hawkes, E. R. Sears, F. Ehrendorfer and T. W. Böcher. Almost every lecture was followed by a lively discussion, mainly in English but also in German and French. A summarizing general discussion was led by Prof. F. Ehrendorfer at the final session.

Unfortunately, the discussions could not be included in the present volume, as their editing would have delayed publication by several months,

while — in our opinion — publishing of the proceedings volume must be accomplished within the shortest possible time.

The order in which the papers are included here follows the order in which they were presented. This was based upon the belief that the sessions should not be overspecialized, and each one should preferably have a paper with more general conclusions.

During and after the Symposium, field excursions were organized to see the submediterranean vegetation around Lake Balaton as well as in the Vértes Hills on the way back to Budapest.

Thanks are due to the Hungarian Academy of Sciences for making this Symposium possible and for the reception held in Hotel Marina, Balatonfüred. We are also grateful to the Tihany Institute of Biology, Hungarian Academy of Sciences, for the accommodation of the Symposium and last but not least to Akadémiai Kiadó, Budapest, for publishing this volume.

Symp. Biol. Hung. 12, pp. 15–21 (1972)

PATTERNS OF GEOGRAPHICAL DISTRIBUTION IN SPECIES OF THE EUROPEAN FLORA

by

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It has long been known that taxonomic species differ greatly amongst themselves in the extent of their geographical distribution. The matter was given prominence by J. C. Willis (1922), who produced and discussed a great many relevant data. Doubtless because of his violently anti-selectionist views, the conclusions of Willis have not been given the importance they deserve. His main thesis, in very general terms, was that in any large group of allied species, such as a genus, the areas occupied by the various species, under natural conditions, were proportional to their age, rather than to their intrinsic characteristics. It is not easy to say whether or not this thesis is generally accepted, either in whole or in part, at the present time. As regards flowering plants, there is certainly general agreement that many widely distributed species, such as those with disjunct distributions in the northern hemisphere, are ancient. *Juncus trifidus* L., found in Europe, Asia and N. America is a good example. On the other hand, there are some local species, with small areas, which were undoubtedly once much more widely distributed, and which are certainly old; and in many cases we cannot know for certain whether local species are old or new.

Nevertheless, there is no doubt about some of the facts to which Willis drew attention. Thus, if one considers any large genus, it is almost invariably true that this will consist of a high proportion of local, endemic species, with small areas of distribution, and a much smaller number of more widely distributed species. Indeed, this is true not only of higher plants but of many other plant and animal groups. Even though the criterion of what constitutes a species varies a good deal from group to group, the geographical pattern of the species which emerges is substantially the same. Willis thought of the endemics as relatively new, or young species, and of the widely distributed species, or 'wides' as he called them, as old species. His objection to explaining the differences in distribution in terms of natural selection was that he could not imagine that the taxonomic character differences between the species were sufficiently significant to explain the differences in success of the species, in terms of area occupied; he could not see why the wides were successful. This objection is still a difficult one to meet. Admitting that the wides have been successful, the characters which have allowed them to be so, i.e. the selective advantages they possess, are not always easy to discover.

In this paper, I should like briefly to discuss this problem, with special reference to the European flora; and I shall begin by presenting some statistics, conveniently drawn from Volumes 1 and 2 of *Flora Europaea*

(Tutin et al. 1964, 1968). It should be noted that the species of *Flora Europaea* are orthodox taxonomic species, defined in morphological terms, and that the subspecies are usually of the nature of geographical races.

Data for 5 genera are set out in Table 1. In the first genus, which is *Salix*, with 69 species in Europe, the number of species endemic to Europe is listed as 14. Of these 14 endemics, 12 are fairly narrow endemics, being confined to 5 countries of Europe or fewer, while 2 are more widely distributed. The percentage of narrow endemics, i.e. those restricted to 1 or 2 countries, is very low, 7 %. In fact, *Salix* may be taken as a good example of a large genus with an exceptionally low degree of endemism in Europe.

Table 1

Endemic species in 5 genera

(data from *Flora Europaea*)

Genus	No. of species	Number and percentage of endemic species	Number of countries or territories in which endemics occur					
			1	2	3	4	5	6
Salix	69	14 (20%)	4	1	1	5	1	2
Cerastium	51	23 (45%)	8	6	2	2	2	3
Silene	166	81 (49%)	31	27	7	7	3	6
Arenaria	51	29 (56%)	17	7	1	3	1	0
Alchemilla	119	98 (83%)	26	19	13	10	8	23

Below *Salix* in Table 1 are placed three large genera of the *Caryophyllaceae*, viz. *Cerastium*, *Silene* and *Arenaria*. These have a much higher proportion of endemic species than *Salix*; it ranges from 45 to 56 %. It is noteworthy that many of these are narrow endemics, restricted to only 1 or 2 European countries or territories; this is a characteristic feature of large genera. Finally in Table 1, there is the predominantly apomictic genus *Alchemilla*. This differs from the others very markedly in its extremely high degree of endemism (83 %).

In making these comparisons, I am making the tacit assumption that the non-endemic species occupy a large area; because of the limitation of the data to the European flora, this is not necessarily true. Thus, some of the species counted as non-endemic in Table 1 do, in fact, occupy only a small area, but are not listed as endemic because they have a few localities outside Europe. However, this factor is not important enough to invalidate the comparison, as is shown by Table 2, which gives data for average areas of endemics and non-endemics, calculated as the mean number of countries or territories occupied in Europe. The 41 countries or territories listed in *Flora Europaea*, which include 6 territories within European Russia, are used as a basis for this calculation. In all the genera, there is a large and consistent difference between the mean areas of endemics and non-endemics. In other words, the endemics, as treated here, do have, on average, a much more restricted distribution than the non-endemics.

Other interesting points which emerge from Table 2 are that the average area occupied by an *Arenaria* species in Europe is less than that for the other

Table 2

Mean areas of species in Europe
(data from *Flora Europaea*)

Genus	Mean number of countries or territories per species occupied by	
	Endemics	Non-endemics
Salix	3·9	10·3
Cerastium	3·0	12·5
Silene	2·8	7·2
Arenaria	1·8	6·7
Alchemilla	4·4	9·8

Table 3

Location of endemics which are restricted to a single country or territory
(data from *Flora Europaea*)

Genus	No. of endemics	Al	Br	Bu	Cr	Ga	Gr	He	Hs	It	Ju	Lu	Po	Rm	Rs (C)	Rs (K)
Silene	31	—	—	—	4	1	14	—	5	2	3	1	—	1	—	—
Alchemilla	26	1	1	2	—	—	2	5	—	—	2	—	2	—	4	7

four genera; and that the average area occupied by the endemic species of *Alchemilla* is greater than in the other four genera.

A final set of data is presented in Table 3. This contrasts for *Silene* and *Alchemilla* the actual distribution of those endemic species which are confined to a single European country or territory. The differences are remarkable; the areas in which the endemic species predominate are quite different in the two genera. This illustrates another well-known and general point that, in any genus, certain geographical areas are noted for their high proportion of endemic species (so-called centres of speciation) and that these areas differ from genus to genus.

I want now to consider these data in very general terms, dealing first with the problem of the wides, and then, at the other extreme, with the narrow endemics and their very restricted areas of distribution. In many ways, the wides are the more interesting, though students of plant geography have tended in the past to pay more attention to the endemics. In considering the wides, we have first to think of their origin and spread. There are certain kinds of species, such as allopolyploids, which may be thought of as sometimes polytopic in origin; but most species probably have a single centre of origin and begin as a single population or linked series of populations, which are isolated from their nearest relatives and have their own distinctive features. If such a species is to spread over a wide area, and to retain its individuality so that it remains recognizably the same, it must have a stable phenotype which is not unduly plastic; and it must at the same time be physiologically tolerant so that it can put up with the new environments which it must, inevitably, encounter in its spread. Straight away we are postulating intrinsic characteristics which are not likely to be

realised in very many species. The species must have other properties, such as regular seed production and efficient dispersal; and conditions for adequate pollination must travel with it, if it has an insect-vector. External conditions must also be suitable; ecological and geographical opportunities for migration must be available. Sometimes these will arise from major geological or climatic events, such as the retreat of the glaciers in N. Europe, or the slow cooling of the climate in the Tertiary period; these will usually be gradual and the migration will be slow and the spread more or less continuous. Sometimes, however, the progress may be more rapid and proceed by jumps, assuming that long-distance migration is a biological possibility; and the large area may come to consist of a number of more or less disjunct, smaller areas. In recent times, the action of man in providing new habitats and new means of migration has been a potent factor in the formation of wides, notably the weeds of cultivation. Some of the wides in all the genera of Table 1 have been carried about in this way, e.g. some species of *Salix* with economic uses, or weedy species of *Alchemilla* in meadows. Nevertheless, if we bear in mind the numerous intrinsic properties and the variety of external conditions all of which have to be fulfilled to allow of the establishment of a single, more or less uniform species over a wide area, it is not surprising that wides are relatively rare.

Wides may give rise to endemics as a result of allopatric divergence which leads to subspeciation or eventually speciation. One of the most interesting questions here is why wides are phenotypically so stable that even when geographically spread over large areas, or separated as disjunct populations for long periods of time, they change so little that they are still placed in the same species. There are many examples of this; thus *Maianthemum bifolium* (L.) Schmidt is found more or less continuously from W. Europe to E. Asia, in a moderate diversity of habitats which includes both coniferous and deciduous forests; yet it is recognizably the same species throughout, with the same chromosome number except at its N. W. margin (Valentine and Hassan, in press). It is possible that the forest environment is one which is exceptionally stable and well-buffered against climatic and other changes, and this may be a partial explanation. Another example, this time of a disjunct distribution, is *Viola rostrata* Pursh, known from the eastern United States and Japan. Taxonomically, the Japanese plants are classed as varietally different from the American, but the difference is very slight, and the geographical disjunction must be of very long standing. Again this is a forest species. In neither of these cases is there any obvious genetic or biological mechanism which might be associated with the stability. The *Maianthemum* is tetraploid, self-incompatible, regularly produces seed and has extensive vegetative reproduction; the *Viola* is diploid, self-compatible, is also a seed-producer and has only slight vegetative spread; both are insect-pollinated. In other cases, a genetic mechanism has been invoked to explain stability; an interesting example is provided by the work of Anway (1969) on the Australian species *Calectasia cyanea* R. Br. (Xanthorrhoeaceae). The eastern and western populations of this plant are separated by 1200 miles, and have probably been separated since Miocene times; there are minor differences between them, and the author gives them varietal status. The plants are autogamous, with a variable proportion of sterile pollen; they all have $n = 9$, with 8 small chromo-

somes and one large, and the long arm of the ninth chromosome has a chiasma suppressor; when the suppressor control is incomplete and crossing-over occurs, genetic lethality eliminates the recombinant products. Thus a large amount of the genetic material in the species, amounting to about 25%, is inherited as a supergene, which allows the maintenance of a permanent heterozygosity; and this can form the basis of a stabilising mechanism.

Of course, geographical isolation does sometimes lead to speciation and there are many examples of this too; taxonomically, the geographic races receive different kinds of recognition, sometimes being classed as species, sometimes as subspecies. A case in point is seen in *Viola* section *Delphiniopsis*, a relic section of S. Europe, in which the plants, which are woody and have very long-spurred flowers, occur in Spain, Albania and Greece. In *Flora Europaea* they are treated as 3 species (*V. cazorlensis* Gand., *V. delphinantha* Boiss. and *V. kosaninii* [Degen] Hayek), and all are narrow endemics; it would be possible to treat them as subspecies, in which case the species which included them, though still endemic to Europe, would approach nearer to a wide. Vicarious species in the floras of Europe, Asia and N. America supply further examples. Sometimes the components of the group are both wides; a good example is *Viola rupestris* Schmidt in Eurasia and *V. adunca* Sm. in N. America (Valentine 1962). Sometimes both have more restricted distributions, approaching that of endemics, as in *Plantago ovata* Forsk. of the Mediterranean region, and *P. insularis* Eastw. of California, recently discussed by Stebbins and Day (1967).

Wides may also give rise to endemics as a result of the formation of local or ecological races over a relatively small geographical area. Thus short-distance speciation may occur along a climatic gradient on a mountain side, as in *Potentilla glandulosa* Lindl. in California (Clausen, Keck and Hiesey 1940), or *Eucalyptus* species in Tasmania (Barber 1955). It may occur on an archipelago of islands, as in the Aegean islands (Runemark 1970); or it may occur on a series of mountains rising from a plain, as in the Afroalpine flora on the tropical mountains of E. Africa, described by Hedberg (1957). It is probable that where there are climatic differences which lead to ecological differences, as on a mountain side, the process of diversification leads first to the formation of ecotypes; and that provided the situation is sufficiently stable, species are sometimes formed. This view would emphasise the importance of selection rather than isolation in species formation; this is the view which has recently been emphasized by Ehrlich and Raven (1969). There is no doubt that the phenotype is highly amenable to selection in contrasting environments, and that plastic responses in such environments can be genetically fixed, leading to morphological as well as physiological change. Provided the differences are large and well-maintained, speciation can occur, even within small areas, provided there is sufficient variation in habitat, including both climate and soil. Many of the endemic species of the *Caryophyllaceae* listed in Table 1 occur on mountains, and they are often restricted to special habitats, or to certain types of rock (dolomite, serpentine). The fact that, as we have seen, isolated populations of the same species in *similar* habitats often diverge little in morphology (e.g. *Viola rostrata*), reinforces the idea of the importance of selection as compared with isolation.

At the same time the views of Runemark and his colleagues, who have

investigated intensively some 7 or 8 genera in the flora of the Aegean islands, must be borne in mind. Runemark (1970) points out that many of the populations of isolated islands have often been very small for longer or shorter periods, and that the role of genetic drift cannot be neglected. Strid (1970) has studied the *Nigella arvensis* complex in the Aegean, and classifies it into 12 taxa, including 5 species with a number of subspecies, many of which are endemic. These more or less allopatric taxa have virtually the same kind of habitat; and the differences between them are attributed by Strid to random, non-adaptive differentiation.

The situation in *Alchemilla*, with its high proportion of endemics, is interesting. The endemic species here are distinguished from one another by few, minute morphological characters which would not have any validity in a sexual species; they only work because the plants are obligate apomicts and true-breeding. Nevertheless, these marker characters are significant in showing that, even at the single gene level, micro-evolutionary changes are going on which are analogous to the larger, multigenic changes in the sexual species. It must also be presumed that the marker characters are linked with physiological characters, for the species are adapted to a series of climates and habitats across Europe, just like the sexual species. Here selection appears to be operating primarily on the physiological characters; it so happens that there is just sufficient morphological change associated with the physiological change to allow the recognition mechanism of the taxonomist to function.

Thus every genus, given the chance, may have the opportunity to undergo evolutionary radiation; and in so doing, it will produce a rather low number of wides and a much higher number of endemics; for, as we have pointed out, the dice are loaded against the formation of wides. A wide is always liable to break up into endemics, and it needs phenomenal luck to remain morphologically coherent. The prime requirement for evolutionary radiation is environmental change, which allows for migration, for the meeting of species of different floras, and for hybridization, followed by still further movement and change. Once this is over, there is a need for a period of relative stability, so that the products of change can sort themselves out, and settle down, each to its appointed area and niche. When the situation is stable, the species can crystallise out, as it were. It is very noticeable that a high proportion of the endemics of the European flora are in S. Europe. This is in part due to the topography, but it is also perhaps due to the fact that the area has remained unglaciated, and has had a climate which has changed relatively slowly. Northern Europe, on the other hand, has been much more violently affected by glaciation, and is inhabited largely by wides. Many of these show interesting variation at the subspecific level, e.g. in the form of chromosome races; but the time for full speciation and the formation of numerous clusters of local endemics has not yet come, or if it has, only in those genera, such as *Alchemilla* and *Taraxacum*, where speciation (because of the species concept and nature of the breeding system) is much more rapid.

In this discussion I have moved rather a long way from the data which were presented in the Tables at the beginning of this paper. I have looked for explanations of the major patterns in general terms, rather than for details. It is perhaps worth asking one or two questions in conclusion about

some of the differences between the genera of Tables 1, 2 and 3. For example, is the low area per species in *Arenaria*, as compared with *Cerastium*, related to habitat, or to the nature of the taxonomic treatment, or to some intrinsic factor? Which are the main centres of speciation in the European flora, and what are the factors which have controlled the process? There is a rich mine of information in floristic works, such as *Flora Europaea*, which is largely untapped and which can provide at least a starting point for evolutionary enquiries of this kind. Combined with monographic studies, these could tell us much more about the history of the European flora than we know at present.

SUMMARY

Data are presented on the relative proportions of wide and endemic species in five genera of the European flora. Possible explanations of the low proportion of wides and the high proportion of endemics are discussed.

REFERENCES

Anway, J. C. (1969): The evolution and taxonomy of *Calectasia cyanea* R. Br. *Austral. J. Bot.* **17** 147–59

Barber, H. N. (1955): Adaptive gene substitutions in Tasmanian Eucalyptus. *Evolution* **9** 1–14

Clausen, J., Keck, D. D. and Hiesey, W. M. (1940): Effect of varied environments on western North American species. *Carnegie Inst. Wash. Pub.* No. 520

Ehrlich, P. R. and Raven, P. H. (1969): Differentiation of populations. *Science* **165** 1228–32

Hedberg, O. (1957): Afroalpine vascular plants. *Symb. Bot. Upsal.* **15** (1) 1–411

Runemark, H. (1970): The role of small populations for the differentiation in plants. *Taxon* **19** 190–201

Stebbins, G. L. and Day, A. (1967): Cytogenetic evidence for long continued stability in the genus *Plantago*. *Evolution* **21** 409–28

Strid, A. (1970): Studies in the Aegean Flora. XVI. Biosystematics of the *Nigella arvensis* complex. *Opera. Bot.* **28**, Lund

Tutin, T. G. et al. (1964): *Flora Europaea*, Vol. 1, Cambridge

Tutin, T. G. et al. (1968): *Flora Europaea*, Vol. 2, Cambridge

Valentine, D. H. (1962): Variation and evolution in the genus *Viola*. *Preslia* **34** 190–206

Valentine, D. H. and Hassan, H. M. (in press): Cytotaxonomy of the genus *Maianthemum*. *J. Bot. Soc. India*

Willis, J. C. (1922): *Age and Area*. Cambridge

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VARIATIONAL PATTERN IN *CLINOPODIUM VULGARE* L.

by

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The variation in *Clinopodium vulgare* was most recently studied by von Bothmer (1967) who divided it into three geographically vicarious subspecies, viz. ssp. *vulgare*, ssp. *villosa* (de Noé) Bothm. in the Southwest, and ssp. *orientale* Bothm. in the Southeast of Europe. Morphologically these subspecies are characterized by differences in size of calyx tube, calyx teeth, and dimensions of leaves. On the map of the distribution of the three subspecies von Bothmer indicates intermediate forms between the two southern subspecies and the ssp. *vulgare*. Such forms are frequent e.g. along the Dalmatian coast.

It is not clear whether the three subspecies are linked together by a clinal type of variation or behave more or less as distinct taxa which occasionally hybridize. While the very conspicuous vegetative characters to be mentioned below probably are due to selection and are of ecological significance, the calyx characters may be neutral or have some connection with a variation in flower biology.

During a period of twenty years, from 1950 to 1970, I have cultivated under uniform conditions a great number of strains of *Clinopodium vulgare* from different European countries as well as a few from North America. I found some of the intermediates from the South which von Bothmer mentions, and besides a striking variation within ssp. *vulgare*. This variation may to some extent be a result of cytological instability, but it is probably due mostly to selective forces. Cytological instability was demonstrated in two strains only, both from Italy. B-chromosomes were present in both strains, and large amounts of dwarf pollen as well as giant pollen. Otherwise the species seemed to be very uniform with regard to chromosome number ($2n=20$), and the pollen was normal in all other strains which were investigated.

The main differences between the various strains found during cultivation concern the development of the plants from seedling to flowering stage, earliness, duration of life, height and vigour, number of internodia, and size of flowers. In most cases the variation in single characters appeared to be clinal or with many small steps. None of the strains were entirely resembling one another, but this is quite natural as the material came from stations scattered over the Continent.

In the following only two characters will be mentioned in detail. These were considered particularly interesting and were found in a single strain which deviated from the rest in such a way that one would be inclined to regard it as a member of a separate taxon.

Fig. 1. The calcareous exposed slope facing west containing *Clinopodium vulgare* ssp. *cimbricum*. The light spots are the dwarf race of *Solidago virga-aurea*. The slope was formed by erosion of the Limfjord during the Stone Age (Littorina period). It is now separated from the fjord by alluvial areas covered with salt marsh

The deviating plants were collected on a calcareous slope facing west and they were very exposed to wind from a wide open area in the Limfjord in the north of Jutland. On the slope the subarctic *Draba incana* is found at its southern limit. The flora contains many other rare and light-requiring species, a fact which indicates that the slope was not covered by continuous wood (cf. further Böcher, Christensen and Christiansen 1946; and Fig. 1).

The *Clinopodium* on this slope resembled an alpine cushion plant but its nature, whether a special race or just a modification, had to be studied in cultivation experiments. Such experiments clearly showed that the deviating *Clinopodium* was not a modification due to wind but a good ecological race. Two characters were most prominent, viz. (1) the reduction in length and number of the internodia resulting in the dense cushion habit, (2) the reduced speed of development from seedling to flowering plant. In all strains, except in the one from the Limfjord slope, flowering took place late in the first year of cultivation. None of the Limfjord slope plants produced flowers in the first year, only rosette leaves, all running thus into a typical reinforcement stage. This character is of particular interest. In *Prunella vulgaris* we have a series of races differing in the speed of development and duration of life. Material from Southern Europe of *Prunella vulgaris* is usually summer-annual if cultivated in Denmark. Plants from Central Europe are very often first year flowering and perennial, biennial, or pauciennial, while those from Northern Europe and subalpine locations in Europe are second year flowering and perennial (Böcher 1949). The *Clinopodium* in question has just this type of development, which in *Prunella* is characteristic of races of boreal or subalpine origin.

I have crossed the cushion race (Cl 1) with two erect races, one from Southern France containing B-chromosomes (No. 6810) and with rather few and broad floral whorls, the other without B's from Central Europe with a normal number and size of the whorls (No. 7169). The normal number

of whorls on the main shoot is three, but in the race from Southern France it was frequently two. Also the cushion race has frequently two, sometimes one whorl only. The F_1 generations were not particularly low, but the plants did not bloom the first summer. Instead they produced very late in September–October some elongate shoots which bloomed. The F_2 segregations were studied carefully and gave a good deal of information about the genetical background of the cushion race. Late in September the first year a segregation in the characters involving flowering or no flowering was very conspicuous. (See Figs 2 and 3 as well as Table 1.)

Table 1

	6810 × Cl 1	7169 × Cl 1
Mainly fruiting stage	1	0
Flowering and fruiting	14	15
Flowering	2	13
Few flowers, many buds	25	26
Only floral buds	6	15
Purely vegetative	51	32

Fig. 2. Two specimens of *Clinopodium vulgare* 6810 from Southern France (to the left), together with two of Cl 1 (ssp. *cimbricum*) from the slopes north of Løgstør, Jutland (to the right). All four specimens are of the same age and in the second year of cultivation

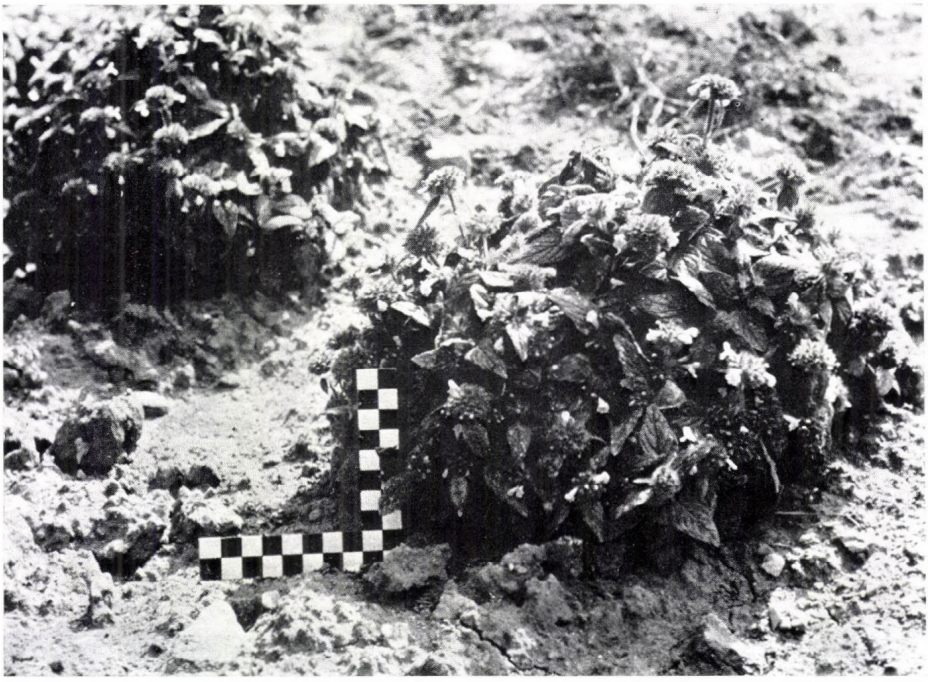

Fig. 3. Full grown specimens of *Clinopodium vulgare* ssp. *cimbricum* growing in the experimental field. The specimens are flowering. The black and white measure is divided into squares of 1 cm²

The two crosses are clearly different with regard to the number of purely vegetative specimens. Among the cultivated strains the character of being vegetative in the first year is very rare, or even unique, and thus fairly important, as from 33% to 50% of the F_2 specimens did not flower the first year.

The mean height of the plants in the cushion race was about 10–14 cm, that of the Southern European race about 30 cm, and that of the Central European one about 50 cm. In F_1–F_2 the average height was greater in the cross involving the Southern European race. This shows that the height depends on a rather complicated genetic system. The Southern European race is a strong and vigorous but not particularly tall race, and this 'vigour' when crossed may be more able to suppress the genes responsible for short internodia and slow growth, originating from the cushion race.

The F_2 contains only a few very low plants which entirely match the cushion race. But there are several almost creeping or decumbent specimens, in which low growth is combined with vigour, so that these plants may e.g. be 14 cm tall and 66 cm broad.

The main impression from these crossings is that the difference between the cushion race and the other races depends on a great many heritable characters. The cushion plant behaves in the same way as several of the ecological races studied by Clausen, Keck, and Hiesey in California. It is

Fig. 4. Type specimen of *Clinopodium vulgare* ssp. *cimbricum* (Botany Museum, Copenhagen)

worth while to mention here that these authors treat such ecological races as taxonomical subspecies.

Describing the cushion race as a new subspecies might accordingly be the right thing to do. The cushion race has been given the name ssp. *cimbricum* (see below and Fig. 4). On the other hand, the population in question is very small and may be of relic nature. The slope in question may not have been covered entirely by woodland and has always had a cool and windy microclimate. It is known that *Clinopodium vulgare* occurred in Northern Europe (e.g. in Ireland; Mitchell 1954) already in late glacial time. It is, therefore, my hypothesis that the cushion race represents the last remains of the late glacial population or it contains at least many genes from that population. In another exposed calcareous slope in Jutland an intermediate *Clinopodium* race occurs with ascending and rather short stems. This may also contain some characters from the late glacial stock. But the majority of *Clinopodium* strains are probably members of wood-steppe populations which came much later and were able to compete with, and in most places by outcrossing to disturb, the original late glacial *Clinopodiums* which were probably heliophilous and more calciphilous.

This implies that the selective forces which produced the ssp. *cimbricum* had probably worked long before, but the characters obtained by this selection were also adapted to windy exposed positions in later periods and were, therefore, able to survive in such places. To put it in another way, the ssp. *cimbricum* which only occurs few in number in a single locality is probably not a response to the recent climate on the slope.

There are other interesting features when we try to analyze the variational pattern in *Clinopodium*, but the most striking thing may be that an abrupt type variation in the case of the cushion type is found together with a clinal or a many-stepped, almost continuous variation in the rest of the species. This also applies to the transatlantic series of forms. The North American section of the species, which was described as var. *neogaea* Fernald 1944, does not seem to differ in any essential way from some of the SW. European forms and may represent populations of European origin, but, with a limited variation, corresponding to what was present of genes in those biotypes which happened to cross the ocean. In the other direction, in China, the ssp. *chinensis* seems to be much more distinct and may, as proposed by Briquet (1897), be considered an independent species. Unfortunately, I have not so far had an opportunity to cultivate Chinese material.

Returning now to ssp. *cimbricum* in Jutland I would like to say a few words about other species occurring in exposed cliffs and dunes along Danish seashores. Among these species there are some which genetically are low-growing and differ from the more widespread races of the same species in a manner which resembles that found in *Clinopodium*.

Ranunculus acris. Low forms on northern slopes resembling the subalpine/sub-arctic races found in the North Atlantic area (ssp. *borealis* [Trautv.] Nyman).

Solidago virga-aurea. Very low and compact race occurring on exposed calcareous slopes and dunes in NW. Jutland. Resembling alpine races by low growth but deviating from the latter by being late blooming. Also occurring abundantly on the slope with the cushion-*Clinopodium* (cf. Fig. 1).

Dactylis glomerata. Dwarf race found on the exposed limestone cliffs of Bulbjerg in NW. Jutland. These cliffs have probably never been covered by wood (cf. Böcher 1961).

Hypochoeris maculata. Very low-growing race found together with the *Dactylis* race on calcareous exposed slope at the sea (the cliffs of Bulbjerg, NW. Jutland).

Silene otites. Low race in the dunes of Jutland. Extremely different from Southern and Central European tall races. No stations in Eastern Denmark.

Koeleria glauca. Low race occurring in the dunes of W. Jutland. No occurrences between the west coast of Jutland and Sweden.

Rosa pimpinellifolia. Low race on slopes and in dunes of W. Jutland. No natural habitats in Eastern Denmark and Sweden.

The first four species are widely distributed but occur in certain exposed slopes as populations composed of very low biotypes. In the case of *Hypochoeris maculata*, similar ones were found on the exposed cliffs on Jersey in the Channel and in the flat alvar of Öland in the Baltic Sea on shallow soil overlying calcareous rocks.

The three species mentioned last, viz. *Silene otites*, *Koeleria glauca*, and *Rosa pimpinellifolia*, all have very wide continental areas, but reach the West coast in W. Jutland. However, in all three cases there are gaps between the W. Jutland occurrences and those towards the East, and in all cases the Jutland race is low. It is, therefore, in my opinion probable that these plants reached our dunes from the South during the late-glacial period, but lost their original continental connections later.

Finally, I may remind of the variation found in *Geranium robertianum*. In Denmark and England a low, decumbent, often reddish race occurs which grows in sunny shingly beaches, while the common erect race grows in woods. In this case the growth habit characters of the decumbent race, which is called ssp. *maritima* (Bab.) H. G. Baker, are dominant when this race is crossed with the woodland race (Böcher 1947). The two races diverge from one another by several genes. They are ecologically almost completely isolated from one another. The shingly beach race is clearly heliophilous. In this case, however, the decumbent type is most abundant in the Southern part of Denmark and is said to occur even in Madeira, a fact which perhaps makes a theory of late glacial arrival less probable.

As a conclusion I may propose the idea that races which are distinct and deviate from the main bulk of biotypes in several genetically fixed characters may not be the results of a recent selection, but have a longer history. They often evolved during other periods which differed climatically from the present period. However, while the prevailing climate of our days may be less favourable, the local climates or microclimates may fit such races. They are, therefore, nowadays closely connected with some deviating small climatic pockets and are rare or have restricted areas. In many ways they have the character of being relics.

Description of ssp. *cimbricum*
Clinopodium vulgare L. ssp. *cimbricum* ssp. nov.

A ssp. vulgari statura pulviniformi et anthesi longe procrastinata imprimis differt. Caules floriferi pulvinum hemisphaericum e caulibus sterilibus internodiis brevibus compositum paulum superantes, in loco naturali 12–16 cm alti, 1 (–2) verticillos gerentes, culti 10–23 cm alti, (1–) 2 (–3) verticillos gerentes. Plantae ex seminibus in horto cultae primo anno non florentes.

Typus (Fig. 4) die 18 Aug. anni 1970 in loco declivi ex oppido Løgstør in septentriones sito regionis Cimbriae peninsulae danicae Jutlandiae lectus in Museo Botanico Hauniensi depositus.

REFERENCES

von Bothmer, R. (1967): Intraspecific variation in *Clinopodium vulgare* L. *Bot. Notiser* **120** 202–8

Briquet, J. (1897): Labiatae im Engler-Prantl: *Natürliche Pflanzenfamilien*, **IV 3a** 183–384

Böcher, T. W. (1947): Cytogenetic and biological studies in *Geranium robertianum* L. *Da. Vidsk. Selsk. Biol. Medd.* **20** No. 8

Böcher, T. W. (1949): Racial divergence in *Prunella vulgaris* in relation to habitat and climate. *New Phytol.* **48** 285–314

Böcher, T. W. (1961): Experimental and cytological studies on plant species VI. *Dactylis glomerata* and *Anthoxanthum odoratum*. *Bot. Tidsskr.* **56** 314–35

Böcher, T. W., Christensen, Tyge and Christiansen, M. Skytte (1946): Slope and dune vegetation of North Jutland. I. Himmerland. *Dan. Biol. Skr.* **4** No. 3, 1–78

Fernwald, (1944):

Maire, R. (1940): Contributions à l'étude de la Flore de l'Afrique du Nord. *Bull. Soc. d'hist. Nat. de l'Afrique du Nord.* **31** 7–49

Mitchell, G. F. (1954): The late-glacial flora of Ireland. *D. G. U. II raekke* **80** 73–86

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RANGE OF CLIMATIC TOLERANCE AS AN INDICATION OF EVOLUTIONARY POTENTIAL IN *MIMULUS* (*SCROPHULARIACEAE*)

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In studying the evolution of a group of plants such as the genus *Mimulus*, one of the recurrent questions is 'how much evolution is possible?', that is, 'what is the actual evolutionary potential of the group?' The purpose of this study is to investigate a small, but significant portion of that interesting overall problem. The scope will be narrowed to the question, 'over how wide a range of climates can different populations of *Mimulus* plants live and reproduce?' and its sequel 'how does interpopulation hybridization affect the range of climates under which *Mimulus* plants can live and reproduce?'

For the investigation thirty populations involved in my other evolutionary studies (Vickery 1951, 1959, 1966, 1967) and two families of their F_1 and F_2 hybrids were selected and grown in the University of Utah greenhouse. Six plants of each population and F_1 hybrid combination and 30 plants of each F_2 hybrid population were chosen and carefully propagated. When large enough, each plant was cloned, i.e. divided into 36 small clone members. All the clone members were flown to Los Angeles, California, where they were established in the Earhart Laboratory, the Phytotron, at the California Institute of Technology, Pasadena. Many of the plants lost clone members due to the rigors of the move and had to be discarded from the experiment. However, 27 plants and one family of F_1 and F_2 hybrids with 30 or more clone members each survived and were studied (Table 1). These plants represented 13 populations belonging to four related species —*Mimulus guttatus* Fischer ex DC., *M. luteus* L., *M. tilingii* Regel, and *M. glabratus* K. The family of F_1 and F_2 hybrids was from a cross between two populations of *M. guttatus* from sharply contrasting localities, the foothills of the hot San Joaquin Valley of California and a spring in the shade of spruce trees in the Hudsonian zone of the Wasatch Mountains of Utah (Table 1).

The experimental design consisted of growing and observing a clone member of each plant in each of 22 different artificial climates (Table 2). The climates ranged from ones with cold days and nights to ones with hot days and nights. All the climates had an 8 hour night period and a 16 hour day period. For most climates the day period had a light intensity of 2000–2500 foot-candles from banks of fluorescent and incandescent lights in the ceilings of the growth rooms (see Went 1957, for a full description of the Earhart Laboratory growth rooms and special greenhouses). For five of the artificial climates the plants received approximately 5000 foot-candles of filtered natural light in the greenhouses for eight hours of each 16

Table 1

Origins of the populations of *Mimulus* grown under controlled temperature conditions

Mimulus gattatus Fischer ex DC.

Culture 5001, $n = 14$, Pacific Grove, Monterey Co., California, U.S.A., 2 m elev., *Vickery 1*
Culture 5003, $n = 14$, Pescadero, Monterey Co., California, U.S.A., 7 m elev., *Clausen 2083*
Culture 5004, $n = 14$, Chew's Ridge, Monterey Co., California, U.S.A., 1500 m elev., *Vickery 3*
Culture 5007, $n = 14$, Yosemite Junction, Tuolumne Co., California, U.S.A., 450 m elev., *Hiesey 539*
Culture 5015, $n = 14$, Mono Lake, Mono Co., California, U.S.A., 2150 m elev., *Clausen 2043*
Culture 5346, $n = 14$, Mt. Oso, Stanislaus Co., California, U.S.A., 330 m elev., *Vickery 190*
Culture 5687, $n = 14$, Kodiak Island, Alaska, U.S.A., ca 200 m elev., *Freeman Aug. 14, 1950*
Culture 5834, $n = 14$, Salt Lake City, Salt Lake Co., Utah, U.S.A., 1470 m elev., *Vickery 330*
Culture 5839, $n = 14$, Big Cottonwood Canyon, Salt Lake Co., Utah, U.S.A., 2350 m elev., *Vickery 334*
Culture 1709, the F_1 hybrid of culture 5346 $\times$ culture 5839
Culture 5923, the F_2 hybrid (1709 $\times$ self) of culture 5346 $\times$ culture 5839

Mimulus luteus L.

Culture 5043, $n = 30 + 0$, 1, or 2. Illapel, Coquimbo Prov., Chile, 600 m elev., *U.S.D.A. Plant Introduction Service no. 144536*

Mimulus tilingii var. *corallinus* (Greene) Grant

Culture 5011, $n = 24$, Porcupine Flat, Mariposa Co., California, U.S.A., 2500 m elev., *Hiesey 576*

Mimulus glabratus var. *utahensis* Pennell

Culture 5048, $n = 15$, Mono Lake, Mono Co., California, U.S.A., 2150 m elev., *Stebbins 714*

Mimulus glabratus var. *parviflorus* (Lindl) Grant

Culture 5041, $n = 46$, Illapel, Coquimbo Prov., Chile, 1220 m elev., *U.S.D.A. Plant Introduction Service no. 144534*

hour day period (Table 2). Occasionally, in artificial climates with sufficient space, the plants were represented by more than one clone member each and, in a few climates in which space was limiting, not all the plants were represented (Tables 2, 3). Each clone member was grown in a plastic cup containing a 1 : 1 mixture of vermiculite and fine quartz gravel. The clone members were kept moist with $\frac{1}{4}$ strength Hoaglund's nutrient solution plus extra de-ionized water as needed in the hotter artificial climates.

In initiating the experiment, care was taken to use clone members of as closely equal size and vigor as possible for each different plant.

Table 2

Comparative growth of *Mimulus* clones under different temperature conditions

Temperature Day/night °C	Populations (flowering or vegetative)							
	5001–30		5001–33		5003–85		5003–86	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	24	2·0 *v*	48	16·0 *f*	67	11·0 *f*	43	7·0 *v*
17/7	33	5·5 *f*	32	3·1 *f*	68	10·0 *f*	42	3·5 *v*
17/10	46	5·4 *f*	47	3·4 *f*	60	8·0 *f*	38	3·6 *v*
17/14	71	6·3 *f*	53	4·4 *f*	82	8·0 *f*	52	2·2 *v*
17/17	26	4·0 *v*	46	5·0 *f*	39	3·5 *v*	54	6·0 *v*
17/20	12	1·1 *v*	—	—	69	5·3 *f*	—	—
17/23	46	4·0 *f*	65	3·0 *f*	48	6·6 *f*	24	0·5 *v*
4/14	7	5·7 *v*	3	1·7 *v*	21	7·1 *v*	7	0·8 *v*
7/14	6	1·6 *v*	21	2·6 *v*	42	8·5 *v*	32	7·5 *v*
10/14	19	3·4 *v*	20	2·5 *v*	54	7·8 *v*	15	1·6 *v*
14/14	39	8·0 *f*	42	5·5 *f*	41	4·6 *v*	29	1·4 *v*
17/14	22	1·3 *v*	47	4·0 *f*	94	8·7 *f*	22	0·4 *v*
20/14	64	5·6 *f*	52	2·3 *f*	64	4·1 *f*	33	1·4 *v*
23/14	28	1·5 *f*	18	1·2 *f*	—	—	10	1·1 *v*
17/14*	44	10·6 *f*	33	—*v*	58	15·6 *f*	24	5·9 *v*
20/14*	49	19·0 *f*	—	—	78	20·0 *f*	—	—
23/14*	17	9·0 *f*	—	—	57	18·0 *f*	—	—
26/14*	11	8·0 *f*	—	—	68	22·0 *f*	—	—
30/14*	13	4·6 *f*	56	17·0 *f*	63	9·7 *f*	39	9·0 *v*
7/7	5	0·2 *v*	35	7·0 *f*	17	10·0 *v*	21	5·0 *v*
7/23	13	5·0 *v*	15	5·0 *v*	29	4·0 *v*	19	3·0 *v*
26/7	4	0·9 *f*	14	0·4 *f*	—	—	2	0·3 *v*
26/23	11	0·2 *v*	25	—*v*	—	—	10	0·1 *v*

Temperature Day/night °C	Populations (flowering or vegetative)									
	5004–32		5004–33		5004–81		5004–83		5007–30	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	38	7·0 *f*	79	5·0 *f*	73	8·0 *f*	103	5·0 *f*	54	6·0 *f*
17/7	42	4·2 *f*	82	7·0 *f*	49	2·0 *v*	111	15·0 *f*	28	2·5 *v*
17/10	58	5·2 *f*	67	4·0 *f*	64	7·0 *f*	87	6·0 *f*	45	3·6 *f*
17/14	49	4·8 *f*	62	4·4 *f*	38	0·7 *v*	104	4·4 *f*	34	2·9 *v*
17/17	—	—	45	3·9 *f*	60	3·5 *f*	56	3·0 *f*	32	3·0 *v*
17/20	—	—	—	—	—	—	93	4·7 *f*	—	—
17/23	55	6·0 *f*	43	6·1 *f*	68	5·6 *f*	68	4·9 *f*	38	3·0 *v*
4/14	8	5·6 *v*	13	—*v*	19	5·6 *v*	36	4·7 *f*	8	4·4 *v*
7/14	24	8·4 *f*	35	7·2 *f*	34	6·1 *f*	28	1·6 *v*	12	2·4 *v*
10/14	26	10·5 *f*	48	7·0 *v*	55	7·0 *f*	82	7·4 *f*	14	2·2 *v*
14/14	58	9·5 *f*	60	6·1 *f*	25	0·6 *v*	76	5·5 *f*	48	6·3 *v*
17/14	38	3·4 *f*	—	4·2 *f*	77	0·9 *v*	116	3·4 *f*	24	0·7 *v*
20/14	55	5·3 *f*	60	5·5 *f*	34	0·5 *v*	94	2·7 *f*	28	2·4 *v*
23/14	13	0·9 *f*	6	0·2 *v*	34	1·2 *f*	10	0·8 *f*	6	0·9 *v*
17/14*	34	10·1 *f*	60	5·5 *f*	64	10·4 *f*	75	8·9 *f*	16	3·1 *v*
20/14*	—	—	—	—	—	—	90	14·7 *f*	—	—
23/14*	—	—	—	—	—	—	91	8·8 *f*	—	—
26/14*	—	—	—	—	—	—	67	6·2 *f*	—	—
30/14*	45	6·2 *f*	37	4·1 *f*	62	5·1 *f*	79	2·0 *f*	27	1·6 *f*
7/7	8	5·0 *v*	38	9·0 *v*	21	9·0 *f*	26	4·0 *f*	15	1·0 *v*
7/23	12	5·5 *v*	30	5·0 *v*	50	4·8 *f*	62	5·9 *f*	19	1·7 *v*
26/7	7	0·3 *v*	—	—	—	—	—	—	4	0·5 *v*
26/23	6	0·3 *v*	—	—	6	0·2 *v*	—	—	8	—*v*

* With higher light intensity for 8 of the 16 hour light period

Temperature Day/night °C	Populations (flowering or vegetative)									
	5007–32		5007–33		5007–83		5011–31		5011–32	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	69	— *v*	48	7·0 *f*	24	0·5 *v*	38	1·0 *f*	18	0·5 *v*
17/7	98	7·0 *f*	47	5·9 *f*	33	1·0 *v*	24	1·0 *v*	17	0·5 *v*
17/10	78	4·0 *f*	26	2·4 *f*	20	0·5 *v*	38	—*v*	19	0·1 *f*
17/14	85	3·6 *f*	67	3·3 *f*	17	—*v*	46	2·3 *f*	15	0·1 *v*
17/17	52	3·8 *v*	41	6·0 *v*	27	1·0 *v*	35	2·0 *f*	18	0·6 *v*
17/20	78	6·5 *f*	—	3·5 *v*	—	—	—	—	—	—
17/23	62	4·7 *f*	29	5·0 *v*	39	2·1 *v*	38	1·8 *f*	14	0·4 *v*
4/14	23	3·4 *v*	8	5·2 *v*	11	1·8 *v*	3	0·1 *v*	8	0·1 *v*
7/14	56	14·2 *f*	13	5·8 *v*	18	0·2 *v*	17	0·6 *v*	13	0·1 *v*
10/14	65	10·8 *f*	19	3·9 *v*	29	0·4 *v*	14	0·3 *v*	12	0·1 *v*
14/14	54	5·1 *v*	28	1·9 *v*	44	1·8 *v*	21	0·7 *v*	8	0·1 *v*
17/14	82	3·6 *f*	42	2·7 *f*	9	0·1 *v*	36	0·4 *f*	11	0·1 *v*
20/14	56	2·0 *v*	38	5·3 *f*	36	0·9 *v*	41	1·4 *f*	24	0·9 *v*
23/14	19	1·1 *f*	10	0·5 *v*	5	0·7 *v*	17	0·3 *f*	21	0·7 *f*
17/14*	65	5·5 *f*	22	1·2 *v*	35	3·3 *v*	17	—*v*	33	1·5 *f*
20/14*	95	14·8 *f*	—	—	—	—	—	—	—	—
23/14*	72	9·5 *f*	—	—	—	—	—	—	—	—
26/14*	82	10·9 *f*	—	—	—	—	—	—	—	—
30/14*	65	2·6 *f*	27	3·2 *f*	18	0·8 *v*	28	1·1 *f*	29	2·0 *f*
7/7	25	7·0 *f*	—	—	14	0·5 *v*	10	—*v*	2	0·01 *v*
7/23	58	7·5 *f*	22	3·1 *v*	32	3·0 *v*	16	0·4 *v*	16	0·4 *v*
26/7	10	1·0 *v*	—	—	—	—	—	—	—	—
26/23	—	—	—	—	—	—	—	—	8	—

Temperature Day/night °C	Populations (flowering or vegetative)									
	5043–30		5043–31		5043–32		5043–33		5048–32	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	16	0·5 *v*	15	5·0 *f*	47	2·0 *f*	39	5·0 *f*	11	—*v*
17/7	25	1·9 *v*	38	3·0 *v*	62	7·0 *f*	35	2·0 *v*	19	0·1 *v*
17/10	43	4·4 *f*	36	2·0 *f*	38	3·5 *f*	38	2·0 *v*	54	3·5 *f*
17/14	56	3·5 *f*	64	3·7 *f*	73	6·1 *f*	—	—	93	7·7 *f*
17/17	34	3·0 *v*	38	3·0 *f*	41	6·0 *f*	37	3·0 *f*	—	—
17/20	—	—	—	—	—	—	—	—	—	—
17/23	45	3·0 *f*	39	3·7 *f*	38	2·2 *f*	32	2·9 *f*	54	1·0 *f*
4/14	9	3·7 *v*	14	4·9 *v*	4	0·1 *v*	7	0·1 *v*	9	1·3 *v*
7/14	18	2·8 *v*	29	2·2 *v*	—	—	10	0·7 *v*	15	1·3 *v*
10/14	23	2·8 *v*	43	4·0 *f*	24	3·3 *v*	—	—	34	1·0 *f*
14/14	29	1·2 *v*	45	2·0 *f*	53	4·2 *f*	53	3·8 *f*	32	0·9 *f*
17/14	45	2·1 *f*	74	2·2 *f*	81	3·3 *f*	69	3·5 *f*	35	1·2 *f*
20/14	41	—*v*	38	0·8 *v*	68	4·4 *f*	52	2·8 *f*	69	4·5 *f*
23/14	14	0·7 *f*	15	3·1 *f*	18	—*v*	—	0·6 *f*	24	0·6 *f*
17/14*	12	0·2 *v*	37	—	52	5·4 *f*	35	3·8 *f*	67	11·8 *f*
20/14*	—	—	—	—	—	—	—	—	—	7·0 *f*
23/14*	—	—	—	—	—	—	—	—	—	—
26/14*	—	—	—	—	—	—	—	—	—	—
30/14*	22	2·0 *f*	23	1·8 *v*	34	5·1 *f*	42	2·7 *f*	24	1·0 *v*
7/7	18	4·0 *v*	9	1·0 *v*	13	4·0 *v*	—	—	20	5·0 *f*
7/23	12	1·2 *v*	22	0·8 *v*	12	0·8 *v*	18	1·1 *v*	38	3·0 *f*
26/7	9	0·3 *v*	—	—	—	—	—	—	23	0·7 *f*
26/23	—	—	—	—	—	—	—	—	20	—*v*

(cont.)

Temperature Day/night °C	Populations (flowering or vegetative)									
	5011–81		5011–82		5015–30		5015–81		5041–81	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	39	2·0 *f*	59	4·0 *f*	68	10·0 *f*	76	—*v*	31	—*v*
17/7	25	0·5 *v*	59	5·0 *f*	61	4·0 *f*	79	3·0 *f*	—	—
17/10	27	3·0 *v*	58	4·0 *f*	62	3·0 *f*	60	4·0 *f*	26	0·8 *v*
17/14	28	1·2 *v*	48	3·0 *f*	43	1·0 *f*	68	4·6 *f*	35	1·9 *f*
17/17	19	2·0 *v*	48	2·3 *f*	57	3·1 *f*	53	4·4 *f*	47	1·3 *f*
17/20	—	—	43	1·3 *f*	55	1·1 *f*	—	—	48	1·9 *f*
17/23	23	4·1 *v*	42	2·9 *f*	40	4·0 *f*	43	1·8 *f*	34	1·0 *f*
4/14	11	0·7 *v*	17	2·8 *f*	4	0·2 *v*	13	1·3 *v*	21	2·1 *v*
7/14	11	0·4 *v*	35	1·0 *f*	—	—	39	7·1 *f*	28	2·9 *f*
10/14	14	0·3 *v*	21	0·8 *v*	64	4·0 *f*	64	3·2 f	31	2·8 *f*
14/14	16	—*v*	57	2·4 *f*	—	—	65	4·6 *f*	30	1·6 *f*
17/14	24	0·4 *v*	49	0·8 *f*	72	2·8 *f*	88	3·7 *f*	26	0·1 *v*
20/14	15	0·7 *v*	49	2·1 *f*	45	2·8 *f*	62	2·5 *f*	—	—
23/14	—	—	29	0·6 *f*	23	—*v*	4	1·0 *f*	—	—
17/14*	16	0·8 *v*	48	4·4 *f*	55	4·0 *f*	57	7·7 *f*	26	2·2 *f*
20/14*	—	—	57	7·0 *f*	65	12·0 *f*	—	—	51	—*v*
23/14*	—	—	45	1·4 *f*	43	15·0 *f*	—	—	28	5·0 *f*
26/14*	—	—	59	2·7 *f*	36	5·0 *f*	—	—	26	3·0 *f*
30/14*	29	0·8 *f*	46	3·3 *f*	17	3·0 *f*	47	4·0 *f*	36	3·0 *f*
7/7	4	—*v*	28	4·0 *f*	4	5·0 *f*	14	1·0 *v*	11	0·5 *v*
7/23	13	0·3 *v*	18	1·2 *v*	45	12·0 *f*	56	15·0 *f*	33	2·0 *f*
26/7	—	—	—	—	—	—	—	—	1	—
26/23	—	—	—	—	20	—*v*	—	—	—	—

Temperature Day/night °C	Populations (flowering or vegetative)									
	5048–33		5687–81		5687–83		5834–32		5834–82	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	83	5·0 *f*	17	1·0 *v*	16	1·0 *v*	64	10·0 *f*	59	7·0 *f*
17/7	73	3·0 *f*	25	1·8 *v*	24	2·3 *v*	87	9·6 *f*	66	6·0 *f*
17/10	70	8·0 *f*	18	3·4 *v*	20	1·4 *v*	63	8·0 *f*	53	10·0 *f*
17/14	56	1·9 *f*	62	1·4 *v*	17	1·3 *v*	64	8·8 *f*	49	—*v*
17/17	57	4·0 *f*	18	1·0 *v*	63	8·0 *f*	55	8·0 *f*	57	4·0 *f*
17/20	—	—	39	1·3 *v*	13	0·3 *v*	51	8·5 *f*	60	2·7 *f*
17/23	45	3·5 *f*	34	4·0 *v*	11	0·5 *v*	52	9·0 *f*	48	2·0 *f*
4/14	13	1·6 *v*	10	0·6 *v*	13	2·0 *v*	22	11·2 *f*	8	0·9 *v*
7/14	39	1·7 *f*	15	3·9 *v*	24	5·2 *v*	37	15·1 *f*	27	4·6 *f*
10/14	66	4·7 *f*	13	1·6 *v*	11	0·8 *v*	40	12·7 *f*	35	5·2 *f*
14/14	56	2·2 *f*	24	0·7 *v*	22	1·9 *v*	58	6·2 *f*	55	3·7 *f*
17/14	67	2·6 *f*	33	1·2 *v*	18	—*v*	77	6·5 *f*	54	3·2 *f*
20/14	60	1·5 *f*	19	2·7 *v*	12	0·7 *v*	58	5·8 *f*	60	3·1 *f*
23/14	28	1·0 *f*	5	0·6 *v*	22	1·2 *f*	23	1·4 *f*	28	0·9 *f*
17/14*	60	0·3 *f*	31	2·6 *v*	12	0·5 *v*	54	7·0 *f*	58	5·5 *f*
20/14*	—	—	36	9·0 *v*	96	28·0 *f*	60	20·0 *f*	68	17·0 *f*
23/14*	—	—	31	9·0 *v*	16	0·2 *v*	73	39·0 *f*	61	12·0 *f*
26/14*	—	—	19	12·0 *v*	10	0·01 *v*	53	30·0 *f*	62	18·0 *f*
30/14*	48	5·0 *f*	13	4·0 *v*	21	2·0 *v*	44	6·0 *f*	51	6·0 *f*
7/7	24	0·01 *v*	5	2·0 *v*	5	1·0 *v*	22	9·0 *f*	6	8·0 *f*
7/23	29	2·0 *f*	15	2·0 *v*	9	1·0 *v*	43	16·0 *f*	35	8·0 *f*
26/7	—	—	—	—	—	—	7	0·5 *f*	—	—
26/23	4	—*v*	—	—	5	—	19	0·4 *f*	—	—

Table

Comparative growth of a family of *Mimulus guttatus* plants under different tempera- (culture 1709), their F_2

Temperature Day/night °C	Populations (flowering or vegetative)							
	5346–31		5346–32		5839–33		1709–1	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	50	2·3 *f*	49	3·1 *f*	22	0·9 *f*	56	2·9 *f*
17/7	51	2·8 *f*	54	—*f*	10	0·4 *v*	61	3·8 *f*
17/10	46	2·1 *f*	33	2·7 *f*	21	1·5 *f*	53	1·7 *f*
17/14	46	2·3 *f*	44	4·5 *f*	13	1·9 *v*	48	1·9 *f*
17/17	18	1·5 *v*	37	2·0 *f*	17	0·8 *v*	32	2·0 *v*
17/20	40	2·9 *f*	41	3·3 *f*	26	0·7 *f*	44	1·8 *f*
17/23	31	2·4 *f*	36	1·7 *f*	15	0·7 *v*	36	2·2 *f*
4/14	5	0·8 *v*	12	—*f*	4	0·5 *v*	3	0·8 *v*
7/14	15	1·6 *v*	7	1·5 *v*	3	0·4 *v*	21	3·1 *f*
10/14	26	3·9 *f*	19	3·1 *v*	3	0·4 *v*	36	4·5 *f*
14/14	30	1·3 *f*	41	3·3 *f*	19	0·2 *v*	28	1·3 *f*
17/14	43	2·5 *f*	31	1·7 *f*	33	0·6 *f*	45	2·5 *f*
17/14*	26	6·1 *f*	35	6·2 *f*	—	—	30	3·3 *f*
20/14*	39	3·3 *f*	37	6·4 *f*	2	0.01 *v*	35	5·3 *f*
23/14*	22	3·3 *f*	37	7·8 *f*	12	0·1 *v*	35	3·9 *f*
30/14*	12	2·7 *f*	41	5·3 *f*	8	0·5 *v*	29	3·2 *f*
7/7	22	1·3 *f*	7	1·0 *v*	—	—	6	1·2 *v*
7/23	24	2·8 *f*	9	1·2 *v*	5	0·01 *v*	22	1·9 *f*
26/7	16	0·3 *f*	22	0·6 *f*	—	—	11	—*f*
26/23	3	0·1 *v*	—	—	—	—	11	0·8 *v*

* With higher light intensity for 8 of the 16 hour light period

Temperature Day/night °C	Populations (flowering or vegetative)									
	5923–13		5923–14		5923–23		5923–25		5923–27	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	56	2·9 *f*	63	4·5 *f*	51	2·1 *f*	59	2·9 *f*	11	0·2 *v*
17/7	46	3·3 *f*	74	5·0 *f*	65	1·6 *f*	56	2·0 *f*	12	1·2 *v*
17/10	57	2·3 *f*	70	3·6 *f*	73	2·8 *f*	73	2·3 *f*	38	2·1 *f*
17/14	42	4·0 *f*	52	3·9 *f*	42	1·0 *f*	43	2·7 *f*	19	0·5 *v*
17/17	45	2·5 *f*	50	2·7 *f*	—	—	40	1·3 *v*	30	2·1 *v*
17/20	39	1·9 *f*	58	5·5 *f*	53	2·3 *f*	67	2·8 *f*	42	2·0 *f*
17/23	36	1·7 *f*	47	4·5 *f*	38	3·8 *f*	36	1·0 *f*	34	1·8 *f*
4/14	12	0·8 *v*	16	3·3 *v*	39	4·6 *f*	8	1·3 *v*	6	0·7 *v*
7/14	23	1·5 *v*	35	—*f*	40	3·6 *f*	18	2·5 *f*	11	2·6 *v*
10/14	33	1·6 *v*	33	6·1 *f*	52	3·8 *f*	30	6·7 *f*	22	3·0 *v*
14/14	41	3·1 *f*	59	4·4 *f*	51	3·3 *f*	25	1·6 *f*	38	2·6 *f*
17/14	52	1·8 *f*	58	6·2 *f*	56	0·9 *f*	72	1·9 *f*	42	1·9 *f*
17/14*	51	5·7 *f*	47	9·3 *f*	56	9·5 *f*	27	6·5 *f*	34	5·1 *f*
20/14*	39	6·6 *f*	45	10·1 *f*	49	7·5 *f*	31	5·8 *f*	50	7·3 *f*
23/14*	49	8·1 *f*	43	9·9 *f*	52	7·3 *f*	35	5·2 *f*	30	4·0 *f*
30/14*	40	3·3 *f*	44	7·9 *f*	7	0·2 *v*	29	2·3 *f*	35	2·1 *f*
7/7	36	2·9 *f*	15	2·0 *v*	39	2·2 *f*	7	0·9 *v*	11	2·6 *v*
7/23	24	1·6 *f*	34	4·7 *f*	48	5·7 *f*	19	4·8 *f*	17	2·2 *v*
26/7	10	—*v*	—	—	—	—	11	0·01 *v*	27	—*f*
26/23	21	—*f*	15	0·4 *v*	—	—	7	0·8 *v*	22	0·3 *f*

ture conditions; two parental populations (cultures 5346 and 5839), their F_1 hybrid hybrids (culture 5923)

Temperature Day/night °C	Populations (flowering or vegetative)									
	5923–7		5923–9		5923–10		5923–11		5923–12	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	34	2·3 *f*	5	0·4 *v*	49	4·6 *f*	38	3·7 *f*	18	2·4 *v*
17/7	41	2·1 *f*	45	0·9 *f*	58	4·1 *f*	47	5·4 *f*	24	1·5 *f*
17/10	26	1·8 *f*	63	1·7 *f*	60	4·0 *f*	41	2·8 *f*	18	0·6 *v*
17/14	27	2·0 *f*	25	0·8 *v*	51	5·3 *v*	41	3·7 *v*	20	1·7 *v*
17/17	—	—	12	6·7 *v*	35	2·6 *f*	21	2·4 *v*	9	1·9 *v*
17/20	14	1·9 *v*	37	1·2 *f*	42	3·2 *f*	27	3·2 *f*	11	0·7 *v*
17/23	30	4·2 *f*	—	—	35	2·4 *f*	28	2·6 *v*	14	1·8 *v*
4/14	7	2·4 *v*	7	1·3 *v*	4	0·3 *v*	8	2·7 *v*	2	0·9 *v*
7/14	11	3·7 *v*	8	1·2 *v*	7	0·9 *v*	19	2·9 *v*	2	1·6 *v*
10/14	6	1·2 *v*	14	3·4 *v*	13	2·5 *v*	32	7·9 *f*	9	1·6 *v*
14/14	20	2·5 *v*	19	0·6 *v*	50	5·1 *f*	22	2·0 *f*	8	1·7 *v*
17/14	20	1·7 *v*	12	0·5 *v*	49	2·4 *f*	47	4·5 *f*	12	1·1 *v*
17/14*	25	7·4 *f*	22	3·6 *v*	40	10·6 *f*	42	10·9 *f*	10	2·5 *v*
20/14*	16	5·6 *f*	21	1·8 *f*	32	8·0 *f*	20	6·0 *v*	16	2·5 *v*
23/14*	21	4·9 *v*	45	2·6 *f*	37	8·0 *f*	19	4·7 *v*	9	—*f*
30/14*	34	4·3 *f*	6	2·2 *v*	30	5·8 *f*	30	2·4 *f*	6	1·4 *v*
7/7	2	0·9 *v*	3	0·6 *v*	5	0·7 *v*	21	1·6 *v*	3	1·1 *v*
7/23	—	—	17	2·7 *v*	11	2·9 *v*	30	6·7 *v*	6	1·4 *v*
26/7	3	0·5 *v*	—	—	26	0·8 *f*	5	0·7 *v*	3	0·1 *v*
26/23	4	0·9 *v*	—	—	23	0·9 *f*	9	0·9 *v*	5	0·4 *v*

Temperature Day/night °C	Populations (flowering or vegetative)									
	5923–28		5923–32		5923–34		5923–47		5923–49	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	44	4·7 *f*	49	3·1 *f*	12	0·4 *v*	30	2·4 *v*	55	3·9 *f*
17/7	62	3·3 *f*	53	3·6 *f*	16	0·6 *v*	29	2·6 *f*	49	3·2 *f*
17/10	56	5·3 *f*	47	2·8 *f*	14	0·7 *v*	35	4·0 *f*	41	—*f*
17/14	63	4·2 *f*	49	3·3 *f*	19	1·8 *v*	27	3·9 *f*	45	4·1 *f*
17/17	62	5·6 *f*	33	2·3 *f*	16	0·2 *v*	24	3·3 *v*	16	1·6 *v*
17/20	48	4·7 *f*	37	4·5 *f*	14	0·5 *v*	25	1·8 *v*	33	3·0 *f*
17/23	46	2·6 *f*	32	2·5 *f*	10	1·6 *v*	21	2·9 *f*	27	2·7 *f*
4/14	29	3·6 *f*	23	1·7 *f*	3	0·4 *v*	11	1·6 *v*	7	2·0 *v*
7/14	35	6·7 *f*	24	3·8 *f*	5	0·8 *v*	16	1·5 *v*	7	2·1 *v*
10/14	34	4·5 *f*	33	6·1 *f*	13	1·1 *v*	15	2·5 *v*	32	6·9 *f*
14/14	63	3·0 *f*	39	4·7 *f*	14	1·0 *v*	19	1·9 *v*	20	2·9 *v*
17/14	55	3·5 *f*	49	2·5 *f*	13	0·3 *v*	25	0·6 *v*	49	1·8 *f*
17/14*	46	8·5 *f*	45	9·2 *f*	12	1·8 *v*	30	5·5 *v*	12	3·2 *f*
20/14*	35	6·6 *f*	30	7·7 *f*	20	1·9 *v*	18	4·5 *v*	28	9·5 *f*
23/14*	66	10·4 *f*	55	2·6 *f*	9	0·8 *v*	50	6·9 *f*	40	9·8 *f*
30/14*	38	4·8 *f*	32	5·8 *f*	9	1·7 *v*	20	1·6 *f*	18	3·2 *f*
7/7	24	2·9 *v*	8	0·4 *v*	4	0·3 *v*	7	2·0 *v*	11	2·0 *v*
7/23	34	6·5 *f*	14	2·9 *f*	11	1·4 *v*	21	3·9 *v*	22	3·2 *v*
26/7	—	—	—	—	4	0·3 *v*	5	—*v*	9	0·9 *v*
26/23	—	—	—	—	2	0·1 *v*	6	0·8 *v*	4	0·4 *v*

Table 3 (cont.)

Temperature Day/night °C	Populations (flowering or vegetative)									
	5923–54		5923–55		5923–56		5923–57		5923–58	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	13	1·1 *v*	57	5·4 *f*	51	3·3 *f*	6	0·01 *v*	14	0·9 *v*
17/7	21	1·8 *v*	69	4·8 *f*	28	1·6 *f*	59	2·2 *f*	12	1·0 *v*
17/10	20	4·3 *v*	52	2·6 *f*	42	2·8 *f*	38	0·8 *f*	22	2·1 *f*
17/14	27	4·9 *v*	58	4·4 *f*	46	1·6 *f*	60	2·1 *f*	37	4·5 *f*
17/17	17	1·2 *v*	54	3·5 *f*	40	1·6 *f*	50	1·1 *f*	8	1·0 *v*
17/20	12	1·3 *v*	57	5·7 *f*	40	2·1 *f*	40	2·4 *f*	23	1·6 *f*
17/23	19	3·5 *v*	45	3·1 *f*	33	2·0 *f*	39	1·8 *f*	11	2·1 *v*
4/14	4	2·8 *v*	20	5·5 *v*	4	1·1 *v*	7	—*v*	5	0·7 *v*
7/14	2	2·5 *v*	26	4·9 *v*	1	0·1 *v*	14	1·2 *v*	8	1·6 *v*
10/14	3	3·1 *v*	36	7·3 *f*	15	1·3 *v*	22	2·4 *f*	7	2·6 *f*
14/14	6	0·5 *v*	57	6·1 *f*	39	1·5 *f*	49	4·4 *f*	10	0·9 *v*
17/14	25	3·8 *v*	40	4·1 *f*	27	1·4 *v*	36	0·7 *v*	15	0·09 *v*
17/14*	24	6·6 *v*	56	9·5 *f*	38	2·5 *f*	36	2·9 *f*	25	—*f*
20/14*	15	3·7 *v*	52	8·8 *f*	37	4·3 *f*	47	4·5 *f*	24	5·0 *f*
23/14*	22	5·3 *v*	68	10·9 *f*	46	2·5 *f*	62	4·7 *f*	35	5·7 *f*
30/14*	9	1·0 *v*	42	6·8 *f*	7	1·6 *v*	1	0·4 *v*	14	1·9 *v*
7/7	5	0·6 *v*	17	3·0 *v*	5	0·7 *f*	6	1·8 *v*	4	0·5 *v*
7/23	23	4·1 *v*	40	6·0 *f*	16	2·8 *f*	10	0·8 *v*	9	1·5 *v*
26/7	—	—	18	—*v*	4	0·4 *v*	19	—*f*	6	0·5 *v*
26/23	—	—	11	0·8 *v*	—	—	4	0·5 *v*	7	0·3 *v*

Temperature Day/night °C	Populations (flowering or vegetative)									
	5923–61		5923–68		5923–70		5923–71		5923–72	
	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm	Height cm	Dry weight gm
17/4	53	3·2 *f*	55	3·7 *f*	62	0·8 *f*	67	4·1 *f*	46	3·1 *f*
17/7	16	0·4 *v*	50	2·4 *f*	65	2·0 *f*	50	3·2 *f*	45	3·1 *f*
17/10	52	3·6 *f*	42	3·1 *f*	46	2·4 *f*	67	5·4 *f*	41	2·9 *f*
17/14	58	2·0 *f*	31	2·9 *f*	47	2·7 *f*	63	4·3 *f*	37	2·9 *f*
17/17	42	3·2 *f*	43	2·1 *f*	52	1·0 *f*	55	2·6 *f*	39	2·1 *f*
17/20	31	3·3 *f*	38	3·7 *f*	38	2·5 *f*	56	4·8 *f*	32	2·0 *f*
17/23	42	3·6 *f*	35	3·8 *f*	41	1·9 *f*	46	3·9 *f*	34	2·5 *f*
4/14	8	3·0 *v*	5	1·7 *v*	2	0·01 *v*	8	2·9 *v*	17	5·2 *v*
7/14	11	1·3 *v*	14	5·2 *f*	13	2·8 *f*	16	3·1 *v*	14	3·0 *f*
10/14	24	3·6 *v*	28	5·5 *f*	26	2·8 *f*	35	4·0 *f*	25	4·0 *f*
14/14	45	5·1 *f*	40	3·4 *f*	53	1·9 *f*	42	5·1 *f*	36	3·4 *f*
17/14	60	3·5 *v*	44	1·3 *f*	60	2·4 *f*	70	3·4 *f*	38	2·3 *f*
17/14*	30	7·8 *f*	38	10·3 *f*	32	5·0 *f*	36	10·1 *f*	39	6·2 *f*
20/14*	44	7·3 *f*	27	5·1 *f*	34	4·5 *f*	22	5·1 *f*	32	6·7 *f*
23/14*	58	13·7 *f*	48	2·3 *f*	40	4·8 *f*	63	10·8 *f*	44	10·4 *f*
30/14*	11	2·4 *f*	27	3·7 *v*	24	1·8 *v*	28	4·4 *v*	35	4·3 *v*
7/7	8	0·4 *v*	9	1·0 *v*	10	0·7 *v*	10	1·0 *v*	8	0·3 *v*
7/23	15	2·1 *v*	19	2·0 *v*	20	2·2 *f*	27	6·4 *v*	25	5·6 *f*
26/7	26	—*f*	16	—*f*	20	0·4 *f*	4	0·5 *v*	21	—*v*
26/23	—	—	15	0·5 *f*	30	0·8 *f*	19	1·2 *v*	23	—*f*

During the experiment, the comparative growth of the plants in each climate was carefully noted at regular intervals. Two experiments were run, the first for the different populations and the second for the family of hybrids. Each experiment was terminated after 60 days and the results scored (Tables 2, 3).

The results of the two experiments showed several general trends. First, artificial climates that included 8 hours of higher light intensity tended to produce much-branched plants with significantly higher dry weights, but not greater heights than the same temperature combinations with lower light intensities (Table 2). Second, speed of flowering was directly correlated with temperature. The warmer the climate the faster flowers were produced and seeds ripened. Third, plants grown under the colder climates tended to be sturdy and robust whereas those grown under the hotter climates tended to be weak and spindly. As in *Poa* (Hiesey 1953) hot night temperatures tended to be deleterious although in general night temperature affected growth less than day temperature. Fourth, artificial climates with the same day and night temperatures often produced weak plants many of which died. This effect was not apparent at cold temperatures but became noticeable at moderate temperatures and pronounced at high temperatures (Table 2; Fig. 1).

Considered by populations the results reveal that the different populations exhibit their optimal growth in from slightly to strongly different artificial climates (Fig. 2; Table 2) as would be expected of populations from such contrasting localities (Table 1). However, the optimal growth conditions found for a population in the experiments did not always correspond to the climate from which the population came. Perhaps other factors such as competition determine in which part of its potential range a population actually grows.

The population results also reveal that the plants of some populations, e.g. culture 5003, are able to grow and flower in a surprisingly wide range of climates whereas the plants of other populations, e.g. culture 5687, are able to grow and flower only under an extremely limited range (see Fig. 1). Thus, some populations are much restricted climatically while others have the potential to grow and reproduce in many climates if other factors permit.

The individual plants of some of the populations, e.g. culture 5004, are nearly alike in their growth responses to each of the climates whereas the plants of other populations, e.g. culture 5011, vary greatly. The climates in which optimal growth of plants of the latter culture occurred differed by as much as 14 °C (Table 2) which is more than the difference in average July maximum temperatures between northern Michigan and southern Florida (Long 1969). Thus, many of the populations appear to have the genetic diversity, at least as far as temperature tolerance is concerned, to occupy new habitats. That they can do so is borne out by the fact that *Mimulus guttatus*, a native of western North America, has become established during the last century or so in Northern Europe, New England, New Zealand, and Tasmania and *M. luteus*, a native of western South America, has become established in England (Grant 1924).

The results for the family of F_1 and F_2 hybrids reveal that the F_1 hybrid's growth responses were close to those of the more vigorous parent (Fig. 1; Table 3). However, the F_2 hybrid plants varied strikingly in their growth

responses. One, 5923–23, was far more vigorous than either parent in all the climates. Another, 5923–34, failed to flower in any of the conditions and another, 5923–68, flowered in all the climates. A few of the F_2 hybrids, e.g. 5923–55 and 5923–27, showed growth optima in artificial climates that are significantly different from those of the parental populations (Fig. 1; Table 3). Thus, interpopulation hybridization produces many poorly adated Fr_2 hybrid plants but it also produces a few plants that grow well and flower in climates in which the parental plants either do poorly or die.

All in all, this study shows that some, but not all, of the wild popula-

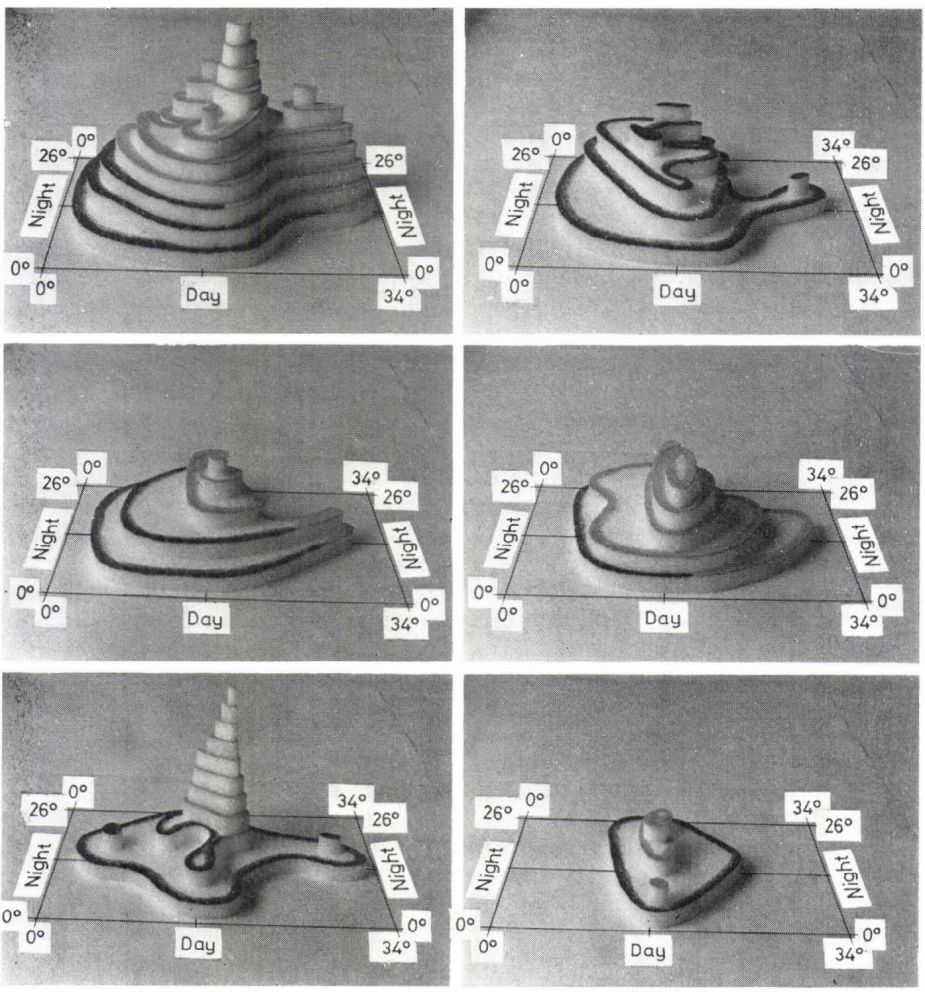

Fig. 1. Models representing the height attained by plants of the various populations in different artificial climates. Each contour line represents 10 cm of height; dark lines represent vegetative growth only; light lines represent flowering plants; upper left: culture 5003–85; middle left: culture 5043–30; lower left: culture 5687–83; upper right: culture 5007–83; middle right: culture 5346–31; and lower right: culture 5839–33

tions of *Mimulus* tested have a wide climatic tolerance or contain a significant amount of genetic variability for climatic tolerance. The study also shows that interpopulation hybridization leads to genetic recombination in the F_2 hybrids that results in plants with climatic optima that exceed the ranges of the parental optima, i.e. that show transgressive variation. Thus, the group as a whole contains a significant amount of evolutionary potential which is actually beginning to be expressed in the colonization of new habitats on three continents.

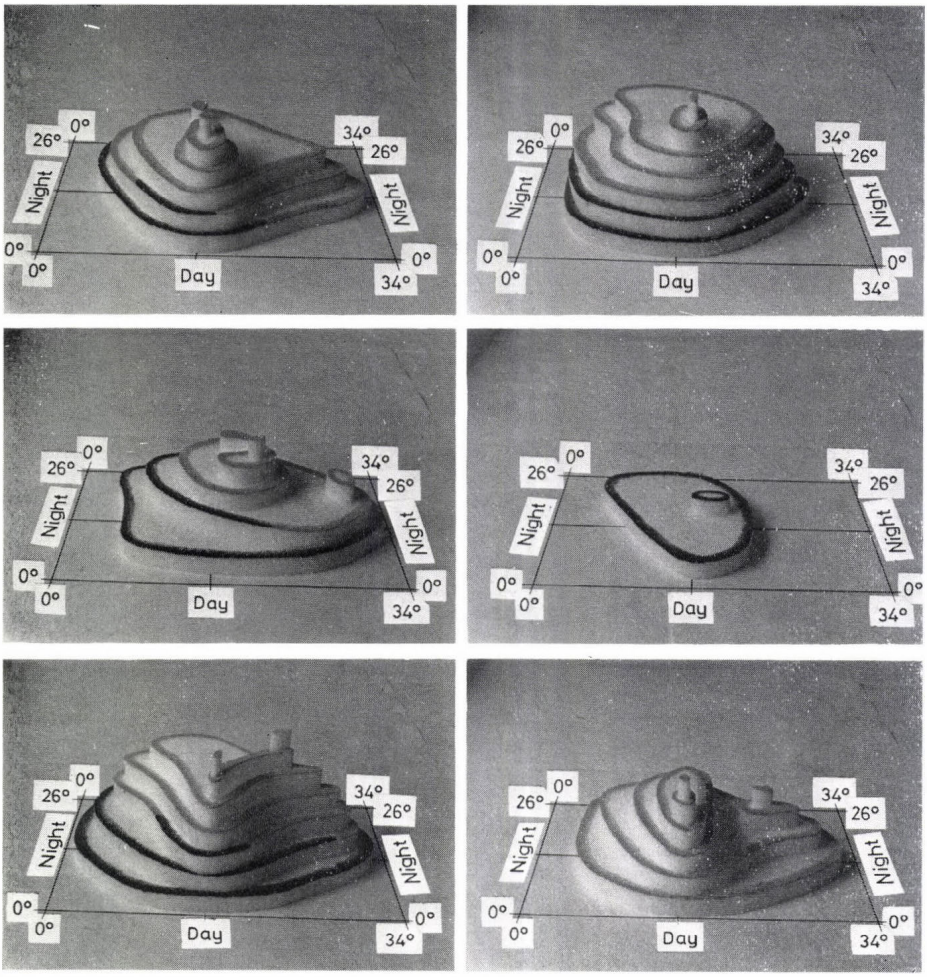

Fig. 2. Models representing the heights attained in the various climates by the F_1 hybrid and selected F_2 hybrids of the interpopulation cross 5346 × 5839. Each contour line represents 10 cm of height; dark contour lines represent vegetative growth only; light lines represent flowering plants; upper left: the F_1 hybrid plant 1709–1; middle left: plant 5923–34; lower left: plant 5923–55; upper right: plant 5923–23; middle right: plant 5923–27; and lower right: plant 5923–68

REFERENCES

Grant, A. L. (1924): A monograph of the genus *Mimulus*. *Annals of the Missouri Botanical Garden* **11** 99–385

Hiesey, W. M. (1953): Growth and development of species and hybrids of *Poa* under controlled temperatures. *American Journal of Botany* **40** 205–21

Long, L. H. (ed.) (1969): *The World Almanac and Book of Facts*. Newspaper Enterprise Assoc., Inc., New York, 932 pp.

Vickery, R. K., Jr. (1951): Genetic differences between races and species of *Mimulus*. *Carnegie Institution of Washington Yearbook* **50** 118–9

Vickery, R. K., Jr. (1959): Barriers to gene exchange within *Mimulus guttatus (Scrophulariaceae)*. *Evolution* **13** 300–10

Vickery, R. K., Jr. (1966): Speciation and isolation in section *Simiolus* of the genus *Mimulus*. *Taxon* **15** 55–63

Vickery, R. K., Jr. (1967): Ranges of temperature tolerance for germination of *Mimulus* seeds from diverse populations. *Ecology* **48** 647–51

Went, F. W. (1957): The experimental control of plant growth. *Chronica Botanica*, Waltham, Mass., 343 pp.

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PESTICIDES—SUBTLE PROMOTERS OF EVOLUTION

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There are an estimated 2 million plant and animal species that occur on the earth today. This is only about 1% of all the species which have evolved; the other 99% have become extinct. Gradually, each species has been replaced by those better adapted to the new environmental conditions. This is a slow evolutionary process taking many, perhaps thousands of years for the development of a new species. However, an increasing number of physical and chemical agents are being found that will alter the genetic constitution of an organism or interfere with its reproductive success, and hence, will affect the rate of natural selection.

The widespread use of pesticides in the control of weeds, insects, and diseases has increased tremendously in the past two decades. For example, the sales of 2,4–D, which is only one of the six most commonly used pesticides, are 'over 25 million dollars annually' in the United States alone. Although crop production and vector control have increased considerably as a result of such practices, data are accumulating to show that the use of pesticides has many secondary consequences. While considerable publicity has been given to the effects of pesticides on our ecosystems, little attention has been paid to the hereditary changes that can be brought about by pesticide usage and the potential evolutionary changes to the flora and fauna. From studies in progress in this laboratory, and elsewhere, it is clear that many pesticides can induce chromosomal aberrations and mutations. Many of the cytological effects on chromosomes are very similar, if not identical, to those produced through irradiation.

The production of morphological and cytological abnormalities as a result of pesticide treatment dates back to 1931 when Kostoff first observed seed set of tobacco plants to be greatly reduced after the plants had been fumigated with nicotine sulphate. In an examination of meiosis he found many chromosome irregularities which lead to the partial sterility of the plants. Subsequently, a number of investigators have made similar observations, many rather incidentally to the main investigation in which they were working.

One class of pesticides known as the carbamates to which the herbicides diallate, barban and propham and the insecticide carbaryl belong, cause chromosome breakage, but like colchicine, are noted for producing polyploid cells. One group of scientists has written a paper on the use of carbamates to induce polyploidy as a classroom exercise in cytology (Storey et al. 1968) and they have also suggested using carbamates for the production of polyploid plants in plant breeding experiments (Mann and Storey 1966).

The primary growth retardant action of some plant growth regulators such as maleic hydrazide, would appear to be a slowing down of nuclear division as a result of the interference of chromosome movement and chromosome breakage resulting in pollen sterility and a lowering of seed set. After tomato seeds had been treated with maleic hydrazide, chromosome bridges were observed in the progeny for three generations. A number of abnormal seedling plants such as dwarf, bushy, narrow leaf and mottled leaf were produced which were identical to known mutants (Grant and Harney 1960). A few other examples to show that pesticides can induce cytogenetic changes in plants are as follows.

In an experimental study after barley seed had been treated with atrazine, chromosome aberrations were produced, and yellow-leaf, striped-leaf and dwarf mutant seedlings were observed in the C_2 progeny (Wuu and Grant 1966). More recently this herbicide has been found at this Institution to cause partial sterility in corn plants grown in the field as a result of the induction of translocations. Similarly, in California, when the herbicide dalapon was applied to the soil prior to the growing season as a pre-emergent weed killer, cold weather prevented the herbicide from dissolving readily and the developing wheat and barley plants were affected. Plants with spike malformations and reduced fertility, and dwarfs, were observed for four generations (Suneson and Jones 1960). Alfalfa (*Medicago sativa* L.) and sunflower (*Helianthus annua* L.) plants are extremely sensitive to the herbicide picloram and can be established as a crop in fields without any mutants appearing only after the soil has had a picloram-free period of five years (Vanden Born 1969).

A number of organic phosphate insecticides have been found to induce chromosome aberrations and mutations. Pea seeds exposed to low vapor concentrations of 'dichlorvos Vapona strips', produce plants with leaf spots showing that this insecticide causes somatic mutations (Blixt and Müller, in Lofroth et al. 1969).

Some fungicides have also been found to cause chromosome abnormalities including the production of polyploid nuclei, mutations and malformed offspring. Mutations have been produced in the fungus *Aspergillus* with ferbam (Prasad and Pramer 1968) and cytological abnormalities (*Vicia faba*) and dwarf plants (*Hordeum vulgare*) have been produced with the fungicide dichloran (Wuu and Grant 1966, 1967b). The fungicide captan can induce chromosome aberrations and has produced teratogenic effects on chicken embryos (Malling and de Serres 1970).

Another factor found in a number of studies is the reduction in fertility after pesticide treatment. This can take the form of decrease in egg shell thickness, in embryo survival, and in seed production (Blus 1970; Lee 1970; Wuu and Grant 1967a) and can be caused by the mutation of one or more genes. For example, Liang and colleagues (Liang et al. 1967) did not observe any chromosomal aberrations in the pollen mother cells of the few partially fertile plants that they found in nearly 3000 second generation progeny derived from atrazine-treated sorghum (*Sorghum vulgare*) plants. This would indicate that the sterility of these plants was genetically controlled and not the result of chromosomal aberrations.

Many more examples of controlled experiments in which pesticides have produced chromosomal aberrations and mutations are known and these

are being summarized by a colleague and myself for publication (Villard and Grant 1972). However, these few examples have been presented in order to illustrate the cytogenetic effects that at least some pesticides will produce.

Let us now turn our attention to the effects of pesticides on the flora and fauna. Our most stable weedy habitats along roadsides, ditches, and utility right-of-ways, have been subject to herbicide control in many areas. Large scale spraying operations by airplanes have occurred in many areas routinely for the control of mosquitoes and other insects, and in forestry applications to control scrub and sagebrush. Considering the foregoing experimental cytogenetic observations, the use of pesticides for the above practices could, theoretically, bring about (1) increased resistance of certain species, (2) the elimination of certain species as a result of their extreme susceptibility and (3) create morphological differences of a nature sufficient for taxonomic recognition.

Resistant plants would become the dominant component of the vegetation, or alternatively, the elimination of one or more species may allow another species to rise, or to enter, and become the dominant species. In addition, treatment for one group of organisms would affect non-target organisms, which likewise might be eliminated, or become resistant to herbicides. Insect pollinators would be a prime non-target organism.

However, there is a wide gap in our knowledge between the experimental results produced in the laboratory in which there is considerable evidence that pesticides can cause cytogenetic damage and the possible effects that pesticides may be playing in nature and their role on the flora and fauna. It is the primary purpose of this paper to draw attention to our limited knowledge in the latter area and for biologists to be on the lookout for evidence on the role that pesticides may be playing in evolution. Nevertheless, data are accumulating to show that pesticides can produce such effects and that they are playing a role in the evolution of plant communities (Grant 1967).

Perhaps most evidence for the role that pesticides are playing has been obtained in the area of gene resistance to insecticides. The group of chlorinated hydrocarbon insecticides to which DDT and dieldrin belong, was first found to produce mutations to resistance under natural conditions and resistant races of houseflies, mosquitoes, ticks, *Drosophila*, cockroaches, bed bugs, blow flies and other insects were soon discovered (Anon. 1964; Oppenoorth and Houx 1968; Webb and Horsfall 1967). As aptly stated in 1967 by Williams in reviewing the early years of DDT, "A few wise men warned that we were living in a fools' paradise and that insects would soon become resistant to DDT, just as bacteria had managed to develop a resistance to the challenge of sulfanilamide. That is just what happened. Within a few years mosquitoes, lice, houseflies and other noxious insects were taking DDT in their stride. Soon they were metabolizing it, then they became addicted to it and were therefore in a position to try harder". Keer (1963) has reported insect resistance to six classes of compounds: (a) DDT and its analogues, (b) BHC, and the cyclodiene derivatives, dieldrin, aldrin, endrin, isodrin, chlordane, heptachlor, toxaphene, (c) organophosphorus compounds, (d) pyrethroids, (e) the carbamates and (f) acaricides. Some 224 species of insects are now known to have developed resistance

and of these 127 are agricultural pests and 97 are pests of medical and veterinary importance (Irving 1970).

What is perhaps not as well documented is the fact that many plants may become resistant to both herbicides and insecticides. A number of barley varieties show major differences in resistance to foliar applications of the insecticide DDT (Hayes 1959; Wiebe and Hayes 1960; Hayes et al. 1965; Wallace et al. 1968). As early as 1947, Albrecht showed some strains of *Agrostis stolonifera*, creeping bent grass, to have greater tolerance to 2,4–D than others. Since this study many plants have been shown resistant to herbicides (Table 1). Varieties of barley have been shown resistant to

Table 1

Relative resistance to 2,4–D and 2,4,5–T (Schacht 1963)

High resistance	Medium resistance	Sensitive
Picea glauca (Moench) Voss	*Pinus banksiana* Zamb.	*Acer negundo* L.
Picea mariana (Mill.) BSP.	*Acer saccharum* Marsh.	*Rhus* sp.
Larix laricina (DuRoi) K. Koch	*Tilia americana* L.	*Corylus americana* Walt.
Abies balsamea (L.) Mill.	*Populus* sp.	*Betula* sp.
Juniperus communis L.	*Ulmus americana* L.	*Alnus rugosa* (DuRoi) Spreng.
Chamaecyparis thyoides (L.) BSP.	*Cornus* sp.	*Prunus serotina* Ehrk.
Pinus strobus L.	*Fraxinus* sp.	*Quercus rubra* L.
Pinus resinosa Ait.	*Lonicera* sp.	*Populus deltoides* Marsh.
	Viburnum sp.	*Salix* sp.

the herbicide barban (Hayes et al. 1965), varieties of maize to atrazine and simazine and varieties of wheat (*Triticum aestivum* L.), rape (*Brassica napus* L.) and mustard (*Sinapis alba* L.) to simazine (Karim and Bradshaw 1968). This resistance in barley and maize has been shown to be under the control of a single recessive gene (Scott and Grogan 1969; Wallace et al. 1968), but polygenes may also play a role (Hayes et al. 1965).

Harper (1956) reported that higher dosages of herbicides were being required to control certain weeds, and that resistant strains were developing in *Cirsium arvense* and *Erechtites hieracifolia*. The latter, a weed of sugar cane, was being controlled by applications of 2,4–D but as resistance developed to this herbicide stronger doses of contact herbicides became necessary to kill it. Jones (1962) has shown that *Dactylis glomerata* and *Lolium perenne* are fairly resistant to applications of paraquat, whereas *Agrostis stolonifera* and *Poa trivialis* are relatively susceptible; six months after treatment the resistant grasses had increased their numbers three to fourfold at the expense of the susceptible species.

Only limited data are available on the effects of pesticides on plant communities. H. G. Baker (personal communication) has stated that in California the roadsides are sprayed each spring to eliminate all living plants. He has noted that certain plants which are dormant at the time of spraying do not appear to have been affected and grow vigorously later in the year. One such plant is *Sorghum halepense* which has an underground storage system. He has found this species to be considerably improved in its performance since it no longer has to compete with other species and has

considerably increased in abundance. Similarly, Douglas (1965) has observed from plot treatment with the herbicide paraquat that the removal of plant competition has resulted in the stimulation of buried rhizomes of *Cirsium arvense* with the resulting increase in numbers of this species. Mulligan (1965) has found that large dense populations of *Carduus* which he and Moore had been studying over a period of years were almost completely displaced by extensive stands of wild carrot, *Daucus carota*, as a result of chemical weed control. In addition, he considered that wild carrot appeared to be taking over new terrain in cases of other species that were being controlled or eradicated by the use of herbicides along the roadsides. Evans et al. (1970) have shown that a mixture of paraquat plus 2,4–D allowed the establishment of wheat grass (*Agropyrum intermedium*) by eliminating established stands of downy brome grass (*Bromus tectorum*) and broadleaf weeds.

Yemm and Willis (1962) in a study of the long term effects of maleic hydrazide (MH) and MH combined with 2,4–D on plant communities along highways found that plots receiving a single MH spray each year after three years showed a steady increase in rhizomatous species (*Festuca* and *Poa*) and a reduction in tufted grasses, such as *Arrhenatherum elatius*, *Dactylis glomerata* and *Zerna erecta*. In the MH plus 2,4–D plots, in addition to the reduction of tufted grasses, there was a marked reduction in dicotyledonous species. *Zerna erecta* and *Holcus lanatus* were eliminated and at the end of the three year study five grasses (*Poa* and *Festuca*) comprised 70% of the population.

The herbicides 2,4–D and 2,4,5–T have received wide publicity over the past year since these herbicides have been widely used in Vietnam for defoliation. In the Rung Sat area of Vietnam southeast of Saigon about 100,000 acres of mangrove trees have been sprayed for several years with a 50 : 50 mixture of *n* butyl esters and of 2,4–D and 2,4,5–T. In the defoliated areas, bamboo is rapidly becoming the dominant component of the vegetation. Such a change will also affect the evolution of the associated animal population. Orians and Pfeiffer (1970) have pointed out that many of the species of animals inhabiting mangroves are restricted to that type of vegetation and would be expected to have higher rates of extinction even under normal conditions than species of more continuous habitats.

One fact which is perhaps not well known is that insects can control the numbers of plants of a species growing in a natural population. In an interesting experiment, Cantlon (1969) has observed that the absolute number of plants of *Melampyrum lineare* Desr. (cow-wheat) is controlled by insects. This species is a herbaceous annual that is hemiparasitic on the roots of woody forest plants and does not complete its life cycle without a host. Nymphs of the katydid (*Atlanticus testaceous*) feed on this plant consuming large amounts of foliage. In addition, some 50 other species of invertebrate animals have been observed to be associated with this plant, especially its shoot systems and seeds. Since most of the invertebrates were considered to be sensitive to chlorinated hydrocarbon insecticides, this population represented an experimental tool for examining the ramifications resulting from their removal. Cantlon marked out a number of 5×5-m plots and each spring treated one plot with granulated aldrin at a rate equivalent to 2 lb/acre. In the first 2 years only, the treated plots also received a light foliage spray every week from mid-May to mid-August with a

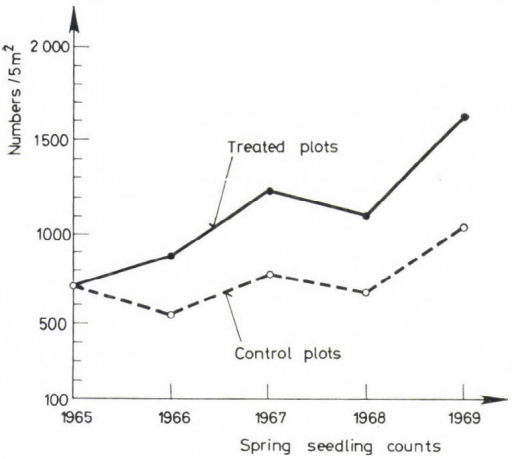

Fig. 1. Numbers of *Melampyrum lineare* seedlings on the approximate date of maximum population density (modified from Cantlon 1969)

50–50 mixture of malathion and DDT. One year after the experiment had begun, the population was twice as large in the treated plots as in the controls and after 2 years they were 3 times as large. The 3rd year the 3-fold difference persisted, and the 4th year the seedling populations on the treated plots were more than 3 times as large as in the control plots (Fig. 1).

We must now ask, how are pesticides promoting evolution? Stebbins (1959) has stated that at least in higher plants and animals, evolution proceeds principally as a result of four indispensable processes, namely, mutation, genetic recombination, natural selection and isolation. Some pesticides have clearly been shown to be mutagens and can induce gene mutations which could lead to speciation. Some pesticides interfere with the reproductive vigor of a species and new strains or species of weeds could evolve under the influence of selection. Some pesticides such as the carbamates and some organophosphorus insecticides, cause a cessation of chromosome separation at anaphase which could lead to species formation. Also, hybridization between individuals in which the reproductive process has been modified by pesticide treatment could lead to speciation per se, or indirectly by chromosome doubling following hybridization. Thus pesticides are agents which have considerable potential for promoting evolution.

Let us now return to our introduction. It is not known how many of the 2 million species in man's environment are necessary for his survival and welfare. The indiscriminate use of pesticides may eliminate many wild species, and yet we are still dependent upon wild species for the continued improvement of our crops. Most species in nature interact in maintaining a life system but we have a very limited knowledge of the complexities of interactions of species in maintaining the biology of their life system. Likewise our knowledge on the synergistic effects of chemicals is very limited (Zavon 1969). Approximately 900 chemicals are registered with the United States Department of Agriculture for use against about 2000 pest species. There is an estimated 200,000 non-target species in the United States alone. The mode of action of pesticides against target organisms is only partially understood, and hence, less so for non-target organisms. I believe we are now only realizing the subtle effects of pesticides in evolution. Perhaps we have been like the lobster. If the lobster is placed in hot water it will immediately jump out. However, if it is placed in cold water which is slowly heated, it does not realize it is being cooked. Therefore as evolutionists we should be on the lookout for the effects of pesticides in the evolution of our plant communities.

REFERENCES

Albrecht, H. R. (1947): Strain differences in tolerance to 2,4–D in creeping-bent grasses. *J. Am. Soc. Agron.* **39** 163–5

Anon. (1964): Genetics of vectors and insecticide resistance. *W.H.O. Techn. Rep. Ser.*, p. 268

Blus, L. J. (1970): Measurements of brown pelican eggshells from Florida and South Carolina. *BioSci.* **20** 867–9

Cantlon, J. E. (1969): The stability of natural populations and their sensitivity to technology. *Brookhaven Sympos. Biol.* **22** 197–205

Douglas, G. (1965): The weed flora of chemically-renewed lowland swards. *J. Brit. Grassl. Soc.* **20** 91–100

Evans, R. A., Holbo, H. R., Eckert, R. E., Jr., and Young, J. A. (1970): Functional environment of downy brome communities in relation to weed control and revegetation. *Weed Sci.* **18** 154–62

Grant, W. F. (1967): Cytogenetic factors associated with the evolution of weeds. *Taxon* **16** 283–93

Grant, W. F. and Harney, P. M. (1960): Cytogenetic effects of maleic hydrazide treatment of tomato seed. *Can. J. Genet. Cytol.* **2** 162–74

Harper, J. L. (1956): The evolution of weeds in relation to resistance to herbicides. *Proc. 3rd Brit. Weed Control Conf.*, Blackpool, 1956, pp. 179–88

Hayes, J. D. (1959): Varietal resistance to spray damage in barley. *Nature* **183** 551–2

Hayes, J. D., Pfeiffer, R. K. and Rana, M. S. (1965): The genetic response of barley to DDT and barban and its significance in crop protection. *Weed Res.* **5** 191–206

Irving, G. W. (1970): Agricultural pest control and the environment. *Science* **168** 1419–24

Jones, L. (1962): Herbicides to aid pasture renovation. *J. Brit. Grassl. Soc.* **17** 85–6

Karim, A. and Bradshaw, A. D. (1968): Genetic variation in simazine resistance in wheat, rape and mustard. *Weed Res.* **8** 283–91

Keer, R. W. (1963): Some recent advances in the study of insecticide resistance. *J. Australian Inst. Agric. Sci.* **29** 31–7

Kostoff, D. (1931): Heteroploidy in *Nicotiana tabacum* and *Solanum melongena* caused by fumigation with nicotine sulphate. *Bull. Soc. Bot. Bulgar.* **4** 87–92

Lee, W. O. (1970): Effect of picloram on production and quality of seed in several grasses. *Weed Sci.* **18** 171–3

Liang, G. H. L., Feltner, K. C., Liang, Y. T. S. and Morrill, J. L. (1967): Cytogenetic effects and responses of agronomic characters in grain sorghum (*Sorghum vulgare* Pers.) following atrazine application. *Crop Sci.* **7** 245–8

Lofroth, G., Kim, C. and Hussain, S. (1969): Alkylating property of 2,2-dichlorovinyl dimethyl phosphate: A disregarded hazard. *Environmental Mutagen Society, Newsletter* **2** 21–6

Malling, H. V. and de Serres, F. J. (1970): Captan — a potent fungicide with mutagenic activity. *Environmental Mutagen Soc. Ann. Meet. Abstr.* **1** 19

Mann, J. D. and Storey, W. B. (1966): Rapid action of carbamate herbicides upon plant cell nuclei. *Cytologia* **31** 203–7

Mulligan, G. A. (1965): Recent colonization by herbaceous plants in Canada, pp. 127–46. *In* H. G. Baker and G. L. Stebbins (ed.): *The Genetics of Colonizing Species*, New York

Oppenoorth, F. J. and Houx, N. W. H. (1968): DDT resistance in the housefly caused by microsomal degradation. *Entomol. Exp. Appl.* **11** 81–3

Orians, G. H. and Pfeiffer, E. W. (1970): Ecological effects of the war in Vietnam. *Science* **168** 544–54

Prasad, I. and Pramer, D. (1968): Genetic effects of ferbam on *Aspergillus niger* and *Allium cepa*. *Phytopath.* **58** 1188–9

Schacht, A. J. (1963): Long-term vegetational changes following aerial applications of 2,4–D and 2,4,5–T in northern Minnesota. *M. Sc. thesis, Univ. of Minnesota*

Scott, G. E. and Grogan, C. O. (1969): Location of a gene in maize conditioning susceptibility to atrazine. *Crop Sci.* **9** 669–70

Stebbins, G. L. (1959): Genes, chromosomes and evolution, pp. 258–90. *In* W. B. Turril (ed.): *Vistas in Botany*, Pergamon Press, N.Y.

Storey, W. B., Jordon, L. S. and Mann, J. D. (1968): Carbamate herbicides—new tools for cytological studies. *Calif. Agric.* **22** (8) 12–3

Suneson, C. A. and Jones, L. G. (1960): Herbicides may produce instability. *Agron. J.* **52** 120–1
Vanden Born, W. H. (1969): Picloram residues and crop production. *Can. J. Plant Sci.* **49** 628–9
Villard, M. W. D. and Grant, W. F. (1972): *A review of the cytogenetic effects of pesticides.* Manuscript in preparation
Wallace, A. T., Rillo, F. O. and Browning, R. M. (1968): DDT resistance in barley, *Hordeum vulgare*. I. Induced mutants for resistance. *Radiation Botan.* **8** 381–8
Webb, R. E. and Horsfall, F., Jr. (1967): Endrin resistance in the pine mouse. *Science* **156** 1762
Wiebe, G. A. and Hayes, J. D. (1960): The role of genetics in the use of agricultural chemicals. *Agron. J.* **52** 685–6
Williams, C. M. (1967): Third-generation pesticides. *Sci. Amer.* **217**(**1**) 13–7
Wuu, K. D. and Grant, W. F. (1966): Morphological and somatic chromosomal aberrations induced by pesticides in barley. *Can. J. Genet. Cytol.* **8** 481–501
Wuu, K. D. and Grant, W. F. (1967a): Chromosomal aberrations induced by pesticides in meiotic cells of barley. *Cytologia* **32** 31–41
Wuu, K. D. and Grant, W. F. (1967b): Chromosomal aberrations induced in somatic cells of *Vicia faba* (Broad Bean) by pesticides. *The Nucleus* **10** 37–46
Yemm, E. W. and Willis, A. J. (1962): The effects of maleic hydrazide and 2,4-dichlorophenoxyacetic acid on roadside vegetation. *Weeds Res.* **2** 24–40
Zavon, M. R. (1969): Interactions. *BioSci.* **19** 892–5

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CYTOTAXONOMY AND GENOME ANALYSIS OF THE EUROPEAN FERNS

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In the first volume of the comprehensive work *Flora Europaea* there are about 85 fern species listed. With very few exceptions they have been studied cytologically somewhere in Europe. The cytologically unknown species are restricted to the Azores or to Iberia, thus we may say that the typical European ferns are basically known, as far as the chromosome numbers are concerned. This is mainly due to Professor Manton and her school who first applied the squash method in studying the meiotic chromosomes of fern spore mother cells. Prior to the publication in 1950 of her book there were 83 fern chromosome records published in 32 papers, but of these counts only ten have proved to be correct in the light of our present knowledge.

A great number of the early mistakes are rather conspicuous (e.g. $n = 32$ instead of 52 for bracken). As many as 21 of the wrong chromosome counts are due to the erroneous belief that ferns ought to have a base number of 32, a number which is now known to be very rare in Pteridophytes. After the publication of Professor Manton's book the number of cytotaxonomical and also cytogenetical papers on Pteridophytes has rapidly increased. Fortunately, the 'mistake period' is now over, and most, although not all, of the recent papers are based on careful cytological observations.

Many cytologists have been studying groups of fern species. In Europe this type of research is being done in Britain (Leeds, Newcastle upon Tyne, Liverpool, etc.) Finland (Helsinki), W. Berlin (Berlin-Dahlem), Hungary (Budapest) and elsewhere. The efficiency of the work very much depends on international co-operation. This has been organized by Professor Reichstein (Basel, Switzerland), who co-ordinates most of the pteridological work, and who has always been helpful to everybody by providing ideas and fern material of known origin for cytological or biosystematic studies.

From the cytotaxonomical point of view the most studied, although by no means the best known, genus is *Asplenium* (Manton, Meyer, Lovis, Reichstein, Sleep, Emmott, Bouharmont and Vida). A number of papers deal with species of *Dryopteris* (Döpp, Manton, S. Walker, Gätzi, Reichstein, Widén, Sorsa and Vida), *Polypodium* (Manton, Shivas, Lenski and Vida) and *Polystichum* (Manton, Reichstein, Sleep and Vida). The European (and Canary Island) representatives of the genus *Cheilanthes* (sensu lato) have recently been studied in a joint paper by Vida, Page, T. Walker and Reichstein (1970). The cytological survey of the genus *Cystopteris* (initiated by Manton and Reichstein and Blasdell) is in progress by Reichstein and Vida (unpubl.). The remaining genera are either composed of very few species

only (*Pteridium*, *Matteuccia*, *Oreopteris*, *Phegopteris*) or they are rich in species (e.g. *Blechnum*, *Thelypteris*), but most of the latter species occur only on other continents, hence, they are not very suitable for cytotaxonomy or for genome analysis in Europe.

Counting the chromosomes assists in answering the following questions: (i) How frequent is polyploidy? (ii) What is the best taxonomic treatment of the polyploid cytotypes? (iii) Is the polyploidy connected with a certain pattern in geographical distribution and ecology? (iv) What is the origin of the polyploids?

Before discussing these questions, let us say a few words about the methods most commonly applied.

METHODS

Meiotic chromosome counts are generally made on squash preparations of developing sporangia, containing spore mother cells at diakinesis or meiotic metaphase I, using the method of Manton (1950). Mitotic chromosomes usually require a pretreatment (with colchicine, oxychinoline, paradichlorbenzene, etc.) and, after fixation in acetic acid alcohol, a softening with snail enzyme (Roy and Manton 1965). By applying this method, precise chromosome counts can be made in ferns having very high chromosome numbers (e.g. *Adiantum reniforme* L., $2n = 300$).

For genome analysis the meiotic pairing behaviour of certain hybrids involving the tetraploid species, or that of haploid sporophytes should be studied. The latter study provides information on the chromosomal homologues present at the gametic level. This is very important as regards the way of origin of polyploid species or races. When analysing wild or synthesized hybrids the maximum proportion of bivalents (sometimes also that of multivalents) has to be considered, since various unfavourable factors are known to reduce the meiotic pairing capacity between homologous or homeologous chromosomes (cf. V. Grant 1952, Wuu and W. F. Grant 1967). The process of analysis consists of the following steps: (a) assembly of the species of a certain taxonomic group (genus, section); (b) registration of chromosome numbers and other meiotic features (pairing, multivalents, secondary associations); (c) induction of haploid sporophytes (e.g. sporophytes with reduced chromosome number in the polyploids), or making remote crosses (e.g. hybrids involving unrelated species with supposedly different genomes), i.e. auto versus alloploid test; (d) synthesis of hybrids using the polyploid (tetraploid) against the most probably related diploid, i.e. progenitor test; (e) resynthesis from the theoretical ancestors; (f) crossing of synthetic and natural polyploids for checking their interfertility as a final test.

Two problems often make these investigations difficult, viz. the hybridization, and the change of ploidy level. Concerning the first, I can refer to the excellent paper of Dr Lovis (1968a), in which details of technique are discussed at length. In reference to the second problem, the well-known method of colchicine treatment for increasing the ploidy level is not very effective in Pteridophytes. However, there is an alternative possibility, namely the induction of apospory on juvenile fronds (cf. Manton 1950,

Meyer 1952, etc.). A gametophyte (including the female and male gametes) developed by the regeneration of the excised frond is already on the chromosome level characteristic of the sporophyte ($2n$). Self-fertilization of such an aposporous gametophyte will therefore produce a sporophyte with doubled chromosome number, as compared with a normal plant. In addition, certain hybrids are capable of producing unreduced spores which give rise to fertile allopolyploids (Wagner and Withmire 1957, Lovis 1968b, Lovis and Reichstein 1968, Lovis 1970). Quite exceptionally spontaneous somatic polyploidization has also been observed (Butters and Tryon 1948, Vida unpubl.*).

Haploid sporophytes can be obtained by inducing apogamy on normal gametophytes. This can be done by preventing the fertilization of the egg cells for an unusually long time (cf. Manton 1950, Manton and S. Walker 1954, Vida 1970), or by adding 1–2% sugar to the sterile culture medium (Whittier and Steeves 1960). Although both methods sound rather simple, till now very few adult sporophytes have successfully been raised in this way.

RESULTS

(I) OCCURRENCE OF POLYPLOIDS AND ANEUPLOIDS IN EUROPEAN FERNS

It is clear from chromosome number compilations (Chiarugi 1960, Fabbri 1963, 1965, Löve and Löve 1961), that at least one half of the European fern species are polyploid or consist of polyploid cytotypes (or cytodemes). In addition, most of the recent base numbers (like $x = 36$, 42, etc.) are regarded by some authors (Chiarugi 1960, Löve and Löve 1961) as ancient polyploids (paleopolyploids). It should be noted, however, that we have no basis to prove this, except arithmetic; but by this way we may reach the conclusion that the original base number was $x = 1$. Although at first this sounds rather trivial, it becomes immediately acceptable if we look far back in the history of evolution, keeping in mind that prokaryotes have only a single so-called 'chromosome' (genophore, also present in chloroplasts and mitochondria of eukaryotes). Nevertheless, this speculation loses interest when the question is about taxonomic or evolutionary relationships of modern fern species and genera. Consequently, it is usually the lowest known gametic chromosome number within a genus that is regarded as base number.

In most genera the base number is fairly stable. There are some exceptions, however, and European representatives of this sort are *Thelypteris* and *Cheilanthes*. Yet, in both these genera, species sharing the same base number can easily be reclassified together (at least on a European scale).

The reason for this high stability is not completely understood. One might expect viable chromosome number deviations (monosomics, trisomics or even nullisomics) in a species having as many chromosomes as $2n = 144$ (*Asplenium trichomanes*, *A. ruta-muraria*) or $2n = 164$ (many *Dryopteris*

* Frequent spontaneous somatic polyploidization has been observed in an apogamously produced diploid *Cystopteris fragilis*, which was completely sterile on the diploid level (polyhaploid).

species). Although the possibility of the existence of such deviations cannot be excluded, an exhaustive research programme which included a precise chromosome counting of more than 300 plants belonging to *Asplenium trichomanes* ssp. *quadrivalens*, *A. ruta-muraria* ssp. *ruta-muraria*, *Cystopteris fragilis* (4× and 6×) failed to show any aneuploids.*

(II) TAXANOMIC TREATMENT OF POLYPLOIDS

After the first excitement, when every new cytotype was regarded by some authors (unfortunately including myself—Vida 1963a) as a new species, an unwritten law is now generally accepted among the majority of pteridobiosystematists that alloploids may have specific rank, but an autoploid (in the broadest sense) should be separated as an infraspecific taxon (usually ssp.) only. This practice is in line with both the morphological species concept and the "biological species concept" (Löve 1964). The requisites of the latter concept are met since an exchange of genes, although on a limited scale between a diploid and its autotetraploid derivate, is still possible.

(III) GEOGRAPHICAL DISTRIBUTION AND ECOLOGY OF POLYPLOID FERNS

A comparison between the percentages of polyploids in different European floras seems to be pointless for various reasons (see for example Stebbins 1950). A more informative approach is to study the distributions of diploids and related polyploids in individual cases. Considering *Asplenium trichomanes*, *A. ruta-muraria*, *A. septentrionale* and *A. ceterach*, where many data are available for mapping, we can conclude that diploids are usually more restricted geographically and sometimes also ecologically than their autotetraploid relatives. The diploids in these cases are most often limited to the south-eastern part of Europe from Italy to the Caucasus, although one of the two diploid ssp. of *A. trichomanes* (the ssp. *trichomanes*) has a much wider distribution, mainly in the cooler part of the continent. This subspecies grows exclusively in non-calcareous soil, while the other diploid of the same species (*A. trichomanes* ssp. *inexpectans* Lovis) prefers calcareous rocks. The widespread tetraploid has no restrictions to certain rocks or soil (Lovis 1964a). The other species mentioned above do not seem to differ in ecological preferences at diploid and tetraploid levels.

Alloploids compared with their known diploid progenitors do not seem to show any general tendency in their geographical distribution. Many allotetraploids are endemics in relation to the more widely distributed diploids (apoendemics—Favarger and Contandriopoulos 1961), as *Asplenium* (*Phyllitis*) *hybridum*, *A. balearicum*, *A. majoricum*, *A. eberlei*, and some of them are very much restricted ecologically (e.g. *A. adulterinum*, growing on serpentine rocks only). On the other hand, the other extreme is also known, when the allopolyploid is frequent and the diploid rare or even possibly extinct (*Dryopteris filix-mas*, *D. carthusiana*, *D. dilatata*).

* Experimental aneuploids have been reported in gametophytes of the low chromosome numbered *Osmunda regalis* L. (Manton 1950).

It is perhaps worth mentioning that in certain cases the diploid progenitors of a European alloploid species are now believed to be somewhere outside of Europe (as in *Polypodium vulgare s.str.* and perhaps in $6\times$ *Cystopteris fragilis* too). These examples illustrate the superiority of certain alloploid combinations over their parental diploids.

(IV) THE ORIGIN OF POLYPLOIDS

The most interesting fern cytological results are concerned with investigations into the origin and types of polyploidy in polyploid complexes. Earlier results in meiotic analyses of interspecific hybrids (Manton 1950) emphasized the importance of alloploidy in many cases. Later studies on some other European ferns (Lovis 1963, 1964b, Lovis and Reichstein 1964, Lovis, Melzer and Reichstein 1966, Lovis, Sleep and Reichstein 1969, Lovis and Vida 1969, Vida 1963d, 1964, 1966a) have demonstrated the importance of autoploidy as well. The examples below will illustrate genomic relationships of diploid and polyploid taxa.

P o l y p o d i u m (Fig. 1). In Europe there are three closely related species of the genus (regarded sometimes as subspecies only, cf. Lenski 1964). The mediterranean *P. australe* is diploid, and, according to the genome analyses made by Manton (1950) and Shivas (1956, 1961a, b), once formed a triploid hybrid with *P. vulgare s.str.* (the common tetraploid species). This sterile hybrid has given rise to a new, fertile hexaploid species: *P. interjectum*. The three species usually require different ecological conditions, but at certain places they meet forming vigorous clones of sterile hybrids (Vida 1963b, Lenski 1964). The problem of origin of the tetraploid *P. vulgare s.str.* is only partly solved.

P o l y s t i c h u m (Fig. 2). Every possible hybrid combination has been found and most of these have been synthesized between the four European species (Sleep 1966). Both tetraploid species seem to be alloploid, but their parentage is known only in the case of *P. aculeatum* (Manton 1950, Manton and Reichstein 1961, Vida 1963c, 1966b, Sleep and Reichstein 1967).

D r y o p t e r i s (Fig. 3). In the *Dryopteris filix-mas* group the situation is complicated by the obligate apogamy present in *D. borreri* (both diploid and triploid cytotypes). Apogamy does not prevent hybridization with other sexual species, because these plants can produce functionable spermatozoids. Apogamy is inherited in the hybrids (Döpp 1932, 1933, 1955, Manton 1950). The parentage of the tetraploid *D.*

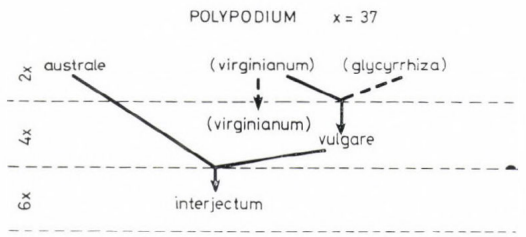

Fig 1.

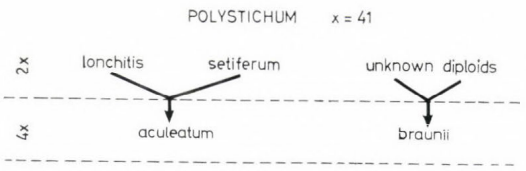

Fig 2.

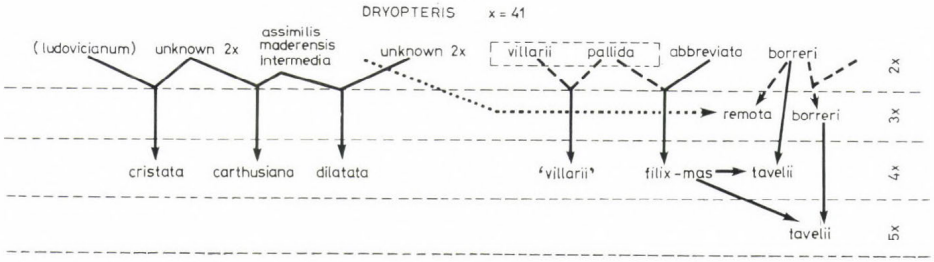

Fig 3.

filix-mas s.str. is only partly known (Manton 1950, Vida 1963c). Its alloploidy has been proved by the cytogenetic study of 2× plants obtained by induced apogamy (Manton and S. Walker 1954).

The origin of the so-called '*spinulosa complex*' (left side of Fig. 3) has been extensively studied (Manton 1950, Manton and S. Walker 1953, S. Walker 1955, 1959, 1961, 1969, Widén, Sorsa and Sarvella 1970). According to S. Walker (1961) there is a phenomenon unknown in the previous schemes whereby three morphologically distinct diploid species (*D. assimilis*, *D. maderensis*, *D. intermedia*) seem to share the same genome. The origin of taxa in the *D. villarii* complex is not yet clear (Vida 1969).

A s p l e n i u m s e n s u l a t o (Figs 4 and 5). In our opinion (Vida 1963a, Lovis and Vida 1969) this includes *Ceterach*, *Phyllitis* and *Biropteris* too. This last named taxon (Kümmerle 1922) is conspecific with *A.* (*Phyllitis*) *scolopendrium* (and not with *A. sagittatum* as suggested by the *Flora Europaea*)

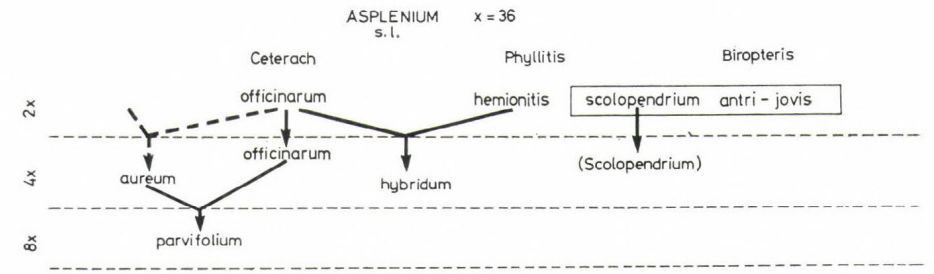

Fig 4.

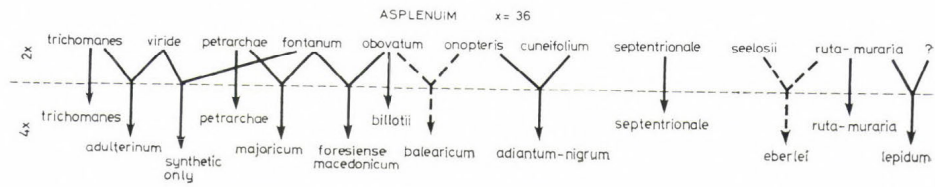

Fig 5.

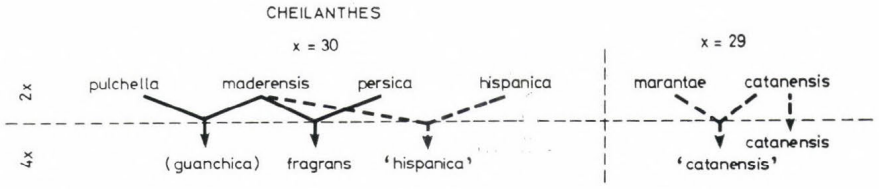

Fig 6.

since their artificial hybrids are fully fertile giving rise to complicatedly segregating F_2 progeny with every intermediate between the two parents (Reichstein and Vida unpubl.) *Asplenium* (*Phyllitis*) *hybridum* is a classic example of successful intergeneric hybridization. Its parentage is now clear (Emmott 1964, Vida 1963a and unpubl.).

The *Ceterach officinarum* complex (=*A. ceterach*) exhibits a series of 2×, 4× and 8× taxa (Vida 1963a, Reichstein and Vida unpubl.). This involves an autotetraploid (*A. ceterach s.str.*), an allotetraploid (*A. aureum*) and their polyploidised hybrid which is an autoallooctaploid (Reichstein and Vida unpubl.)

The genus *Asplenium* sensu stricto is rich in species in Europe. Most of the tetraploids are now of known origin. Autoploids and alloploids are equally common in the genus (Lovis 1963, 1964, Lovis, Melzer and Reichstein 1965, 1966, Lovis and Reichstein 1969, Lovis, Sleep and Reichstein 1969, Lovis and Vida 1969, Sleep 1966, 1967, Vida 1963d, 1964, 1966a, 1971). *A. adulterinum* has also been resynthesized by Lovis (1968b). Another synthetic allotetraploid (*A. viride* × *fontanum* doubled, Lovis 1970) has never been found in nature.

C h e i l a n t h e s (Fig. 6). Genome analysis is in progress in Budapest (Vida unpubl.). Here again, both autoploidy and alloploidy are involved foten in the same complex (cf. Vida, Page Walker and Reichstein 1970).

C y s t o p t e r i s (Fig. 7). The genomic relationship is very much obscure in the *C. fragilis* complex (Manton 1950, Manton and Reichstein 1965, Blasdell 1963). The basically alloploid nature of the tetraploid *C. fragilis* has been proved both by induced apogamy and by hybridization with the American species *C. protrusa* (Vida 1970a), but the situation is complicated by the recent discovery of a morphologically distinct octaploid taxon (Reichstein and Vida unpubl.). A hybridization programme is in progress in Budapest to analyse the genomic composition of the *C. fragilis* complex.

It is surprising that in most cases fern polyploids are quite easy to classify either as auto- or as alloploids. There are, however, a few allotetraploid

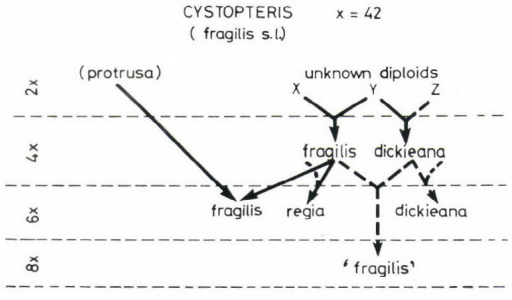

Fig 7.

species which show some degree of autosyndetic pairing capacity (*Cystopteris fragilis, Asplenium adiantum-nigrum*). On the other hand, some tetraploids which cytologically behave like autoploids show remarkable morphological distinction allowing their taxonomic separation from their supposed diploid progenitors (*A. scolopendrium* 2×, 4×; *A. billotii* 2×, 4×).

The importance of polyploidy in evolution is often discussed. In the case of homosporous ferns polyploidy is a very important evolutionary factor to "create and maintain genetic variation in the face of the homozygotizing effects of habitual self-fertilization in the monoecious gametophytes of these plants" (Klekowski and Baker 1966). Besides, polyploidy increases 'biochemical versatility' at the molecular level (cf. Barber 1970) which is a fundamental prerequisite for speciation.

REFERENCES

Barber, H. N. (1970): Hybridization and the evolution of plants. *Taxon* **19** 154–60

Blasdell, R. (1963): A monographic study of the fern genus *Cystopteris*. *Mem. Torrey Bot. Club* **21** 1–102

Bouharmont, J. (1968): Les formes chromosomiques d'*Asplenium trichomanes* L. *Bull. Jard. Bot. Nat. Belg.* **38** 103–14

Butters, F. K. and Tryon, R. M., Jr. (1948): A fertile mutant of a *Woodsia* hybrid. *Amer. Journ. Bot.* **35** 132

Chiarugi, A. (1960): Tavole cromosomiche delle *Pteridophyta*. *Caryologia* **13** 27–150

Döpp, W. (1932): Die Apogamie bei *Aspidium remotum* A. Br. *Planta* **17** 86–152

Döpp, W. (1933): Weitere Untersuchungen an apogamen Farnen. I. *Aspidium filix-mas* Sw. var. *crist. hort. Ber. Deut. Bot. Ges.* **51** 341–47

Döpp, W. (1955): Experimentell erzeugte Bastarde zwischen *Dryopteris filix-mas* (L.) Schott und *Dryopteris paleacea* (Sw.) C. Christensen. *Planta* **46** 70–91

Fabbri, F. (1963): Primo supplemento alle Tavole cromosomiche delle *Pteridophyta* di Alberto Chiarugi. *Caryologia* **16** 237–335

Fabbri, F. (1965): Secondo supplemento alle Tavole cromosomiche delle *Pteridophyta* di Alberto Chiarugi. *Caryologia* **18** 675–731

Favarger, C. and Contandriopoulos, J. (1961): Essai sur l'endémisme. *Bull. Soc. Bot. Suisse* **71** 384–408

Emmott, J. I. (1964): A cytogenetic investigation in a *Phyllitis–Asplenium* complex. *New Phytologist* **63** 306–18

Gätzi, W. (1961): Über den heutigen Stand der Dryopterisforschung. *Ber. St. Gallen. Naturwiss. Ges.* **77** 7–73

Grant, V. (1952): Cytogenetics of the hybrid *Gilia millefoliata* × *achilleaefolia*. I. Variations in meiosis and polyploidy rate as effected by nutritional and genetic conditions. *Chromosoma* **5** 372–90

Klekowski, E. J., Jr. and Baker, H. G. (1966): Evolutionary significance of polyploidy in the *Pteridophyta*. *Science* **153** 305–7

Kümmerle, J. B. (1922): Pteridologische Mitteilungen. *Magyar Botanikai Lapok (Budapest)* **21** 3–10

Lenski, I. (1964): Merkmalsprüfungen an den europäischen Zytotypen von *Polypodium vulgare* L. s. lat. *Flora* **154** 245–66

Lovis, J. D. (1963): Meiosis in *Asplenium* × *murbeckii* from Borrowdale. *Brit. Fern Gaz.* **9** 110–13

Lovis, J. D. (1964a): The taxonomy of *Asplenium trichomanes* in Europe. *Brit. Fern Gaz.* **9** 147–60

Lovis, J. D. (1964b): Autoploidy in *Asplenium*. *Nature* **203** 324–25

Lovis, J. D. (1966): *Asplenium* × *stiriacum*. D. E. Meyer emend. und die zwei *Asplenium lepidum* × *trichomanes*-Bastarde. *Bauchinia (Basel)* **3** 87–101

Lovis, J. D. (1968a): Fern hybridists and fern hybridising. II. Fern hybridising at the University of Leeds. *Brit. Fern Gaz.* **10** 13–20

Lovis, J. D. (1968b): Artificial reconstruction of a species of fern *Asplenium adulterinum*. *Nature* **217** 1163–65
Lovis, J. D. (1970): The synthesis of a new *Asplenium*. *Brit. Fern Gaz.* **10** 153–57
Lovis, J. D., Melzer, H. and Reichstein, T. (1965): *Asplenium adulteriniforme* hybr. nov. = diploides *Asplenium trichomanes* L. × *A. viride* Hudson. *Bauchinia (Basel)* **2** 231–7, 315–21
Lovis, J. D. and Reichstein, T. (1964): A diploid form of *Asplenium ruta-muraria*. *Brit. Fern Gaz.* **9** 141–46
Lovis, J. D. and Reichstein, T. (1968): Über das spontane Entstehen von *Asplenium adulterinum* aus einem natürlichen Bastard. *Naturwissenschaften* **55** 117–20
Lovis, M. D. and Reichstein, T. (1969): Der Farnbastard *Asplenium* × *orellii* hybr. nov. = *Asplenium majoricum* Litard. × *A. trichomanes* L. subsp. *quadrivalens* D. E. Meyer und die Abstammung von *A. majoricum*. *Berichte Deut. Bot. Ges.* **79** 335–45
Lovis, J. D., Sleep, A. and Reichstein, T. (1969): Der Farnbastard *Asplenium* × *sollerense* hybr. nov. = *Asplenium majoricum* Litard. × *A. petrarchae* (Guérin) DC. subsp. *petrarchae*. *Ber. Schweiz. Bot. Ges.* **79** 369–76
Lovis, J. D. and Vida, G. (1969): The resynthesis and cytogenetic investigation of × *Asplenophyllitis microdon* and × *A. jacksonii*. *Brit. Fern Gaz.* **10** 53–67
Löve, A. (1964): The biological species concept and its evolutionary structure. *Taxon* **13** 33–45
Löve, A. and Löve, D. (1961): Chromosome numbers of central and northwest European plant species. *Opera Botanica* **5** 1–581
Manton, I. (1950): Problems of cytology and evolution in the *Pteridophyta*. Cambridge Univ. Press, pp. 316
Manton, I. and Reichstein, T. (1961): Zur Cytologie von *Polystichum braunii* (Spenner) Fée und seiner Hybriden. *Ber. Schweiz. Bot. Ges.* **71** 370–83
Manton, I. and Reichstein, T. (1965): Die Chromosomenzahlen von *Cystopteris sudetica* A. Br. et Milde von Berchtesgaden (Bayern) sowie von *Cystopteris dickieana* Sim. s. l. vom Foostock (Kanton Glarus, Schweiz). *Bauchinia* (Basel) **2** 307–12
Manton, I. and Walker, S. (1953): Cytology of the *Dryopteris spinulosa* complex in eastern North America. *Nature*, **171** 1116–17
Manton, I. and Walker, S. (1954): Induced apogamy in *Dryopteris dilatata* (Hofm.) A. Gray and *D. Filix-mas* (L.) Schott emend. and its significance for the interpretation of the two species. *Ann. Bot. n.s.* **18** 377–83
Meyer, D. E. (1952): Untersuchungen über Bastardierung in der Gattung *Asplenium*. *Bibliotheca Bot.* **123**
Roy, S. K. and Manton, I. (1965): A new base number in the genus *Lygodium*. *New Phytol.* **64** 286–92
Shivas, M. (1956): Some problems in cytology and taxonomy of species of *Polypodium* in Europe and North America. *PhD. Thesis* (unpubl.), University of Leeds
Shivas, M. (1961a): Contributions to the cytology and taxonomy of species of *Polypodium* in Europe and North America. I. Cytology. *Journ. Linn. Soc. London (Bot.)* **58** 13–26
Shivas, M. (1961b): Contributions to the cytology and taxonomy of species of *Polypodium* in Europe and North America. II. Taxonomy. *Journ. Linn. Soc. London (Bot.)* **58** 27–38
Shivas, M. (1969): A cytotaxonomic study of the *Asplenium adiantum-nigrum* complex. *Brit. Fern Gaz.* **10** 68–80
Sleep, A. (1966): Some cytotaxonomic problems in the fern genera *Asplenium* and *Polystichum*. *PhD. thesis* (unpubl.), University of Leeds
Sleep, A. (1967): A contribution to the cytotaxonomy of *Asplenium majoricum*. *Brit. Fern Gaz.* **9** 321–29
Sleep, A. und Reichstein, T. (1967): Der Farnbastard *Polystichum* × *meyeri* hybr. nov. = *Polystichum braunii* (Spenner) Fée × *P. lonchitis* (L.) Roth und seine Cytologie. *Bauchinia (Basel)* **3** 299–374
Stebbins, G. L. (1950): *Variation and evolution in plants*. Columbia Univ. Press, New York
Vida, G. (1963a): A new *Asplenium* (sectio *Ceterach*) species and the problem of the origin of *Phyllitis hybrida* (Milde) C. Christ. *Acta Bot. Acad. Sci. Hung.* **9** 197–215
Vida, G. (1963b): The biosystematics of the Hungarian *Polypodium vulgare* s.l. *Acta Biol. Acad. Sci. Hung.*, Suppl. **5** 26–7

Vida, G. (1963c): A *Dryopteris* s.l. nemzetség szisztematikája (Systematics of the genus *Dryopteris* s.l.). *Botanikai Közlemények (Budapest)* **50** 125–33
Vida, G. (1963d): Zytogenetik der ungarischen *Asplenium*-Bastarde. *Botanikai Közlemények (Budapest)* (Sitzungsberichte) **50** 235
Vida, G. (1964): Cytogenetical studies in *Asplenium* hybrids found in Hungary (TAX). *Tenth Int. Bot. Congr. Edinburgh* 1964 (Abstracts), p. 500
Vida, G. (1966a): Az evolució genetikai alapjai (Genetic bases of evolution). *MTA Biol. Oszt. Közl. (Budapest)* **9** 133–66
Vida, G. (1966b): Cytology of *Polystichum* in Hungary. *Botanikai Közlemények* **53** 137–44
Vida, G. (1969): Tetraploid *Dryopteris villarii* (Bellardi) Woynar ex Schinz et Thell. in Rumania. *Botanikai Közlemények (Budapest)* **56** 11–6
Vida, G. (1970a): Genome analysis of *Cystopteris fragilis* by means of hybridization and induced apogamy. Abstracts of the lectures delivered at the 9th Hungarian Congress of Biology, Budapest, 6–8 May, 1970. *Publ. Demographic Res. Inst.* **32** 51
Vida, G. (1970b): The nature of polyploidy in *Asplenium ruta-muraria* L. and *A. lepidum* C. Presl. *Caryologia* **23** 525–47
Vida, G., Page, C. N., Walker, T. G. and Reichstein, T. (1970): Cytologie der Farn-Gattung *Cheilantes* in Europa und auf den Canarischen Inseln. *Bauchinia (Basel)* **4** 223–53
Wagner, W. H. and Withmire, R. S. (1957): Spontaneous production of a morphologically distinct, fertile alloploid by a sterile diploid of *Asplenium ebenoides*. *Bull. Torrey Bot. Club* **84** 79–89
Walker, S. (1955): Cytogenetic studies in the *Dryopteris spinulosa* complex. I. *Watsonia* **3** 193–209
Walker, S. (1959): Cytotaxonomic studies of some American species of *Dryopteris*. *Amer. Fern Journ.* **49** 104–11
Walker, S. (1961): Cytogenetic studies in the *Dryopteris spinulosa* complex. II. *Amer. Journ. Bot.* **48** 607–14
Walker, S. (1969): Identification of a diploid ancestral genome in the *Dryopteris spinulosa* complex. *Brit. Fern Gaz.* **10** 97–9
Whittier, D. P. and Steeves, T. A. (1960): The induction of apogamy in the bracken fern. *Canad. Journ. Bot.* **38** 925–30
Widén, C. J., Sorsa, V. and Sarvella, J. (1970): *Dryopteris dilatata* s. lat. in Europe and the Island of Madeira. *Acta Botanica Fennica* **91** 1–30
Wuu, K. D. and Grant, W. F. (1967): Chromosomal aberrations induced by pesticides in meiotic cells of barley. *Cytologia* **32** 31–41

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THE LOSS OF A SPECIES THROUGH BREAKDOWN OF A CHROMOSOMAL BARRIER*

by

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Clarkia nitens Lewis & Lewis was described in 1955 as a species distinct from *C. speciosa* Lewis & Lewis on the basis of numerous morphological differences and the knowledge that artificially produced hybrids were nearly sterile. Both species had the same chromosome number ($n = 9$), but their genomes were known to differ by at least seven interchanges based on the observation that F_1 hybrids during meiosis formed a ring of sixteen chromosomes and one pair. These large rings showed a frequency of non-disjunction sufficiently high to account for the very low fertility of the hybrids. Herbarium records indicated that the range of distribution of the two species overlapped by at least twenty km and because of the sterile hybrids it was assumed that no effective gene exchange occurred between them. Seldom has a species been described with more knowledge than that on which *C. nitens* was based. We are now convinced, however, on the basis of additional evidence, that although *C. nitens* and *C. speciosa* were once distinct species, they have since merged into one. Our reasons for this conclusion and our interpretation of the interactions that have occurred between *C. nitens* and *C. speciosa* form the basis for this paper.

Our present study began with the discovery that *C. speciosa* included two chromosome races which differed from each other by at least seven interchanges. Hybrids between them formed a maximum association of a ring of sixteen and one pair at meiosis and like the hybrids between *C. nitens* and *C. speciosa*, were nearly sterile. One of the chromosome races was found to include all of the several subspecies of *C. speciosa* endemic to the Coast Ranges of California as well as the populations in the southern half of the range of *C. speciosa polyantha*, the subspecies which occurs in the foothills on the east margin of the San Joaquin Valley. The other chromosome race was found to include the populations of *C. s. polyantha* in the northern half of its range. Populations in the region of contact between the two chromosomal races were found to be morphologically indistinguishable and no more variable in appearance than populations from outside this area. Furthermore, the northern chromosome race of *C. s. polyantha* was shown to have the same chromosome arrangement as *C. nitens* and to form fully fertile hybrids with it.

This information led to an examination of wild populations in the area

* For more details see 'Reciprocal translocations and interpopulational gene exchange in *Clarkia speciosa*' by the same authors, to be published in *Chromosomes Today* **3** (supplement to Heredity).

where *C. nitens* and *C. s. polyantha* were presumed to overlap. Contrary to earlier expectations, the two taxa were found to intergrade morphologically over a wide area. These field observations, together with hybridization studies in the garden, indicate beyond a reasonable doubt that this intergradation is the result of hybridization and genetic recombination between the two taxa.

Having determined that the chromosomal discontinuity which was thought initially to coincide with the morphological differences between two species was actually located about 100 km south of the zone of conspicuous morphological intergradation, attention was turned to the boundary between the two chromosome races. Since hybrids are readily produced in the garden and are cytologically identifiable, we attempted to locate the area of contact between the two chromosomal races by examining meiosis in samples from ten populations along a transect about 35 km long across the known boundary area, but no interracial hybrids were found; nor were they found among the progenies produced by crossing individuals from adjacent populations. We did find, however, that populations from the transect compared to others have a high frequency of individuals heterozygous for one or two interchanges, recognizable by the presence of rings of four or six at meiosis, and one population was chromosomally exceptionally variable.

The exceptional population had a much higher average level of heterozygosity than any other; in addition to a very high frequency of individuals with small rings of four or six, this population also included a few plants with a ring of eight and one individual was found to have a ring of ten. Ten different arrangements were identified from this population of which the five most frequent accounted for more than 80 percent of all arrangements in the population and were those which in various combinations generally produced small rings. The arrangements which in combination would produce larger rings were found in low frequency. In each of the other populations sampled, no arrangements were identified which, in combination with other arrangements in the same population, would produce an association larger than a ring of six.

Hybridization between individuals from the highly heterozygous population and from a series of populations to the north and south of it indicated that each arrangement had a distribution determined by its effect on fertility when in combination with other arrangements. Arrangements that differ by one or two interchanges and produce rings of four or six have relatively little effect if any on fertility because they show a high frequency of regular alternate segregation whereas larger rings show a much higher frequency of nondisjunction and a corresponding decrease in fertility with increase in the size of the ring. As a result, the most frequent arrangements in any population are those that in combination produce a ring of four or at most a ring of six. Furthermore, the most frequent arrangement in any one population was found to differ by no more than one interchange from the most frequent arrangement in the colonies nearest to it. Consequently, nearly every individual in all populations is highly fertile, produces fertile progeny with other individuals from the same population, and also produces fertile hybrids with individuals from neighboring colonies. Contrary to our expectation, no chromosomal barrier to gene exchange between adjacent popu-

lations was found in the boundary area between the two chromosome races.

The relationships among the various arrangements identified from the boundary area cannot be explained as a sequence of changes leading from the southern race to the northern or vice versa because arrangements characteristic of the center of the boundary area differ from both races by as many interchanges as the races differ from each other. The most reasonable explanation for the pattern of chromosomal relationships is that two cytologically differentiated species came into contact and hybridized. These species, we believe, were morphologically and cytologically comparable to *C. s. polyantha* as it now exists south of the area between the two chromosome races and *C. nitens* as it now exists to the north of the zone of intergradation with *C. s. polyantha*. Starting from this assumption we suggest the following course of events.

Hybridization between the two species may have come about as a result of changing environmental conditions which permitted *C. s. polyantha* to migrate northward and get into contact with the southern margin of *C. nitens* in the area now marked by the cytological boundary. Because the *C. s. polyantha* phenotype subsequently moved northward, we believe that *C. s. polyantha* was better adapted than *C. nitens* to the area of initial contact. Since no barriers to hybridization are known between *C. nitens* and *C. speciosa* from throughout their respective ranges of distribution, hybrids were presumably formed as readily as conspecific progeny at the point or line of initial contact. As a result, *C. speciosa*, although better adapted to the area, could not invade sites occupied by *C. nitens* because a hybrid produced in a population of *C. nitens* from pollen of *C. speciosa* would ordinarily leave no progeny, and seedlings of *C. speciosa* that might become established in a colony of *C. nitens* would produce mostly if not exclusively sterile hybrids.

The continued production of frequent hybrids at points of contact might have led to selection for barriers to hybridization but in this instance evolution took the course of selection for an increase in the fertility of hybrids, the increase being due to new chromosome arrangements which produced smaller rings with the parental arrangements and among themselves. As subsequent arrangements arose, which formed smaller rings and gave higher fertility in combination with one another, there was a gradual displacement and eventual elimination of the original arrangements from the contact zone. Until now they are separated by a considerable distance but are linked by a large number of populations consisting of individuals nearly all of which are fully fertile and capable of producing highly fertile hybrids with individuals from adjacent populations.

Gene exchange between the two species became possible at an increasing rate as the system of interchanges improving interfertility evolved. But regardless of rate, gene exchange involved crossing over and not chromosome substitution, except perhaps for the chromosome pair that was common to both. The occurrence of populations that have the phenotype of *C. s. polyantha* and the chromosome arrangement of *C. nitens* means that there has been a massive introgression of *C. s. polyantha* genes into *C. nitens* and a reconstruction of genotypes comparable to those of *C. s. polyantha* that have not been subjected to dissociation. Since gene recombination

between the two taxa is now free from the chromosomal barrier, the rate, direction, and degree of introgression are determined only by the interaction between recombinant genotypes and their relative fitness.

The system of interchanges that evolved is geographically stable and undoubtedly arose in the area in which it is now found. This assumption is based on the observation that the arrangements appear to be independent of the genotype to the extent that different arrangements have indistinguishable phenotypes. Consequently, the primary if not the only effect of the various arrangements is to reduce fertility in individuals heterozygous for more than one or two interchanges. As a result the spatial distribution of each arrangement is determined by its effect on fertility in combination with other arrangements and unlike the genotype will be relatively unaffected by the external environment. Although the frequency and distribution of existing arrangements may change, particularly at the margin of the system or in relation to the establishment of a new arrangement, this is unlikely to affect the system as a whole.

The stable system of interchanges, which marks the position of the initial contact between *C. nitens* and *C. s. polyantha*, provides a basis for determining the direction and the extent of introgression. Without such a marker one would not suspect that introgression had been so extensive or that the zone of interaction was now located about 100 km north of where it began.

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EVOLUTIONARY RELATIONSHIPS IN WILD TUBER-BEARING *SOLANUM* SPECIES

by

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The genus *Solanum* is one of the largest in the plant kingdom. Its distribution is world wide but the concentration of diversity lies in the American continent, as it does for the family *Solanaceae* itself.

Four of the six sub-genera in *Solanum* are monocontinental, though there are two world-wide ones (*Solanum*, *Stellatipilum*). Some 75% of the sections and subsections of these are, again, monocontinental. This adds considerable weight to the hypothesis that a number of widely spread genera, including *Solanum*, may have already been in existence before the fragmentation of Gondwanaland in at least early Cretaceous times, some 100 million years ago (Hawkes and Smith 1965).

Opinions vary as to the number of species in the genus, since no one person has been courageous enough to monograph it since Dunal's treatment in 1852, which is inadequate by present-day standards. About 2000 species is the usual estimate, and of these not more than one tenth belong to the tuber-bearing sub-section, *Hyperbasarthrum*, of the section *Tuberarium*. These tuber-bearing species are of particular interest economically, since one of them, *Solanum tuberosum* L., is one of the most important world crops; and most of the rest are of interest to plant breeders for the various types of resistance to disease and greater adaptation to climatic extremes which they possess. There is thus a practical as well as a theoretical reason for interesting ourselves in the evolutionary diversity of wild and primitive cultivated potatoes; and because of this interest, breeders, cytogeneticists and experimental taxonomists have accumulated a fairly large body of information on evolutionary pathways in this group of species.

Within the group of tuber-bearing *Solanums* we find a wide range of morphological variation, mirrored by biochemical and serological diversity; there is a polyploid series based on $x = 12$, ranging from diploid to hexaploid in the wild species and from diploid to pentaploid in the cultivated ones; and the range of ecological adaptation and resistance to fungi, bacteria, viruses, insects and nematodes is also very considerable.

This rich variability is no doubt largely due to the wide range of climatic and other selection pressures which have acted on this group of plants over periods of millions of years. The species are found as far north as Colorado and Utah in the U.S.A. and as far south as the island of Chiloé in Southern Chile. They are found from sea level up to over 4500 m in the Andes of South America. Some are found in the subtropics and even in the drier regions of the tropics (*S. calvescens*). Others occur in the cold 'alpine' zone of the Andes and are resistant to frost (*S. acaule*). Others

again occur in dry scrub and semi-deserts or dry intermont basins, (*S. chacoense*, *S. infundibuliforme*, *S. kurtzianum*) and others in high-rainfall mountain forests (*S. oxycarpum*, *S. microdontum*). Some aestivate for 9 months in the year on the desert coast of Peru, waiting for the two or three months of sea mists which by condensation provide sufficient water for them to grow and set tubers and berries (*S. wittmackii*, *S. weberbaueri*); and one species has even become adapted to growth as an epiphyte in the mountain rain forests of Mexico and Guatemala (*S. morelliforme*).

In a discussion of the possible mode of evolution of potato species consideration must be given to their reproductive biology. Potatoes, and especially the wild species, reproduce both sexually and asexually. The diploid species are self-incompatible allogamous species, incapable of self-fertilization. The even-number polyploids are self-fertile potentially but, apart from the almost obligatorily self-pollinating *S. acaule*, most in fact are out-pollinating. This outbreeding system ensures that gene flow will take place through large populations and seems to have been responsible for maintaining a high degree of intraspecific variability, whilst providing the basis for rapid evolutionary change. In a stable environment with optimum conditions, on the other hand, genetic stability is maintained for a well-adapted genotype by vegetative reproduction. A large population of genetically identical individuals can build up in a few vegetative generations.

Thus vegetative reproduction is at a premium in a stable environment, whilst if the environment is changing, or if competition or selection is more intense, then sexual reproduction will be favoured. A delicate balance is thus preserved between stability and change. We can liken this to the process of facultative apomixis or inbreeding combined with occasional outbreeding—two processes which seem to have occurred with such frequency and success in other flowering plant genera.

In studying evolutionary pathways in different plant groups investigators have always been able to identify breeding barriers which isolate groups of populations from others, preventing gene flow between them and leading eventually to the production of well-defined biological or taxonomic species.

Most species of potatoes are diploids, and with almost all of these the primary barriers which isolate one from the other are eco-geographical. Species generally occur in well-defined altitudinal belts, are separated spatially by mountain, forest or desert barriers, or are adapted to a rather clearly defined habitat range. However, artificial hybrids are generally very easy to make in the experimental field or glasshouse and the F_1 plants are quite fertile, with regular bivalent pairing at meiosis and abundant seed production. This has often been used as evidence to show that such species are not 'good' or 'valid', since they are not separated by sterility barriers of the usual type. However, apart from differences in species concepts one must make two points in favour of retaining the species as generally defined.

Firstly, 'F_2' hybrids resulting from F_1 sib-matings between most morphologically defined potato species show 'genetic breakdown', with seedlings ranging from inviable, extremely unthrifty or poorly developing plants, right through to ones as vigorous as the parents. This seems to be evidence of a difference in the genetic background or architecture, such that blocks of genes cannot substitute for each other in every combination of F_2

segregants to provide healthy vigorous individuals. Stebbins (1945) has postulated that chromosomes of species where F_1 hybrids show regular pairing have evolved by cryptic structural change too small to prevent chromosome pairing but nevertheless real enough in genetic terms.

Further evidence comes from studies by Swaminathan (1953) who analysed quadrivalent frequencies in artificial autotetraploid plants of diploid species, comparing them with the amphiploids derived from diploid × diploid crosses and subsequent colchicine doubling. Significantly, the quadrivalent frequencies in the autotetraploids and in hybrids between species not considered to be distinct ranged from 3·45 to 4·56; on the other hand, they were very much lower in the amphiploids, varying from 0 to 1·19. This is a clear indication of a cryptic genomic difference between species which is unassessable in the F_1 hybrids but visible from F_2 progeny testing and autotetraploid/amphiploid comparisons.

One can assume then, with some certainty, that a chromosome in the presence of its exact partner or homologue will pair with it in preference to a similar chromosome or homeologue from another species. Hence the multivalent formations in amphiploids will be low, as we have seen. In a diploid F_1 where no homologue is present the chromosome will pair with its homeologue, giving the false impression that there are no genome differences or mating barriers of any kinds between species.

We have hitherto been examining hybridization in the experimental field. When one studies populations of potato species in the wild, one finds evidence of frequent hybridization there, too, even though physiological and genetical barriers to gene flow can be discerned by careful study.

On Anderson's hypothesis (Anderson 1949) where species have evolved under ecological and/or geographical isolation any natural or man-made changes of the environment which result in a blurring of the natural habitats may bring together previously ecologically isolated species and allow them to hybridize. Under intermediate habitat conditions hybrids may be able to survive for which there would have been no appropriate ecological niche previously. Partially fertile hybrids would be more likely to backcross with the fully fertile parents than with each other, and this would result in limited gene flow or introgression of some genes from one species to another.

Together with a Danish colleague, J. P. Hjerting, I investigated variability in an Argentine wild potato species, *S. chacoense* (Hawkes 1962; Hawkes and Hjerting 1969). We discovered strong evidence for introgression of genes of *S. microdontum* into *S. chacoense* in the medium altitude northwestern valleys of Argentina. *S. chacoense* is a species of the plains of Argentina and Paraguay at altitudes of 500 m or much less. The mountain forms occurring at above 500 m differ very markedly from the plains forms, and by means of Anderson's extrapolated correlates we demonstrated that the contaminating species was *S. microdontum*, which occurs primarily in high altitude forests but evidently spreads down into the fields and waste areas derived from man's activities, into which *S. chacoense* also migrated. Natural hybrids can be seen in many areas, and forms of *S. chacoense* with introgression from *S. microdontum* can be clearly recognized. Evidence of introgression of virus Y resistance genes can also be found, this time probably from *S. chacoense* to *S. microdontum* (Cockerham, in Anon. 1962, 1965).

In certain years hybrids between species in the wild seem very frequent

and are not only confined to those species I have just mentioned. Thus, referring again to the Argentine species, Hjerting observed large quantities of hybrids in 1956 but hardly any in the same localities in 1966 (Hawkes and Hjerting 1969, Appendix III). The 1966 season was a particularly dry one, and it seems likely that because of the rigorous conditions the hybrids died out, since they were not so well adapted to their environmental conditions as the parents. If this hypothesis is correct, namely, that the hybrids do not possess such combinations of genes for perfect physiological adaptation as the parents, then the fluctuations of environmental conditions from season to season might be all that is necessary to prevent mass hybridization, with a consequent complete blurring of the species boundaries. This would not prevent introgression, since the well-adapted segregants would be selected for the same adaptive peaks as the parents. This mechanism, it seems to me, would account for the elimination of hybrids and the maintenance of clear species boundaries even between species which overlap and form natural hybrids with some frequency. It would be valuable to know how far it was taking place also in European plants, and indeed it would be much easier to monitor populations of hybrids and parents from year to year in Europe than it is in the remote mountains of South America.

A curious phenomenon in very many of the diploid potato species is the occurrence of autotriploids. These occur with the diploids and are extremely common in certain species (*S. maglia*, *S. commersonii*, *S. cardiophyllum*, etc.) but have been seen in many others when tuber collections from the wild have been investigated. It would seem that 'unreduced' gametes are not infrequent in potatoes and that under certain conditions triploid hybrids from the union of reduced and 'unreduced' gametes are at a selective advantage and persist vegetatively, colonizing vast areas by clonal reproduction. In a sense, they represent an evolutionary 'dead end'. However, because they seem to be slightly more vigorous than their parent diploids they can become very frequent, especially in the vicinity of large cities, where the environment has been so changed by man and the natural competition with other species so reduced, that they are able to survive for probably very long periods. Under conditions of stronger competition with natural vegetation where potatoes are not so well adapted, vegetative propagation is less important and the triploids are not frequent. Even there, however, we have reason to believe that they are produced, but do not survive for long.

We have spoken about 'cryptic' genome evolution in potato species, which seems to be the only situation in almost the whole of the South American species. However, the Mexican wild potatoes, which include allotetraploid and allohexaploid groups of species, show considerable genome differences. Hawkes (1958) postulated the genome A_1 for diploid South American species; A_2A_3 for the tetraploid South American species *S. acaule;* A_1B for the tetraploid Mexican species *S. stoloniferum* and its relatives; and A_1A_1B for the hexaploid Mexican *S. demissum* and its relatives. This was of course a tentative hypothesis but in the subsequent 12 years no satisfactory alternative has been advanced.

One might envisage that the tuber-bearing species as a whole originated in Mexico, where the widest range of morphological variation can be seen, where two distinct crossability groups exist and where the strongest serological differences between species can be found. From Mexico one might

further envisage that one section of the *A* genome migrated to South America in pre-Eocene times. From Eocene to Pliocene, North and South America were completely severed from each other but the land bridge was restored at the end of that period. One may then envisage two waves of migration of the *A* genome northwards, one by hybridization, forming the tetraploid A_4B species, and the second more recent one forming the A_1A_4B species. It is of interest to note that the hexaploid species all possess one identical genome derived from the diploid Mexican *S. verrucosum*. This latter is postulated as the recent immigrant from South America, whose genome is of the same type as that of the diploid South American species (Marks 1955).

Although there are present-day climatic belts in Central America over which *S. verrucosum* could not migrate we may assume with some certainty that conditions during the Pleistocene were considerably different. It is known, for instance that glaciers of certain magnitude were developed in Costa Rica, where none now exist (R. Weyl 1955) and that these were synchronous with the last or Wisconsin glaciation. With glaciation in mountains of no more than 3400 m when present glaciations begin at altitudes of some 5000 m, we can satisfy ourselves that migrations of cold-adapted potato species over the Central American isthmus would present no problems.

To conclude, it is clear that we have arrived at some understanding of the course of evolution in wild potatoes, their breeding mechanisms and barriers to gene flow. We know something about hybridization and introgression in the better studied areas such as Mexico and Argentina. We have begun to understand genome differences in a few of the diploid South American species, but much more cytological work on auto- and allo-tetraploids is needed. And finally we can postulate in outline the historical sequences of migration and species group formation from North to South America and back again.

REFERENCES

Anderson, E. (1949): *Introgressive hybridization*. New York

Cockerham, G. (1962): (in Anon.) *Rec. Scott. Pl. Breed. Stn.* 5–27

Cockerham, G. (1965): Ibid. 7–25

Dunal, M. F. (1852): (in De Candolle) *Prod. Syst. nat. Regni. veg.* **13** I. Paris

Hawkes, J. G. (1958): (in Kappert, H. and Rudorf, W.) *Handbuch der Pflanzenzüchtung*. 2nd ed., Vol. III, Chapter 1. Potatoes: taxonomy, cytology and crossability. pp. 1–43

Hawkes, J. G. (1962): Introgression in certain wild potato species. *Euphytica* **11** 26–35

Hawkes, J. G. and Smith, P. (1965): Continental drift and the age of Angiosperm genera. *Nature (Lond.)* **207** 48–50

Hawkes, J. G. and Hjerting, J. P. (1969): *The potatoes of Argentina, Brazil, Paraguay and Uruguay*. Oxford

Marks, G. E. (1955): Cytogenetic studies in tuberous *Solanum* species. I. Genome differentiation in the group *Demissa*. *J. Genet.* **53** 262–69

Stebbins, G. L. (1945): The cytological analysis of species hybrids. *Bot. Rev.* **11** 463–86

Swaminathan, M. S. (1953): Studies on the inter-relationships between taxonomic series in the section *Tuberarium*, genus *Solanum*. I. *Commersoniana* and *Tuberosa*. *Amer. Potato J.* **30** 271–81

Weyl, R. (1955): Geologische Studien in der Cordillera de Talamanca von Costa Rica. *Neues Jahrbuch für Geol. und Palaeontol. Monatsheft* **6** 262–69

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MULTIPLE MOLECULAR FORMS OF PERIOXIDASES AND ESTERASES AMONG *NICOTIANA* SPECIES AND AMPHIPLOIDS*

by

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SUMMARY

Electrophoretic patterns of 61 species of the genus *Nicotiana* were analyzed for seedling root peroxidases demonstrated in starch gels, and 55 for esterases extracted from dry seeds and separated in polyacrylamide gels. Each species had a unique band pattern. In all, 33 peroxidase and 25 esterase bands were determined; and in any one species the range was from 3 to 10 peroxidase bands and 3 to 15 esterase bands. No single specific band was common to all *Nicotiana* species.

Statistical methods, based on a hypergeometric distribution model, were used to assess the degree of phylogenetic association within vs. between taxonomic sections in terms of matching species bands. The probability that the observed band matching was due to chance was less among species within a section, thus indicating a closer genetic relationship in agreement with the established taxonomy of the genus.

Seventeen amphiploids were synthesized and their peroxidase and esterase band patterns were compared with those of their parental species. Seventy-five percent of the amphiploid bands showed the same mobility as in one or both parents; while 25 percent were new (possibly hybrid) bands. The number of bands of the amphiploid that matched those of the sum of the band positions in the diploid parents was greater than could be due to chance. It was concluded that this method of band assessment is a reliable measure of genetic similarity.

The band patterns of three species of amphiploid origin (*N. rustica*, *N. arentsii*, and *N. tabacum*) were compared with those of the sum of their putative diploid progenitors. The number of matched bands was higher than could be attributed to chance, thus substantiating the ancestry predicated on evidence from cytogenetics and morphology.

Addendum: Since completion of this paper, a publication has appeared that reports similar objectives and materials (S. J. Sheen 1970, Peroxidases in the genus *Nicotiana*. *Theoretical and Applied Genetics* **40** 18–25). The plant parts used, separation and staining methods, analysis of data, and conclusions are largely different from those presented here, except for agreement that many different peroxidase bands are found among species of the genus *Nicotiana*.

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THE NATURE OF MUTATION IN HEXAPLOID WHEAT*

by

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INTRODUCTION

It was shown by Stadler (1928a, b) more than 40 years ago that mutations are easily induced in diploid plants by ionizing radiation. This finding has since been amply confirmed by the work of many investigators.

Of the mutations which can be induced in diploids, one conspicuous class that occurs in substantial frequency is chlorophyll aberration. Because chlorophyll mutations are easily scored at the seedling stage, they are often used as a measure of mutation rate, and the relative frequencies of different kinds of chlorophyll mutations are used in comparing the effects of different mutagens.

Various lines of evidence suggest that the large majority of the radiation-induced chlorophyll mutations are simply deficiencies for loci essential to chlorophyll formation. There are evidently scores of such loci in each diploid species.

In polyploids of fairly recent origin, such as hexaploid wheat, quite a different situation obtains. Indeed, Stadler (1929) found no chlorophyll mutations at all in hexaploid wheat in an experiment that he calculated would have yielded at least 40 mutations if the material had been diploid. Subsequent experiments of many investigators have confirmed that good, simply inherited chlorophyll mutations are extremely rare in hexaploid wheat following irradiation. MacKey (1954), for example, while obtaining very high frequencies of some so-called peripheral mutations, such as speltoidy, found almost no chlorophyll mutations.

Stadler concluded that the absence of chlorophyll mutations in hexaploid wheat was a consequence of triplication of the loci concerned in chlorophyll production. Deletion of any one locus had no detectable effect because there were still two loci left to carry out that particular step in chlorophyll synthesis. All subsequent results are in accord with this explanation. In particular, it is clear from the normal chlorophyll content of the nullisomics and tetrasomics of the variety Chinese Spring that at least in this variety there is no one locus that is essential to normal chlorophyll production or that leads to chlorophyll abnormality when duplicated.

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CLASSES OF GENES

In dealing with the nature of mutation in hexaploid wheat, we shall find it useful to classify the genes of wheat according to their degree of duplication and their expressivity at various dosages. As pointed out by Morris and Sears (1967), at least three classes can be distinguished:

(1) Triplicated genes with no increased effect at dosages above four. — (Normal dosage equals six.) As would be expected from the fact that most wild-type genes are dominant in diploids, where a dosage of one equates with a dosage of three in the hexaploid, the large majority of genes in the hexaploid have as great an effect at four doses as at five or six and thus belong in this class. All, or nearly all, of the genes essential to chlorophyll production belong here, along with the other 'vital' genes (MacKey 1954) essential to the viability of the plant. Homozygous deficiency for only one locus has no effect, because four doses remain. These genes are therefore highly intractable to mutation by radiation, but some mutate spontaneously and respond to chemical mutagens.

(2) Triplicated genes with a dosage effect beyond the level of four. — This class is relatively small, but the genes concerned are responsible for most of the characters of the nullisomics. Nullisomy reduces to four the dosage of several different series of these genes, bringing about a particular complex of changed characteristics. Since the other two loci of each series are located, as a rule, on the two homoeologous chromosomes, nullisomy for any one of the three homoeologues has substantially the same effect as nullisomy for either of the other two.

An example of such a series of triplicates is the genes on chromosomes 2A, 2B, and 2D that promote awn development. Each nullisomic has shortened awns and each tetrasomic lengthened awns, but all the possible nullisomic-tetrasomics involving group-2 chromosomes have normal awns. Mutations of such genes are of course easily obtained, a simple deletion or duplication being all that is required.

A few genes in this class may actually show a greater increase in effectiveness at levels beyond six than between four and six. In fact, the awn-promoting genes just mentioned make no awn at all (in the Chinese Spring background) at four doses, produce awns up to 2 mm long at six doses, and make awns up to 20 mm at eight doses. Such genes are more likely to reveal themselves through duplication mutations than deficiency mutations. The *q* series of inhibitors of speltoidy is apparently such a series, at least with respect to its effect on square-headedness. Thus Muramatsu (1963) was able to show that nine doses of *q* had approximately the same effect as four *q* plus two *Q*, and that *Q* was therefore very probably a duplication or triplication of *q*. Deficiencies of *q* in lines with six doses of *q* and none of *Q*, on the other hand, are apparently very hard to detect.

(3) Genes that behave as though they were not triplicated or even duplicated. — Two subclasses may be distinguished here. The first includes loci that have become diploidized through loss or inactivation of one or both of the duplicates on other chromosomes. For example, McIntosh and Baker (1968) studied a line in which nullisomy for chromosome 7B resulted in albinism. This particular line must retain only a single locus (on 7B) of a series essential for chlorophyll production. Similarly, Natarajan et al.

(1958) found a strain of wheat which yielded a high frequency of albino mutations following radiation. Here again the strain concerned has presumably already become deficient for all but one of a series of triplicate loci, perhaps the same series as in McIntosh and Baker's line. Although other examples could be cited, it appears that few series of homoeo-alleles have undergone this kind of diploidization.

The second subclass is more important and consists of genes that have become diploidized through mutation rather than loss. Included here are the few major genes that distinguish the various types of hexaploid wheat: *Q*, which differentiates the aestivum wheats from the speltas; *C*, which distinguishes compactum from aestivum; *s*, which separates sphaerococcum from aestivum; and B_1, B_2, and *Hd*, which suppress awn development. Also belonging here is the gene on chromosome 5B that suppresses homoeologous pairing of chromosomes and thereby makes polyploid wheat diploid-like and stable.

All of the genes in this second subclass are active alleles, whose deficiency has a pronounced effect. They are all believed to be mutants which have occurred since the formation of polyploid wheat. All are easily mutated through simple loss, but such loss mutation only restores approximately the ancestral condition.

Q and B_1 are the only genes in this subclass whose normal alleles have been shown (Muramatsu 1963; Sears 1944, 1954) to have the same effect as the parent alleles but of reduced intensity. The pairing suppressor is very likely an antimorphic mutation, with an effect opposite to that of the gene from which it arose, and other genes of the group may well be of this type. Although only *Q* and the pairing suppressor are known to have normal alleles which are duplicated on the homoeologous chromosomes, the same may well be true of the other genes of the group.

NEATBY'S VIRESCENT

Of the three classes of genes just described, the first, triplicated genes with little or no increased effect of six doses over four, is of the greatest interest from an evolutionary point of view. Not only is this class by far the largest, but it is the class which is believed to have given rise through mutation to all the major genes acquired during the evolution of the polyploid wheats. Presumably there are other class-1 genes that are capable of mutating in useful ways.

Let us now examine a known mutation of a class-1 gene, Neatby's virescent. This gene is chosen not because of any evolutionary value it might have, but because it has been more thoroughly studied than any other and can perhaps give us some clues as to what to expect at other loci.

Neatby's virescent is a simple Mendelian recessive, v_1, located on the long arm of chromosome 3B (Sears 1956, Steinitz–Sears, 1963). Unlike most chlorophyll mutations in diploids, it is not a mere deficiency for a gene essential to chlorophyll production; it is an active gene with a pronounced dosage effect: one dose (the hemizygote) has no effect under normal conditions, two doses cause virescence, and three doses lead to extreme virescence or albinism.

The normal allele of v_1 proves to be a member of a triplicate series, with V_2 on chromosome 3A and V_3 on 3D (Sears 1957). That V_1, V_2, and V_3 are involved in chlorophyll production was established by combining deficiency for V_1 with nullisomy for chromosome 3A (Sears 1963). The resulting plants, carrying only V_3V_3, were virescent, though less severely so than Neatby's virescent itself. A spontaneous virescent mutation obtained and kindly supplied by Dr. J. G. Hermsen appears also to be deficient for V_1 and V_2 (Sears and Sears 1968), and is, as expected, less extreme than Neatby's virescent.

The mutant allele v_1 competes with its normal allele V_1 and also with V_2 and V_3 (Table 1). Thus $V_1v_1v_1$ is a less extreme virescent than v_1v_1. Tetrasomic 3A or 3D, with two extra doses of V_2 or V_3, is green though v_1v_1. On the other hand, monosomic-3A v_1v_1 is an extreme virescent, and mono-3D v_1v_1 is an embryo lethal. It should be noted that one dose of v_1 cancels the effect of between one and two doses of V. It has the same effect as deficiency for V but is more extreme.

Table 1

Expression of Neatby's virescent v_1 at various dosages of V_1, V_2, and V_3

Genotype			Phenotype
V_1v_1	V_2V_2	V_3V_3	Green
v_1v_1	V_2V_2	V_3V_3	Virescent
$V_1v_1v_1$	V_2V_2	V_3V_3	Less extreme virescent
v_1v_1	$V_2V_2V_2V_2$	V_3V_3	Green
v_1v_1	V_2V_2	$V_3V_3V_3V_3$	Green
v_1v_1	V_2	V_3V_3	More extreme virescent
v_1v_1	V_2V_2	V_3	Embryo lethal

OTHER CHLOROPHYLL MUTATIONS

Several other chlorophyll mutations are now available in hexaploid wheat. First may be mentioned another virescent, induced with ethyl methanesulfonate by Prabhakara Rao and Washington (unpublished) and analyzed by Washington (unpublished). This mutant closely resembles Neatby's virescent but is perhaps a little less extreme. It is located on chromosome 3A, and complementation tests indicate that it is a mutation of V_2 to v_2.

Four *chlorina* mutants have been studied. One of these, *chlorina*-1, induced with EMS by Shama Rao and Sears (1964), is located on the long arm of chromosome 7A (Sears and Sears 1968, and unpublished). Like the virescent mutants, it is an active gene. It causes a slight paleness when hemizygous, yellowness when homozygous, and a gold color when present in three doses. It too competes with its normal allele, for the heterozygote is more nearly normal than the hemizygote.

Driscoll's *chlorina* is a spontaneous mutant allelic to the one just described (Driscoll; personal communication). Its effect is considerably more extreme than that of *chlorina*-1.

Two other EMS-induced *chlorinas* were studied by Washington (unpublished). One proved to be located on chromosome 7B and the other on 7D. Complementation studies indicate that the loci concerned are duplicates of the one on 7A. Thus the *chlorinas* establish a second triplicate series affecting chlorophyll production.

The one other mutant, also EMS-induced, that Washington studied, was also a virescent, but of a different type. It tended to develop white sectors in some of the intermediate leaves. The gene concerned appeared not to be located on any of the group-3 chromosomes.

DISCUSSION

Although more mutants must clearly be studied, it seems fairly safe to say that the genes of hexaploid wheat concerned with chlorophyll production do not mutate at random. As mentioned before, there must be scores of chlorophyll loci in diploid wheat [Smith (1939) induced 23 different chlorophyll mutants in a modest experiment]. We may assume that all or nearly all of these many loci are present in triplicate in the hexaploid, yet all four *chlorina* mutants available involve only a single triplicate series, and the two virescents only one other such series. We may tentatively conclude that most of the chlorophyll genes of the hexaploid mutate at low rates or not at all.

Perhaps we ought to be surprised that any chlorophyll genes in hexaploid wheat can be mutated. The nullisomics show that there are no genes whose absence causes chlorophyll aberration. The mutated gene cannot simply fail to function, as in a deficiency; it must have a more drastic effect. What can happen to a gene that is more drastic than deletion?

Stern (1943) long ago advanced an explanation for the action of genes such as these, which reduce the effectiveness of their normal alleles. From his results with a series of *cubitus interruptus* alleles in *Drosophila*, he suggested that a locus may operate on a limited substrate and that a mutant allele may be very efficient at tying up substrate but very inefficient at converting the substrate to the next product in the sequence. Such an allele is then more effective than a deficiency or a null mutation, because there is such a reduced amount of substrate in the heterozygote that the normal allele cannot function at its full capacity. We may assume that in the extreme case the mutant allele would give rise to no product at all, or to a product which could not be utilized in the process concerned.

In trying to apply the limited-substrate theory to the chlorophyll mutants of hexaploid wheat, we must face the fact that the substrate itself is in all probability under genetic control. Deletion of one of the genes concerned should reduce the amount of substrate and thereby the amount of chlorophyll produced; but we know that there are no genes in hexaploid wheat whose deficiency results in a reduced amount of chlorophyll. It seems best to look elsewhere for an explanation of how a change in a gene can be more effective than a deficiency for that gene.

Now it is important to remember that, while many genes give rise to enzymes, they do not do so directly. The primary product of a gene is messenger RNA, and this, with the aid of a few ribosomes, gives rise to a polypeptide. In almost every case, the polypeptide, called a monomer,

must then combine with one or more other monomers, like or similar to itself, before it becomes an enzyme.

It is reasonable to assume that some at least of the triplicated chlorophyll genes give rise to monomers which are able to combine with each other at random, and thus that the final enzyme molecules are made up of monomers from the different genes in proportions which, for any particular molecule, are determined by chance. It may also be assumed that mutations occur spontaneously (or may be induced by EMS and other chemicals) which result in the production of a defective monomer, and that when such a defective monomer combines with a normal monomer or monomers, a defective enzyme molecule is the result (Sears 1969). Thus the mutant gene itself not only fails to produce normal enzyme, it also prevents a portion of the product of the duplicate loci from doing so. If too little normal enzyme is produced, there will be a reduction in the amount of chlorophyll produced.

With one of three loci homozygous for a defective monomer, the amount of defective enzyme produced will depend upon the number of monomers of which the completed enzyme molecule is composed: the more monomers included in each enzyme molecule, the greater the percentage of the latter with one or more defective monomers (Table 2). Since enzymes are known to be overproduced, sometimes greatly so, it may well be that only genes that give rise to enzymes formed from larger numbers of monomers can be mutated.

There are other circumstances that would render a triplicate series nonmutatable. Obviously the extent to which the enzyme concerned is overproduced would be a determining factor. If only five percent of the enzyme is required for normal function, as has been shown to be true in one instance in *Drosophila* (Glassman and Pinkerton 1960), no effect of rendering one locus defective would be seen even if the enzyme were a heptamer (Table 2).

It is probable that the monomers produced by some triplicate series are sufficiently changed in structure that, while still producing enzymes with the same function, each monomer combines preferentially or exclusively with other monomers from the same locus. Mutation of one locus to a

Table 2

Effect of complexity of enzyme on amount of defective enzyme produced when monomers from triplicate loci combine at random and one locus gives rise defective monomer

No. of monomers per enzyme molecule	Percent defective enzyme
2	55
3	70
4	80
5	87
6	91
7	94
8	96

defective allele can therefore only reduce the amount of enzyme produced by one-third, no more than is accomplished by deletion of the locus.

From the fact that chloroplasts contain DNA, it is reasonable to assume that much of the information required for the synthesis of chlorophyll is coded in chloroplast DNA rather than in the nuclear DNA. Many of the nuclear genes which affect chlorophyll production may then be regulators, which simply turn the chloroplast genes on and off. Since the polynucleotides produced by regulator genes are believed to act directly as monomers, rather than first combining to form polymers, there would be no opportunity for the product of a defective locus to tie up the product of duplicate loci and render them less effective. A defective locus could therefore be no more than equivalent to a deficiency.

It is probable that some enzymes tolerate substantial changes in structure without losing their effectiveness. Mutants would clearly be difficult to get for genes responsible for such enzymes.

Thus the defective-monomer hypothesis predicts that some, perhaps nearly all, of the triplicated genes involved in chlorophyll production in hexaploid wheat should be non-mutatable. With the limited data now available, this prediction appears to be satisfied.

There seems to be no good reason why different mutations at the same locus should not differ in their effectiveness. Monomers defective in different ways may well differ in the ease with which they combine with normal monomers. Also, some types of defect may render an enzyme molecule completely ineffective whereas other defects allow it to retain a portion of its normal function. Thus the fact that Driscoll's *chlorina* is clearly different from its allele *chlorina*-1 is in accord with the defective-monomer hypothesis.

A serious difficulty in the hypothesis lies in the results obtained from EMS treatment of diploid plants. At least some of the many chlorophyll genes of diploids must also operate through the production of multimeric enzymes. Following deletion of one member of a pair of such genes, the remaining normal gene provides enough monomers to form all the enzyme that is needed for normal activity; hence the deficiency mutant is recessive. If, however, one of the genes becomes changed in such a way that it gives rise to a defective monomer, this monomer should combine with normal monomers produced by the remaining normal allele of the heterozygote and give rise to defective enzyme molecules. With random union of defective and non-defective monomers, 75% of a dimeric enzyme would contain one or more defective components, and a level of 97% defective would be reached with only a pentameric enzyme (Table 3).

Therefore some EMS-induced mutants in diploids would be expected to be dominant. But not only have standard mutation experiments with barley and maize, in which an occasional dominant mutant could have been overlooked, failed to yield dominant chlorophyll mutations, but special maize experiments, that could not have failed to reveal any dominant mutants which had been induced, have failed to produce any (Ficsor and Neuffer, personal communication). However, if only a few of the chlorophyll genes actually operate through the production of enzymes rather than regulators, none of these few may involve enzymes which are of just the right degree of complexity to cause a locus producing defective monomers to be effective but not lethal when heterozygous. The virescent mutant v_1,

Table 3

Effect of complexity of enzyme on amount of defective enzyme produced when a diploid is heterozygous for a gene that gives rise to defective monomer

No. of monomers per enzyme molecule	Defective enzyme %
2	75
3	87
4	94
5	97

for example, would probably be a dominant lethal in a diploid, for V_1v_1 should be even more defective than $v_1v_1V_2V_2V_3$, which is already lethal (cf. Table 1).

Whatever the nature of the EMS-induced chlorophyll mutations — whether or not the mutant alleles give rise to defective monomers — it is clear that the chemical produces a kind of mutation in hexaploid wheat not obtainable in significant frequency with radiation. This kind of mutation appears to be equivalent to the simultaneous deletion of two or more members of a series of triplicate loci. By repeated use of radiation over several generations, Kao and Caldecott (1966) obtained chlorophyll defects in hexaploid wheat, but their mutants were presumably not simple in inheritance, and it is likely that there were associated aberrations due to deficiency for more than just the loci of the chlorophyll genes.

What is of course necessary for really progressive evolution is that genes change in such ways as to acquire new functions. Certainly genes have done this in the past, and polyploids have been suggested as organisms in which this kind of change ought to take place relatively frequently (Haldane 1932). This is because gene duplication provides loci which are no longer essential to the organism and are therefore free to mutate to alleles which are radically different, perhaps with a new function. The logic of this reasoning cannot be denied, but we must not assume that changes of the sort indicated occur in substantial frequency, even under the influence of chemical mutagens. Enzymes are extremely complicated, and it must surely be true that constructive changes in them must be very rare indeed, compared to inactivating changes.

Although it may be unrealistic to expect useful frequencies of chemically induced mutations to alleles with new functions, this is not to say that genes of evolutionary value may not be obtained. Since wheat is a cultivated plant, its evolution consists in its becoming more useful to man. This may take the direction of increased yield, wider adaptability, or improved food value. Most of the genes of wheat are apparently triplicated, but there is little reason to believe that this is the best level in every case. Reducing the dosage of some genes may lead to a more favorable balance. And because the chemical mutagens can give rise to mutations that are more drastic than the simple deficiencies caused by radiation, the chemicals may well prove to be the more useful mutagens.

SUMMARY

Several simply inherited virescent and *chlorina* mutations have appeared in hexaploid wheat, either spontaneously or following treatment by ethyl methanesulfonate. The virescent mutations involve triplicate loci on homoeologous chromosomes 3A, 3B, and 3D, and the *chlorinas* triplicate loci on 7A, 7B, and 7D. The mutant genes are not simple deficiencies but are active alleles, each of which competes with its normal allele and with the normal allele's duplicates on the other two homoeologues. Each mutant gene is thought to give rise to a defective polypeptide (monomer), which may combine with normal monomers from the normal allele and its duplicates to produce a defective multimeric enzyme molecule. In this way a mutant gene can be as effective, or more so, than simultaneous deficiency for two of the three loci concerned.

REFERENCES

Glassman, E. and Pinkerton, W. (1960): Complementation of the *maroon-like* eye color locus of *Drosophila melanogaster*. *Science* **131** 1810–1

Haldane, J. B. S. (1932): *The Causes of Evolution*. Longmans, Green and Co., London, 234 pp.

Kao, F. T. and Caldecott, R. S. (1966): Genetic effects of recurrent irradiation in diploid and polyploid *Triticum* species. *Genetics* **54** 845–58

Mac Key, J. (1954): Neutron and X-ray experiments in wheat and a revision of the speltoid problem. *Hereditas* **40** 65–180

McIntosh, R. A. and Baker, E. P. (1968): Cytogenetical studies in wheat. II. An analysis of chlorophyll abnormalities in hexaploid wheat. *Genet. Res. Cambr.* **12** 11–9

Morris, R. and Sears, E. R. (1967): The cytogenetics of wheat and its relatives. In *Wheat and Wheat Improvement* (K. S. Quisenberry and L. P. Reitz, eds., Amer. Soc. Agron.), 19–87

Muramatsu, M. (1963): Dosage effect of the *spelta* gene *q* of hexaploid wheat. *Genetics* **58** 469–82

Natarajan, A. T., Sikka, S. M. and Swaminathan, M. S. (1958): Polyploidy, radiosensitivity, and mutation frequency in wheats. *Proc. 2nd UN Int. Conf. Peaceful Uses Atom. Energy*, Geneva **27** 321–31

Sears, E. R. (1944): Cytogenetic studies with polyploid species of wheat. II. Additional chromosomal aberrations in *Triticum vulgare*. *Genetics* **29** 232–46

Sears, E. R. (1954): The aneuploids of common wheat. *Mo. Agr. Exp. Sta. Bul.* **572** 58

Sears, E. R. (1956): Neatby's virescent. *Wheat Inform. Serv.* **3** 5

Sears, E. R. (1957): Effect of chromosomes XII and XVI on the action of Neatby's virescent. *Wheat Inform. Serv.* **6** 1

Sears, E. R. (1963): Gene evolution in polyploid wheat. *Proc. XIth Int. Congr. Genet.* **1** 123–4

Sears, E. R. (1969): Wheat cytogenetics. *Ann. Rev. Genet.* **3** 451–68

Sears, L. M. S. and Sears, E. R. (1968): The mutants *chlorina*-1 and Hermsen's virescent. *Proc. 3rd. Int. Wheat Genet. Symp., Canberra, 1968. Austral. Acad. Sci.* 299–304

Shama Rao, H. K. and Sears, E. R. (1964): Chemical mutagenesis in *Triticum aestivum*. *Mut. Res.* **1** 387–99

Smith, L. (1939): Mutants and linkage studies in *Triticum monococcum* and *T. aegilopoides*. *Mo. Agr. Exp. Sta. Res. Bul.* **298** 26

Stadler, L. J. (1928a): Genetic effects of X-rays in maize. *Proc. Nat. Acad. Sci. U. S.* **14** 69–75

Stadler, L. J. (1928b): Mutations in barley induced by X-rays and radium. *Science* **68** 186–7

Stadler, L. J. (1929): Chromosome number and the mutation rate in *Avena* and *Triticum*. *Proc. Nat. Acad. Sci. U. S.* **15** 876–81

Steinitz-Sears, L. M. (1963): Cytogenetic studies bearing on the nature of the centromere. *Proc. XIth Int. Congr. Genet.* **1** 123
Stern, C. (1943): Gene action as studied by means of the effects of different doses and combinations of alleles. *Genetics* **28** 441–75

Note added in proof. — The unpublished works referred to in the section 'Other Chlorophyll Mutations' is now in print, as follows:

Pettigrew, R. and Driscoll, C. J. (1970): Cytogenetic studies of a chlorophyll mutant of hexaploid wheat. *Heredity* **25** 650–5.
Prabhakara Rao, M. V. and Washington, W. J. (1969): EMS-induced chlorophyll defective sectors in hexaploid wheat. *Proc. Symp. on Radiations and Radiomimetic Substances in Mutation Breeding (Bombay)* 228–33.
Washington, W. J. (1971): Homoallelism in *Triticum aestivum*. *Canad. J. Genet. Cytol.* **13** 169–72.
Washington, W. J. and Sears, E. R. (1970): Ethyl methanesulfonate-induced chlorophyll mutations in *Triticum aestivum*. *Canad. J. Genet. Cytol.* **12** 851–9.

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ON THE DEVELOPMENT OF INCOMPATIBILITY AND SEX SYSTEMS IN HIGHER PLANTS AND THEIR EVOLUTIVE MEANING

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I. INTRODUCTION

It is generally considered (Crowe 1964) that the evolution of incompatibility systems proceeds according to the following rules:

(1) One locus gives two loci (by duplication)
(2) Many alleles give few (e.g. two) alleles
(3) Gametophytic control shifts to sporophytic control
(4) Intergametic incompatibility becomes style-pollen incompatiblity
(5) Self-incompatibility gives dioecy or gynodioecy
(6) Self-incompatibility gives self-compatibility.

These rules lead to a genealogy of the incompatibility systems in angiosperms which suits a monophyletic origin; one must suppose, at the beginning, a theoretical phylum with an intergametic incompatibility with many alleles at one locus and gametophytic control. The *Theobroma* type derives from the theoretical phylum by a switch from gametophytic to sporophytic control of both sexes; the *Oenothera* type,which is the most common, as far as we know derives from the transfer of the production, of the incompatibility substance from the female gamete to the style. The latter gives the *Physalis* type by duplication of an incompatibility locus and, again by a shift to the sporophytic control (pollen only) the *Parthenium* type. The loss of all the alleles but two gives the dimorphism of *Primula* and, from there, all the heteromorphic systems, including those with sexual specialization.

I would like to examine the preceding six 'rules' or points.

It is not necessary to go into details concerning point one. We do not see any way by which the genes of the modern species could have appeared if not by a sequence of events such as duplication; this remains true, *a fortiori*, for two loci involved in the same incompatibility system, therefore having probably similar roles.

Neither will I discuss point three. The anteriority of gametophytic systems seems to be well demonstrated (Pandey 1960).

The selective advantages of the shift of the site of expression of the incompatibility function from the female gamete to the style (point four) are obvious. Indeed, these advantages are so important that this shift must have occurred as soon as the female gamete was wrapped in somatic tissue, before the appearance of a style. It probably occurred in some angiosperms but others must have inherited it from ancestors with ovules protected in a less sophisticated way. However, it seems somewhat illogical to put, at the origin of the incompatibility of the angiosperms, an hypothetic organism which is self-compatible. In this supposed ancestor, the

homozygosity of the incompatibility locus is excluded, not self-fertilization. What seems illogical to me, let me insist on this fact, is by no means to suppose that such an organism exists or has existed, but to admit that it is (alone) at the root of the whole affair.

Point six is, undoubtedly, the most important and it is the most firmly established. Incompatibility is obviously a specific function which may be lost by mutation. If the incompatible plant is isolated either by distance or absence of a pollen vector, the mutated gene is efficiently screened and rapidly fixed. The shift to the autogamous state is then complete: the species has been preserved by the incompatibility against the inbreeding hazards; not one of the secondary characters which, enhances outbreeding without compelling to it, has been selected. Sugar beet breeders (Desprez 1960) are familiar with these forms, in which it is practically impossible to prevent selfing, which is followed by a dramatic loss of vigour. This fact adds some weight to the interpretation by D. Lewis (1956) of the origin of *Passiflora suberosa*, a self-compatible species with small dull flowers from a genus known for its adaptation to the entomophilous pollination. The two remaining points (two and five) must be examined in a more detailed manner.

II. THE EVOLUTION OF ALLELE NUMBER

The multiallelic systems anteriority hypothesis is based upon two arguments.

The first one refers to the species the incompatibility system of which is connected with heterostyly; the allele number is then, generally, two per locus. These species are sparsely distributed in families in which most of the other species are homomorphic. Among these, some, at least, have multiallelic systems. The monophyletic and exclusively diverging evolution of angiosperms being admitted, it means that the two-allelic systems evolved recently and repeatedly from the multiallelic ones.

Since one is looking for a proof of a monophyletic and diverging evolution of the incompatibility systems in angiosperms, it seems difficult to use this first argument, which hypothetically excludes that the general evolution of the group might be reticulate and polyphyletic. Let us add that systematicists seem, as far as I know, to have been frequently obliged to give up the idea of a unique origin for each one of their units of classification.

The second argument results from the fact that the loss of the incompatibility function has been frequently observed, while the apparition of new alleles, even after mutagenesis, has not been observed. This second argument is worth more consideration but is subject to the following objections.

(A) The argument applies to the mutations of any known gene. As far as I know, all the mutations which have been observed are more or less complete losses of functions. This may mean either that the events which lead to the birth of new functions are too rare to be observed, or that they do not occur under the conditions of observation.

The two reasons must play their part and we have no reason to choose one of them for a given function; in the present state of our knowledge on the relations between the structure and the function of a protein, this would be especially risky.

(B) However, the setting of a new functional *S* allele in a population is, all things being equal, less unlikely than for a new functional allele of another gene. In fact, this last event implies: (1) the random formation of a new functional protein molecule; (2) an environment of the organism in which this new protein is more useful than the one specified by the original gene or in which it co-operates with the original gene.

The first condition also holds for the new *S* allele. On the other hand, the second one is always fulfilled, since the new allele replicates more than the already existing ones and thus it is functional, as long as its frequency is inferior to the equilibrium frequency.

(C) This difference between *S* and other genes is, indeed, so conspicuous that one may wonder how it happens that systems with so few alleles (such as the plus-minus one of the Ascomycetes) exist.

It seems that in a population with incompatibility alleles the number of these may only increase, without regard to the selective value of this increase for the population as a whole. Consequently, the future of a new functional allele is not determined by the choice of one or another member of the population but by the advantage that the population, as a whole, will gain from it over the other populations (group selection).

The question, therefore, is to know if a population with a high number of alleles is at a selective premium when compared with a population with fewer number. The advantage of the self-incompatibility is to force outbreeding; this leads to heterozygotes and these, by segregation, generally yield, if the gametes differ in more than one locus, *recombined* products able to put together the selective superiorities of both parents. The increase of the allele number leads to an increase in the number of compatibility groups, which means the number of plants with which a given plant is compatible; in a population of 1000 plants, this is about 500 for two alleles and two equiprobable groups; it is near to 1000 for 40 or 50 alleles of the *Nicotiana* or *Oenothera* type. One may think that, for recombinational purposes only, the latter system is not very superior to the first. There is only loss of one time generation in the formation of an optimum genotype if the qualities to be put together exist, in the first system, in plants belonging to the same group. The superiority of the second system becomes evident, if the possible recombinations are not the unique advantage of the formation of heterozygotes and if the heterozygosity 'per se' (even in a unique locus, where the effects of the two alleles may then add) brings with itself an advantage. Consequently, the average heterozygosity of the population is higher. This, however, supposes that the biological cycle phase which mainly withstands the selective pressure can be heterozygous, which means that the homologous genes exist in every cell unit, a condition which is fulfilled in dikaryotic or diploid cells.

There is, then, no surprise that multiallelic systems are found in *Basidiomycetes* (Whitehouse 1949). Therefore, if there has been during the course of evolution one unique moment during which multiallelic systems appeared, one may think that it was following the extension of the phases with two (or more) homologous loci rather than after the appearance of the angiosperms, undoubtedly far more recent. One may also think that the well known plus-minus system of the *Ascomycetes* is a very honourable putative ancestor for the multiallelic as well as for the other diallelic

systems. Of course, there is no objection to the idea that the transformation occurred more than once, each time, for instance, when the syncytium, with its disorderly distributed nuclei, has been replaced by a dikaryotic or diploid cell.

On the other hand, it becomes difficult to believe that the angiosperms have inherited from a unique ancestor a unique system and this, in turn, causes us to believe that they have more than one ancestor. Most of the angiosperms would have originated from multiallelic ancestors; others, less numerous because they were not so well-adapted to the angiosperm situation, would have been provided with a two-allelic system. The two categories of systems would have been distributed among the groups as were other characters; sympetaly, for instance, following the reticulations of its evolution.

(D) Finally, even if one can see how a multiallelic system can break down and give place to a unique gene of compatibility, one sees with much more difficulty how certain functional alleles disappear while others persist. Whatever may be the modification of the primitive gametophytic system with individual stylar action, either dominance or sporophytic control, *as long as the incompatibility function may work*, a rare allele tends to reproduce itself more than the others and this increases its frequency each time it becomes less than the equilibrium frequency. A possible way would be the spatial isolation of a genotype such as S_1S_2 *together* with the occurrence of a mutation rendering, say, S_1 dominant on S_2. Such a mutation would be selected against in normal conditions, as bringing about a partial breakdown of incompatibility but would lead here to a diallelic system with one self-compatible (S_1 S_2) and one self-incompatible (S_2S_2) genotype. Since, contrary to the mutation of functional to compatibility alleles, such a modification of dominance does not seem to have been observed, one may think that this set of circumstances represents a very rare event, not more probable, *a priori*, than the appearance of a new diallelic system.

However, my purpose is not to exclude any of the two possibilities but rather to exclude the possibility that one of the two occurred alone; my feeling is that the two occurred before as well as after the appearance of angiosperms.

III. THE EVOLUTION OF SEX

It seems logical to consider first that an organism with separated sexes stems from a hermaphroditic ancestor by loss of one sexual function by certain individuals, and of the other function by other individuals. Such a conception meets two objections.

(1) Sterility is, by itself, a drawback which is always selected against if it does not bring a selective advantage; for a sterility induced by a recessive gene, such an advantage must lead to the production of more than twice as many efficient gametes of the other sex which Darlington (1958) considers too unlikely to happen. In the case of a sterility induced by cytoplasmic information, either alone or in connection with a genic system, it does not seem that one may expect an equilibrium to establish itself as long as the population remains panmictic (Valdeyron et. al. 1970).

(2) Up to now, there is no available record of cases where a vegetal phylum exhibits a spontaneous evolution from hermaphroditism to dioecy through the loss of one of the sexual functions.

For these reasons, one has aimed to develop theories deriving directly from the known systems of sex separation, specially gynodioecy and dioecy, from incompatibility systems.

Bateman (1952) has suggested, as a possible origin for gynodioecy, a diallelic system with dominance of S_1 on S_2, in the style and gametophytic control of pollen. There are, then, two genotypes, S_1S_2 self-compatible (since fertilizable by S_2 and giving $\frac{1}{2} S_1S_2 + \frac{1}{2} S_2S_2$) and S_2S_2 self-incompatible (fertilized by S_1 and giving S_1S_2). At the equilibrium, the frequency of S_1S_2 is such that

$$\alpha = \frac{1}{2}\alpha + 1 - \alpha$$

which gives $\alpha = 2/3$, so that one has $2S_1S_2 : 1S_2S_2$.

Once this system is established, the male-sterility recessive genes tightly linked to S_2 and the recessive lethal genes tightly linked to S_1 are not selected against; the male-sterility of S_2S_2 makes useless the incompatibility function, which then disappears; there remain S_1 and S_2 gametes fertilizing S_1S_2 to give $\frac{2}{3} S_1S_2 + \frac{1}{3} S_2S_2$ (S_1S_1 being lethal) and S_2S_2 to give $\frac{1}{2} S_1S_2 + \frac{1}{2} S_2S_2$. At equilibrium,

$$\alpha = \frac{2}{3}\alpha + \frac{1}{2}(1 - \alpha)$$

from where $\alpha = \frac{3}{5}(3S_1S_2 : 2S_2S_2)$.

Another model, based on a gametophytic control of the female gametes and on a sporophytic control with dominance of the male gamete, has been suggested by Crowe (1964).

It seems to me that it is difficult to accept these models for the following reasons.

(1) They imply the occurrence of very complex and improbable events. Bateman's model (1952) involves at its origin the same situation as the one discussed in the preceding section; Crowe's model involves a very improbable and disadvantageous step backward to an expression of the incompatibility gene at the fertilized egg-cell level; of course, this argument alone would not be sufficient.

(2) The numerical segregations anticipated in these models do not seem to have been observed, either in bulk, or in individual progenies; on the contrary very different segregations have been observed with *Thymus vulgaris* (Assouad and Dommée 1970).

(3) Taking into account the fact that one deals with outbreeding mechanisms involving functional, pollen vectors, one does not see what selective

advantage the population may gain from transformations which always imply a partial breakdown of incompatibility.

(4) There are few actual situations to compare with these models. The appearance of homostyles in *Primula vulgaris* (Crosby 1949) might be an interesting exception; I am also deeply impressed by the pollen size dimorphism in gynodioecious *Silene maritimum* (Crowe 1964).

(5) Lastly and above all, the building of complex models is only justified if one considers it unlikely that a sterility gene for one sex brings about a better fertility of the other. On the other hand, if one admits that the same chain of substrates is used by the plant to manufacture gametes of both sexes (which is not unplausible and which would be highly desirable, but probably rather difficult, to be verified) such a coincidence may normally be supposed. Observations on *Asparagus officinalis* (Thevenin 1967a, b) and on *Thymus vulgaris* (Assouad 1968) seem to prove that this supposition might be sound. Simpler models may then be constructed without difficulty (Valdeyron 1967).

The model which appeals the most to me (Valdeyron 1968) may be used to explain the evolution from incompatibility to dioecy. Starting from a hermaphroditic self-incompatible species, there is loss of incompatibility by fixation of the compatibility allele *Sf* following the mechanical prevention of cross-fertilization. This loss brings about a strong inbreeding depression, thus rendering selectively desirable the return to outbreeding. Nonetheless, a sterility mutation for one sex is selected against, unless it involves a doubling of the numbers of efficient gametes produced by the other sex. There are, of course, more chances for this to occur with male sterility and female fertility simply because the probability for a pollen grain to be efficient is far smaller than the corresponding probability for the ovule.

We thus may imagine that a common substrate *Pc*, synthesized by a chain of reactions RC_1, RC_2 ... be used in the hermaphrodite in two chains of reactions RM_1, RM_2 ... and RF_1, RF_2 ... in order to elaborate the metabolites P_m and P_f, necessary for the production of male and female gametes. A mutation in RM_2, for instance, has no other consequence than the male sterility; on the other hand, the interruption of RM_1 will let *Pc* be totally available for an increase in the female fertility. In an anemophilous plant, in which a hypertelic selection of appropriate modifiers has brought about an exaggerated pollen production at the expense of the ovule production, this secondary effect might be very important.

The frequency of hermaphrodites is linked to the superiority of female selective value of male-steriles, ω, by the simple formula

$$\alpha = \frac{1}{2\left(1 - \frac{1}{\omega}\right)},$$

which, since α must be such as $0 < \alpha < 1$, implies that $\omega > 2$, as already said.

Now, such a situation being set, if a mutation occurs which brings about a lowering of the female selective value of the hermaphrodite, it may be expected that this mutation be selected against: ω increasing, α decreases and there is a risk of shortage of pollen for the population. It is probably

what actually happens when the quantity of pollen may be considered as a limiting factor, as it is probably in entomophilous species: many gynodioic species belong to families known for their adaptation to insect pollination (e.g. *Labiatae*).

When the pollen production is, on the other hand, more than sufficient, it seems that there is no drawback to the hermaphrodite's becoming progressively female-sterile, its frequency becoming correlatively near to 1/2 (as ω increases). At the limit, the population becomes dioic.

Of course, the genes for female sterility must express themselves in male-fertile individuals only. This may be obtained by the chromosomal linkage of the proper allele, which must then be dominant, with the gene of which the recessive allele induces male sterility when homozygous. This is the situation discovered by Westergaard (1958) in *Melandrium*. The dominant female suppressor Su^F and the M_1 gene of Westergaard, tightly linked by some crossing-over suppressor, then prime the evolution of a *Y*-chromosome.

However, the linkage between male fertility and female sterility may be obtained by another way. Let us return to the preceding metabolic model and consider a hermaphroditic anemophilous plant in which the hypertelic development of the pollen production has brought about an exaggerated depletion of the common substrate *Pc*, which is no longer available for the production in sufficient quantity of the metabolite *Mf* necessary for the female function. One may imagine that a set of emergency circuits CF_1, CF_2, CF_3 ... permits the plant, thanks to the selection of modifiers, to complete *Mf* production from substrates other than *Pc*. A loss of function occurring in one of these circuits will decrease the female fertility only inasmuch as RM_1 will be in function, that is to say if there is no male sterility.

It seems self-evident that the well-known system described by Jones (1934), giving rise to a dioecious maize, follows a determinism of this type.

The case is probably the same in *Asparagus officinalis*. This species is considered as dioic (Thevenin 1967a, b). In reality, if the populations observed comprise effectively a complete male sterile form, making up the female individuals, the individuals bearing staminate flowers can never be considered as definitively male. It seems almost always possible, sooner or later, to obtain berries, if necessary by placing plants in particularly favourable growth conditions. There is no sharp environment independent limit between ordinary male individuals and the hermaphrodites known to occur with a frequency of 1–2% in most populations. When trying to select these hermaphrodites, there is no difficulty in eliminating male sterility; self-fertilization gives rise to 1 male-sterile for 3 male-fertile of which one breeds true for male fertility. Female fertility, on the other hand, gives rise to sharp segregation; the speed of the fixation of this female fertility varies according to the individuals on which selection has been started. One can suppose, therefore, that the male fertility is, in this system, determined by a gene *F*, the recessive allele of which brings about the male-sterility while the female fertility depends on a large number of genes, independent and of more or less additive effect which express themselves only in the presence of *F*. It should be noted that in order to confirm the point stated above, the hermaphrodites producing the largest amount of

berries still produce some hundred times fewer berries than the average female. The gene *f* seems, therefore, owing to its presence, actually to increase female fertility (this suffices to give a high value to *f*, resulting in a value very close to 1/2 for α, just as in the *Ficus carica*; Valdeyron 1967).

The occurrence of hermaphrodites in small quantities in otherwise dioecious populations is known in several species (*Ceratina siliqua*, *Populus alba*, etc.), a fact which suggests that situations of the preceding type are not exceptional. One of the remarkable points with *Asparagus*, however, is that the *officinalis* situation might give the example, which was lacking, of a gynodioecious link in a continuous chain going from hermaphroditism, in *A. albus*, up to strict dioecism, in *A. acutifolius*. *A. officinalis* seems to have, as *Ficus carica*, a system which is nothing else than gynodioecism, which constitutes, here, an intermediate stage on the way to dioecysm. We know (Westergaard 1958) how, starting from simple determinism, *Ecballium elaterium* evolves toward the formation of a more and more differentiated *Y*-chromosome.

Must we conclude, from what has been said above that dioecism has always that origin? I do not think so. *Primula vulgaris* homostyly gives arguments for a direct evolution from incompatibility to gynodioecism; in the same manner, the model suggested by Crowe (1964) for the origin of dioecism is likely and rests on real situations. If, a *Primula* type system, with two alleles with pollen sporophytic determination and dominance in pollen and style, gives place to individual action in the gametes of one sex, the efficient gametes of that sex come from the homozygote genotype. The genes for sterility of useless gametes are not selected against and they settle. The dioecious heterostyled species in which the male is long-styled (*Rhamnus lanceolatus*) or short-styled (*Aegiphila obdurata*) seem to confirm the soundness of this hypothesis.

IV. CONCLUSION

From the three points discussed the same conclusion has been arrived at; that is, that the same system may have many origins. It is my impression that this conclusion eventually will apply to all biological mechanisms and, especially, to the ones used as a basis for classification. Angiospermy, in this sense, would not be a situation; it would be a way in which plants could explore a given possibility of evolution. This way may have been taken by more than one phylum. If this view is correct, each successful evolutionary step (or the type which produces adaptive radiation and, as a by-product, the divisions of taxonomy) would be the result of the cooperation of many organisms. As Teilhard de Chardin pointed out for anthropoids, divergence always led to extinction. Recombination and any possible way of re-assembling the potentialities of different, even if similar organisms would be, conversely, the true preparation for the evolutionary future.

REFERENCES

Assouad, W. (1968): *Etude de la répartition des formes sexuelles chez le thym, Thymus vulgaris* L. Ronéotypé, Montpellier, 22 pp.

Assouad, W. and Dommée, B. (1970): In preparation

Bateman, A. J. (1952): Self-incompatibility systems in angiosperms. I. Theory. *Heredity (London)* **6** 285–310

Crosby, J. L. (1949): Selection of an unfavourable gene complex. *Evolution (Lancaster)* **3** 212–30

Crowe, L. C. (1964): The evolution of outbreeding in plants. *Heredity (London)* **19** 435–57

Darlington, C. E. (1958): *Evolution of Genetic Systems*. 2nd ed., London, Oliver and Boyd, 265 pp.

Desprez, M. (1960): Personal communication

Jones, D. F. (1934): Unisexual maize plants and their bearing on sex differentiation in other plants and animals. *Genetics (New York)* **19** 552–67

Lewis, D. (1956): Genetics and plant breeding. *Brookhaven Sym. Biol.*, **9** 89–100

Pandey, K. K. (1960): Evolution of gametophytic and sporophytic systems of self-incompatibility in angiosperms. *Evolution (Lancaster)* **14** 98–115

Thevenin, L. (1967a): Contribution à l'étude de la sexualité et de l'haploïdie chez l'asperge cultivée, *Asparagus officinalis* L. Thèse, Ronéotypé, Montpellier, 226 pp.

Thevenin, L. (1967b): Les problèmes d'amélioration chez *Asparagus officinalis* L. I. Biologie et améloiration. *Annales de l'Amel. des Pl. (Paris)* **17** 33–66

Valdeyron, G. (1967): Sur le système génétique du figuier, *Ficus carica* L. Essai d'interprétation évolutive. *Annales de l'Inst. Nat. Agron. (Paris)* **5** 1–167

Valdeyron, G. (1968): On a possible pathway of evolution from hermaphroditism towards sex separation in plants. Abstr. in *Proc. Intern. Congr. Genetics (Tokyo)*

Valdeyron, G., Assouad, W. and Dommée, B. (1970): Coexistence des déterminismes genique et cytoplasmique de la stérilité-mâle. Recherche d'une hypothèse explicative. Symposium sur la sterilité mâle en horticulture. *Eucarpia (Versailles)*. Sous presse

Westergaard, M. (1958): The mechanism of sex determination in dioecious flowering plants. *Advances in Genetics (New York)* **9** 217–81

Whitehouse, H. L. K. (1949): Multiple allelomorph heterothallism in the fungi. *New Phyt. (Oxford)* **48** 212–44

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EVOLUTION OF GARDEN *CANNAS*

by

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In comparison to crop plants, there exists a relatively better understanding of the origin and evolution of ornamentals because in them the transformation from wild to the cultivated condition has taken place in historical time and more often the intervening events are reasonably well documented and stages often well preserved. During domestication, most favourable conditions exist for the survival of the deviating types which may normally get eliminated in nature because of lack of selective value. This is particularly true of *Canna* in which all deviants can be preserved clonally even though they may carry a high degree of heterozygosity and reproductive sterility. The purpose of the present study is to bring out such events, and to present a coherent picture of the origin and evolution of the garden cannas.

ANCESTORS

Out of about 51 species belonging to the genus *Canna*, only five, *C. glauca*, *C. indica*, *C. iridiflora*, *C. warscwiczii* and *C. flaccida*, constitute what may be called as elemental, basal or ancestral species, which have been responsible for the origin of the garden cannas now included under two artificial or synthetic collective species of hybrid origin, *C.* ? *generalis* and *C.* ? *orchiodes* (Khoshoo and Mukherjee 1970b). All the five species belong to the subgenus *Eucanna*, Section *Trialatae* and distributed in four subsections *Glaucae*, *Coccineae* (or *Indicae*), *Elatae* and *Achirida*. An important character shared by all of them is the presence of 3 petal-like staminodia, one lip and one standard, all of which together form the showy part of the canna flower.

The five elemental species are indigenous to the West Indies and tropical-subtropical Americas, but ornamental cannas were developed from them under altogether different environmental conditions of temperate Europe, particularly in France and Italy. From their indigenous habitats, they were introduced in Europe beginning with *C. indica* (1 in Plate I) in 1596 by Gerard, followed by *C. glauca* whose exact year of introduction is not known but it was illustrated by Piso in 1648 (Baker 1893b). Next came *C. flaccida* from the South Atlantic States of the USA in 1788, *C. iridiflora* from the Andes of Peru brought by Lambert in 1816 and finally *C. warscwiczii* from Costa Rica by Von Warscwicz in 1849 (Anonymous 1893; Baker 1893a).

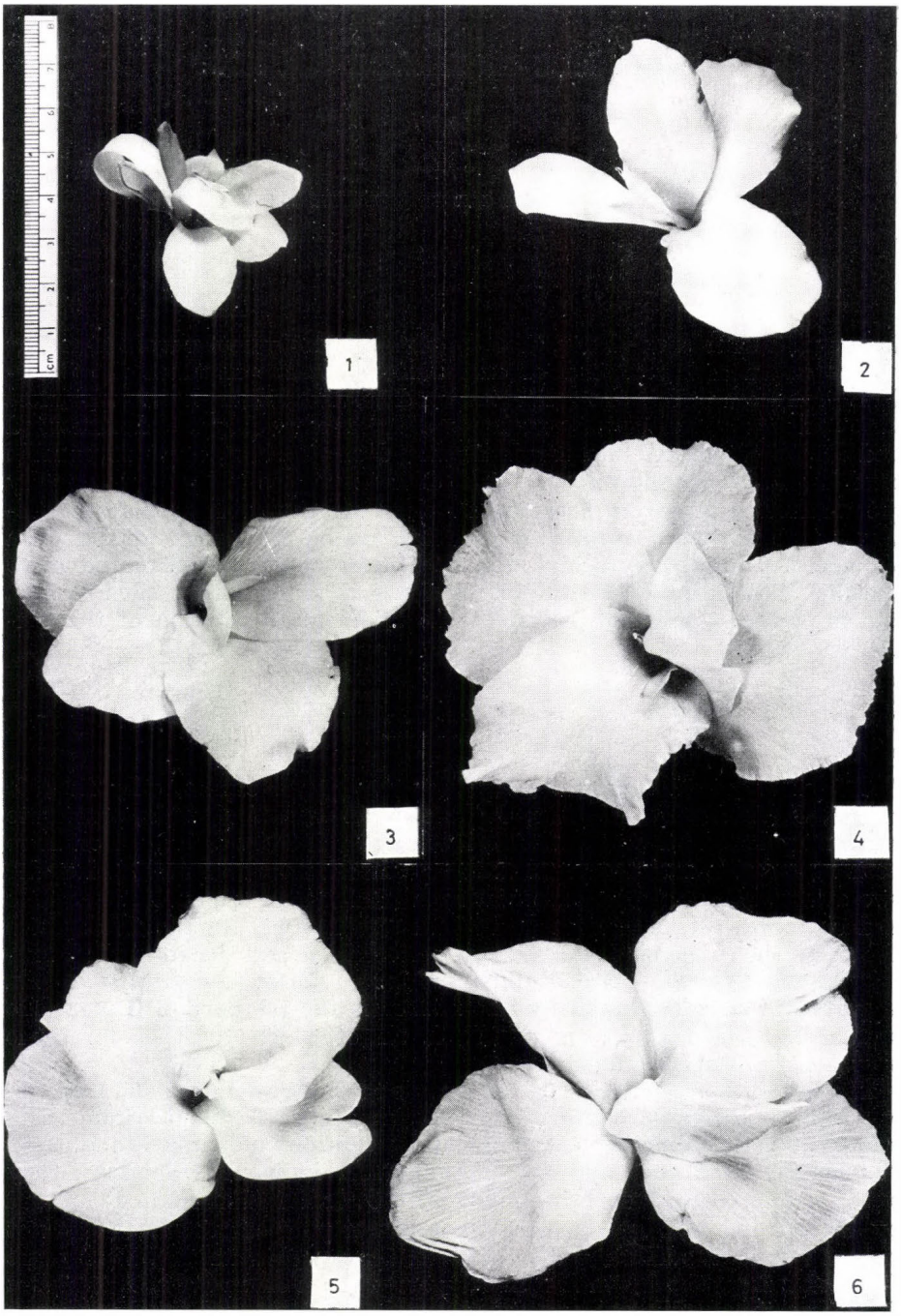

Plate I. Range in flower size in some elemental species and diploid and triploid cultivars; 1. *C. indica* (2x) × 2/3; 2. *C. glauca* × *indica* (2x) × 2/3; 3. *C.* x *generalis* 'Rajaji' (2x) × 1/2; 4. *C* x *orchiodes* 'Bharat' (asynaptic 2x) × 1/2; 5. *C.* x *generalis* 'Plume' (autotriploid) × 1/2; 6. *C.* x *orchiodes* 'Wintzer's Colossol' (segmental allotriploid) × 1/3

Most of these species were cultivated with a view to impart tropical effect to the European gardens. They were often tall (90–500 cm), leafy, long-jointed with comparatively small flowers arranged in simple lax racemes generally with only a few flowers.

Most of the species are structurally predisposed for self-pollination because stamen and stigma are situated at about the same level and pollen is deposited very near or on the stigma itself. Although flowers are visited by insects, the species are predominantly self-pollinated and self-fertile. Whether this represents the original condition characteristic of the species in their native habitats, or is an adaptation to the temperate regions of Europe, is not known.

All the five species are diploids ($2n = 18$) with 9 bivalents and 17·08 to 17·40 chiasmata per cell, followed by regular meiosis and normal pollen and seed fertility.

ANNEÉ AND EHMANN CANNAS

M. Anneé of France was the principal cultivator of cannas from 1840 to 1865 and was the first to raise a canna hybrid, *C. glauca* x *C. indica* (2 in Plate I) in 1848 which was named as *C.* x *annaei*. This canna was about 360–390 cm in height with long internodes; large leaves erect peduncles with many racemes with flowers salmon-yellow, orange-yellow or tinged with rose-red that were about the same size as in *C. indica*. From this stock arose a large number of forms grown primarily for their foliage which was from green to red-purple. These cannas were so popular for decorative purpose that more than 20,000 tufts were planted in parks and public squares in Paris in 1861 (Baker 1893b).

Ehmann cannas, *C.* x *ehmanni*, were also hybrids (*C. iridiflora* x *C. warscwiczii*) originally raised by M. Anneé in 1863 in Paris but distributed by M. Kolb in Munich. These were of medium height (180 cm), rather colourful, having somewhat pendulous crimson flowers like the female parent and with a short tube resembling *C. warscwiczii*. They were distinct from the typical species in size, form and colour.

CROZY, GLADIOLUS OR FRENCH DWARF CANNAS

Although Anneé and Ehmann cannas were a distinct improvement over the elemental species, they were still small-flowered and major improvement came around 1868 when Crozy cannas were released. This group is rather polyphyletic in origin involving principally four distinct botanical species, namely *C. indica*, *C. glauca*, *C. warscwiczii* and *C. iridiflora*. Essentially Crozy cannas were developed from hybrids between *C.* x *annaei* and *C.* x *ehmanni* and their backcrosses to parents in several permutations and combinations. *C.* x *ehmanni* played an important role in the origin of this group and this species together with its backcrosses to *C. warscwiczii* resulted in red flowered types, while yellow types emanated from crosses between *C.* x *ehmanni* and *C. glauca*, and (*C. warscwiczii* x *C. indica* 'Aureo-picta') x *C. indica*. Further intercrossing within and between

yellow and red types followed by inbreeding and judicious selection resulted in Crozy hybrids. In a short time Crozy raised about 180–200 hybrids.

Crozy cannas selected for their hardy characters are, therefore, easy to culture in open in Europe. They are dwarf in habit, never more than 120 cm, foliage is green or bronze and spikes are stiff and floriferous loaded with very showy large flowers (11–15 cm) with broad staminodia of varied, brilliant and glowing colours (3, 5 in Plate I). With this change, canna became an effective ornamental and nearly 92% of cultivars belong to this group.

Several French, British, German and American breeders have contributed materially to the development of this group, but the principal architect has been M. Crozy of France, who, on this account, was known in France as 'Papa Canna'. Crozy cannas were introduced in India around 1889 and many varieties were raised by cross-breeding (Percy Lancaster 1967).

Most of the Crozy cannas are free flowering. This character emanates from stigma being 0·5–1·9 cm higher than the stamen and no seed is set unless pollen is deposited on the stigma either by hand or after cross-pollination by insects or sunbirds. The greater this difference, the more a cultivar is free flowering, because of lesser chances of seeding. However, like the parental species all these are self-compatible. This is a significant, change from the inbreeding in elemental species to outbreeding in Crozy cannas.

In 80% of cultivars meiosis is perfectly normal with 9 bivalents with chiasma frequency lower (15·65–17·50 per cell) than the elemental species. In 3% of cultivars there is an interchange multiple of 4 and 7 bivalents which is also found in the hybrid *C. glauca* x *C. indica*. The interchange complex generally forms a non-disjunctional ring. The cultivars showing interchanges have colourful flowers which in one case is accompanied by pygmy habit (Khoshoo and Mukherjee 1970a).

Seed set in Crozy cannas is poorer after self than after cross-pollination. The reduced seed set after self-pollination may be the result of accumulation of sterility and other factors accompanying selfing in the cultivars.

From the above data it appears that the elemental species are sufficiently close genetically with almost free exchange of genes. However, they are also reasonably differentiated and there are genic and/or minute cryptic chromosomal differences between them which may account for the lower chiasma frequency and fertility. The latter may be the result of disharmonious combinations arising from incompletely homologous chromosomes.

Earlier Crozy cannas were diploid (3 in Plate I) but soon with increased emphasis on the durability of blooms due to thicker flower parts, types that were triploid appear to have been preferred (5 in Plate I). The triploids, which constitute about 9% of cultivars, had rather larger flowers with intense colours. With the existence of a close chromosomal homology between the parental types, triploids were autotriploid ($2n = 27$) in character with, on the average, 7·32–8·24 trivalents per cell out of the maximum 9 expected. One interchange heterozygote was also found among the Crozy triploids. This had associations of 5–6 chromosomes in the form of rings and chains (Khoshoo and Mukherjee 1970a).

It is evident from the foregoing account that hybridization has played

a dominant and decisive role in the origin of Crozy cannas. This has been rendered possible by the lack of efficient genetic barriers between the parental species coupled with a good deal of recombination associated with reasonably high fertility in the hybrid segregates. Hybridization has been important in two ways. Firstly, as is clear from the work of Honing (1923) and our own, genetical differences in flowers between species like *C. indica* are controlled by at least 23 genes (Khoshoo and Mukherjee 1970b). These involve colour genes proper, their intensifiers, inhibitors, lethals, etc. From recombination of such a wide range of genes segregating simultaneously and involving a complex segregation, a wide array of genotypes with new colours and colour combinations are expected to arise. Furthermore, apart from flower colour, similar segregation is expected to arise in plant height, blooming period, flower size, texture of staminodia, etc. Under the circumstances recovery of parental types is difficult and new character combinations with new phenotypes are expected to arise.

Recombination between the two basic colours red and yellow in the genus is of particular interest. The red colour is an anthocyanin and is sap soluble, while yellow is a plastid pigment and structurally different from the former. There is no direct interaction between red and yellow but in absence of red anthocyanin, plastid pigment is responsible for flower colour. However, in the presence of red, plastid pigment acts as a background colour. Although, red is monogenic dominant, its intensity, flaking, etc. are controlled by several genes whose ratios are disturbed by linkage, lethals, etc. Thus besides segregation in other characters, 11 shades of red colour were observed under the influence of different shades of yellow (Honing 1923; Khoshoo and Mukherjee 1970b).

Much genetic diversity has been released due to recombination, which probably also enabled release of latent mutations in the new genetic background, and probably there was an increase in mutation rate in the hybrid condition, perhaps as a result of elimination of mutation suppressors affecting red colour and changes in cell pH and emergence of a great variety of colours from the original yellow and red.

Secondly, hybridization has been responsible for transgressive segregation particularly in the length and breadth of leaves and staminodia. This is clear from the data of Honing (Tables 1, 2, 17 and 18 in his paper of 1923) on the F_1 and F_2 progeny of *C. indica* x *C. glauca*. Furthermore, what is important, in the backcrosses to *C. glauca*, the length of staminodia registered further increase in the mean. In such cases of transgression there is perhaps an accumulation of dominant favourable genes and/or co-adapted heterozygous combinations which cover recessives responsible for the size bottlenecks in the parents. However, whatever the cause of transgression such recombinants are very useful and through repeated cycles of hybridization which led to the breakage of size and other barriers that seem to have been exploited continuously till very large flower size was steadily built up. This was combined with other useful vegetative and floral characters, like colour and number of flowers per inflorescence, extended blooming period, cold resistance, etc. Because of the efficient vegetative propagation, fixation of the useful genotypes was no problem, although they may contain a high degree of heterozygosity and sexual sterility.

A plateau was reached in genetic improvement of Crozy cannas when continued intercrossing, inbreeding and selection yielded no significant improvement, and 'new blood' in the form of *C. flaccida* was introduced by C. Sprenger of Italy and L. Burbank of USA with a view to 'revitalise' Crozy cannas. Both of them worked independently and pollinated Crozy cannas with *C. flaccida*. The cross succeeded only in this direction and the resultant hybrids evoked widespread interest (Khoshoo and Mukherjee 1970b).

Italian cannas are robust, 120–200 cm in height, highly vigorous and very floriferous. The flowers range from 12·5 to 17·5 cm in diameter, with strongly reflexed corolla lobes, and very broad staminodia (4, 6 in Plate I). The flowers were broadly open with a flattened face like the orchid *Cattleya* or a Japanese iris, a shape unknown in the genus *Canna*. They constitute about 8% of the canna cultivars.

Among the first two cultivars raised by Sprenger in 1893 (Anon. 1898; Clayton 1895) are 'Italia' and 'Austria' which were selected out of 1000 seedlings. The former was unusual in the size of flower with beautiful golden vermillion colour, while in the latter the colour was yellow shaded with purple. L. Burbank raised 'Burbank' which was yellow with heavy red spotting on the inner staminodium. 'Bharat' (4 in Plate I) is an Indian cultivar of Italian cannas (Percy Lancaster 1967). In spite of the overall improvement and magnificent look, flowers in these Italian cannas are night-flowering, soft, evanescent and fragile, characters which came from the night-flowering *C. flaccida*. All the above and other initial cultivars (3%) of Italian cannas are asynaptic non-seeded diploids (Khoshoo and Mukherjee 1970a). These show karyotypic heteromorphicity with an average 8·88–12·24 (range 4–16) univalents per cell out of a total of 18 chromosomes. Irregular meiosis follows and leads to total sterility. These properties imply that the genome of *C. flaccida* appears to be well-differentiated from those of the other species.

With the above undesirable characters in the first asynaptic diploid Italian cannas, Sprenger (1901) tried to improve them by using their pollen on Crozy cannas and was able to raise new hybrids with still larger, more beautiful and resistant flowers, and flowering was more abundant than in the earlier Italian cannas (6 in Plate I). The first such cultivar is 'King Humbert' followed by others, which, in contrast to the diploid asynaptics, opened like Crozy cannas in the early morning hours. These were triploid in constitution and out of the total of 8% of Italian cannas, triploids are about 5%.

As expected, these triploids showed allo- or segmental allotriploid characters because of the non-homologous genome of *C. flaccida*. In contrast to autotriploid Crozy cannas, the Italian triploids are karyotypically heteromorphic with only 2·32–4·92 loosely associated trivalents per cell during meiosis. The remaining associations are in the form of bivalents and univalents. Highly irregular meiosis follows with 22·8–40·6% pollen fertility and total seed sterility.

All Italian cannas, whether diploid or triploid, show a strong influence of *C. flaccida*. In comparison with Crozy autotriploids, flowers in Italian

segmental allotriploids are large, somewhat delicate and short lived, fewer per inflorescence and are better suited to Southern Europe (Italy) and subtropical and tropical countries, but do not perform well under northern climate. Further, in comparison with Crozy cannas, the Italian cannas have a relatively larger plant body and unusually large flowers. This is not the effect of triploidy *per se* but due to luxuriance (*sensu* Dobzhansky 1950, 1952) that accompanies introduction of *C. flaccida* through hybridization both at diploid and triploid levels. In fact the cultivar 'Wintzer's Colossol' with flowers 21 cm across belongs to the Italian group (6 in Plate I).

CONCLUDING REMARKS

If we define plant breeding as plant evolution under the direction of man, then the two differ in their speed and direction. As seen from the foregoing account, the garden cannas evolved during the 44 years between 1848–1892 A.D. and in particular the last 24 years (1868–1892). There were opportunities for very rapid evolution, during which large part of the transformation took place and the garden varieties became so significantly modified in comparison with their progenitor species that they are not expected to persist in wild state. From an evolutionary point of view, such tremendous changes have taken place in a very short time. Such a rapid burst of evolution must have been accompanied by an accumulation of a good deal of genetic variability.

The very first factor to provide such opportunities was the cultivation since 1596 of *Canna* species in European environments to which they were not adapted. European gardeners imported the seeds/rhizomes of these species but not their environment and pollinators. Evidently the pressure of natural selection, whatever it be, was removed and ideal conditions provided for deviants to survive in the gardens. This could be the result of activation of a considerable unexpressed variation, which may have been aided by the limited size of the breeding group and consequent enforced inbreeding. *Canna* species now growing in European and American gardens are inbreeders; whether this is also the case in their natural habitats, or is an after-effect of cultivation under European conditions, is not known. Finally, canna began to be selected for characters not beneficial under conditions of natural selection. Hybridization between species which are not strongly differentiated, genetically coupled with selection, helped in the release of tremendous amounts of new variability through mutation, recombination and segregation, particularly transgressive segregation and luxuriance. Hybridization was, therefore, the most important single factor responsible for the origin of garden cannas. Next to it are triploidy, followed by chromosomal repatterning (through interchange heterozygosity) and somatic mutations. All these have played a relatively secondary role.

The direction of evolution of garden cannas was provided by the shift of emphasis from cannas as foliage plants, up to the middle of the nineeenth century, to cannas for colourful and large flowers and greater adaptability to hardy and cold climate. Naturally, canna was selected for reduction in height, form and colour of leaves, extended blooming period,

large spikes well above foliage, free flowering, erect, circular, rather flat and self-shedding flowers, and increase in size, colour diversity and durability of flowers. It was this shift that was instrumental in the rise of cannas from tall, long-jointed and small flowered, foliage plants imparting a tropical effect to the European gardens up to the middle of the nineteenth century, to summer flowering plants in Europe with medium to dwarf habit, close, compact growth and prominently-held free flowering inflorescences of very large and highly colourful circular, erect, durable and self-shedding flowers that open on all sides. Vegetative multiplication could enable fixation and perpetuation of almost any genotype irrespective of the extent of fertility and heterozygosity, provided, however, it has some selective value.

Lastly, selection for the two principal uses of canna involves not only different organs but, what is important, has been undertaken in contrasting environments. While in ornamental cannas, selection for floral parts has been made in European environments, a habitat unknown to cannas, that for starch content has involved rhizome but under its own native habitat in West Indies and South American tropics-subtropics. It is interesting to find that different purposes of selection under contrasting conditions have both ended in triploidy which in ornamental types has enlarged flowers and not so much rhizome, while in starch-yielding types it has enlarged fleshy rhizome, increased good flavour and starch content three times and significantly decreased tannins and fibre contents but affected flower to a very limited extent. Perhaps it means that the highest effective level of polyploidy possible in the genetic system of cultivated canna is triploidy (Khoshoo and Mukherjee 1970b).

SUMMARY

A picture of origin and evolution of garden cannas has emerged from a morphological, cytological and genetical analysis of the elemental species, primary hybrids and Anneé, Ehmann, Crozy and Italian cannas.

There has been a rise of cannas from tall, long jointed, small flowered foliage plants imparting tropical effect to the European gardens, to summer-flowering plants with medium or dwarf habit, close, compact growth and prominently-held inflorescences of very large and highly colourful circular flowers. The underlying genetic factors have been primarily hybridization, and secondarily triploidy and interchange hybridity. Hybridization between species which are not strongly differentiated genetically coupled with selection, helped in the release of a tremendous amount of new variability through mutation, recombination and segregation, particularly transgressive segregation and luxuriance.

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Anonymous (1893): Cannas, new dwarf *gladiolus*-flowered. *Gdnrs' Chron.* Aug. **12** 189–90

Anonymous (1898): Cannas: The 'Italian' or 'Orchid flowering' cannas. *Gdnrs' Chron.* Jan. **1** 2

Baker, J. G. (1893a): A synopsis of the species of cannas. *Gdnrs' Chron.* Jan. **14** 42–3

Baker, J. G. (1893b): On the species and garden forms of *Canna*. *J. Roy. Hort. Soc.* **2** 178–88

Clayton, J. (1895): Italian Cannas. *Gdnrs'. Chron.* Dec. **14** 703–5

Dobzhansky, Th. (1950): Genetics of natural populations. XIX. Origin of heterosis through natural selection in populations of *Drosophila pseudoobscura*. *Genetics* **35** 288–302

Dobzhansky, Th. (1952): Nature and Origin of heterosis. In *Heterosis*, pp. 330–5. Iowa State College Press, Ames, Iowa

Honing, J. A. (1923): Canna crosses. I. *Mededeelingen Landbouwhoogeschool* **26** 1–56

Khoshoo, T. N. and Mukherjee, I. (1970a): Genetic-evolutionary studies on cultivated cannas. III. Variation in meiotic system. *La Cellule* **68** 109–34

Khoshoo, T. N. and Mukherjee, I. (1970b): Genetic-evolutionary studies on cultivated cannas. IV. Origin and evolution of ornamental taxa. *Theoret. Appl. Genet.* **40** 204–17

Percy Lancaster, S. (1967): The giant-flowered cannas. *Indian Horticulture* **12** 30–1

Sprenger, C. (1901): Sur l'histoire des cannas à fleures d'orchidées. Dits cannas Italiens. *Revue Horticol.* **1** 446–8

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CYTOLOGY OF THE FERN GENUS *CHEILANTHES* IN EUROPE AND IN THE CANARY ISLANDS*

by

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SUMMARY

The cytology of all known representatives of the genus *Cheilanthes* described in the rank of subspecies and above from Europe and the Canary Islands has been investigated.

Cheilanthes fragrans (L. fil.) Schwartz is a tetraploid species ($n = 60$, $2n = 120$), which according to hybridisation experiments (Vida, in preparation), is an allotetraploid containing two genomes of *C. maderensis* and two of *C. persica*.

Cheilanthes maderensis Lowe has proved to be a diploid ($n = 30$, $2n = 60$), and is believed to be one parent of *C. fragrans*. It therefore cannot be classified as a subspecies of *C. fragrans*, but must instead be attributed specific rank, in spite of the small morphological difference between these two taxa.

Cheilanthes hispanica Mett. appears to exist in two different cytotypes ($n = 30$, $2n = 60$ and $n = 60$, $2n = 120$). On morphological grounds the tetraploid may be an autotetraploid, but more material of different origins is necessary to clarify this problem.

Cheilanthes persica (Bory) Mett. ex Kuhn is diploid ($n = 30$, $2n = 60$).

Cheilanthes marantae (L.) Domin subsp. *marantae* was already known to be diploid. Subsp. *subcordata* (Cav.) Benl & Poelt which replaces subsp. *marantae* in the Canary Islands and Madeira (and Cap Verdes?), has the same chromosome number ($n =$ ca. 29, $2n = 58$).

Cheilanthes catanensis (Cosent.) H. P. Fuchs has proved to be an aggregate species but correct naming of the different taxa must be postponed. We refer to them all provisionally as *C. catanensis* s. l. Plants from various parts of Mediterranean Europe and from the Canary Islands were found to be tetraploid ($n = 58$, $2n = 116$), and a similar count was found by Manton (in preparation) for plants from Madeira. However, a diploid taxon ($n = 29$, $2n = 58$) was detected in Spain and in some islands of the Canaries. The Madeira tetraploid differs morphologically from the Spanish diploid in being much less hairy, whilst the Spanish diploid is macroscopi-

* Paper presented by T. Reichstein at the Symposium. The full paper has been published in *Bauchinia* (*Basel*) **4** 223–53.

cally indistinguishable from the tetraploid plants ($2n$ = ca. 116) from Greece and the Pyrenees.

Cheilanthes pulchella Bory ex Willd., which, though formerly reported also from Madeira, is today only found on the Canary Islands, is a diploid ($n = 30$, $2n = 60$).

Cheilanthes guanchica Bolle and *C. sventenii* Benl. Originally assumed for morphological and geographical reasons to be a (diploid) hybrid of *C. maderensis* × *pulchella*, *C. sventenii* has proved to be a tetraploid species ($n = 60$, $2n$ = ca. 120), most probably derived from this postulated hybrid by alloploidy. The long known *C. guanchica* Bolle is also tetraploid ($n = 60$, $2n = 120$), and genetically probably identical with *C. sventenii*. In our view the small morphological differences between these two taxa are not sufficient to justify specific separation, and we suspect that *C. sventenii* will have to be accepted as a synonym of *C. guanchica*. Further experiments are in progress to resolve this question.

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ZUSAMMENHANG ZWISCHEN DER EVOLUTION DER GATTUNG TRITICUM, DER NEOLITHISCHEN REVOLUTION UND DEN URKULTUREN KLEINASIENS

von

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Seitdem zu Beginn der zwanziger Jahre Percival die »*Aegilops*-Hypothese« aufgestellt hat, sind einige Phasen der Evolution der Gattung *Triticum* geklärt worden. Die genetischen vergleichend-morphologischen und resynthetisierenden Versuche haben klarstellen lassen, daß der Träger des Genoms »A«, der 14 Chromosomen besitzende *Triticum boeoticum* ist. Die Genom- Zusammensetzung der zweiten Weizenreihe ist »AB«. Das Genom »B« entstammt wahrscheinlich der *speltoides*-Art der Gattung *Aegilops* derart, daß *Aegilops* der befruchtete Partner bei der Kreuzung war, d. h. von ihm rührt das Zytoplasma der meisten Arten der Tetraploidreihe her. Die diploiden und tetraploiden Artengruppen sind also anisoplasmatisch.

Am wichtigsten ist die Hexaploidreihe, diese hat die Genomzusammensetzung »ABD«. Das Genom »D« ist ebenfalls aus der *Aegilops*-Gattung in den Weizen gelangt. Hier war der Donor *Aegilops squarrosa*. Das bedeutet soviel, daß das Plasma der hexaploiden Weizen gleichfalls der *Aegilops*-Gattung entstammt.

Die drei Weizengenome sind verwandt, darauf deutet die Homeologie der Chromosomen. Trotz der Homeologie existiert unter normalen Umständen nur homologe Paarung. Am längeren Arm des Chromosoms 5 von Genom »B« wurde ein auch im hemizygotischen Zustand wirksames Gen identifiziert, welches die homeologe Paarung verhütet und so für die Ordnung bei der Teilung der 21 Chromosomenpaare der allohexaploiden Weizenarten sorgt. In der Art *Aegilops speltoides*, von dem das Chromosom 5B stammt, ist ein derartiges Gen noch nicht enthalten. Dies führt zu der Annahme, daß es sich um eine im Laufe der Evolution zustandegekommene glückliche Mutation handelt, die zu der Aufrechterhaltung der Hexaploidreihe bedeutend beigetragen hat.

In botanischen Expeditionen hat man klären können, wo die Urheimat des 14 Chromosomen besitzenden Weizens bzw. der die »B«- und »D«-Genome gebenden *Aegilops*-Arten war. Sowohl die archäologischen Funde, wie auch die botanischen Sammlungen beweisen, daß sich das Entstehungsgebiet von *Triticum boeoticum* in Kleinasien vom nordöstlichen Küstengebiet des Mittelmeeres bis zu den Zagrosketten halbkreisförmig erstreckt. Die Urheimat von *Ae. speltoides* stimmt fast völlig mit diesem Gebiet überein, sie dehnt sich nur in südwestlicher Richtung etwas weiter aus. Es ist offentsichtlich, daß der 28 Chromosomen besitzende Weizen-Urahn, *T. dicoccoides*, gleichfalls in dieser Gegend entstanden war. Die Befunde bekräftigen des weiteren, daß die ökologische Anpassungsfähigkeit dieser

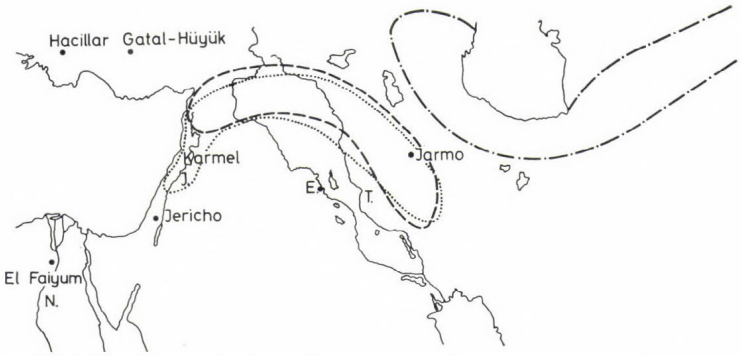

Abb. 1. Die Landkarte Kleinasiens. Das mit – – – umgrenzte Gebiet ist die Urheimat des *T. boeoticum*. Die mit . . . . und – · – · – umgrenzten Gebiete sind die Urareale von *Ae. speltoides* und *Ae. squarrosa*

polyploiden Art größer war, als die der beiden Komponenten und sie sich infolgedessen weit über deren natürliches Areal hinaus ausbreitete.

Die Urheimat von *Ae. squarrosa*, der dritten Komponente des hexaploiden Weizens, beginnt mehr nördlich und dehnt sich weiter nach Osten aus. Diese Art ist an der südlichen Küste des Kaspischen Meeres, am Südhang des Kaukasus heimisch; ihr Areal erstreckt sich in nordöstlicher Richtung ganz bis zum Hindukusch. Sein Fundort kommt also mit dem Areal von *T. boeoticum* und *Ae. speltoides* nicht in Berührung. Diese Feststellung bereitet aber in evolutionstheoretischer Hinsicht dennoch keine Schwierigkeit, denn *T. dicoccoides* hat — wie erwähnt — infolge ihres größeren Anpassungsvermögens auch in das Areal von *Ae. squarrosa* übergreifen können, so daß im Raum zwischen dem nördlichen Lauf des Tigris und dem Kaspischen Meer einer spontanen Kreuzung nichts im Wege stand.

Das Fundmaterial der kleinasiatischen archäologischen Erschließungen beweist, daß das erste Getreide des hier lebenden *Homo sapiens sapiens*, neben der Gerste, der über 14 und 28 Chromosomen verfügende Weizen war. Der hexaploide Weizen dürfte erst später aufgetreten sein und erst zu Beginn der historischen Zeiten allmählich das Einkorn und den Emmer verdrängt haben. Die evolutionsgenetische Erklärung für das Zustandekommen der drei Weizenreihen ist also evident und auch ihr Entstehungsareal läßt sich deutlich umreißen.

In der letzten Abkühlungsperiode der Würm-Eiszeit überdeckten die Gletscherströme den nördlichen Raum Mitteleuropas. Die Gebirgszüge des Kaukasus, Pontus, Zagros und Hindukusch trugen auch eine dicke Schnee- und Eisdecke. Unter dem kühlenden Einfluß der gewaltigen zusammenhängenden Eisfelder war das Klima Nordafrikas und Kleinasiens wesentlich kühler und niederschlagsreicher als heutzutage. Im gesamten Raum lebte eine reiche Flora und Fauna. Der Urmensch Kleinasiens sorgte damals für seinen Unterhalt durch die Jagd auf Großtiere. Die Bewohner der Karmelhöhlen, der Siedlungen Hazer-Merd, Shanidar u. a. jagten nach ihrer Beute noch in Wäldern mit üppiger Vegetation. Die Überwärmung des Klimas von Nordafrika und Kleinasien und die Desikkation setzte

ein, als vor etwa 30 000 Jahren in Europa die langsame Erwärmung begann und die Gletscher sich nach Norden zurückzogen. Im 12. Jt. v. u. Z., als auch Skandinavien von seiner Eisdecke befreit war, nahmen im Raum zwischen der östlichen Mittelmeerküste und den Zagrosketten infolge der Erwärmung und des Austrocknens die Wälder schon einen lockeren Charakter an. Die Vegetation der Wiesen bestand aus dürretolerierenden einkeimblättrigen Pflanzen mit kurzer Vegetationsdauer. Die Gattungen *Triticum* und *Aegilops* dürften in den vorangegangenen Jahrtausenden in diesem Raum entstanden sein. Hieraus ist zu schließen, daß das 12. bis 11. Jt. v. u. Z. jene Epoche gewesen sein muß, in der *T. dicoccoides*, der tetraploide Weizen entstanden war.

Aus dem 9. Jt. v. u. Z., von den Höhlenmenschen des Karmelgebirges, stammt die erste, aus Knochen und Kieselstein angefertigte Sichel und der erste Mahlstein. Der Höhlenmensch des Karmelgebirges hat das Getreide bereits geerntet, als er an einen Anbau desselben noch gar nicht dachte. In den Lichtungen der immer lockerer werdenden Wälder gedieh wahrscheinlich schon in großen zusammenhängenden Populationen die Gerste und die Primitivform des 14 und 28 Chromosomen tragenden Weizens.

Die Werkzeuge und Getreiderelikte der untersten Schichten von Jericho, Catal-Hüyük, Jarmo und Faiyum beweisen, daß im 6. bis 5. Jt. v. u. Z. im heutigen Anatolien, Kurdistan, Palestina und am unteren Nillauf die diploiden und die tetraploiden Weizen nicht nur geerntet, sondern bereits auch angebaut wurden. In diesen Jahrtausenden erfolgte eigentlich jene Wandlung, wo der Mensch, der im Pleistozän noch vorwiegend Fleischesser war, sich immer mehr mit pflanzlicher Nahrung zu ernähren begann, und seine Hauptnahrung war das Getreide. Außer den zuvor erwähnten wichtigeren Fundorten ist noch eine ganze Reihe von Ursiedlungen freigelegt worden, deren Geräte und Getreideüberreste beweisen, daß diese schicksalsentscheidende Wendung tatsächlich hier stattgefunden hat. Die Ausgrabungen von Hacilar, Ras-Shamra, Alaca-Hüyük, Tell-Halaf, Ugarit, Bogasköy, Quades, Ninive, Samarra und Babylon legen sämtlich Zeugnis hierfür ab.

In der Periode vom 7. bis 4. Jt. v. u. Z. war also das Getreide jene Pflanze, welche die entscheidende Veränderung der menschlichen Lebensform ermöglicht und die Grundbedingungen der gesellschaftlichen und kulturellen Entwicklung gesichert hatte.

Es ist kein Zufall, daß seinerzeit im gleichen Raum, dort, wo die Urevolution der Gattungen *Hordeum* und *Triticum* zum Abschluß gelangt war, auch die neolithische Revolution begann. Das Getreide war nämlich die erste Nahrung, die auf einem relativ kleinen Gebiet eine sehrdichte Bevölkerung ernährte. Dank seiner leichten Speicherfähigkeit, ermöglichte es die Anreicherung von Vorräten, wozu bis dahin der Mensch im Laufe seiner eigenen Evolution nie imstande war.

Vom 4. Jt. v. u. Z. an waren die sich nahe der großen Flüsse Kleinasiens niederlassenden und in steter Vermehrung begriffenen Menschen bereits Getreideesser. Die gleichmäßige und systematische Nahrungsaufnahme beschleunigte die Fortpflanzung. Die Existenzunsicherheit hatte aufgehört. Der bislang nomadisch lebende Mensch wurde seßhaft, an die Scholle gebunden. Hiermit waren die Voraussetzungen für eine dauerhafte Nieder-

lassung gegeben und die Urbanisierung konnte beginnen. Das Getreide ermöglichte die Herstellung von Überschüssen, die einen Lebensunterhalt auch den sich nicht unmittelbar mit dem Anbau beschäftigenden Arbeitern, Handwerkern, Kaufleuten, Beamten, Soldaten und Priestern boten. Auf diese Weise gelangten Schichten zum Broterwerb, die ihre Energie der Zivilisation und Kultur, der Ausübung der Religion widmen konnten. Doch all dies geschach nur dort, wo massenhaft Getreide angebaut werden konnte, in Mesopotamien, im Niltal und den Jordan entlang. Dem Getreideanbau ist es zu verdanken, daß an den Ufern des Euphrat und Tigris die sumerische und akkadische und den Nil entlang die ägyptische Urkultur erblühen konnte.

Die Archäologie hat schon seit langem klargestellt, daß die Wiege der Kultur Eurasiens in Kleinasien stand, in jenem Gebiet, wo die sogenannte neolithische Revolution begann. Wir wissen auch, daß eben dieses Gebiet auch die Urheimat des Ackerbaus und zum Teil der Viehzucht war, doch wird die Bedeutung der Phylogenese der Gerste- und besonders der Weizengattungen und der so unerwarteten Beschleunigung des Tempos der kulturellen Entwicklung des Menschen nicht miteinander in kausale Beziehung gebracht.

Sollte sich tatsächlich die neue Feststellung von Richard E. Leaky bewahrheiten, wonach der in Mittelafrika, im östlichen Uferbereich des Rudolfsees lebende Vormensch schon vor zweieinhalb Jahrmillionen steinerne Werkzeuge, Schopper, hergestellt hat, so hat es zweieinhalb Millionen Jahre gedauert, bis der Mensch zur neusteinzeitlichen Technologie gelangt war. Danach bedurfte es kaum noch 3000 bis 4000 Jahre, um aus ihm ein Kulturwesen werden zu lassen. Es ist offensichtlich, daß in dieser unglaublichen Beschleunigung der menschlichen Evolution zahlreiche Faktoren eine Rolle gespielt haben, daß aber die Bedeutung des Getreideanbaus bzw. der Übergang zur Getreidekonsumption der grundlegendste ist, kann kaum in Zweifel gezogen werden. Nur das Getreide — und in erster Linie der Weizen — vermochte jene Nahrungs- bzw. Energiequelle zu sichern, die zu einem derart rapiden Entwicklungstempo unerläßlich war. Daß die Entwicklung gerade in Kleinasien einsetzte und ihren Abschluß fand, dazu hat in entscheidender Weise der Umstand beigetragen, daß sich auch die Evolution der Gattung *Triticum* hier vollzogen hatte.

Der *Homo* war — seinem körperlichen Aufbau entsprechend — ursprünglich Omnivore. Trotz seiner Geschicklichkeit, seiner Waffen und Werkzeuge hat er die eigene Evolution Zehntausende von Jahren als Karnivore, sogar als Raubtier durchgemacht.

Die Evolution des Getreides, vor allem der Gattung *Triticum*, hat ihm die Rückkehr zu seiner ursprünglichen Ernährungsform ermöglicht.

Es ist durchaus begründet, die Wissenschaft nicht nur auf die wirtschaftliche, kulturelle und historische, sondern auch auf die human-evolutiongenetische Bedeutung dieses Zusammenhanges aufmerksam zu machen. Die Rückkehr des Menschen zu pflanzlicher Nahrung, zum Getreide bzw. zum Brot, hat auf seine somale, geistige und auch auf seine genetische Entwicklung die tiefste Wirkung ausgeübt.

Kihara, H. (1949): Genomanalyse bei *Triticum* und *Aegilops*. *Cytologia* **17** 135–44

Kihara, H. (1968): Cytoplasmic relationships in the *Triticale*. *Third International Wheat Genetics Symposium, Canberra*, pp. 124–34

MacFadden, E. S. and Sears, E. R. (1946): The origin of *T. spelta* and its free-threshing hexaploid relatives. *J. Hered.* **37** 81–9, 107–16

MacKey, J. (1954): Neutron and X-ray experiments in wheat and a revision of the speltoid problem. *Hereditas* **40** 60–180

Percival, J. (1921): *The wheat plant*. A monograph. Duckworth and Co., London

Riley, R., Unrau, J. and Chapman, C. (1958): Evidence of the origin of the B genome of wheat. *J. Hered.* **49** 91–8

Riley, R. and Chapman, V. (1958): Genetic control of the cytologically diploidlike behaviour of polyploid wheat. *J. Hered.* **52** 22–5

Sarkar, P. and Stebbins, G. L. (1955): Morphological evidence concerning the origin of the B genome in wheat. *Amer. J. Bot.* **43** 297–303

Suemoto, H. (1968): The origin of the cytoplasm of tetraploid wheat. *Third International Wheat Genetics Symposium, Canberra*, pp. 141–52

Yamashita, K., Kihara, H. and Tanaka, H. (1965): *Morphological, physiological, genetical and cytological studies in Aegilops and Triticum, collected from Pakistan, Afganistan and Irak*. Kyoto University, Kyoto, Japan

Symp. Biol. Hung. 12, pp. 111–133 (1972)

DIE MÖGLICHE BEDEUTUNG DER EXTRACHROMOSOMALEN VERERBUNG FÜR DIE EVOLUTION

von

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Das *Plasmon*, das heißt die Summe der genetisch wirksamen Faktoren, die außerhalb des Zellkerns und der Chromosomen in der Zelle gelegen sind, ist ein Faktor, der bisher in der Genetik noch nicht die Beachtung gefunden hat, die er verdient, obgleich bis heute bereits eine größere Anzahl von Arbeiten vorliegt, die schon einiges Wesentliche über Beschaffenheit, Wirkungsweise und Bedeutung dieser extrachromosomalen Erbträger aussagt. Bei der Erörterung der genetischen Kräfte, welche das Evolutionsgeschehen steuern, wird das Plasmon im allgemeinen noch weniger in Betracht gezogen. Es erscheint daher wichtig, an Hand der bisher bekannten Tatsachen einmal kurz die wesentlichen Beobachtungen zusammenzufassen, aus denen sich ersehen läßt, welche Bedeutung diese extrachromosomalen genetischen Faktoren für die Evolution der Organismen haben können.

Die ersten Anhaltspunkte dafür, daß neben den Chromosomengenen noch andere Faktoren existieren, die am Zustandekommen der Vererbungsvorgänge beteiligt sind, wurden bereits kurze Zeit nach der Wiederentdeckung der Mendelschen Vererbungsgesetze erhalten (Baur 1909, Correns 1909a, b). Inzwischen haben sich die Beweise für das Vorkommen extrachromosomaler genetischer Faktoren stark vermehrt und geben uns heute bereits einige Klarheit über Wesen, Funktion und genetische Wirksamkeit dieser außerhalb des Zellkerns gelegenen Erbfaktoren (Hagemann 1964, Jinks 1967, Schötz 1967).

Das Vorhandensein eines genetisch wirksamen Prinzips außerhalb des Kerns konnte auf verschiedene Weise nachgewiesen werden. Einmal ließ sich schon früh zeigen, daß mitunter bei höheren Pflanzen reziproke Kreuzungen verschiedene Ergebnisse erbrachten: Die F_1-Pflanzen wa-

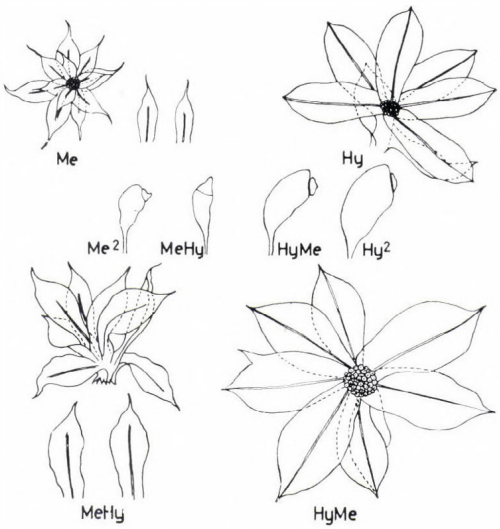


Abb. 1. Gametophyten und Sporogone von *Funaria mediterranea*, *F. hygrometrica;* reziproke Bastardsporogone und diploide Bastardgametophyten. — Vergr. 10×, Sporogone 4×. (Nach F. v. Wettstein)

Abb. 2. Der Bastard *Epilobium hirsutum* Sippe Jena ♀ × Sippe München ♂ (links) und reziprok (rechts). Die beiden Eltern ähneln der Pflanze rechts. (Nach Michaelis)

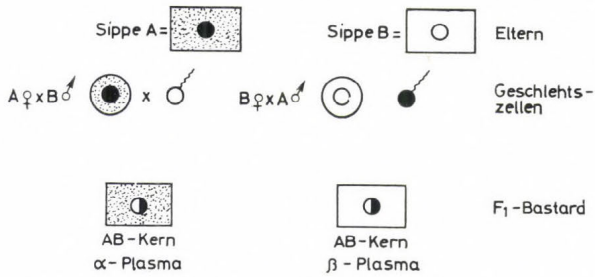


Abb. 3. Schema einer reziproken Kreuzung. (Nach Michaelis)

ren reziprok verschieden, und zwar zeigten sie in der Regel im gesamten Habitus oder in einzelnen Merkmalen entweder eine mehr oder minder starke Mutterähnlichkeit (Abb. 1) und diese Matroklinie blieb auch in der F_2- und in den folgenden Generationen erhalten, oder ein Kreuzungsprodukt war normal entwickelt, das reziproke war mißgebildet (Abb. 2), und in noch anderen Fällen führte nur die eine Kreuzung zu lebensfähigen Samen, die reziproke gelang überhaupt nicht.

Da der männliche und der weibliche Elter quantitativ und qualitativ die gleiche Menge an Chromosomen und damit an Kerngenen zum Genom der F_1-Pflanzen beisteuern (Abb. 3), konnten die in dieser und in den folgenden Generationen beobachteten Unterschiede zwischen den Produkten der reziproken Kreuzungen nicht auf Verschiedenheiten im Genom beruhen. Sehr verschieden ist dagegen bekanntlich die Plasmamenge in den weiblichen und den männlichen Keimzellen: Während die Eizellen reich an Plasma sind, ist der Plasmagehalt der männlichen Keimzellen recht gering und es scheint darüber hinaus, daß in einer Reihe von Fällen bei der Befruchtung mit dem männlichen Kern nur wenig oder gar kein Zytoplasma in die Eizelle eindringt. Aus diesen Befunden wurde schon früh der Schluß abgeleitet, daß nicht nur dem Kern, sondern auch dem Plasma irgendeine genetische Funktion innewohnen müsse.

In anderen Fällen wurde beobachtet, daß bestimmte Merkmale nur durch einen der beiden Partner eines Sexualaktes, bei höheren Pflanzen in der Regel von dem weiblichen Elter, übertragen werden. Derartige Beispiele, die weitere Beweise für das Vorhandensein im Plasma gelegener

Erbfaktoren erbrachten, ergaben sich u. a. aus der Analyse des genetischen Verhaltens verschiedener Algen- und Pilzarten. So gibt es bei der einzelligen, zu den *Volvocales* gehörenden Grünalge *Chlamydomonas reinhardi* zwei Paarungstypen mt^+ und mt^-, die nur miteinander zu kopulieren vermögen. Bei der Kopulation verschmelzen die äußerlich völlig gleichen Zellen miteinander und bilden eine diploide Zygote, aus der nach Reduktionsteilung vier haploide Zellen hervorgehen, von denen zwei zum Paarungstyp mt^+, zwei zum Paarungstyp mt^- gehören. Auch die anderen Merkmale, in denen die Algen verschiedenen Paarungstyps sich unterscheiden, zeigen eine typische Mendelspaltung.

Ganz anders verhalten sich streptomycinresistente oder streptomycinbedürftige Mutanten dieser Art. Aus der Kreuzung einer streptomycinresistenten Mutante mit der Wildform gingen nur resistente Nachkommen hervor, wenn der resistente Elter eine mt^+-Form war; es entstanden nur anfällige Nachkommen, wenn als resistenter Elter eine mt^--Form gewählt wurde. Der Paarungstyp und alle übrigen Eigenschaften spalteten in dem für monohybride Vererbung üblichen Zahlenverhältnis von 1 : 1 (Abb. 4). In gleicher Weise erfolgte bei *Chlamydomonas reinhardi* auch die Übertragung der Streptomycinbedürftigkeit.

Ein anderer Fall nichtmendelnder Vererbung ist von bestimmten Mutanten der Bierhefe *Saccharomyces cerevisiae* bekannt. Diese Mutanten, deren Atmungssystem geschädigt ist, bilden Zwergkolonien. Die eine dieser Mutanten »neutral petite« bildet bei Kreuzung mit der Wildform Zygoten, die sich durch Sprossung weitervermehren und schließlich nach Herunterregulierung der Chromosomenzahl in der Meiosis 4 Ascosporen bilden, die hinsichtlich des Kreuzungstyps ganz normal spalten, in der Größe der Kolonien aber sämtlich dem Wildtyp angehören. Die mangelhafte Bildung der Atmungsfermente und das Wachstum der Zellkolonien wird hier also durch extrachromosomale Faktoren bestimmt, wobei sich die Faktoren des Wildtyps vollständig gegenüber denen der Mutanten

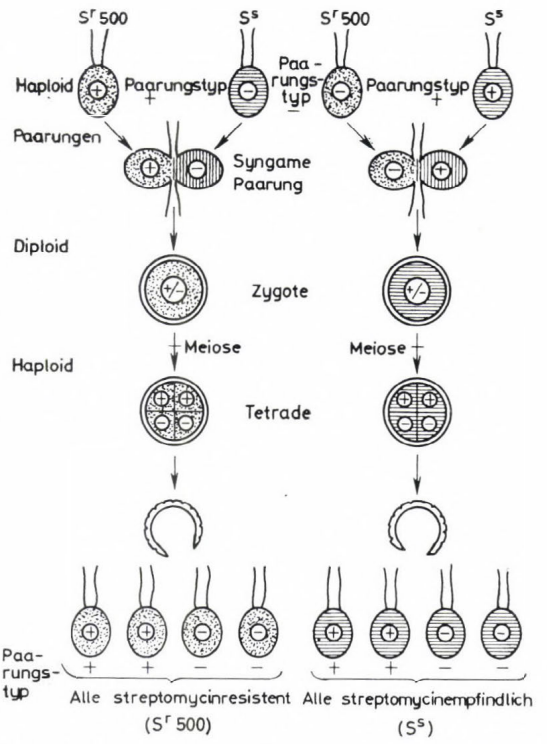


Abb. 4. Vererbung der Streptomycinresistenz (S^r 500). Die Plus- und Minuszeichen bezeichnen den Paarungstyp, der monogen vererbt wird. Die Nachkommenschaft gleicht mit wenigen Ausnahmen in der Streptomycinresistenz dem Plus-Elter, der Unterschied im Paarungstyp spaltet in jeder Tetrade im Verhältnis 1:1. (Nach Jinks)

durchsetzen. Diese beiden Beispiele zeigen, daß nichtmendelnde Vererbung, die durch extrachromosomale Faktoren bestimmt wird, nicht unbedingt auf Unterschieden in der Plasmamenge der weiblichen und der männlichen Keimzellen beruht und sich daher auch nicht in reziproker Verschiedenheit der Bastarde äußern muß, sondern sich auch in Übertragung durch nur einen der beiden Geschlechtspartner bzw. in rein mütterlicher Vererbung äußern kann, wie dies etwa beim status albomaculatus bei *Mirabilis* oder *Antirrhinum* der Fall ist.

Wenn die in ihrer Gesamtheit als Plasmon bezeichneten Elemente der extrachromosomalen Vererbung für die Evolution von Bedeutung sein sollen, müssen sie eine hochgradige erbliche Konstanz besitzen. Daß dies tatsächlich der Fall ist, zeigten bereits 1908 Untersuchungen von Correns an gynodiözischen Pflanzen wie *Satureja hortensis* oder *Cirsium oleraceum*. Die Populationen dieser Gynodiözisten setzen sich zur Hälfte aus rein weiblichen, zur Hälfte aus Pflanzen mit Zwitterblüten zusammen. Die zwittrigen Pflanzen bestäuben sich selbst und bringen wieder Zwitterpflanzen hervor. Die Nachkommenschaft der weiblichen Pflanzen, die mit den Pollen der Zwitterpflanzen befruchtet wurden, besteht ausschließlich aus weiblichen Pflanzen.

Correns konnte diese Erscheinung darauf zurückführen, daß das Plasmon bei den weiblichen und den Zwitterpflanzen verschieden ist. Die von Kerngenen induzierte Anlage zur Ausbildung zwittriger Blüten kann sich in dem Plasmon der weiblichen Pflanzen nicht voll auswirken, und diese Hemmung führt zur Unterdrückung der männlichen Blütenorgane. Da die weiblichen Pflanzen seit ungezählten Generationen von den zwittrigen bestäubt, also ständig zurückgekreuzt werden und sich die Gynodiözie trotzdem erhalten hat, muß das Plasma dieser Arten extrachromosomale Faktoren enthalten, die von den im Kern gelegenen genetischen Faktoren unabhängig und auch über sehr lange Zeit vom Genom nicht beeinflußbar sind. Diese plasmatischen Faktoren dürften damit genauso konstant sein, wie es die Kerngene sind.

Weitere Beweise für die potentielle Konstanz des Plasmons ergaben Arbeiten von F. von Wettstein (1930) und von P. Michaelis (1940, 1956, 1963). Beide kreuzten reziprok verschiedene Bastarde zwischen Moosarten und zwischen verschiedenen Arten und Sippen von *Epilobium* solange mit dem männlichen Elter zurück, bis jeder Rest des mütterlichen Genoms verschwunden sein mußte und nur noch die Kerngene des väterlichen Elters vorhanden sein konnten (Abb. 5). Auch in diesen Fällen zeigte sich, daß das Plasmon und die von ihm ausgehende Wirkung die Kerngene auch nach längerer Einwirkung nicht zu verändern vermochte.

Es erhebt sich nun die Frage, ob diese im Plasma vorhandenen Träger erblicher Funktionen an bestimmte korpuskuläre Teilchen des Plasmas gebunden und welches diese Teilchen sind. Gelingt es, das Plasmon als Gesamtheit aller extrachromosomalen genetischen Faktoren in Einzelkomponenten zu zerlegen und diese, wenn möglich, mit bestimmten Organellen in Verbindung zu bringen, so sind damit wesentliche Voraussetzungen für die Analyse der extrachromosomalen Vererbungserscheinungen geschaffen. Bei der Suche nach bestimmten Zellbestandteilen, die der Sitz von Teilkomponenten des Plasmons sein könnten, hat sich die Aufmerksamkeit verständlicherweise zunächst auf die Plastiden als die größten Zellorga-

nellen gerichtet, die in allen grünen Organen auftreten und deren Hauptfunktion die Photosynthese ist. Renner hat bereits 1934 darauf hingewiesen, daß die Plastiden »selbständige Elemente der genetischen Konstitution« sind. Auf eine solche zumindest verhältnismäßig starke genetische Selbständigkeit der Plastiden deutet u. a. die Beobachtung hin, daß die Chloroplasten eine korpuskuläre Kontinuität besitzen. Dies geht einmal daraus hervor, daß bei Blütenpflanzen im Meristem und in den Embryonen Proplastiden vorhanden sind, aus denen sich dann am Licht die Plastiden entwickeln. Zum anderen zeigt die Analyse der Weißbuntheit in den Fällen, in denen diese rein mütterlich vererbt wird (status albomaculatus), daß hier zwei Sorten von Chloroplasten in den Zellen vorhanden sind, normal grüne und mutierte, die nicht zu ergrünen vermögen (Abb. 6). Bei den Zellteilungen in den Vegetationsspitzen werden diese Plastiden zufallsgemäß verteilt und es entstehen so Gewebsteile, die beide Chloroplastentypen oder jeweils nur einen dieser Typen enthalten, und auf diese Weise kommt durch Entmischung der Chloroplasten die typische Scheckung der Gewebe zustande.

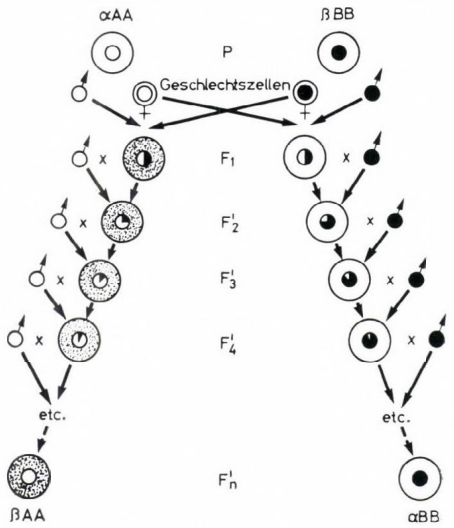


Abb. 5. Kernaustausch mit Hilfe der Rückkreuzung

Die in den Plastiden enthaltene genetische Information, die in ihrer Gesamtheit als *Plastom* bezeichnet wird, hat zunächst einmal Einfluß auf Form und Funktion dieser Organellen selbst. Hierüber geben Plastommutanten eindeutige Auskunft. So führen bei *Oenothera* verschiedene Plastommutanten, welche die Ergrünung der Plastiden beeinflussen, zu einer unterschiedlichen Färbung der Blätter, und auch bei *Antirrhinum majus* gibt es verschiedene weiß-grün gescheckte Stämme, die sich zum Teil deutlich voneinander unterscheiden (Hagemann 1964). Aus diesen Feststellungen läßt sich freilich noch nicht ableiten, ob es sich in diesen Fällen um verschiedene Mutationsschritte, also um multiple Allele des gleichen Plastidengens handelt oder um Mutationen verschiedener Gene. In einigen Fällen können wir allerdings mit verhältnismäßig großer Sicherheit sagen, daß es sich höchtwahrscheinlich um Mutationen in verschiedenen Loci handelt. So hat W. Stubbe (1959) für *Oenothera* einen Fall beschrieben, in dem zwei verschiedene und voneinander unabhängige Plastommutationen auftreten, eine, die eine gelbgrüne Färbung der Plastiden verursacht, und eine andere, die im Zusammenspiel mit bestimmten Genotypen bei Bastarden bleiche Färbung der Blätter hervorruft. Ferner beobachteten Wild (1958) bei *Antirrhinum* und Schötz (1955) sowie Kandler und Schötz (1956) bei *Oenothera*, daß der Ablauf des Photosyntheseprozesses durch verschiedene Plastommutationen an sehr unterschiedlichen Stellen

gestört sein kann, was darauf hindeutet, daß hier wohl Mutationen verschiedener Loci im Plastom vorliegen.

Das Plastom beeinflußt aber auch Merkmale, die nichts mit den Plastiden und ihren Funktionen zu tun haben. So fand Renner (1919a, b) bei *Oenothera*, daß bestimmte Genome in fremdem Plasma den Pollen unfähig zur Befruchtung machen. W. Stubbe (1959, 1960) konnte später zeigen, daß diese Inaktivität des Pollens durch das Plastom verursacht wird. Ferner konnte von Schwemmle und Mitarbeitern (1938) nachgewiesen werden, daß unter dem Einfluß fremden Plastoms bestimmte Gene inaktiviert, andere Gene in ihrer Wirksamkeit modifiziert werden. Für die Evolution dürfte von Bedeutung sein, daß Eigenschaften, wie das Längenwachstum, die photoperiodische Reaktion und auch die selektive Befruchtung, durch das Plastom beeinflußt werden können.

Diese Ergebnisse zeigen, daß die Plastiden zweifellos eine Reihe von Genen enthalten, die nicht nur deren Bildung, Form und Funktion bestimmen oder mitbestimmen, sondern auch andere wichtige Merkmale der Pflanze beeinflussen können. Diese »Plastogene« können offenbar mutieren und Allele bilden, die sich in einer veränderten genetischen Wirkung des Plastoms äußern. Über die Zahl der in einem Plastom enthaltenen »*Plastgene*« wissen wir noch nichts.

In Zellkern und Chromosomen ist die DNS der Träger der genetischen Information. In neuerer Zeit gelang der Nachweis, daß auch die Chloroplasten DNS in Form von feinen Fibrillen enthalten (Abb. 6 und 7). Diese treten in bestimmten Teilen der Plastiden auf und werden bei deren Tei-

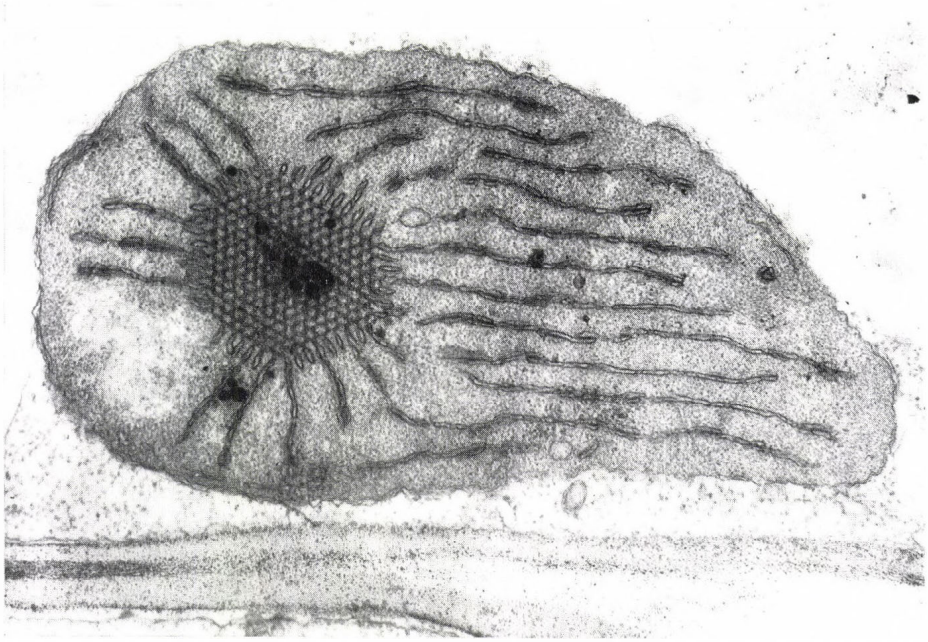


Abb. 6. Elektronenmikroskopische Aufnahme eines Chloroplasten. Die helle Zone an der linken Seite der Chloroplasten enthält die DNS-Fibrillen. (Nach Sprey)

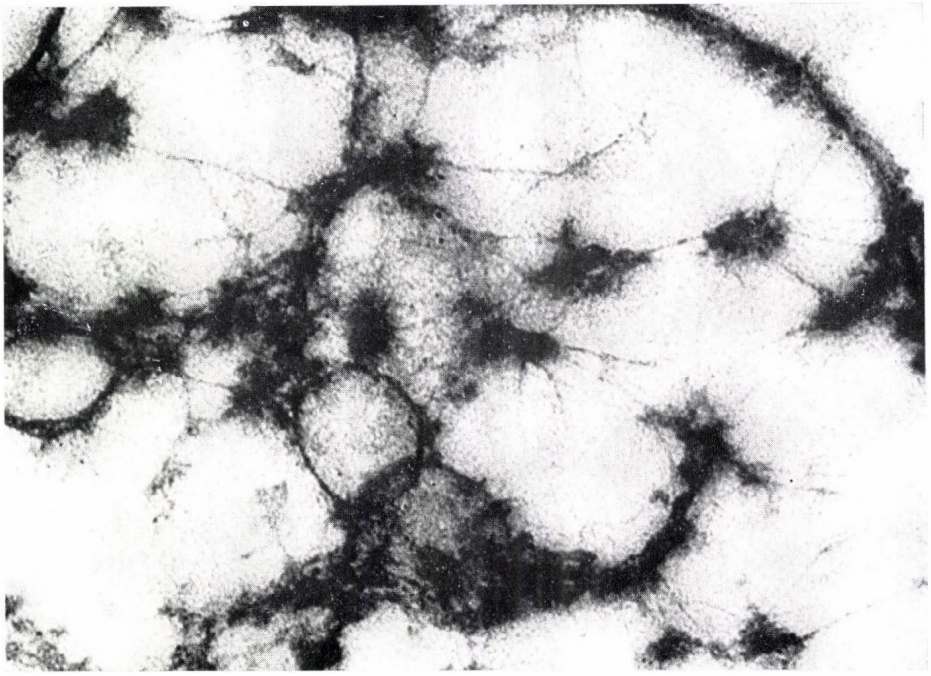


Abb. 7. Stark vergrößerter Ausschnitt aus der DNS-haltigen Zone eines Chloroplasten. Die überall im Bildfeld sichtbaren Fäden sind Teile von DNS-Molekülen. (Nach Sprey)

lung auf die Tochterplastiden verteilt (Abb. 8). Bei der Umformung des in der Kern-DNS enthaltenen genetischen Codes in Fermente, die den Aufbau und die Funktionen des Organismus regulieren, spielen die verschiedenen Sorten der DNS eine entscheidende Rolle. Nun wurden auch in der Matrix der Chloroplasten RNS-haltige Partikeln gefunden, Chloroplastenribosomen, die kleiner sind, als die Ribosomen im Zytoplasma und sich auch in der Basenzusammensetzung von diesen unterscheiden. Dagegen zeigen sie in der Größe und ihrer Zusammensetzung gewisse Übereinstimmung mit den Ribosomen der Bakterien und Blaualgen. Dies ist vom phylogenetischen Standpunkt gesehen nicht uninteressant, da bekannt ist, daß in verschiedenen Fällen farblos gewordene Algen wie *Glaucocystis*, *Paulinella*, *Cyanophora* und verschiedene andere Algen, vor allem Flagellaten, in fester Symbiose mit Cyanellen, blaualgenähnlichen Gebilden leben, die allein nicht mehr lebensfähig sind (Abb. 9). Im Rahmen der seit langer Zeit immer wieder entwickelten Vorstellungen, wonach die Chloroplasten letzten Endes nichts anderes sind als symbiontische einzellige Algen, die im Laufe der Zeit ihre Selbständigkeit verloren haben, sind diese Tatsachen zweifellos nicht uninteressant. Schließlich muß noch erwähnt werden, daß in den Chloroplasten auch eine lösliche RNS nachgewiesen wurde, die wohl als Messenger-RNS angesehen werden darf. Damit sind in den Chloroplasten alle Voraussetzungen für eine genetische Autonomie gegeben: Eine spezifische DNS als Träger von Informationen, Messenger-RNS, die den gene-

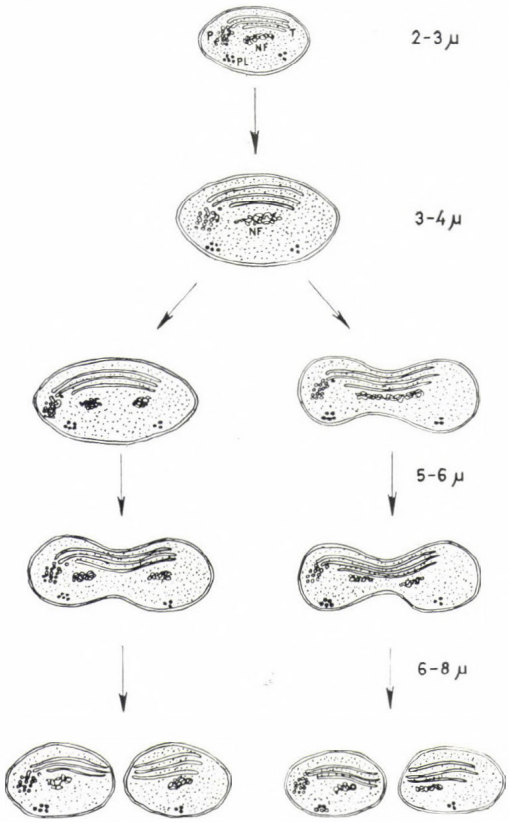


Abb. 8. Aufteilung der DNS-Fibrillen (NF) während der Teilung eines Chloroplasten auf die Tochterchloroplasten. (Nach Sprey)

tischen Code auf eigene Ribosomen übertragen, an denen dann eine eigene Proteinsynthese erfolgen kann.

Weitere Träger genetischer Information außerhalb des Zellkerns sind die Mitochondrien, kugelförmige bis längliche Gebilde, die von zwei Membranen umgeben sind und deren Inneres durch Einstülpung der inneren Membranen in Form von Lamellen oder röhrenförmigen Gebilden eine stark vergrößerte innere Oberfläche hat. Ähnlich wie die Chloroplasten steuern sie wichtigste Stoffwechselvorgänge der Zelle, so spalten sie Fette und Kohlenhydrate zu leichter oxydierbaren Verbindungen und oxydieren organische Säuren zu CO_2. Ihnen kommt somit bei der Atmung eine entscheidende Rolle zu, kurz das Mitochondrion ist »das Energiezentrum der Zelle« (Jinks).

Auch die Mitochondrien sind selbständige Träger spezifischer genetischer Informationen. Dies zeigt einmal das Vorkommen rein mütterlich vererbter Mutationen, wie der »petite« Mutanten bei *Saccharomyces* (Abb. 10) und ähnlicher, gleichfalls im Wachstum gehemmter Mutanten von *Neurospora crassa*, die beide mit Störungen in der Bildung wichtiger Atmungsfermente verbunden sind. Der Atmungsstoffwechsel ist aber, wie bereits erwähnt wurde, eng mit den Mitochondrien verbunden.

Es ist ferner in letzter Zeit gelungen, auch in den Mitochondrien DNS nachzuweisen, und mit Hilfe isolierter Mitochondrien-DNS ließ sich zeigen, daß diese in ihrer Zusammensetzung sowohl von der Kern-DNS wie von der DNS in den Chloroplasten verschieden ist. Da auch in den Mitochondrien Messenger-RNS und Transfer-RNS nachgewiesen wurden und da ferner gezeigt werden konnte, daß isolierte Mitochondrien zur Proteinsynthese befähigt sind, dürfen wir auch die Mitochondrien als selbständige Träger genetischer Informationen betrachten. Man glaubt, daß diese sich aus Einzelkomponenten, den Chondriogenen zusammensetzen, die in ihrer Gesamtheit das Chondriom bilden. Die erwähnten »petite« Mutanten bei *Saccharomyces* und bei *Neurospora* sind auf Mutationen im Chondrium zurückzuführen.

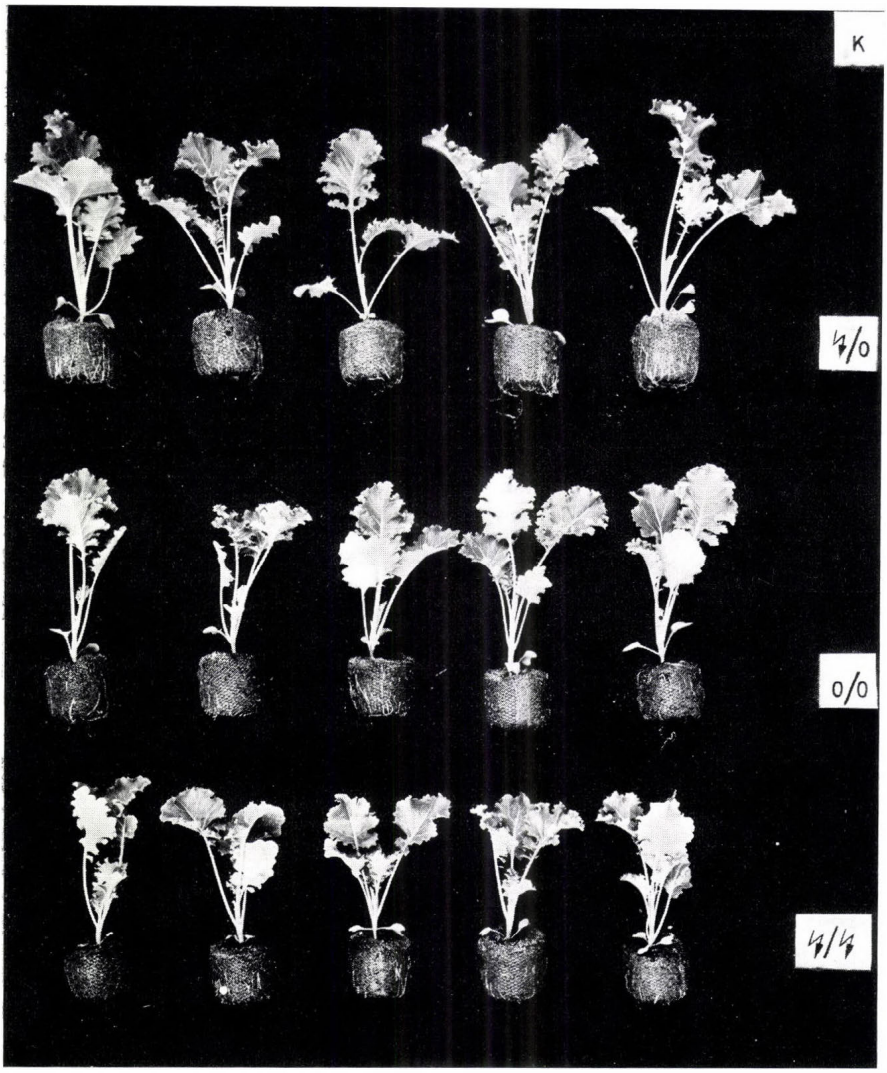


Abb. 9. Obere Reihe: Nachkommen von Grünkohlpflanzen (x_2-Pflanzen), die in der vorhergehenden Generation eine hohe Strahlendosis (75 kR) erhalten hatten. Mittlere Reihe: Kontrollpflanzen. Untere Reihe: Jungpflanzen von Grünkohl, die in der vorhergehenden und in dieser Generation eine hohe Strahlendosis erhalten hatten

Von den weiteren Organellen der Zelle seien die RNS-haltigen *Ribosomen* erwähnt, die die Träger der Proteinsynthese sind. Sie bestehen aus einer RNS-Kette, die von einer Proteinhülle umgeben ist, ihr Bau entspricht also dem der einfachsten Viren. Wieweit die Ribosomen, die nach Beobachtungen an Colibakterien aus kleineren Gebilden, den Eosomen entstehen, sich selbst replizierende Organellen mit einem eigenen genetischen Code

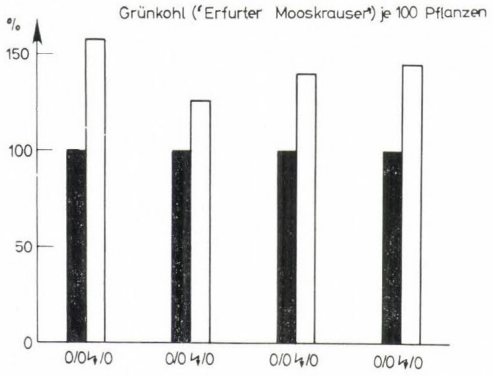


Abb. 10. Stimulierung des Wachstums junger Grünkohlpflänzchen durch Bestrahlung der Samen in der vorhergehenden Generation mit einer hohen Dosis von Röntgenstrahlen. Vier Wiederholungen. Die Werte der Kontrollen wurden gleich 100 gesetzt. Zeichenerklärung: 0/0 = Kontrolle, ↳/0 = in der vorhergehenden Generation bestrahlt

sind, muß noch offen bleiben. Das gleiche gilt für die weiteren Bestandteile des Zellplasmas, das *endoplasmatische Reticulum*, die *Kinetosomen*, den *Golgiapparat*, die *Microsomen* oder *Sphaerosomen* und die *Lysosomen*.

Sicher erscheint jedenfalls, daß mit den Plastiden und den Mitochondrien die Summe der außerhalb der Chromosomen gelegenen Informationen nicht erschöpft ist, und daß wir auch in dem Rest des Zytoplasmas, von Höfler (1960) als Hyaloplasma bezeichnet, noch genetische Funktionen erwarten dürfen, die wir bisher allerdings nicht mit bestimmten Strukturen verbinden können. Das Hyaloplasma als Träger genetischer Informationen und Funktionen wird als *Cytoplasmon* bezeichnet.

Über die DNS-Menge in Plastiden und Mitochondrien ist einiges bekannt. Sie beträgt in den Chloroplasten im Durchschnitt 10^{-11} bis 10^{-12} mg, was etwa der DNS-Menge einer Bakterienzelle entspricht. Der Anteil der Plastiden-DNS an der Gesamt-DNS der Zelle ist im einzelnen sehr verschieden, er kann von 1% bis 25% gehen. Bei den Mitochondrien liegt der DNS-Gehalt bei 10^{-13} bis 10^{-14} g je Mitochondrium und entspricht so etwa dem DNS-Gehalt eines T_2-Phagen. Die Mitochondrien-DNS beträgt etwa 0,2% der Gesamt-DNS der Zelle.

Die Struktur der DNS-haltigen Teile der Plastiden entspricht weitgehend derjenigen der Nucleoide der Bakterien und der Chromatin-Elemente der Cyanophyceen. Wieweit diese Plastiden-DNS polytän oder polyploid ist, also homologe DNS-Stränge in ihr mehrfach oder in größerer Zahl vorhanden sind, läßt sich mit Sicherheit noch nicht sagen. Bei der Mitochondrien-DNS scheint dies tatsächlich der Fall zu sein, denn die Kleinkoloniemutanten der Hefe besitzen in ihren Mitochondrien nur etwa ein Zehntel der DNS-Menge, die sich in den Mitochondrien der Normalform findet, und man nimmt an, daß in den Mitochondrien der Mutante von zehn DNS-Molekülen nur noch eines vorhanden ist. Da bei den Kleinkoloniemutanten die Mitochondrien noch teilungsfähig und — wenigstens zu einem gewissen Teil — noch funktionsfähig sind, erhebt sich hier die Frage, ob diese in den normalen Mitochondrien vorhandenen zehn DNS-Moleküle — die gleiche Zahl wurde übrigens auch bei *Neurospora* gefunden — nicht weitgehend homolog sind. Das würde aber bedeuten, daß zumindest die Mitochondrien polyenergid oder polyploid sind. Das gleiche scheint auch bei den Chloroplasten der Fall zu sein; besonders beachtlich aber ist hier die Angabe, daß bei den Chloroplasten der Polytänie- oder Polyploidiegrad der DNS offenbar beträchtlich schwanken kann (Herrmann 1969).

Bei der Erörterung der Plastiden als Träger genetischer Information wurde bereits eine Reihe von Merkmalen erwähnt, die vom Plastom abhängig sind. Wichtig scheint in diesem Zusammenhang die Tatsache, daß es bei den Euoenotheren fünf verschiedene Plastome gibt (Stubbe 1959, 1960), die offenbar durch Mutation aus einem Urplastom hervorgegangen sind. Diese unterschiedlichen Plastome wirken mit den einzelnen *Oenothera*-Genomen sehr verschiedenartig zusammen. Harmonische Beziehungen zwischen Genom und Plastom führen zur Entstehung vitaler Pflanzen. Passen Genom und Plastom nicht zueinander, so treten je nach dem Grade der Inkompatibilität geringere oder stärkere Störungen in der Entwicklung auf, die zur Unfähigkeit der Plastiden zu ergrünen sowie sich zu teilen führen kann, was wiederum das Absterben der betreffenden Kombinationen zur Folge hat. Plastommutationen können somit einen Isolationsmechanismus schaffen, der die unabhängige evolutionäre Entwicklung genetisch verschiedener Populationen fördern, ja erzwingen kann. Zum anderen aber zeigen die Arbeiten von Stubbe, daß die Analyse des Zusammenwirkens verschiedener Genome mit verschiedenen Plastomen einen Einblick in die Evolution der betreffenden systematischen Gruppe geben kann.

Entsprechende Isolationsmechanismen, die aber auf Unterschieden im Plasmon beruhen — von Plasmon sprechen wir im folgenden immer dann, wenn Fälle extrachromosomaler Vererbung vorliegen, die nicht oder noch nicht auf Vererbung durch das Plastom oder das Chondriom zurückgeführt werden können —, konnten von Lamprecht (1944, 1948) zwischen *Phaseolus vulgaris* und *Ph. coccineus* und von Sirks (1938a, b) zwischen *Vicia faba major* und *minor* aufgezeigt werden. Da die genetische Isolierung ein wichtiger Faktor bei der Differenzierung und Auseinanderentwicklung der Arten sein kann, dürfte mutativen Änderungen der extrachromosomalen Faktoren schon aus diesem Grunde eine gewisse Bedeutung für die Evolution zukommen.

Bedeutungsvoll für die Evolution kann das Plasmon auch dadurch werden, daß es an dem Zustandekommen von Heterosiseffekten mitzuwirken vermag (Michaelis und Kaplan 1950). Auch die Höhe der spontanen Mutationsrate der Kerngene spielt zweifellos bei der Evolution eine Rolle, ist doch die Zahl der je Zeiteinheit entstehenden Mutanten ein Faktor, der einen Einfluß auf das Tempo der Evolution haben kann, besonders beim Eindringen einer Art in eine neue ökologische Nische. Unter diesen Umständen scheint es bemerkenswert, daß H. Stubbe (1935), Kihara (1951) und Michaelis (1953) feststellten, daß durch das Plasmon die Mutabilität der Kerngene erhöht werden kann.

Abgesehen von seiner Fähigkeit zur Isolierung verschiedener Genotypen voneinander sowie seiner Befähigung zur verstärkten Auslösung von Mutationen und zur Herbeiführung von Heterosiswuchs, vermag das Plasmon auch verschiedene wichtige Einzeleigenschaften des Organismus zu beeinflussen, wie Vitalität, Wachstum, Verzweigung, Wuchsform, Blütenbildung und Blütenbau, Geschlechtsverhältnis, zahlreiche physiologische Eigenschaften und anderes mehr.

Über Mutationen des Plastoms und des Chondrioms wurde bereits gesprochen. Plastommutationen sind in größerer Zahl bekannt geworden. Dies ist verständlich, da diese Mutationen leicht erkennbar sind. Auf Chondriommutationen wurde bereits hingewiesen. Aber auch andere, nicht

an bestimmte Organellen lokalisierbare extrachromosomale Mutationen sind bekannt geworden. So beobachtete Sirks (1937) eine solche Mutation bei *Phaseolus* und Gelin (1956) erhielt durch Röntgenbestrahlung eine Plasmonmutation, die Gigaswuchs verursacht.

In diesem Zusammenhang muß das Problem der Beziehung zwischen Genom und extrachromosomalen Faktoren kurz gestreift werden. Auf die unterschiedliche Kompatibilität zwischen verschiedenen Plastomen und Genomen bei *Oenothera* wurde bereits hingewiesen. Bei *Epilobium* konnte Michaelis zeigen, daß auch das Zytoplasmon ähnliche Wirkungen hat. Dort, wo Zytoplasmon und Genom aufeinander angepaßt sind, entstehen normale Pflanzen, dort, wo dies nicht der Fall ist, entstehen Typen mit herabgesetzter Vitalität. Auch das Zytoplasmon vermag also genetische Barrieren zu schaffen, die die Ursache von Formentrennung und unabhängiger evolutionärer Weiterentwicklung werden können.

Darüber hinaus läßt sich ganz allgemein sagen, daß der Idiotypus als Summe der Kerngene und der extrachromosomalen Faktoren ein in sich ausgewogenes Ganzes ist, dessen normale Funktion vom harmonischen Zusammenspiel beider Komponenten abhängt.

In diesem Zusammenhang sei noch erwähnt, daß bestimmte Gene bzw. Allele Mutationen im extrachromosomalen System hervorrufen können, daß umgekehrt aber durch den Plasmotyp auch der Genotyp verändert werden kann, und zwar geschieht dies vor allem mit den Genen, die nicht zu dem betreffenden Plasmotyp »passen«. Diese Veränderungen des Genoms durch das Plasmon, die von verschiedenen Forschern beschrieben wurden, sind von einer Art, die uns sonst im gesamten Erbgeschehen unbekannt und deren Mechanismus uns bisher unklar ist: Es handelt sich hier in allen Fällen um eine allmähliche Veränderung des Genoms durch das Plasmon (Hagemann 1964). Auch der experimentelle Austausch von Kernen zwischen zwei Amoebenarten zeigte, daß sowohl der Kern das Plasmon als auch das Plasmon den Kern verändern kann, wobei die Wirkung des Plasmas stärker war als die des Kerns.

An dieser Stelle ist es nötig, einmal kurz über die Unterschiede zu sprechen, die zwischen der Übertragung der im Zellkern gelagerten Gene und der extrachromosomalen Faktoren bestehen. Die DNS der Kerngene ist in einer bestimmten Zahl von DNS-Molekülen in einer artspezifischen Zahl von Chromosomen vereinigt, die in der Mitose, bei der Befruchtung und bei der Meiosis gesetzmäßig so verteilt und wieder kombiniert werden, daß die Erhaltung und unveränderte Weitergabe des in den Chromosomen vorhandenen genetischen Materials weitgehend gesichert ist. Bei den extrachromosomalen Faktoren ist dies nicht der Fall. Die Organellen, die Träger derartiger genetischer Faktoren sind, finden sich in größerer, weitgehend variabler Zahl in der Zelle. In den Organellen selbst sind darüber hinaus homologe DNS-Fäden mehrfach bis vielfach vorhanden. Da jeder dieser DNS-Fäden an den verschiedenen Loci mutieren kann, dürfen wir einmal damit rechnen, daß bereits im genetischen System der Organellen selbst eine mehr oder minder starke Heterozygotie besteht. Des weiteren dürften sich aber auch die einzelnen Organellen selbst in ihrer genetischen Konstitution voneinander unterscheiden. Werden Mutationen in diesen Organellen ausgelöst, so werden sie sich häufig nicht manifestieren können, weil im Organell und in der Zelle selbst eine so große Menge an »Wild«-Allelen

vorhanden ist, daß sich die mutierten Allele nicht ohne weiteres sogleich auswirken können. Da ein so exakt verlaufender Aufteilungsmechanismus, wie er von den Chromosomen bekannt ist, hier offenbar fehlt, ist auch nicht mit einem regelmäßigen Herausspalten der Mutanten zu rechnen. Eine durch steigende Zahl von Allelen im genetischen System der Organellen induzierte Heterozygotie in den Organellen selbst und im extrachromosomalen genetischen System der Zelle aber könnte zu zunehmender Heterosis führen — wir haben oben darauf hingewiesen, daß das Plasmon am Zustandekommen von Heterosis beteiligt sein kann. Da die bekannten Elemente der extrachromosomalen Vererbung ganz wesentliche Lebensprozesse, wie Photosynthese, Atmung und vielleicht auch die Eiweißsynthese mit steuern, dürfte eine Heterosis in diesen Organellen die Leistungsfähigkeit des betreffenden Organismus verbessern.

Einige eigene Experimente scheinen uns in diese Richtung zu weisen. Bestrahlt man Samen von Kohl oder von Tomaten mit hohen Dosen von Röntgenstrahlen, so erhält man in der bestrahlten Generation, der x_1, zunächst starke Störungen im Wachstum sowie in der Sexualität und Fertilität. Diese strahleninduzierten somatischen Schäden werden im Laufe der Zeit äußerlich mehr oder weniger ausgeglichen. In der nächsten Generation, der x_2, zeigten die Nachkommen der bestrahlten Pflanzen bei Grünkohl eine gegenüber der Kontrolle erhebliche beschleunigte Jugendentwicklung (Abb. 9 und 10). Bei Tomaten wurde das gleiche gefunden (Abb. 11), nur kam hier noch hinzu, daß auch die Wuchsform sowie die Blattform verändert wurde (Abb. 12), daß die Zahl der Früchte um 34%, das mittlere Fruchtgewicht um ungefähr 20% (hochsignifikant gesichert) gesteigert war, und daß die Pflanzen überdies beträchtlich frühreifer waren. Ferner war die Nachkommenschaft der bestrahlten Grünkohl- und Tomatenpflanzen strahlenresistenter als die der Kontrollpflanzen. Charakteristisch ist, daß, wenn man von durch Mutation von Kerngenen auftretenden Mutanten absieht, alle Nachkommen der bestrahlten Pflanzen die gleichen Veränderungen zeigten.

Wurde das von dieser x_2 erhaltene Saatgut wieder bestrahlt, so blieb die Förderung des vegetativen Wachstums und die erhöhte Strahlenresistenz eine weitere Generation hindurch erhalten. Die Fertilität der Pflanzen nahm in

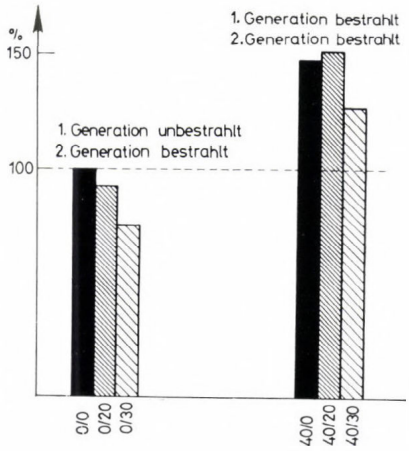
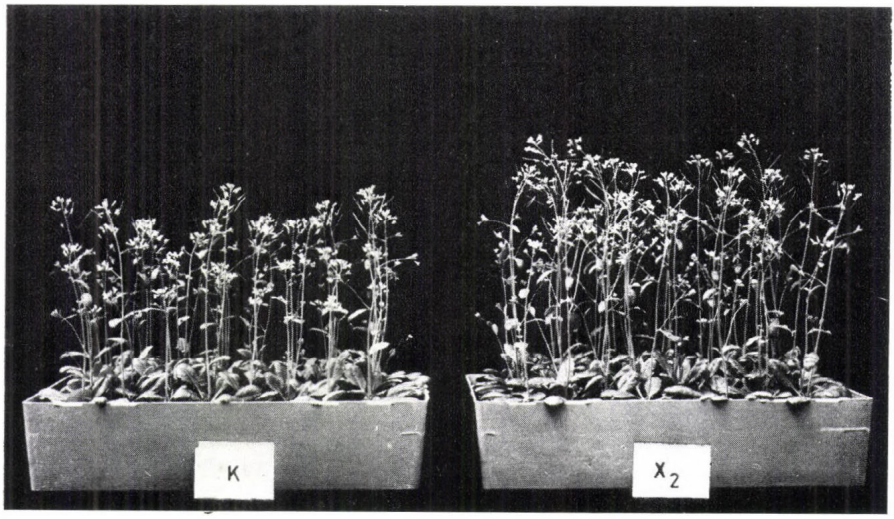


Abb. 11. Förderung des Wachstums und der Strahlenresistenz bei Tomaten durch Bestrahlung der vorhergehenden Generation. Mittleres Frischgewicht in % der unbestrahlten Kontrolle. Zeichenerklärung: 0/0 = in der vorhergehenden und der folgenden Generation unbestrahlt (= Kontrolle); 0/20 = in der vorhergehenden Generation unbestrahlt, in der folgenden mit 20 kR bestrahlt; 0/30 = in der vorhergehenden Generation unbestrahlt, in der folgenden mit 30 kR bestrahlt; 40/0 = in der vorhergehenden Generation mit 40 kR bestrahlt, in der folgenden unbestrahlt; 40/20 = in der vorhergehenden Generation mit 40 kR, in der folgenden mit 20 kR bestrahlt; 40/30 = in der vorhergehenden Generation mit 40 kR, in der folgenden mit 30 kR bestrahlt

Abb. 12. Tomatensorte »Professor Rudloff«. Von links nach rechts: Kontrolle (weder in dieser noch in einer früheren Generation bestrahlt); Pflanzen erstmals in dieser Generation bestrahlt (x_1); Pflanzen nur in der vorhergehenden Generation bestrahlt (x_2); Pflanzen in der vorhergehenden und in der folgenden Generation bestrahlt

diesem Falle jedoch bereits ab (vergl. Abb. 12). Erhielt auch die dritte Generation die gleiche hohe Strahlendosis, wie die beiden vorhergehenden Generationen, so trat wieder eine Schädigung des Wachstums und der Entwicklung ein, die allerdings etwas geringer war als bei erstmals bestrahlten Pflanzen.

Eine entsprechende Wachstumsförderung konnte auch bei *Arabidopsis thalliana* Sippe Enkheim gefunden werden. Auch hier zeigten alle untersuchten x_2-Pflanzen eine Wachstumsförderung und ein früheres Blühen und Reifen. Diese Entwicklungsförderung blieb bis in die x_4 unverändert erhalten (Abb. 13), in der x_5 war sie nur noch in Spuren vorhanden. Im



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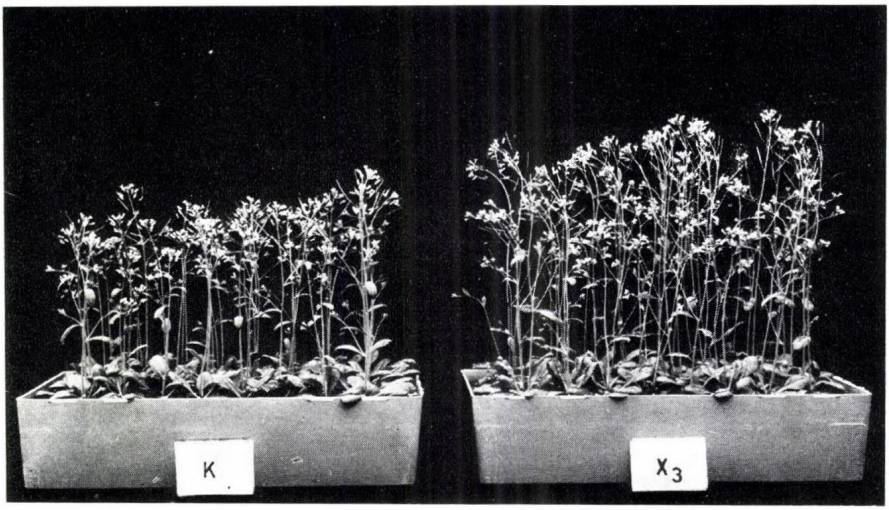

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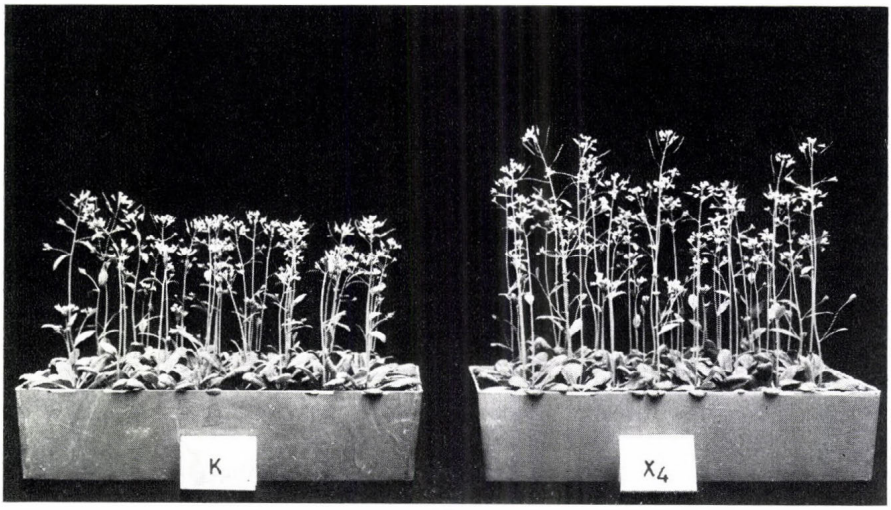

13c

Abb. 13. *Arabidopsis thaliana*. Übertragung der strahleninduzierten Entwicklungsförderung bis in die x_4. (Nach Conrad und Schwanitz)

Gegensatz zu dem Verhalten des Kohls und der Tomaten wurde durch die Bestrahlung hier jedoch die Strahlenresistenz vermindert, und diese strahleninduzierte Herabsetzung der Strahlenresistenz blieb gleichfalls bis in die x_4 erhalten (Abb. 14).

Auf Grund dieser Ergebnisse wurden bei Tomaten reziproke Kreuzungen zwischen bestrahlten und unbestrahlten Pflanzen vorgenommen; über die Ergebnisse dieser Kreuzungen werden wir in Kürze berichten können. Reziproke Kreuzungen zwischen bestrahlten und unbestrahlten Pflanzen

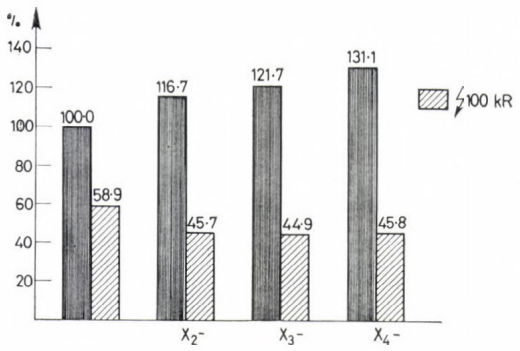

Abb. 14. Förderung der Entwicklung und Verringerung der Strahlenresistenz bei *Arabidopsis thalliana* in der x_2, x_3 und x_4. Die linke Kolumne wiedergibt jeweils die Sproßlänge unbestrahlter Pflanzen (die Werte der $x_1 = 100$ gesetzt), die zweite die Werte von Pflanzen, die außer der Bestrahlung in der x_1 in der jeweiligen Generation (x_2, x_3 oder x_4) nochmals eine Bestrahlung mit 100 kR erhielten. (Nach Conrad und Schwanitz)

von *Begonia semperflorens* erbrachten F_1-Bastarde, die in zwei quantitativen Eigenschaften, im Wachstum und in der Blütenzahl, eindeutig ein der jeweiligen Mutter gleiches Verhalten zeigten. Zusammen mit der bei der Nachkommenschaft aller bestrahlten Pflanzen völlig gleichen Reaktion auf die Bestrahlung spricht dies dafür, daß in diesen Fällen durch die Bestrahlung erbliche Veränderungen im extrachromosomalen System dieser Pflanzen eingetreten sind.

Wie läßt sich nun dieses Verhalten auf Grund der oben beschriebenen Besonderheiten der extrachromosomalen Partikeln deuten? Wir dürfen davon ausgehen, daß alle DNS und RNS in der Lage sind zu mutieren, ganz gleich, ob sie als genetische Information in den Zellkernen oder in anderen genetisch wirksamen Zellbestandteilen enthalten sind. So wird eine ionisierende Bestrahlung auch in den extrachromosomalen Trägern genetischer Funktionen ebenso mutagen wirken, wie in den Zellkernen. Bei steigenden Strahlendosen wird vermutlich auch hier die Zahl der Mutationen steigen, und bei hohen, subletalen Dosen wird sie vermutlich auch entsprechend hoch sein. Die Art und Zahl der Mutationen wird in jedem homologen DNS-Faden verschieden sein, so daß jedes dieser Organellen ein anderes Spektrum an Mutationen besitzt. Einige dieser Mutationen vermögen vielleicht allein oder im Zusammenspiel mit anderen Mutationen in der gleichen Organelle diese — etwa durch Produktion eines »giftigen« Proteins — zu schädigen. Andere werden in ihrer Funktion durch den polytänen oder polyploiden Charakter des in ihnen enthaltenen genetischen Materials unverändert bleiben und in noch anderen entsteht durch die induzierte Heterozygotie ein Heterosiseffekt, der die Funktion und vielleicht auch die Vermehrungsrate dieser Organellen günstig beeinflußt. Ferner ist besonders bei Blütenpflanzen, die eine Blattscheckung zeigen, die auf Plastomwirkung zurückgeht, immer wieder eine Entmischung der zunächst in den Zellen im Gemisch vorhandenen genetisch verschiedenen Chloroplasten beobachtet worden, und auch bei verschiedenen Pilzen konnten Entmischungsvorgänge extrachromosomaler Faktoren gefunden werden.

Nimmt man an, daß stärker heterozygot gewordene Organellen eine höhere Teilungsrate besitzen als genetisch defekte, aber auch als normale Organellen — unterschiedliche Vermehrungsraten sind im Plastom von verschiedenen Chloroplasten von *Oenothera* bekannt —, so könnten im Verlauf der Zellteilungen während der Ontogenese in den Organellen populationen innerhalb der Zellen vielleicht die infolge Heterosis vitaleren Orga-

nellen quantitativ immer mehr die Oberhand gewinnen und für die Leistung der Zelle und des ganzen Organismus entscheidend werden. Diese gesteigerte Leistungsfähigkeit bliebe ständig erhalten und könnte erblich konstant bleiben, wenn sämtliche Organellen in gleicher Weise erblich verändert wären. Ist dies nicht der Fall, so ist es möglich, daß im Laufe der Generationen durch Entmischung der extrachromosomalen Faktoren und eine allmähliche Verringerung der Heterozygotie in den Organellen bei deren Teilungen die ursprünglich erlangte Leistungshöhe wieder herabgesetzt wird, wie wir dies bei *Arabidopsis* beobachtet haben. Entsprechende Entmischungsvorgänge könnten auch das Verschwinden der von Sirks bei *Phaseolus* beobachteten Plasmonmutante nach einigen Generationen verständlich machen.

Fassen wir kurz einige wichtige Tatsachen zusammen: Wir haben im Zytoplasma Gruppen von in Mehrzahl oder Vielzahl auftretenden Organellen, die Träger bestimmter genetischer Funktionen sind; hinzu kommt das restliche Plasma, das Zytoplasmon, das gleichfalls genetische Wirkung hat. Diese Organellen können durch Mutation genetisch voneinander verschieden sein, so daß sich in der Zelle eine Population von untereinander genetisch verschiedenen Faktoren befindet. Durch ungleichmäßige Aufteilung der Organellen während der Zellteilungen oder durch einseitige Förderung oder Verminderung bestimmter Organellentypen (Abb. 15) kann bereits während der Ontogenese eine Veränderung in der genetischen Zusammensetzung dieser Organellenpopulation eintreten. Eine derartige Veränderung aber kann nach allem, was wir über die extrachromosomale Vererbung wissen, zu quantitativen und zu qualitativen Veränderungen im Phänotypus der Pflanze führen. Diese Veränderungen in der Organellenpopulation können nach den Vorstellungen von Jinks, wenn sie nur schwach sind, zu Modifikationen bzw. Phänokopien führen, sind sie stärker, so treten Dauermodifikationen bzw. erbliche Dauermodifikationen auf, und gehen diese Verschiebungen in der Organellenpopulation soweit, daß

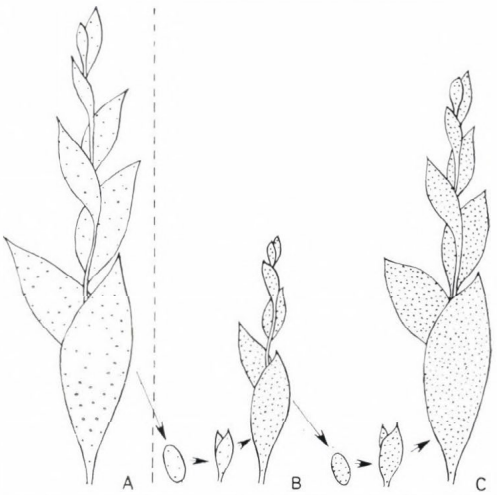

Abb. 15. Schematische Darstellung der Selektion bestimmter Typen von extrachromosomalen Faktoren während der Ontogenese und ihrer Folgen. Das Schema zeigt die Pflanzen A, B und C, die Samen der Pflanzen A und B sowie die aus ihnen gezogenen Sämlinge B und C. Die Punktdichte entspricht der Konzentration der Plasmagene. Es wird angenommen, daß die kälteren Bedingungen, unter denen die Pflanze B wächst, die Teilungsgeschwindigkeit der Zellen verlangsamt, aber auf das Vermehrungstempo der Plasmagene keinen Einfluß hat. B enthält deshalb weniger und kleinere Zellen als A, jedoch ungefähr die gleiche Menge an Plasmagenen. Im Ergebnis haben die Samen der Pflanze B und die daraus gezogenen Sämlinge eine höhere Konzentration an Plasmamengen. Auf diese Weise ist die Pflanze C schon von Anfang an besser an die Kälte angepaßt als die Pflanze B und zeichnet sich durch besseres Wachstum aus. (Aus Crosby 1956)

nur noch Organellen mit gleicher genetischer Konstitution vorhanden sind, so ist die betreffende Komponente des Plasmons stabil geworden.

Wirken auf einen Organismus, der in seinem extrachromosomalen System starke genetische Verschiedenheit aufweist, extreme Außenbedingungen ein, so ist es möglich, daß diese auf sämtliche Zellen einwirken und auch deren genetisch wirksame Organellen intensiv beeinflussen. Es wäre aber denkbar, daß es Organellen gibt, deren genetische Konstitution so beschaffen ist, daß sie von den extremen Bedingungen weniger stark betroffen werden als andere. Sie würden dann auch unter den ungünstigen Bedingungen besser funktionieren und sich besser vermehren können als Plasmonkonstituenten mit einer weniger vorteilhaften genetischen Konstitution. Durch die fortgesetzte scharfe Auslese würden sie innerhalb des Individuums während der Ontogenese immer stärker angereichert, und so könnte durch eine solche intraindividuelle Selektion extrachromosomaler genetischer Faktoren eine Veränderung des Plasmons herbeigeführt werden, die zu einem besseren Angepaßtsein des Organismus und u. U. auch seiner Nachkommen an die veränderten Umweltbedingungen führen kann (vergl. Abb. 15). Erinnern wir uns daran, daß in verschiedenen Fällen festgestellt worden ist, daß durch ein bestimmtes Plasmon das Genom in Richtung auf dieses Plasmon allmählich verändert werden könne, so scheint die Vorstellung von einer umweltinduzierten erblichen Veränderung des Organismus im Sinne einer direkten Anpassung an diese Umweltverhältnisse gar nicht so abwegig, wie es uns noch vor einiger Zeit erschienen sein mag. Diese Erkenntnisse, die wir auf dem Gebiet der extrachromosomalen Vererbung erlangt haben, erlauben es uns meines Erachtens durchaus, derartige lamarckistische Vorstellungen in das Bild der modernen Genetik einzufügen.

Endlich sei eine eigene Versuchsreihe angeführt, die mir durchaus für diese Vorstellungen zu sprechen scheint. Eine Einzelpflanze von *Lycopersicon pimpinellifolium* var. *ribesoides* wurde geklont, und der Klon wurde zum Teil normal ernährt, zum Teil lange Zeit hindurch extremem Nährstoffmangel ausgesetzt. Die von diesen Pflanzen erhaltenen Samen wurden dann jeweils zur Hälfte bei normaler Nährstoffversorgung, zur Hälfte bei Nährstoffmangel zur Keimung gebracht und weiter kultiviert. Abb. 16 gibt das Ergebnis wieder. Es zeigt sich deutlich, daß die Pflanzen, die aus Samen von Hungerpflanzen stammen, den schlechten Ernährungsbedingungen wesentlich besser angepaßt sind, als die Pflanzen, die von normal ernährten Pflanzen stammen. Daß durch den Nährstoffmangel auf die nächste Generation übertragbare Veränderungen entstanden sind, geht auch aus dem Verhalten der normal ernährten Pflanzen hervor. Obgleich die Nachkommen der Hungerformen seit ihrer Keimung ausgezeichnet mit Nährstoffen versorgt waren, wichen ihr Wuchstyp und ihre Blattform von dem der Nachkommen normal ernährter Pflanzen beträchtlich ab und blieben so weitgehend bis zum Ende des Versuchs nach etwa einem Jahr erhalten. Ähnliche Ergebnisse wurden mit einer Kulturtomate erzielt. Eine neue Serie dieser Versuche, deren Ergebnisse uns völlig unerwartet waren, läuft zur Zeit, an ihr sollen auch reziproke Kreuzungen durchgeführt werden. Es darf schließlich nicht unerwähnt bleiben, daß sowohl von Crosby (1956) wie von Feiginson (1959) darauf hingewiesen wurde, daß auf Grund des Vorhandenseins und des genetischen Verhaltens der extra-

Abb. 16. Einwirkung von normaler Ernährung und Hunger auf die Nachkommenschaft eines Klons von *Lycopersicon pimpinellifolium* var. *ribesoides*. Die Beeinflussung der Wuchs- und Blattform sowie der Fähigkeit, mit geringeren Nährstoffgaben auszukommen, wird deutlich. Von links nacht rechts: *Freiland*/Hunger = die Klonpflanzen wurden im ersten Jahr bei guter Ernährung im Freiland gezogen, die Nachkommen bei starkem Nährstoffmangel; *Hunger*/Hunger = die Klonpflanzen wurden im ersten Jahr bei extremem Nährstoffmangel gezogen, desgleichen ihre Nachkommen im zweiten Versuchsjahr; *Freiland*/gut ernährt = die Klonpflanzen wurden im ersten Jahr bei guter Ernährung im Freiland gezogen, die Nachkommen gleichfalls bei guter Ernährung; *Hunger*/gut ernährt = die Klonpflanzen wurden im ersten Jahr bei extremem Nährstoffmangel gezogen, die Nachkommen bei guter Ernährung

chromosomalen genetischen Faktoren eine »Vererbung erworbener Eigenschaften« durchaus vorstellbar wäre.

Fassen wir kurz zusammen, welche Möglichkeiten einer Beeinflussung der Evolutionsvorgänge durch die extrachromosomalen Faktoren gegeben sind. Einmal steuern sie selbst wichtige Lebensprozesse und es besteht damit die Möglichkeit, daß durch Mutationen im extrachromosomalen System die Leistungsfähigkeit des Organismus erhöht wird. Im Zusammenspiel mit dem Genom beeinflussen sie wichtige morphologische und physiologische Eigenschaften und Mutationen im Plasmon oder die Übertragung des Genoms in ein ihm fremdes Plasmon können diese Eigenschaften mehr oder weniger stark verändern. Ferner vermag das Plasmon eine genetische Kreuzungsbarriere zu schaffen, was zur Isolierung und letzten Endes zur getrennten Entwicklung ursprünglich gleichartiger Populationen führt. Von großer Bedeutung für die Evolution kann die Tatsache sein, daß die Träger genetischer Informationen außerhalb des Kerns in jeder Zelle in größerer Zahl enthalten sind, daß homologe DNS-Moleküle in ihnen in größerer Zahl vorhanden sind, und daß sich diese Populationen von Or-

ganellen während der Zellteilung zu entmischen vermögen bzw. daß sich die Zusammensetzung dieser Populationen ändern kann. Wenn dies unter dem Einfluß bestimmter Außenbedingungen geschieht, könnten sich gerichtete genetische Veränderungen im Plasmon vollziehen, die dem entsprechen, was wir als »Vererbung erworbener Eigenschaften« zu bezeichnen pflegen. Die Möglichkeit einer gerichteten Veränderung des Genoms durch das Plasmon wäre ein weiterer Schritt in dieser Richtung.

Alle diese Vorstellungen sind vorläufig nicht viel mehr als Arbeitshypothesen. Sie scheinen mir aber doch in ihrer möglichen Tragweite für die Evolution so bedeutungsvoll, daß ich es für wichtig hielt, einmal die ihnen zugrundeliegenden Tatsachen kurz zusammenzufassen, um zu zeigen, daß die extrachromosomale Vererbung zwar ein bisher recht vernachlässigtes Gebiet der Genetik ist, daß sie aber dazu beitragen kann, unsere Erkenntnisse und Vorstellungen von den der Evolution zugrundeliegenden Vorgängen wesentlich zu bereichern.

Ganz zum Schluß sei noch kurz auf die Vorstellungen von der Evolution der Träger der extrachromosomalen genetischen Information selbst hingewiesen. Es wurde bereits erwähnt, daß Chloroplasten und Mitochondrien zuweilen auf Grund ihrer morphologischen Struktur und der Beschaffenheit ihrer DNS als Zellsymbionten angesehen werden, die ihre Selbständigkeit verloren haben, und die Symbiose farbloser Algen mit Cyanophyceen oder doch wohl von diesen abgeleitete Formen scheint für eine solche Möglichkeit zu sprechen. Die Chloroplasten von *Euglena* bilden einen Übergang von dieser zur nächsten Gruppe: Sie werden bei der Zellteilung regelmäßig an die Tochterzellen weitergegeben, sind aber offenbar nicht lebensnotwendig. Für das Vorkommen von Viren, die als erbliche Symbionten in verschiedenen Wirtsarten leben und in diesen wie extrachromosomale Faktoren wirken, sei nur an die Kappa-Partikeln bei *Paramaecium*, die Sigma-Partikeln bei *Drosophila melanogaster* und den SR-Faktor bei *Drosophila willistoni* und anderen *Drosophila*-Arten erinnert. Die virösen und nichtvirösen Episome endlich können »die Lücke zwischen Vererbung und Infektion, zwischen chromosomaler und extrachromosomaler Vererbung« schließen (Jinks). Denken wir noch an die Möglichkeiten der Übertragung fremden genetischen Materials durch Transformation und Transduktion, so wird klar, daß für den Einbau neuer genetischer Informationen in ein fremdes Plasma und letzten Endes auch in ein fremdes Genom offenbar eine ganze Reihe von Möglichkeiten besteht. Die Möglichkeit, daß fremde Organismen auf dem Umweg über Parasitismus und Symbiose feste Bestandteile des extrachromosomalen Systems der Zelle geworden sind, ist jedenfalls kaum noch von der Hand zu weisen. So erweist sich der extrachromosomale genetische Apparat alles in allem als ein sehr plastisches genetisches System, das für die Evolution ganz besondere Möglichkeiten bietet.

LITERATUR

Baur, E. (1910): Vererbungs- und Bastardierungsversuche mit *Antirrhinum*. *Zschr. indukt. Abstamm.-Vererb.lehre* **3** 34

Correns, C. (1909a): Vererbungsversuche mit blass (gelb) grünen und buntblättrigen Sippen bei *Mirabilis Jalapa*, *Urtica pilulifera* und *Lunaria annua*. *Zschr. indukt. Abstamm.-Vererb. lehre* **1** 291–329

Correns, C. (1909b): Zur kenntnis der Rolle von Kern und Plasma bei der Vererbung. *Ibid.* **2** 331–340

Crosby, J. L. (1956): A suggestion concerning the possible role of plasmagenes in the inheritance of acquired adaptations. *Journ. Genetics* **54** 1
Ephrussi, B. (1953): *Nucleo-cytoplasmic relations in microorganisms.* Oxford
Feiginson, N. I. (1959): *Kritik des modernen Neodarwinismus.* Jena
Gelin, O. E. V. (1956): Problems relating to plant breeding by means of mutation. *Agr. Hort. Gen.* **14** 127
Gibor, A. and Granick, S. (1964): Plastids and mitochondria: Inheritable systems. *Science* **145** 890
Hagemann, R. (1964): *Plasmatische Vererbung.* Jena
Herrmann, R. G. (1970): Multiple amounts of DNA related to the size of chloroplasts. I. *Planta (Berl.)* **90** 80
Höfler, K. (1960): Meiosomes and groundplasm. *Protoplasma* **52** 295
Jinks, J. L. (1967): *Extrachromosomale Vererbung.* Stuttgart
Kandler, O. und Schötz, F. (1956): Untersuchungen über die photooxydative Farbstoffzerstörung und Stoffwechselhemmung bei *Chlorella*-Mutanten und panaschierten Oenotheren. *Zschr. Naturf.* **11b** 708
Kihara, H. (1951): Substitution of nucleus and its effects on genome manifestations. *Cytologie* **16** 177
Kirk, J. T. O. (1964): DNA-dependent RNS synthesis in chloroplast preparations. *Biochem. biophys. Res. Commun.* **14** 393
Kirk, J. T. O. (1967): *The plastids, their chemistry, structure, growth and inheritance.* London and San Francisco
Kislev, N., Swift, H. and Bogorad, L. (1965): Nucleic acids of chloroplasts and mitochondria in swiss chard. *J. Cell Biol.* **25** 327
Lamprecht, H. (1944): Die genisch-plasmatische Grundlage der Artbarriere. *Agri Hortique Genetica* **II** 75-142
Lamprecht, H. 1948: Zur Lösung des Artproblems. Neue und bisher bekannte Ergebnisse der Kreuzung Phaseolus vulgaris L. x coccineus K. und reziprok. *Agri Hortique Genetica* **VI** 87-141
Michaelis, P. (1940): Über die reziprok verschiedenen Sippenbastarde bei *Epilobium hirsutum.* II. Über die Konstanz des Plasmons der Sippe Jena. *Zschr. indukt. Abstamm.-Vererb.lehre* **78** 223
Michaelis, P. (1949): Über Abänderungen des plasmatischen Erbgutes. *Zschr. indukt. Abstamm.-Vererb.lehre* **83** 36
Michaelis, P. (1950): Grundzüge der intraindividuellen Plasmon-Umkombination. *Protoplasma* **39** 260
Michaelis, P. (1951): Interactions between genes and cytoplasm in *Epilobium. Cold Spring Harbor Symp. Quant. Biol.* **16** 121
Michaelis, P. (1953): Das labile Gen Pallidovariabile von *Epilobium*, seine Manifestation und Entstehung in verschiedenen Plasmonabänderungen. *Zschr. indukt. Abstamm.-Vererb.lehre* **85** 282
Michaelis, P. (1954a): Versuche über die Ursachen der Plasmon-Umkombinationen. *Zschr. indukt. Abstamm.-Vererb.lehre* **86** 101
Michaelis, P. (1954b): Cytoplasmic inheritance in *Epilobium* and its theoretical significance. *Adv. Genet.* **6** 287
Michaelis, P. (1956): Plasma-Vererbung. *Hb. Pflanzenzüchtung, Bd. I,* 140
Michaelis, P. (1958a): Untersuchungen zur Mutation plasmatischer Erbträger, besonders der Plastiden. I. Teil. *Planta* **51** 600
Michaelis, P. (1958b): Untersuchungen zur Mutation plasmatischer Erbträger, besonders der Plastiden. II. Teil. *Planta* **51** 722
Michaelis, P. (1958c): Über die Bedeutung des plasmatischen Erbgutes für die Mannigfaltigkeit der Gattung *Epilobium. Biol. Zbl.* **77** 165
Michaelis, P. (1959): Cytoplasmic inheritance and the segregation of plasmagenes. *Proc. Xth Int. Congr. Genet. Vol.* **1** 375
Michaelis, P. (1961): Genetische, entwicklungsgeschichtliche und zytologische Untersuchungen zur Plasmavererbung. I. Über zufallsgemäße und einseitige Verteilung plasmatischer Erbträger während der Zellteilungen, zugleich ein Beitrag zur Analyse intraindividueller Scheckungsmuster. *Flora* **151** 162
Michaelis, P. (1963): Probleme, Methoden und Ergebnisse der Plasmavererbung. *Naturwiss.* **50** 581
Michaelis, P. und Michaelis, G. (1948): Über die Konstanz des Zytoplasmons bei *Epilobium. Planta* **35** 467

Michaelis, P. und Kaplan, R. W. (1950): Manifestationswechsel beim Zusammenwirken chromosomaler und plasmatischer Erbfaktoren. *Naturwiss.* **37** 494
Nass, M. M. K. and Nass, S. (1963a): Intermitochondrial fibers with DNA characteristics. I. Fixation and electron microscopy staining reactions. *J. Cell Biol.* **19** 593
Nass, M. M. K. and Nass, S. (1963b): Intermitochondrial fibers with DNA characteristics. II. Enzymatic and other hydrolytic treatments. *J. Cell Biol.* **19** 613
Oehlkers, F. (1938): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. I. Plasmatische Vererbung und die Geschlechtsbestimmung von Zwitterpflanzen. *Zschr. Bot.* **32** 305
Oehlkers, F. (1940): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. III. Neue Ergebnisse über die Genetik von Wuchsgestalt und Geschlechtsbestimmung. *Ber. Dtsch. Bot. Ges.* **58** 76
Oehlkers, F. (1941): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. IV. Weitere Untersuchungen über Plasmavererbung und Geschlechtsbestimmung. *Zschr. Bot.* **37** 158
Oehlkers, F. (1952): Neue Überlegungen zum Problem der außerkaryotischen Vererbung. *Zschr. indukt. Abstamm.-Vererb.lehre* **84** 213
Oehlkers, F. (1953): Außerkaryotische Vererbung. *Naturwiss.* **40** 78
Oehlkers, F. (1956): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. V. Phänotypische und genotypische Geschlechtsbestimmung bei dem Bastard *Str. (Wendlandii × Rexii). Zschr. indukt. Abstamm.-Vererb.lehre* **87** 722
Oehlkers, F. (1957): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. VI. Die genischen und plasmonischen Grundlagen der Blütenschlitzung verschiedener *Streptocarpus*-Bastarde sowie über die Konstitution des Plasmons. *Zschr. indukt. Abstamm.-Vererb.lehre* **88** 1
Oehlkers, F. (1961a): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. VIII. Neue Untersuchungen über die Blütenschlitzung. *Zschr. Vererb.lehre* **92** 233
Oehlkers, F. (1961b): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. IX. Neue Untersuchungen über die Geschlechtsbestimmung bei *Streptocarpus*. *Zschr. Vererb.lehre* **92** 445
Oehlkers, F. und Ebell, U. (1958): Bastardierungsversuche in der Gattung *Streptocarpus* Lindley. VII. Die genischen und plasmonischen Grundlagen für die Pollensterilität verschiedener *Streptocarpus*-Bastarde. *Zschr. Vererb.lehre* **89** 559
Parthier, B. und Wollgiehn, R. (1966): Nucleinsäuren und Proteinsynthese in Plastiden. In: *Funktionelle und morphologische Organisation der Zelle.* Berlin—Heidelberg—New York
Renner, O. (1919a): Zur Biologie und Morphologie der männlichen Haplonten einiger Oenotheren. *Zschr. Bot.* **11** 305
Renner, O. (1919b): Über das Sichtbarwerden der Mendelschen Spaltung im Pollen von *Oenothera*-Bastarden. *Ber. Dtsch. Bot. Ges.* **37** 129
Renner, O. (1925): Untersuchungen über die faktorielle Konstitution einiger komplexheterozygotischer Oenotheren. *Bibliotheca genetica* **9** 168
Renner, O. (1929): *Artbastarde bei Pflanzen. Handb. d. Vererbungswissenschaft.* Bd. II A, Berlin
Renner, O. (1934): Die pflanzlichen Plastiden als selbständige Elemente der genetischen Konstitution. *Ber. Verh. sächs. Akad. Wiss. Leipzig, Math.-phys. Kl.* **86** 241
Renner, O. (1937): *Zur Kenntnis der Plastiden- und Plasmavererbung.* Cytologia Fujii Jub. Vol., Pars II. 644
Renner, O. (1946): Artbildung der Gattung *Oenothera*. *Naturwiss.* **33** 211
Ris, H. (1963): Ultrastructure of the cell nucleus. In: *Funktionelle und morphologische Organisation der Zelle.* Berlin—Göttingen—Heidelberg
Ris, H. and Plaut, W. (1962): Ultrastructure of desoxyribonucleic acid containing areas in the chloroplast of *Chlamydomonas*. *J. Cell Biol.* **13** 383
Schötz, F. (1955): Untersuchungen an panaschierten Oenotheren. I. Über die photosynthetische Leistungsfähigkeit der Chloroplasten in den blassen Arealen einiger Plastidenmutanten und Bastardschecken. *Zschr. Naturf.* **10b** 100
Schötz, F. (1962): Zur Kontinuität der Plastiden. *Planta* **58** 333
Schötz, F. (1967): Extrachromosomale Vererbung. *Ber. Dtsch. Bot. Ges.* **80** 523
Schwemmle, J. (1940): Plastidenmutationen bei Eu-Oenotheren. *Zschr. indukt. Abstamm.-Vererb.lehre* **79** 171
Schwemmle, J. (1941): Weitere Untersuchungen an Eu-Oenotheren über die genetische Bedeutung des Plasmas und der Plastiden. *Zschr. indukt. Abstamm.-Vererb.lehre* **79** 321

Schwemmle, J. (1943): Plastiden und Genmanifestation. *Flora* **137** 61
Schwemmle, J. (1952): Der Einfluß des Plasmas auf die Affinität zwischen Samenanlagen und Pollenschläuchen. I. *Biol. Zbl.* **71** 487
Schwemmle, J. (1957a): Der Einfluß des Plasmas auf die Affinität zwischen Samenanlagen und Pollenschläuchen. II. *Biol. Zbl.* **76** 443
Schwemmle, J. (1957b): Der Einfluß des Plasmas und der Plastiden auf die Affinität zwischen Samenanlagen und Pollenschläuchen. III. *Biol. Zbl.* **76** 529
Schwemmle, J., Haustein, E., Sturm, A. und Binder, M. (1938): Genetische und zytologische Untersuchungen an Eu-Oenotheren. Teil I—VI. *Zschr. indukt. Abstamm.-Vererb.lehre* **75** 358
Sirks, M. J. (1937): Plasma-Änderung als Ursache einer Knospenvariation. *Zschr. indukt. Abstamm.-Vererb.lehre* **73** 367
Sirks, M. J. (1938a): A case of bud-variation in *Phaseolus* caused by a transitory plasmatic change. *Genetica* **20** 121
Sirks, M. J. (1938b): Plasmatic inheritance. *Botan. Rev.* **4** 113
Sprey, B. (1968): Zum Verhalten DNS-haltiger Areale des Plastidenstromas bei der Plastidenteilung. *Planta* **78** 115
Stubbe, H. (1935): Über den Einfluß artfremden Plasmas auf die Konstanz der Gene. *Zschr. indukt. Abstamm.-Vererb.lehre* **70** 161
Stubbe, W. (1959): Genetische Analyse des Zusammenwirkens von Genom und Plastom bei *Oenothera*. *Zschr. Vererb.lehre* **90** 288
Stubbe, W. (1960): Untersuchungen zur genetischen Analyse des Plastoms von *Oenothera*. *Zschr. Bot.* **48** 191
Stubbe, W. (1962): Sind Zweifel an der genetischen Kontinuität der Plastiden berechtigt? Eine Stellungnahme zu den Ansichten von Mülethaler und Bell. *Zschr. Vererb. lehre* **93** 175
Stubbe, W. (1963a): Die Rolle des Plastoms in der Evolution der Oenotheren. *Ber. Dtsch. Bot. Ges.* **76** 154
Stubbe, W. (1963b): Extrem disharmonische Genom-Plastom-Kombinationen und väterliche Plastidenvererbung bei *Oenothera*. *Zschr. Vererb.lehre* **94** 392
Stubbe, W. (1966): *Die Plastiden als Erbträger. Probleme der biologischen Reduplikation.* Berlin–Heidelberg–New York
Wettstein, F. v. (1927): Über die plasmatische Vererbung sowie Plasma- und Genwirkung. *Nachr. Ges. Wiss. Göttingen* 1926, *Math.-phys. Kl.* **250**
Wettstein, F. v. (1928a): Morphologie und Physiologie des Formwechsels der Moose auf genetischer Grundlage. II. *Bibliotheca genetica* **10** VI, 216, Berlin
Wettstein, F. v. (1928b): Über plasmatische Vererbung und über das Zusammenwirken von Genen und Plasma. *Ber. Dtsch. Bot. Ges.* **46** 32
Wettstein, F. v. (1930): Über plasmatische Vererbung, sowie Plasma- und Genwirkung. II. *Nachr. Ges. Wiss. Göttingen, Math.-phys. Kl. Fachgr. VI (Biologie)* **2** 109
Wettstein, F. v. (1937): Die genetische und entwicklungsphysiologische Bedeutung des Cytoplasmas. *Zschr. indukt. Abstamm.-Vererb.lehre* **73** 349
Wild, A. (1958): Experimentelle Beeinflussung des Granamusters einer abweichenden Plastidensorte von *Antirrhinum majus*. *Planta* **50** 379

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ZUR ENTWICKLUNG DER GATTUNG PEDICULARIS L. IM EUROPÄISCHEN RAUME

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Die Gattung *Pedicularis* L. wird in neuester Zeit, wohl mit Recht, meist als selbständige Subtribus *Pedicularinae*, ganz an den Anfang der halbparasitischen Rhinanthoideen gestellt, und sie umfaßt, insoweit man heute die Situation einigermaßen übersehen kann, etwa 500 bis 600 Arten. Obwohl unsere Gattung in ihren morphologischen Merkmalen gegenüber den nächst verwandten Gattungen relativ gut abgegrenzt ist, ihre weitere taxonomische Unterteilung ist trotzdem recht uneinheitlich und noch heute ziemlich offen. Die sehr zahlreichen Sippen zeigen nämlich in ihren vegetativen und reproduktiven Merkmalen ein fast unübersehbares Gemisch von analogen und homologen Ausbildungen auf, die untereinander, meist ohne sichtbare Korrelationen, kombiniert sind. Es wurde bisher noch kein ernstlicher Versuch unternommen, die umfangreiche Gattung *Pedicularis* in Untergattungen aufzugliedern.

Die älteren Systeme der Gattung *Pedicularis* beruhen auf verschiedenen Grundlagen und sind, da sie meist nur auf einzelnen morphologischen Merkmalen aufgebaut sind, recht ungleichartig ausgefallen. Ihr Wert liegt zwar in einer erleichterten Übersichtlichkeit, die jedoch ausgesprochen künstlich erscheint.

So wurde die Gattung *Pedicularis* von Steven (1823), Bunge (1849), Maximovicz (1877, 1888), Prain (1890), Bonati (1918) und Limpricht (1924) aufgegliedert auf Grund der Beschaffenheit der Blütenkrone, besonders nach ihrer Oberlippe, wobei meist die zahnlosen *Anodontae*, die mehr oder minder zweizähnigen *Bidentatae*, die kurzgeschnäbelten *Rhyncholophae* sowie die langschnabeligen *Longirostres* in verschiedener Umgrenzung und mit unterschiedlicher Benennung aufgestellt wurden. Bonati (1918) und Limpricht (1924) haben die genannten Gruppen in je eine wirtelig (»verticillatae«) bzw. eine wechselig (»alternifoliae«) beblätterte Untergruppe weiter unterteilt.

Li (1948–1949) versuchte dagegen eine neue Gliederung auf Grund der Beblätterung auszubauen, während Tsoong und Chang (1965) ihr System der Gattung *Pedicularis* vorwiegend nach palynologischen Merkmalen aufstellten.

Von allen bisherigen Systemen, die in neuerer Zeit eine naturgemäße Gliederung der Gattung *Pedicularis* anstreben, verdient wohl dasjenige von Tsoong (1955–1956, 1961) besondere Beachtung, da es sich nicht nur durch eine gleichmäßigere Heranziehung von mehreren morphologischen Merkmalen, sondern auch durch die Einführung von zwei Blüten-Grundformen (*Capitata* bzw. *Flammea*-Typ) auszeichnet, wodurch eine zuver-

lässige Grundlage für einen weiteren Ausbau eines natürlichen Systems der Gattung gegeben ist. Nach Tsoong (1955–1956) wird die Gattung *Pedicularis* in 13 Greges mit etwa 100 Serien aufgeteilt und weicht dadurch ganz wesentlich von allen anderen Großgliederungen der Gattung ab.

Andererseits aber ist es bemerkenswert, daß, im Gegenteil zu den recht ungleichartigen Großgliederungen, innerhalb der niedrigsten taxonomischen Rangstufe der Gattung, im Bereiche der Serien, eine fast allgemeine und recht auf fällige Übereinstimmung über ihre morphologische und taxonomische Umgrenzung hervortritt.

Auch die cytologischen Kenntnisse über die Gattung *Pedicularis* sind einstweilen noch zu dürftig, um eine annehmbare Erklärung über ihre stark explosive und polymorphe, sowohl allgemeine als auch lokale Entwicklung aussagen zu können. Nach den entsprechenden Angaben, die Darlington und Wylie 1955, Löve und Löve 1961, Ornduff und Mitarb. (1967–1969), Fedorow und Mitarb. (1969), Moore und Mitarb. (1970) und Löve (1967–1970) entnommen sind, geht nämlich hervor, daß nur für insgesamt 52 *Pedicularis*-Taxa, also für kaum ein Zehntel aller bekannten Arten, die Chromosomenzahlen gezählt bzw. bekannt sind.

Trotzdem aber ergibt sich aus der bereits vorliegenden cytologischen Übersicht die interessante Tatsache, daß der schon oben erwähnten starken morphologischen Plastizität eine recht einheitliche, also keinesfalls bewegte cytologische Gestaltung gegenübersteht. 46 Arten, also der weitaus größte Teil der untersuchten Taxa, weist nämlich die einheitliche Zahl $2n = 16$ auf. Als tetraploid erwiesen sich mit $2n = 32$ weitere vier Arten, und zwar *P. apodochila* Maxim. (Ostasien), *P. villosa* Ledeb. (Sibirien) und *P. groenlandica* Retz. (Arkt. Nordamerika) sowie die auch in Europa vorkommende *P. sceptrum-carolinum* L.*

Als stärker abweichend, mit $2n = 12$, treten nur zwei Arten hervor, nämlich die in Eurasien und Nordamerika weit verbreitete *P. verticillata* L. sowie die bisher meist übersehene *P. carnosa* Wall. (West-Himalaya).

Die Basis-Chromosomenzahl ist nach dem Gesagten für die Gattung *Pedicularis* mit $x = 6 = 8$ anzugeben.

Als primäres Entwicklungszentrum der Gattung *Pedicularis* wird meist Asien mit seinen zentralen und östlichen Gebieten angesprochen; in ihnen wurden mehr als die Hälfte der bisher bekannten Taxa vorgefunden und beschrieben. Alle Vebreitungsgebiete der *Pedicularis*-Taxa in den weiteren Teilen von Asien, Europa und Amerika wären demnach als sekundäre Entfaltungszentren zu betrachten, obwohl auch andere Deutungen, besonders auf Grund der zirkumarktischen Verbreitung, möglich sind.

In Europa ist die Gattung *Pedicularis* mit 67 Taxa vertreten, von denen meist 55–58 als gute Arten, die restlichen als Unterarten bewertet werden. In cytologischer Hinsicht sind bisher 24 Taxa untersucht worden, wobei bei 22 Arten** die Chromosomenzahl $2n = 16$ beträgt und je eine Art mit $2n = 32$ *(P. sceptrum-carolinum)* bzw. $2n = 12$ *(P. verticillata)* hinzukommen.

* Kürzlich haben Gadella und Kliphuis (1968) in Holland auch eine tetraploide Population ($2n = 32$) von *P. sylvatica* L. festgestellt.

** Auf eine abweichende tetraploide Population von *P. sylvatica* wurde schon oben hingewiesen.

Während nun im nördlichen Teil Europas fast nur zirkumpolare oder euroasiatische Arten mit umfangreichen Arealen vertreten sind, haben sich in den Alpen und in den davon südlicheren Gebieten im Bereich einiger Gruppen lokale Entfaltungszentren herausgebildet, die eine größere Anzahl von endemischen Taxa hervorgebracht haben. So sind die beiden anodonten Serien *Limnogenae* und *Roseae* rein europäisch und die anodonten *Foliosae*, die bidentaten *Comosae* und die rhyncholophen *Rostratae* treten durch ihren Arten- und Endemitenreichtum im europäischen Raum hervor.

Ein informativer Überblick über die in Europa vorkommenden *Pedicularis*-Taxa und ihre ebenfalls kurzgefaßten chorologischen Verhältnisse, der teils nach Steininger (1886–1887), Maly (1907, 1932), Limpricht (1924, 1927), Hayek (1929), Klaštersky (1928), Mayer (1969) und Hartl (1969), teils nach eigenen Untersuchungen zusammengestellt ist, ergibt folgendes Bild:

Ser. ***Acaules*** (3 Arten): *P. acaulis* Scop., südostalpin–illyrisch (Endemit).

Ser. ***Gloriosae*** (7 Arten): *P. sceptrum-carolinum* L. ($2n = 32$), nord-eurasisch (bis Zentraleuropa).

Ser. ***Foliosae*** (7 Arten): *P. foliosa* L. ($2n = 16$), südeuropäisch (Endemit); *P. hoermanniana* Maly, illyrisch–zentralbalkanisch (Endemit); *P. hacquetii* Graf, südalpin–karpatisch (Endemit); *P. exaltata* Besser, zentral-osteuropäisch (Endemit).

Ser. ***Limnogenae*** (2 Arten): *P. recutita* L. ($2n = 16$), alpin (Endemit); *P. limnogena* L., ostkarpatisch–zentralbalkanisch (Endemit).

Ser. ***Roseae*** (2 Arten): *P. rosea* Wulf. subsp. *rosea* ($2n = 16$), süd- und ostalpin (Endemit), subsp. *allionii* (Reichenb. fil.) E. Mayer, westalpin (Endemit); *P. orthantha* Griseb., zentral-balkanisch (Endemit).

Ser. ***Hirsutae*** (9 Arten): *P. dasyantha* Hadač, arktisch–eurasisch (auch Spitzbergen); *P. hirsuta* L. ($2n = 16$), arktisch–eurasisch–nordamerikanisch; *P. oederi* Vahl ($2n = 16$), eurasisch–nordamerikanisch (Nordeuropa, Alpen, Karpaten, Balkangebirge); *P. flammea* L. ($2n = 16$), arktisch–nordamerikanisch–nordwesteuropäisch.

Ser. ***Verticillatae*** (20 Arten): *P. verticillata* L. ($2n = 12$), eurasisch–nordamerikanisch.

Ser. ***Amoenea*** (5 Arten): *P. amoena* Adams, arktisch–eurasisch; *P. arguteserrata* Vveden., osteuropäisch–sibirisch.

Ser. ***Palustres*** (10 Arten): *P. palustris* L. subsp. *palustris* ($2n = 16$), eurasisch–nordamerikanisch, subsp. *opsiantha* (Ekman) Almquist, nordeuropäisch (Endemit), subsp. *borealis* (J. W. Zetterst.) Hylander, nordwesteuropäisch (Endemit); *P. karoi* Freyn, osteuropäisch–sibirisch; *P. labradorica* Wirsing ($2n = 16$), arktisch–eurasisch–nordamerikanisch; *P. sylvatica* L. subsp. *sylvatica* ($2n = 16, 32$), west–zentraleuropäisch (Endemit), subsp. *lusitanica* (Hoffmanns. und Link) Coutinho, iberisch (Endemit), subsp. *hibernica* Webb, hibernisch (Endemit).

Ser. ***Sudeticae*** (9 Arten): *P. sudetica* Willd. ($2n = 16$), nordeurasiatisch–arktisch–nordamerikanisch (isoliert in Zentraleuropa im Gebirge Krkonoši [= Riesengebirge]).

Ser. ***Comosae*** (ca. 40 Arten): *P. comosa* L., südeuropäisch (Endemit); *P. campestris* Griseb. und Schenk, südosteuropäisch (Endemit); *P. kaufmannii* Pinzger, osteuropäisch (Endemit); *P. sibthorpii* Boiss., osteuropäisch–südwestasiatisch; *P. uralensis* Vveden., nordosteuropäisch–westsibirisch; *P. schizocalyx* (Lange) Steining., iberisch (Endemit); *P. asparagoides*

Lapeyr., pyrenäisch–iberisch (Endemit); *P. brachyodonta* Schloss. und Vukot. subsp. *brachyodonta*, illyrisch–zentralbalkanisch (Endemit), subsp. *moesiaca* (Stadlm.) Hayek, südostbalkanisch (Endemit); *P. malyi* Janka, illyrisch (Endemit); *P. grisebachii* Wettst., zentralbalkanisch (Endemit); *P. heterodonta* Pančić, zentralbalkanisch (Endemit); *P. leucodon* Griseb. subsp. *leucodon*, zentralbalkanisch (Endemit), subsp. *occulta* (Janka) E. Mayer, ostbalkanisch (Endemit); *P. physocalyx* Bunge, osteuropäisch–sibirisch–zentralasiatisch; *P. dasystachys* Schrenk, osteuropäisch–sibirisch; *P. graeca* Bunge, südbalkanisch (Endemit); *P. friderici-augusti* Tommasini, illyrisch–apenninisch (Endemit); *P. petiolaris* Ten., balkanisch–apenninisch (Endemit); *P. ferdinandii* Bornm., zentralbalkanisch (Endemit).

Ser. ***Compactae*** (14 Arten): *P. compacta* Steph. ($2n = 16$), osteuropäisch–sibirisch–zentralasiatisch; *P. lapponica* L. ($2n = 16$), nordeurasisch–nordamerikanisch.

Ser. ***Rostratae*** (ca. 30 Arten): *P. tuberosa* L. ($2n = 16$), südwesteuropäisch–alpin (Endemit); *P. elongata* Kerner ($2n = 16$), südalpin (Endemit); *P. julica* E. Mayer, südostalpin (Endemit); *P. ascendens* Gaud. ($2n = 16$), westsüdalpin (Endemit); *P. baumgartenii* Simonkai, südkarpatisch (Endemit); *P. rostrato-spicata* Crantz subsp. *rostrato-spicata* ($2n = 16$), ostalpin (Endemit), subsp. *helvetica* (Steining.) O. Schwarz, westalpin–pyrenäisch (Endemit); *P. rostrato-capitata* Crantz subsp. *rostrato-capitata* ($2n = 16$), ostalpin–westillyrisch (Endemit), subsp. *glabra* Kunz, südalpin (Endemit); *P. kerneri* Dalla Torre ($2n = 16$), zentralwestalpin–pyrenäisch (Endemit); *P. pyrenaica* Gay ($2n = 16$), pyrenäisch (Endemit); *P. mixta* Grenier, pyrenäisch (Endemit); *P. cenisia* Gaud., westalpin–apenninisch (Endemit); *P. gyroflexa* Vill. subsp. *gyroflexa* ($2n = 16$), westsüdalpin–pyrenäisch (Endemit), subsp. *praetutiana* (Levier in Steining.) Kunz und E. Mayer, apenninisch (Endemit); *P. elegans* Ten., apenninisch (Endemit); *P. portenschlagii* Sauter, ostalpin (Endemit); *P. asplenifolia* Floerke ($2n = 16$), ostalpin (Endemit).

Ser. ***Resupinatae*** (ca. 12 Arten): *P. resupinata* L. ($2n = 16$), osteuropäisch–sibirisch–ostasiatisch.

Diese Übersicht stellt nur eine bewußt kurzgefaßte Zusammenfassung der bisherigen Kenntnisse über die Gattung *Pedicularis* im europäischen Raum dar. Aus unseren Untersuchungen, die vor allem im Bereich der *Comosae* und *Rostratae* aus verschiedenen Alpen- und südeuropäischen Gebieten im Gange sind, erhoffen wir in absehbarer Zeit eine weitere Beleuchtung mehrerer offener taxonomischer und entwicklungsgeschichtlicher Probleme zu bekommen.

LITERATUR

Bonati, G. (1918): Le genre *Pedicularis* L. *Morphologie, classification, distribution géographique, évolution* et *hybridation*. Univ. Nancy, Diss. 48

Bunge, A. (1849): *Pedicularis* L. In: C. F. Ledebour, *Flora Rossica* **3** 268–303

Darlington, C. D. and Wylie, A. P. (1955): *Chromosome Atlas of Flowering Plants*, 2nd ed.

(Fedorow, A. A. und Mitarb.) Федоров, А. А. и сотр. (1969): Хромосомные числа цветковых растений АН СССР, Бот. инст. В.Л. Комарова.

Hartl, D. (1969): *Pedicularis* L. In: G. Hegi: *Illustr. Flora von Mitteleuropa*. 2. Aufl. Bd. 6, 261–315

Hayek, A. (1929): *Prodromus Florae peninsulae Balcanicae* **2** (**2**) 192–7. *Feddes Repert. Beih.* **30** (**2**)
Klaštersky, I. (1928): Les espèces européennes du groupe des *Foliosae* (Maxim) du genre *Pedicularis*. *Bull. int. Acad. Sci. Bohême* **1928** 1–29
Li, H.-L. (1948–1949): A revision of the genus *Pedicularis* in China. *Proc. Acad. Nat. Sci. Philadelphia* **100** 205–378 (1948), **101** 1–214 (1949)
Li, H.-L. (1951): Evolution in the flowers of *Pedicularis*. *Evolution* **5** 158–64
Limpricht, W. (1924): Studien über die Gattung *Pedicularis*. *Feddes Repert.* **20** 161–265
Limpricht, W. (1927): Nachträge zu *Pedicularis*. *Feddes Repert.* **23** 333–9
Löve, A. (1967–1970): IOPB Chromosome number reports. *Taxon* **16, 17, 18, 19**
Löve, A. and Löve, D. (1961): Chromosome numbers of Central and Northwest European plant species. *Opera Bot.* 5
Maly, K. (1907): Über *Pedicularis Hoermanniana* und verwandte Arten. *Magyar Bot. Lapok* **6** 143–9
Maly, K. (1932): Ein Beitrag zur Kenntnis einiger *Pedicularis*-Sippen Illyriens. *Glasn. Bot. zav. bašt. Univ. Beograd* **2** (**1/2**) 94–103
Maximovicz, C. J. (1877): *Pedicularis* L. Species Asiae orientalis cum totius generis conspectu. Diagnoses plantarum novarum asiaticarum 2. *Bull. Acad. Imp. Sci. Pétersb.* **24** 51–89
Maximovicz, C. J. (1882): Addenda et emendanda ad *Pedicularium* conspectum. Diagnoses plantarum novarum asiaticarum 4. *Bull. Acad. Imp. Sci. Pétersb.* **27** 510–21
Maximovicz, C. J. (1888): *Pedicularis* L. Synopsis generis nova. Diagnoses plantarum novarum asiaticarum 7. *Bull. Acad. Imp. Sci. Pétersb.* **32** 515–619
Mayer, E. (1969): Notulae ad floram Jugoslaviae III. Conspectus generis *Pedicularis* L. *Acta bot. Croatica* **28** 437–48
Moore, R. J. et al. (1970): Index to plant chromosome numbers for 1968. *Reg. veg.* **68**
Ornduff, R. et al. (1967–1969): Index to plant chromosome numbers for 1965, *Reg. veg.* **50** (1967); for 1966 *Reg. veg.* **55** (1968); for 1967 *Reg. veg.* **59** (1969)
Prain, D. (1890): The species of *Pedicularis* of the Indian Empire and its frontiers. *Ann. Bot. Gard. Calcutta* **3** 1–196
Steininger, H. (1886–1887): Beschreibung der europäischen Arten des Genus *Pedicularis*. *Bot. Centralbl.* **28** (1886); **29** (1887); **30** (1887)
Steven, C. (1823): Monographia *Pedicularis*. *Mém. Soc. Nat. Moscou* **6** 1–60
Tsoong, P.-Ch. (1955–1956): A new system for the genus *Pedicularis*. *Acta Phytotax. Sinica* **4** 71–147 (1955); **5** 41–73, 239–78 (1956)
Tsoong, P.-Ch. (1961): A new system for the genus *Pedicularis* (continued). *Acta Bot. Sinica* **9** 230–74
Tsoong, P.-Ch. and Chang, K. T. (1965): Palynological study of *Pedicularis*, and its relation with the taxonomic system of the genus. *Acta Phytotax. Sinica* **10** 257–81, 357–74

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DIE INTROGRESSIVE HYBRIDISATION IN DER GATTUNG PICEA A. DIETR.

von

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Die systematische Einteilung der Gattung *Picea*, die Klassifikation und sogar die Differenzierung ihrer Arten bereiten öfters große Schwierigkeiten; einen Grund dafür findet man in der Hybridisation der Arten, die in dieser Gattung öfters vorkommt. Die gewöhnlichen Fälle der Artenhybridisation, die sowohl in der Natur als auch in Dendrarien, das heißt in Kulturverhältnissen vorkommt, haben in dieser Hinsicht keine große Bedeutung. Ihre wesentliche Bedeutung besteht eher darin, daß sie die genetische Nähe der Arten und ihre physiologische Übereinstimmung bezeugen, sogar in Fällen, wenn diese Arten zu verschiedenen Sektionen der Gattung gehören.

Die Erscheinung der introgressiven Hybridisation aber, die früher nicht verstanden, derzeit aber in dieser Gattung endlich erkannt wurde, rief und ruft auch jetzt noch zahlreiche Klassifikationsschwierigkeiten hervor. An die introgressive Hybridisation bei den Fichten hat erstmalig der Verfasser dieses Artikels hingewiesen (Bobrow 1944), und in letzter Zeit wurde sie auch von kanadischen Gelehrten beschrieben. Wir wissen jetzt, daß auf den großen, weit ausgedehnten Territorien des europäischen Teils von Rußland, in den Gebieten Nordamerikas, die an den Atlantischen und den Stillen Ozean grenzen, wie auch im Fernen Osten, Fichten verbreitet sind, deren Artenzugehörigkeit unbestimmt ist. Wir werden später noch ausführlicher darüber sprechen, an dieser Stelle bemerken wir nur, daß dieser Erscheinung auch aus florogenetischem Aspekt große Bedeutung zukommt. Wie gesagt, ist die Hybridisation zwischen den Fichtenarten keine seltene Erscheinung: es sind solche Fälle unter natürlichen Verhältnissen bekannt und Hybriden werden auch in Baumschulen und Dendrarien erhalten, wo eine künstliche Kreuzung vorgenommen wird. In der neuesten Übersicht von Dallimore und Jackson (1966) werden folgende Hybriden erwähnt:

1. *P.* × *hurstii* — eine natürliche Hybride zwischen *P. engelmannii* und *P. pungens*.

2. *P.* × *lutzii* — eine natürliche Hybride auf Alaska und auf der Halbinsel Kinai, wo die *P. glauca* und *P. sitchensis* zusammen wachsen. Diese Arten wurden auch in Europa künstlich gekreuzt. Sehr interessant ist, daß die genannten Arten zu verschiedenen Sektionen der Gattung gehören.

3. *P.* × *saaghii* — eine Hybride von *P. jezoensis* und *P. glauca*, einer japanischen und einer amerikanischen Art aus verschiedenen Sektionen. Sie wurde zum ersten Mal 1917 registriert.

4. *P.* × *notha* — eine Hybride zwischen *P. hondoensis* und *P. glehnii*, die nur in Kultur bekannt ist. Sie könnte aber im Fernen Osten auch unter

natürlichen Verhältnissen entdeckt werden. Die Eltern gehören zu verschiedenen Sektionen der Gattung.

5. *P.* × *mariorica* — eine Hybride der amerikanischen *P. mariana* und der serbischen *P. omorica*. Wurde in einer Baumschule Deutschlands im Jahre 1925 erhalten.

6. *P. mariana* × *P. glauca* — eine natürliche Hybride, welche in Minnesota bekannt ist.

7. *P. glehnni* × *P. jezoensis* — eine in Kultur bekannte Hybride. Es ist aber möglich, daß hier von *P.* × *notha* die Rede ist, bei welcher der eine Elter *P. jezoensis* ist. Die letztere wird von einigen Autoren von *P. hondoensis* nicht unterschieden.

Mit dieser Liste ist die Zahl der *Picea*-Hybriden selbstverständlich nicht erschöpft. Hier ist es angezeigt, die Aufmerksamkeit auf einige Fälle der Hybridisation zu lenken, welche vollkommen unerwartet und sogar unmöglich erscheinen. In der Literatur (Gaussen 1966, S. 653) findet man einen Hinweis auf die Hybridisation zwischen *Picea sitchensis* und *Tsuga heterophylla*. Es wird mitgeteilt, daß diese Hybriden *(Tsuga=Picea hookeriana)* im oberen Gürtel des Küstengebirges vom Felsengebirge (Rocky Mountains) von Alaska bis Kalifornien verbreitet ist.

Gaussen weist auch auf die Kreuzung der genannten Hybriden mit *Picea engelmannii* hin. Diese dreifache Hybride *(Tsuga=Picea crassifolia)* kommt in Kalifornien und Nevada vor. In derselben Arbeit gibt Gaussen einen Hinweis auf die Hybridisation der chinesischen *Tsuga chinensis* mit der Art der Gattung *Keteleeria evelyniana* aus Südostasien. Diese Hybride ist in einer Gebirgsgegend von Südchina weit verbreitet. Wie merkwürdig auch diese Tatsachen erscheinen mögen, sie zeugen von der Möglichkeit einer intergenerischen Hybridisation bei Coniferen. Anscheinend ist die Hybridisation zwischen *Picea* und *Tsuga* und zwar der zwei obengenannten Fichten aus der Sektion *Casicta* und einigen *Tsuga*-Arten aus der Sektion *Hesperopeuce* nicht zu bezweifeln. Die intergenerische gegenwärtige Hybridisation *Picea=Tsuga* gibt einen Grund zur Vermutung, daß solche Hybridisationen auch in der Vergangenheit stattfinden konnten, im Neogen und sogar im Paleogen, und zwar nicht nur im Felsengebirge, sondern auch in anderen fernen Gebieten, zum Beispiel in Nordasien oder in Europa, wo die Gattung *Tsuga* im Tertiär weit verbreitet war. Die Möglichkeit der Hybridisation zwischen *Picea* und *Tsuga* ist auch deshalb ein verlockender Gedanke, weil sie die Entstehung der Fichten der Sektion *Omorica* erklären könnte. Ist man sich auch über die Verschiedenheiten der beiden Gattungen im klaren (Pollenbau und andere Merkmale), muß man doch eine gewisse Ähnlichkeit im Aufbau der Zapfen zugeben, und zwar bestehen die Zapfen aus holzartigen lockeren Schuppen. Man darf vermuten, daß an dieser Hybridisation verschiedene *Tsuga*-Arten teilgenommen hatten.

Beispielsweise darf man die Tatsache nicht übersehen, daß die Zapfen der rezenten *Tsuga mertensiana* (Bong.) Carr. den Zapfen der kaukasischen Fichte *Picea orientalis* (L.) Link sehr ähnlich sind. Die Zapfen dieser letzten Art sind in ihrer Form von den Zapfen der Fichten der *Omorica*-Sektion derart verschieden, daß die Autoren der neuesten Übersichten die *P. orientalis* aus der Sektion *Omorica* ausschließen und sie in der typischen Sektion unterbringen. Wir halten es aber für angezeigt, die kaukasische Fichte in der Sektion *Omorica* zu belassen.

Wenn man die hybridische Teilnahme von *Tsuga* in der Genesis der *Picea*-Arten der Sektion *Omorica* zuläßt, kann man auch zugeben, daß an dieser Hybridisation verschiedene *Tsuga*-Arten teilgenommen hatten, daß heißt, daß die verschiedenen *Picea-Arten* der Sektion *Omorica* als das Resultat der Hybridisation einiger *Picea*-Arten und einiger *Tsuga*-Arten entstanden waren. Wir werden dieses Problem hier nicht weiter erörtern, weil es doch rein spekulativ erscheint und gründlicher Erforschung bedarf.

In der Arbeit über die Eigenartigkeit der Flora des erratischen Gebietes des europäischen Teils der Sowjetunion (Bobrow 1944), wurde die hybridische Vermischung einiger Artenpaare gezeigt, die mit den Ereignissen im Pleistozän und mit der Pflanzenbesiedlung der Territorien, die von der Eisdecke befreit waren, zusammenhängt. Diese Erscheinung, welche wir als hybridische Vermischung der Arten bezeichnen, ist als Folge der Hybridisation von einzelnen Artenpaaren bei deren Gegenmigration im Verlauf der Besiedlung von weiten freien Territorien zu betrachten; ihre hybridische Wechselwirkung dauerte viele Jahrhunderte und sogar Jahrtausende. Unter diesen Verhältnissen konnten die Resultate der Hybridisation, wie wir bereits 1944 schrieben, auf großen Territorien und in geographischen Maßstäben in Erscheinung treten.

Die hybridische Vermischung der Arten läßt sich am deutlichsten im Norden des europäischen Rußlands an Hand eines *Picea*-Artenpaares der westeuropäischen *P. abies* (L.) Karst. und der sibirischen *P. obovata* Ledeb. darstellen. Es handelt sich darum, daß während des Rückzugs der Gletscher und der Verringerung der periglazialen Zone sich für *P. abies* und *P. obovata* die Möglichkeit einer Erweiterung ihres Ansiedlungsgebietes eröffnet hatte: die europäische Art konnte weiter nach Nordosten und die sibirische nach Westen vordringen. Die Erweiterung ihres Areals während der Wärmesteigerung wurde durch die Reduktion desselben beim Eintreten neuer Vergletscherungen abgelöst. Die Pulsation der Areale, die sich, wie es scheint, in den Interstadialen zusammenschlossen, endete mit ihrer Fusion nach dem Rückzug des letzten Gletschers. Bei ihrem Vorrücken nach Westen traf *P. obovata* in dem erratischen Gebiet *P. abies*, die ihrerseits nach Nordosten vordrang. Dort begann ihre hybridische Vermischung, infolge welcher die große Vielfalt der bekannten Übergangsformen oder der Zwischenformen dieser beiden Arten entstanden war.

Das spezielle Studium der Übergangsformen (D. N. Danilow 1943) zeigte die Transgression ihrer Merkmale. Danilow kam zu der Schlußfolgerung, daß »... bei der Bewegung in Richtung der Breitegrade vom Ural zu den westlichen Grenzen ... die Merkmale von *P. excelsa* ständig und ununterbrochen zunehmen, während die Merkmale von *P. obovata* abnehmen. Der Mittelwinkel der Zuspitzung der Fruchtschuppen verändert sich ganz regelmäßig: mit einer Verringerung der Länge um 1 Grad nimmt dieser Winkel um 3° ab. Außer der Schuppenform verändert sich auch die Zapfengröße: ihre Länge und ihr Gewicht nehmen beim Vordringen in Westrichtung ständig zu«. In den Schlußfolgerungen der obenerwähnten Arbeit von E. G. Bobrow heißt es, daß die weitgehende Hybridisation nicht nur für den Norden des europäischen Teils der Sowjetunion charakteristisch ist, sondern auch in den anderen Erdteilen vorkommen soll, wo die Entstehung der Pflanzendecke unter ähnlichen Bedingungen erfolgt war. Diese Bedingungen sind: Gegenmigration physiologisch übereinstimmender Arten, anhaltende hybri-

dogene Wechselwirkung und Vorhandensein von verhältnismäßig freien Standorten, wo sich die hybridische Nachkommenschaft ansiedeln konnte.

Später haben wir gezeigt (Bobrow 1961), daß die hybridische Vermischung der Arten in Baikal-Sibirien weit verbreitet ist, da man in seiner Flora mehrere Dutzend Exemplare aufzählen kann, deren hybridogene Genesis zweifellos ist. Als besonders krasse Beispiele dieser Hybridisation in der Baikal-Flora können die Gattungen *Larix*, *Betula* und *Adenophora* gelten, aus denen Dutzende von »Arten« beschrieben wurden, die in Wahrheit Hybriden sind. Wir haben erfahren, daß die von uns entdeckte hybridische Vermischung der Arten (Bobrow 1944) von E. Anderson (1949) auch in den Vereinigten Staaten beschrieben und als »introgressive Hybridisation« bezeichnet wurde. Anderson hat diese Erscheinung auf genetischer Grundlage gedeutet und hat als »introgressive Hybridisation« die »Infiltration des Embryoplasmas der einen Art in das der anderen Art, als eine Folge von Hybridisation und wiederholter Rückkreuzung« bezeichnet.

Andersons »introgressive Hybridisation« und Bobrows »hybridische Vermischung der Arten« bezeichnen ohne Zweifel verschiedene Aspekte ein- und derselben Erscheinung, wobei aber E. Anderson vom genetischen und E. G. Bobrow vom systematischen und pflanzengeographischen Standpunkt ausgehen.

In unseren späteren Artikeln wurden auch andere Fälle der introgressiven Hybridisation erörtert, wodurch gezeigt wurde, daß diese Erscheinung durchaus nicht selten ist (Abb. 1).

Sehr wichtig erscheint uns, daß auch im Ausland die Aufmerksamkeit auf die introgressive Hybridisation in der Gattung *Picea* gelenkt wurde. Über die Hybridisation von *P. glauca* (Moench) Voss. und *P. engelmannii* Engelm. in Britisch-Kolumbien wurde eine spezielle Arbeit (E. H. Garman 1957) vom Forst Department von Kanada publiziert. Garman hat die morphologischen Merkmale der beiden Arten (es sei erwähnt, daß sie zu verschiedenen Sektionen gehören) sowie die morphologischen Eigentümlichkeiten der Übergangsformen (Zwischenvarianten) und die Verbreitung aller dieser Formen in Britisch-Kolumbien sehr ausführlich erörtert.

Zwei Jahre später wurde in einer anderen offiziellen kanadischen Ausgabe die Arbeit von K. W. Horton (1959) veröffentlicht.

Dieses sehr sorgfältig ausgeführte Studium bewies unzweifelhaft, daß die von Garman beschriebene Hybridisation einen typischen Fall der introgressiven Hybridisation darstellt. Unter den graphischen Darstellungen im Artikel von Horton ist die Karte des südwestlichen Teils von Kanada und des Nordostens der Vereinigten Staaten besonders interessant, weil sich dort die Verbreitungsgebiete von *Picea glauca* und *P. engelmannii* berühren. Auf dieser Karte ist auch die Verbreitung ihrer Übergangsformen auf dem größten Teil von Britisch-Kolumbien, im Hochgebirge vom südwestlichen Teil von Alberta und in den territorial nicht großen Hochgebirgsgegenden des Staates Montana gezeigt. Die introgressive Hybridisation der Fichten in Nordamerika beschränkt sich nicht nur auf den begrenzten Teil des Felsengebirges. Im Jahre 1964 wurde eine ähnliche Arbeit über die Introgression von zwei *Picea*-Arten veröffentlicht, die auch in anderen Teilen dieses Kontinents stattfindet. Die Forstfakultät der Universität in Toronto veröffentlichte die Arbeit von Morgenstern und Farraz (1964), die das Gebiet im extremen Südosten von Kanada und im extremen Nord-

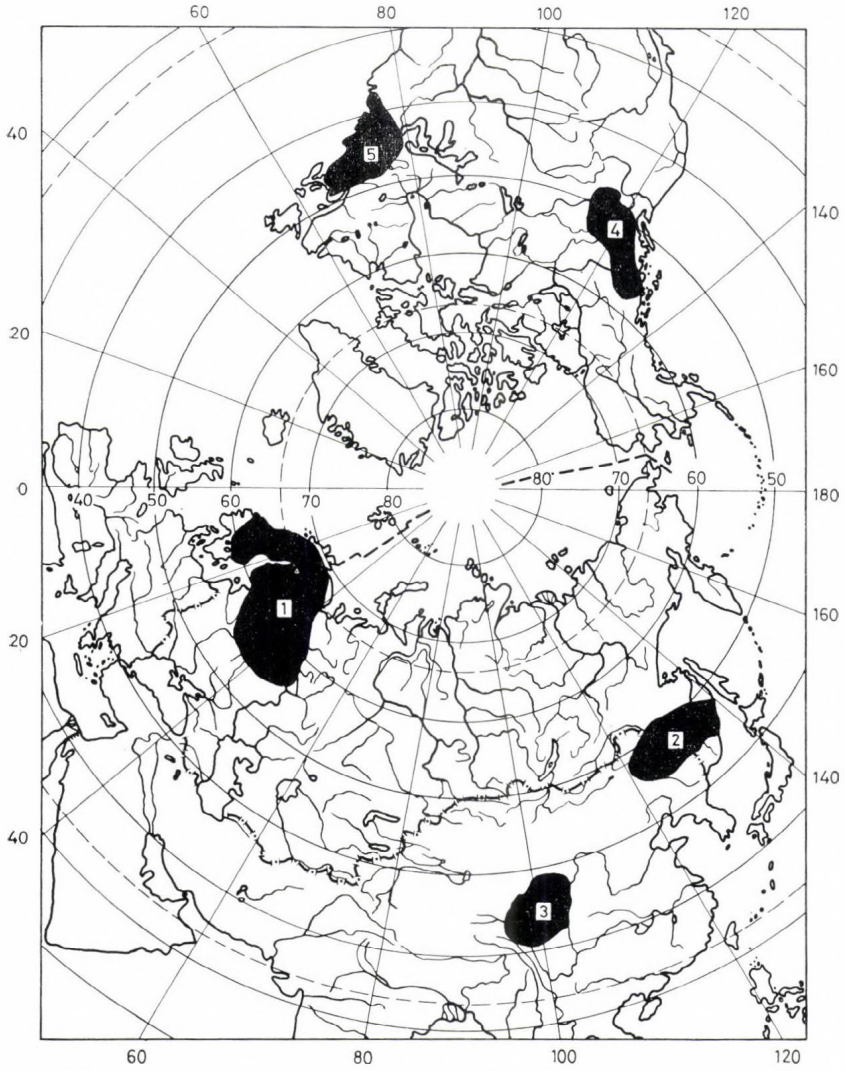

Abb. 1. Die Gebiete der introgressiven Hybridisation der *Picea*-Arten: 1. *P. abies* (L.) Karst. und *P. obovata* Ledeb. — 2. *P. obovata* Ledeb. und *P. ajanensis* (Lindl. et Gord.) Fisch. ex Carr. im Norden; *P. obovata* Ledeb. und *P. koraiensis* Nakai im Süden und anscheinend auch *P. ajanensis* und *P. koraiensis* im Süden des sowjetischen Küstengebietes des Fernen Ostens. — 3. *P. asperata* Mast. und *P. likiangensis* (Franch.) E. Pritz. — 4. *P. glauca* (Moench.) Voss und *P. engelmannii* Engelm. — 5. *P. mariana* (Mill.) Britt., Sterns and Pagg. und *P. rubens* Sarg.

osten der Vereinigten Staaten erforscht hatten, und zwar die Territorien, die ostwärts von den Great Lakes liegen und wo die Areale von *Picea mariana* (Mill.) Britt., Stearn et Pogg. und *P. rubens* Sarg. miteinander in Kontakt treten.

Die spezielle Untersuchung vieler Populationen in der Natur, die hybridologische Analyse derselben und die Beobachtungen in den Baumschulen zeugten mit voller Sicherheit von der Introgression zwischen den beiden Arten. Die Verfasser hoben dabei besonders hervor, daß die Introgression dieser Arten nach der pleistozänen Vereisung eingesetzt hat. Die räumliche Ausdehnung der Introgression ist im Westen wie im Osten des Kontinents sehr bedeutend, erreicht geographische Maßstabe und kommt in dieser Beziehung der Introgression der *Picea*-Arten im europäischen Rußland und in Skandinavien nahe. Aus den Angaben unserer Karte kann man sich überzeugen, daß die Territorien, welche von den Introgressanten eingenommen sind, sich etwa auf 1000 Kilometer erstrecken und im Durchmesser 300 bis 500 Kilometer betragen.

Wir sehen also, daß die introgressive Hybridisation in der Gattung *Picea* durchaus keine Seltenheit ist, im Gegenteil, sie scheint der normale Zustand zu sein. Dennoch wird sie, ungeachtet dessen, daß sie in einigen Verbreitungsgebieten der *Picea*-Arten geradezu auffällig ist, immer noch nicht erkannt.

Als wir im Jahre 1961 das Herbarmaterial von *P. obovata* aus dem Gebiet vom oberen Lauf des Amur, das heißt von der südöstlichen Verbreitungsgrenze dieser Art studierten, fiel uns seine Eigenartigkeit auf. Unter diesen Herbarexemplaren befanden sich einige mit Pollen, den auf unser Ersuchen D. B. Archangelsky einer speziellen Untersuchung unterzog (1962); er vermochte unsere Vermutung die hybridische Genesis dieser Arten betreffend zu bestätigen. Archangelsky wies auch auf die große Zahl der deformierten Pollenkörner in den Präparaten hin.

Wir haben alle Ursache anzunehmen, daß im Amurgebiet und im anliegenden Teil Nordostchinas im Kontaktgebiet von *P. obovata* und *P. ajanensis* eine introgressive Hybridisation stattfindet. Weiter nach Osten — in Nordostchina, auf dem kontinentalen Teil des sowjetischen Fernen Ostens und auf der Halbinsel Korea — kann man mit Sicherheit die Introgression der Arten feststellen. Hier sind als Teilnehmer dieses Prozesses *Picea ajanensis* und *P. koraiensis* zu nennen. Es läßt sich vermuten, daß die Arten, welche im Jahre 1941 aus Korea beschrieben wurden, und zwar: *P. tonaiensis* Nakai, *P. pungsanensis* Uyeki ex Nakai und *P. intercedens* Nakai, Hybrid-Introgressanten darstellen. Ferner ist es durchaus möglich, daß die aus dem Küstengebiet des sowjetischen Fernen Ostens (Primorje) beschriebene *P. komarovii* Vassil. (1955) auch eine solche Hybride ist.

P. mandshurica, die im Jahre 1943 von T. Nakai beschrieben wurde, ist vermutlich ein Produkt der hybridischen Vermischung von *P. obovata* und *P. koraiensis*.

Alle diese Probleme sind äußerst interessant und man wird sich erst dann darüber Klarheit verschaffen können, wenn man *Picea*-Populationen in der Natur erforscht hat. Diese Probleme sind lösbar, denn jede der echten Arten nimmt eine bestimmte ökologische Nische ein und weist konstante morphologische Merkmale auf. Den Erforschern der Flora des Fernen Ostens eröffnet sich — wie wir sehen — ein hochinteressantes, wichtiges und notwendiges Forschungsgebiet.

Die introgressive Hybridisation der zwei obenerwähnten Artenpaare im Fernen Osten muß man desgleichen mit den Ereignissen des Quartärs in Verbindung stellen. Die Vereisung von Gebirgen war dort durch die Senkung des Kontinentrandes auf 2 500–3 000 Meter erschwert. Die

Pflanzendecke aus dunklen Nadelwäldern, welche zu dieser Zeit im Hochgebirge entstand, kam in den niederen Gebirgsgegenden und auf dem Flachland in unmittelbaren Kontakt mit der Pflanzendecke der letzteren, und die *Picea*-Arten, die den Bestand dieser Wälder bilden, konnten miteinander hybridisieren.

Unsere Aufmerksamkeit wurde noch auf ein geräumiges Territorium gelenkt, wo die introgressive Hybridisation der *Picea*-Arten offensichtlich auch in Erscheinung tritt, und zwar auf die ausgedehnten Gebirgsgegenden der Provinzen Hupe und Szetschwan in Südchina.

An der Introgression nehmen dort dem Anschein nach die Arten der Serien *Asperatae* und *Likiangenses* teil, die, wie man bemerken muß, zu verschiedenen Sektionen der Gattung gehören. Wir haben in diesen Gebieten das Vorliegen der introgressiven Hybridisation deswegen angenommen, weil aus diesen Provinzen eine sehr große Zahl von »Arten« festgestellt wurde, deren Unterschiede ganz gering sind.

Beispielsweise werden für die Provinz Szetschwan 15 *Picea*-Arten angegeben, und dabei nur aus der Umgebung der Stadt Da-Dzien-Lu 8 Arten.

Es sei erwähnt, daß J. W. Wright über eine intensive Hybridisation der Fichten in diesen Gebieten geschrieben hat, wie S. G. Harrison (Dallimore und Jackson 1966) mitteilt.

Die introgressive Hybridisation der Fichten in Südchina kann man gleichfalls mit den Ereignissen im Pleistozän in Verbindung stellen. Im Gegensatz zu den fernöstlichen Territorien, wurden die Territorien von Südchina im Quartär stark emporgehoben und die Vereisungen in den Gebirgen hingen mit den Veränderungen der Feuchtigkeitsverhältnisse zusammen. Alle diese Faktoren haben anscheinend die Verschiebungen der Pflanzendecke, welche gegen Ende des Pliozäns bereits ausgebildet war, hervorgerufen und zu der Introgression der *Picea*-Arten geführt.

Aus dem Gesagten läßt sich folgern, daß die Erscheinung der introgressiven Hybridisation für die Arten der Gattung *Picea* sehr charakteristisch ist.

Diese Tatsache hat selbstverständlich große wissenschaftliche Bedeutung und verdient die erhöhte Aufmerksamkeit der Forstwissenschaftler, weil sie die Möglichkeit einer weiteren Auslese der in dieser oder jener Beziehung mehr produktiven, für die Kultur notwendigen Formen (Notomorphen) bietet. In der letzten Zeit haben die kanadischen Forscher ihre Aufmerksamkeit auf die chemischen Unterschiede der Introgressanten, im Vergleich zu den Ausgangsarten, gelenkt.

LITERATUR

Anderson, E. (1949): *Introgressive hybridization*. New York

(Archangelsky, D. B.) Архангельский, Д. Б. (1962): Einige palynologische Daten betreffend die Erscheinung der introgressiven Hybridisation. *Бот. Жур.* **47** (7) (russ.)

(Bobrow, E. G.) Бобров, Е. Г. (1944): Über die Eigenartigkeit der Flora des erratischen Gebiets. *Сов. Ботаника* **2** (russ.)

(Bobrow, E. G.) Бобров, Е. Г. (1961): Die introgressive Hybridisation in der Flora von Baikal-Sibirien. *Бот. Журн.* **46** (3) (russ.)

Dallimore, W. and Jackson, A. B. (1966): *A Handbook of Coniferae and Ginkgoaceae*. 4th ed., revised by S. G. Harrison, London

(Danilow, D. N.) Данилов, Д. Н. (1943): Die Veränderlichkeit der Zapfenschuppen von *Picea excelsa* Link. *Бот. Журн.* **28** (5) (russ.)
Garman, E. H. (1957): The occurrence of spruce in the interior of British Columbia. *Techn. Publ. Dept. Lands and Forests Brit. Columb. Forest Service* **49**
Gaussen, H. (1966): *Les Gymnosperms actuelles et fossiles* **8** Toulouse
Horton, K. W. (1959): Characteristics of subalpine spruce in Alberta. *Techn. Note Dept. North Affairs and Nat. Resources, Forestry Branch* **76**
Morgenstern, E. K. and Farraz, J. L. (1964): Introgressive hybridization in red spruce and black spruce. *Techn. Rep. Fac. Forest. Univ. Toronto* **4**

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BIOSYSTEMATIK DER *DIANTHUS PLUMARIUS* L. (SENSU LATO) IN UNGARN

von

L. Baksay

BUDAPEST*

EINFÜHRUNG

Die Conspecies *Dianthus plumarius* L.** ist in den Gebirgsgegenden von Mitteleuropa, im östlichen Teil der Alpen und in den Karpaten einheimisch. Infolge ihres speziellen ökologischen Anspruches (Felsen und Felsenrasen) und ihrer Verbreitung, gliedert sie sich in mehrere kleinere Arten, die als Subspecies zu betrachten sind.

Die Felsenfedernelken gehören, samt den weißblühenden Sandfedernelken, zu der Sektion *Fimbriatus*. Die Arten der beiden ökologischen Gruppen stehen einander nahe. Um ihre Verwandtschaft und Differenzierung besser zu verstehen, ist es zweckmäßig, die Untersuchungen an lebendem Material vorzunehmen. Taxonomisch sind beide Gruppen außerordentlich kompliziert, weil sie im Berührungsgebiet ihrer Verbreitung nicht nur mit den Arten der eigenen Sektion, sondern auch mit denen anderer Sektionen hybridisationsfähig sind. Dank den gründlichen Arbeiten und Monographien von F. A. Novák (1915 bis 1929) sind zwar von den europäischen Nelken die Arten der Sektion *Fimbriatus* am besten bearbeitet, eine zeitgemäße Umwertung ist jedoch beinahe unvermeidlich.

UNTERSUCHUNGSGEBIET UND MATERIAL

Die Felsennelken sind im Ungarischen Mittelgebirge verbreitet. Dieses niedrige Gebiet, mit 300 bis 500 Meter Meereshöhe, umfaßt jenen Teil des ungarischen Florenreiches, der pflanzengeographisch Pannonicum oder Urmatra genannt wird. Es ist ein nordöstlich-südwestlicher Bergzug; im nördlichen Teil, an der Landesgrenze, berührt er den slowakischen Karst und erstreckt sich in 450 km Länge bis zum südlichen Ende des Balatonsees. Seine Gesteine, auf denen die Nelken gedeihen, bestehen aus Kalkstein, an einer Stelle aus Basalt und Dolomit; letzterer kommt vom Donauknie bis zum südlichen Ende des Balatons oft vor.

Das lebende Material wurde aus 5 wichtigen Populationen gesammelt und im Zuchtgarten und Glashaus angepflanzt. Die Sandnelken der Ebene stammen von kalkhaltigem (zwei Stellen) und saurem Sand (aus der Umgebung von Fenyőfő, Transdanubien). Es wurden morphologische, ökologische, pflanzengeographische, blütenbiologische und cytologische Untersuchungen durchgeführt und diese mit herbarischer Besichtigung ergänzt.

* Adresse: Budapest, IX. Ráday u. 33b.

** Nomenklatorisch kann man zwar gegen die Beibehaltung des Namens Einwand erheben, wegen der Zusammenfassung der Unterarten ist er dennoch nötig, worauf auch Novák in seiner Monographie hingewiesen hat.

Im nördlichen Teil des untersuchten Gebietes (Abb. 1) gedeiht *Dianthus plumarius* L. ssp. *praecox* (Kit.) Pawl. Diese subalpine Pflanze ist in den Nordkarpaten endemisch. Die ungarischen Fundorte sind die südlichsten Verbreitungsgrenzen dieser Subspecies und fallen im Mittelgebirge mit der südlichsten Grenze der diploiden *Festuca glauca* Lam. zusammen. Der Standort dieser Pflanze ist in Ungarn der Felsenrasen *Festucetum glaucae subcarpaticum* und im slowakischen Gebiet *Festucetum glaucae carpaticum*, und sie ist die Charakterart der Assoziation *Diantho-Seslerietum subcarpaticum*.

Die vom Dolomitfelsen des Felsens Feketekő (Pilis Gebirge im Donauknie) gesammelten Pflanzen entsprechen morphologisch, blütenbiologisch vollkommen der Beschreibung der *Dianthus lumnitzeri* von Wiesbaur, die *Dianthus plumarius* ssp. *lumnitzeri* (Wiesb.) Dom. genannt wird. Ihr natürlicher Standort ist heute eine kleine herausragende nördliche Felsenspitze, wo eine sehr kleine Fläche, kaum 25 bis 35 Quadratmeter, für die Entwicklung des Felsenrasens zur Verfügung steht, da der übrige Teil der Umgebung von Wald bedeckt ist. Sie ist eine Charakterart des Felsenrasens *Sesleria sadleriana-Festuca pallens* Host.; die letztere ist ein tetraploider Cytotyp der *Festuca glauca*. Die spp. *lumnitzeri* ist eine endemische Art der Kleinen Karpaten und der nördlichste Punkt ihrer Verbreitung liegt, zusammen mit dem der tetraploiden *Festuca pallens*, neben Brezova. Der zweite Fundort, außerhalb des Areals, war 1920 der Basaltberg neben dem Balaton, aber infolge Hybridisation ist sie von dort verschwunden.

Die wichtigsten morphologischen Merkmale der ssp. *praecox* (Abb. 2c) sind: die Grundblätter der sterilen Triebe sind meergrün, hellgrün, fahlgrün, lose rasig, etwas grasartig. Die Blätter sind 4 bis 6 cm lang, 2 bis 3 mm breit, beinahe flach, verschmälern sich allmählich in eine lange Spitze. Der Stengel hat 3 bis 4 Blätterpaare; die Nodi enthalten, wenn sie jung sind, Anthocyan, sonst sind Kelch und Kelchschuppen rötlich, die Blüten weiß, beim Verblühen ein wenig rosafarbig (weitere Merkmale siehe Tabelle 1).

Die Grundblätter und sterilen Triebe der ssp. *lumnitzeri* sind graubereift,

Tabelle 1

Einige wichtige morphologische Merkmale der pannonischen

Taxon	Kelch		Kelchschuppen	Pollen	
	Länge	Breite	Länge	Größe	leer
	(mm)		(mm)	in μ	%
D. plumarius					
ssp. *praecox*	21–25	3,5–4,5	7,5–8	54	10–15
ssp. *lumnitzeri*	23–25	4	7–8	55	10–20
ssp. *regis-stephani* ♂	27–28	3–3,3	7	60	5
ssp. *regis-stephani* ♀	21–23	3	7	—	—
var. soói	21–23	3,5	7–8	54	20
D. arenarius					
ssp. *borussicus*	23–25	2,5–3	6–7	54	—
D. serotinus	26–28	2,8–3	6–7	56,5	10

bläulich-grün, mit Wachs überzogen, eventuell grünlich-grau, dicker, rinnig, 3 bis 3,5 mm breit und 2,5 bis 3,5 cm lang, der Blattrand ist in der ganzen Länge oder bis zur Hälfte rauh, das Blatt verschmälert sich plötzlich in eine Spitze. Am grauen Stengel finden sich 4 bis 5 Paar Blätter, der Kelch ist grün, die Blüte weiß. Bei der rosafarbigen Form (f. *eosinus* Gáy.) sind die Nodi und die Kelchschuppen rötlich, am Ende der Blüte sehr blaß rosafarbig (Abb. 2d und Tabelle 1). Für beide Arten oder ssp. ist charakteristisch, daß an der jungen Knospe die Kelchschuppen abstehen, und nicht eng dem Kelch anliegen. Auf Grund dieser Merkmale sind ihre Hybriden zu erkennen.

Für die Dolomitfelsen des Ungarischen Mittelgebirges ist auch eine niedrige, einblütige Federnelke charakteristisch, die ebenfalls zu *D. plumarius* gehört und den vorigen Unterarten zwar ähnlich aber dennoch anders ist. Sie wurde i. J. 1922 von R. Rapaics *Dianthus regis Stephani* genannt und bekommt jetzt den Rang einer Subspecies. Phytozönologisch ist sie eine Charakterart der Assoziation *Festucetum pallentis hungaricum*, sie wächst nur auf Dolomit. Novák (1923, 1927a, b, 1928) ordnete sie unter dem Einfluß früherer Autoren (Neilreich, Hegi u. a.) der Sandnelke *D. serotinus* zu und seine Auffassung hatte zahlreiche Anhänger. Ihre unterscheidenden Merkmale, gegenüber den vorigen Unterarten, sind: ein mehr xeromorpher Charakter, dichter polsteriger Wuchs, 2 bis 2,5 cm lange, schmale, steife, grau-bereifte oder grünlich-graue Blätter mit sich allmählich verschmälernder, stechender Spitze. Der Kelch ist grün bzw. samt dem Stengel graulich, die Kelchschuppen schmiegen sich auch im Knospenzustand dem Kelch an. Die Kronenblätter sind weiß bis weißlich, schmaler und berühren sich nicht mit den Rändern (Abb. 2a und 2e, Tabelle 1).

Unter Berücksichtigung der Klimaänderungen der Eiszeit und damit des Schicksals und der gegenwärtigen Verbreitung der Pflanzenarten, bin ich der Meinung, daß die in den Karpaten gedeihende ssp. *praecox* während der letzten Würm-Eiszeit aus den Karpaten in das Gebiet des ungarischen Mittelgebirges, ein damaliges Refugium, einwanderte, und daß auch die ssp. *lumnitzeri* gezwungen war, dorthin einzuwandern. Im Kontaktgebiet

Repräsentanten der Gattung Dianthus sectio Fimbriatus

Samen/Kapsel	Gewicht von 500 Samen (mg)	Chromosomenzahl $2n$	Standort
18–30	561	90	Osztramos (Nordost-Ungarn)
18–30	593	90	Pilisgebirge: Feketekő
18–30	586	90	Budaörs in der Nähe von Budapest
30–45	—	—	Budaörs in der Nähe von Budapest
18–30	—	90	Keszthely
45–50	305	60	Fenyőfő (Bakonygebirge)
45–50	310	90	Insel Csepel, Csévharaszt

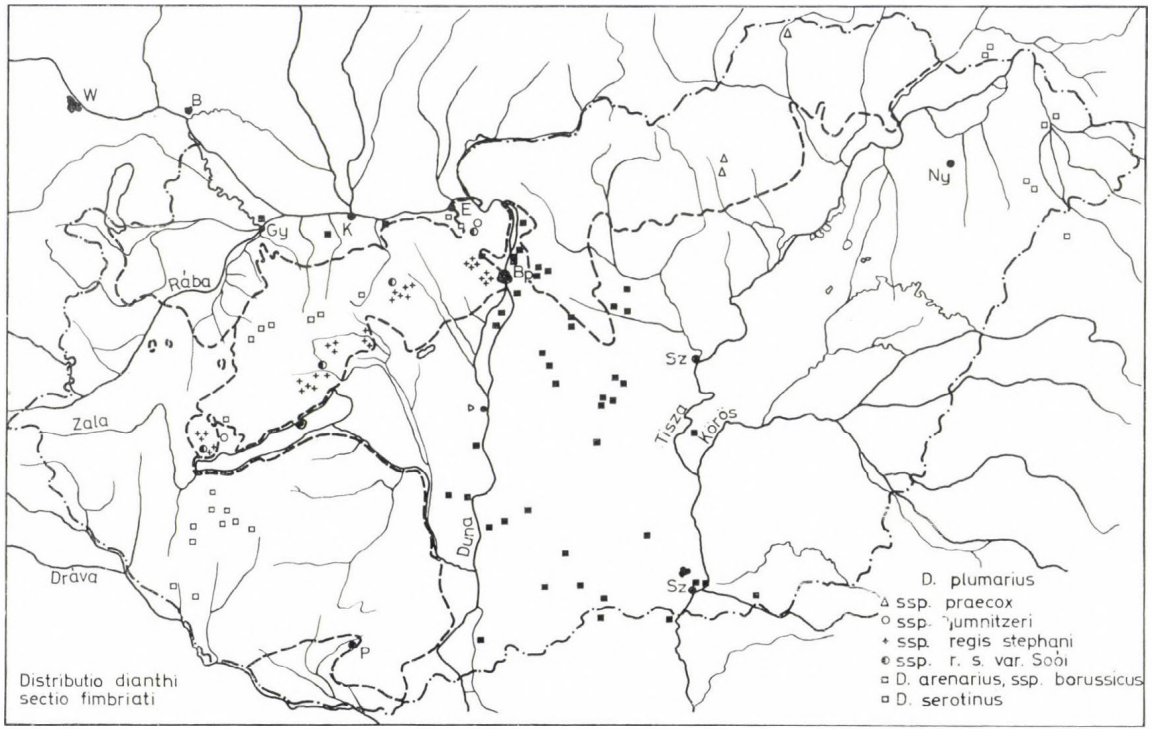


Abb. 1. Verteilung der Vertreter der Sektion *Fimbriatus* (Genus *Dianthus*) in Ungarn

der beiden Unterarten, südwestlich vom gegenwärtigen Donauknie, entstand durch Hybridisation, als jüngstes Glied der *Dianthus plumarius*-Gruppe, die ssp. *regis-stephani* (Rapcs.), und sie stabilisierte sich unter dem Einfluß der natürlichen Selektion.

Das Zustandekommen der Hybridisation an der Kontaktlinie der Elternarten und die Verminderung der elterlichen Populationen kann man auch an den heutigen Populationen feststellen. Im Untersuchungsgebiet von der Donau bis Keszthely (Südende des Balatons) gibt es fünf Stellen, wo die Pflanzen dem einen Elter z. B. *D. lumnitzeri* näher stehen, wo also eine Introgression erfolgte. Dies hat auch S. Jávorka bemerkt, aber er dachte an einen Übergang zwischen *Dianthus serotinus* und *D. lumnitzeri*, obwohl diese zwei Unterarten sich bei uns nicht berühren. Die Kronenblätter dieser Varietät sind breiter, ein wenig hellrosafarbig. Andere Merkmale sind unter var. *soói* in Tabelle 1 zu sehen. Die Fundorte sind isoliert und das Fortbestehen der Pflanzen ist noch nicht gefährdet.

Die Beobachtung der Introgression in Richtung der ssp. *praecox* ist schwieriger. Man kann annehmen, daß auf der nördlichen steilen Basaltwand des Szentgyörgyberges, der in der Balatongegend inselähnlich hervorragt und ziemlich reich an Raritäten ist, und auf dem Gipfel ein überraschend kühles Mikroklima für die Vegetation bietet, sich auch die ssp. *praecox* für längere Zeit erhalten haben dürfte, während sie von den anderen Gebieten verschwunden ist. Die gegenwärtige Population zeigt auf den ersten Blick eher den Einfluß der ssp. *praecox*. Im Herbarium habe ich ein Exemplar aus 1920 gefunden, das aber ssp. *lumnitzeri* zu sein scheint. Leider wurde auf diesem Standort nur in wenigen Fällen gesammelt, und wir sind nicht in der Lage, das Schicksal dieser Population in den einzelnen Jahrzehnten zu verfolgen. Noch bedauernswerter ist es, daß ein einziges Exemplar der Kulturvarietät *Dianthus gratianopolitanus* Vill. im Garten des Touristenhauses unterhalb der Felsen, durch zufällige Kreuzung die natürliche Population zerstört hat, und es ist schwer, zwei gleiche Individuen zu finden (Abb. 2b). Auf Grund der Untersuchung der Herbarien waren ähnliche Fälle überall vorgekommen, wo in der Nähe der natürlichen Felsen Gärten vorhanden sind. Ein solcher Bastard kommt auch auf dem Berg Sashegy bei Budapest vor, ist aber auch auf dem Mödlinger Felsen in der Nähe des Klosters zu finden.

CYTOLOGISCHE UND BIOLOGISCHE EIGENSCHAFTEN

Die Chromosomenzahl der *D. plumarius*-Gruppe ist schon von vielen Autoren untersucht worden (Rohweder 1934, Carolin 1957, Gentscheff 1937 [ex Carolin], Blackburn und Morton 1957, Borhidi 1968), und es wurden einerseits $2n = 90$, anderseits $2n = 60$ gefunden. Ich habe Pflanzen von natürlichen Populationen untersucht, wobei die Chromosomenzahl in der Wurzelspitze bei ssp. *lumnitzeri* und bei ssp. *regis-stephani* $2n = 90$ betrug, und auch ssp. *praecox* war hexaploid. Diese Zahl entspricht völlig der nahen Verwandtschaft und auch der Chromosomenzahl von ssp. *spiculifolius* (Schur), die ebensoviel ausmacht. Letztere Unterart ist ssp. *praecox* sehr ähnlich, wächst endemisch in den Ost- und Südkarpaten und wird gleichfalls stellenweise von Hybridisation beeinflußt. Die Chromosomenzahl der in den Ostalpen einheimischen ssp. *neilreichii* (Hayek) Hegi ist den österreichischen Cytotaxonomikern wahrscheinlich ebenso bekannt,

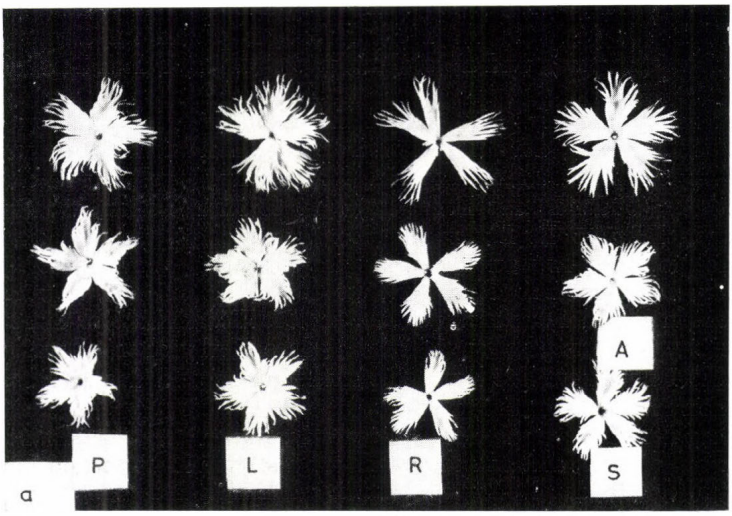
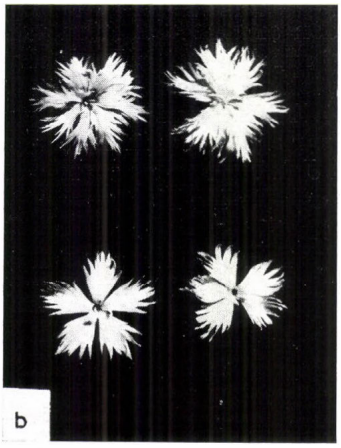


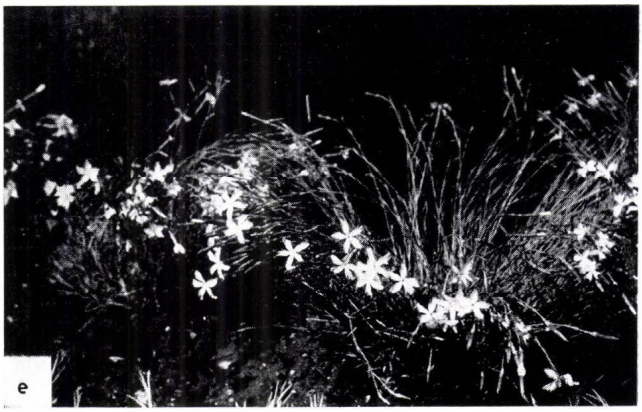
Abb. 2. (a) Blüten von *D. plumarius*, *D. serotinus* und *D. arenarius*; P = *D. plumarius* ssp. *praecox*; L = *D. plumarius* ssp. *lumnitzeri*; R = *D. plumarius* ssp. *regis-stephani*; S = *D. serotinus*; A = *D. arenarius* ssp. *borussicus*



(b) Blüten der Hybride *D. plumarius* ssp. *lumnitzeri* × *D. gratianopolitanus* vom Berg Szentgyörgyhegy in der Nähe des Balatons

(c) *D. plumarius* ssp. *praecox* in Kultur gezüchtet

(d) *D. plumarius* ssp. *lumnitzeri* f. *eosinus*



(e) *D. plumarius* ssp. *regis-stephani* vom gleichen Standort

(f) Künstliche Hybride zwischen *D. plumarius* ssp. *regis-stephani* und *D. serotinus*. Männlich sterile F_1-Pflanze

und sie muß auch hexaploid sein. Die abweichende Angabe über die tetraploide Form bezieht sich möglicherweise auf aus botanischen Gärten stammendes Material oder auf eine nicht erkannte Hybride, deren Chromosomenzahl abreguliert wurde (Rohweder 1934). Untersuchungen über die Meiose führte ich nur in geringerem Maße durch. Eine Analyse ist die Aufgabe der Zukunft. Bei der PMZ-Meiose von ssp. *praecox* und ssp. *lumnitzeri* hat man in einigen Fällen 2 bis 3 multivalente Assoziationen beobachtet, charakteristisch sind ferner für die hexaploiden Taxa die häufigen Doppelassoziationen. Die Störungen in der Meiose widerspiegeln sich in der Pollenqualität (Tabelle 1). Die Unterarten können reziprok miteinander erfolgreich gekreuzt werden, wodurch ein freier Genaustausch möglich wird. In der natürlichen Population der ssp. *lumnitzeri* und ssp. *regis-stephani* sind männlich sterile Individuen vorhanden.* Die Entwicklung dieses Mechanismus dürfte aus den ökologischen und populationsdynamischen Eigenschaften der Pflanzen folgen. Sie leben immer in offenen Pflanzengesellschaften, am nackten Felsenboden oder in Felsenrissen, und die Individuenzahl ist in den einzelnen Populationen gering. Trotz der niedrigen Individuenzahl bleibt die Variabilität durch Fremdbefruchtung erhalten (D. Lewis 1941, Stebbins 1958, Jain 1959). Wir setzen die Untersuchungen über die Natur der männlichen Sterilität fort und erwägen ihre Bedeutung auch in bezug auf die Differenzierung.

In der Blütezeit der drei Unterarten zeigen sich zwar kleinere Differenzen, aber alle blühen im Mai–Juni. Die ssp. *regis-stephani* beginnt erst zu blühen, wenn die zwei anderen Unterarten schon in voller Blüte stehen. Die Kronenblätter werden vom Aufblühen bis zum Abblühen immer größer und so können sie die zweifache Aufblühgröße erreichen (Abb. 2a). Die Staubblätter ragen an aufeinander folgenden Tagen empor und streuen den Pollen nach und nach aus. Dieses Stadium dauert auch in den wärmsten Zeiten 2 bis 3 Tage. Nachdem der letzte Staubbeutel leer geworden ist, beginnt sich die Narbe zu heben, und wieder vergehen 3 bis 4 Tage, bis sie die volle Reife erreicht.

Die Kronenblätterspreite ist am Anfang der Blüte fein geteilt aber bis zu der Befruchtung werden die Fransen immer breiter, verlängern sich und so kann man auf derselben Pflanze unterschiedlich geteilte Petalen beobachten, wodurch diese Eigenschaft als Merkmal labil wird (Abb. 2a). Die Form der männlich sterilen Blüten ist demgegenüber konstant und sie sind natürlich kleiner, weil die verkümmerten Staubblätter kein Auxin erzeugen, das sonst das Wachstum der Kronenblätter fördert. Charakteristisch ist weiterhin, daß in dieser Gruppe die Kronenblätter, auch wenn sie weiß sind, mit normaler Salzsäure Anthocyanreaktion geben.

Weitere einheimische Arten der Sektion *Fimbriatus* sind die Federnelken auf den Sandböden der Ebene. Sie unterscheiden sich sowohl morphologisch als auch ökologisch von der vorigen Gruppe. Novák betrachtet diese Arten in seiner Monographie (1927a) innerhalb der Sektion *Fimbriatus* als eine separate Gruppe und betont, daß die Verwandtschaft eine fernere sei.

* Rohweder (1934) beobachtete, daß in der natürlichen Population 25% der zu verschiedenen taxonomischen Gruppen gehörenden Nelken männlich steril ist; auch ich habe das gleiche Verhältnis ermittelt.

Von ökologischen und historisch-pflanzengeographischen Überlegungen ausgehend habe ich einen Teil des lebenden Materials vom kalkigen Sand zwischen Donau und Theiß gesammelt; hier gedeiht *Dianthus serotinus* W. et K. Den anderen Teil habe ich von den niedrigeren (200 bis 250 m) sauren Sandböden des transdanubischen Bakonygebirges gesammelt, wo *Pinus silvestris* einheimisch ist. Dort, wo die schönsten Bestände dieser *Pinus*-Art stehen, habe ich die *D. arenarius* L. ssp. *borussicus* (Vierh.) Kleop. gefunden. Die beiden Arten unterscheiden sich verhältnismäßig wenig voneinander, wie sich eben innerhalb einer polyploiden Reihe die tetraploiden und hexaploiden Typen unterscheiden können. Darin ist die Ursache der Verwechslung der beiden Arten zu sehen, denn seit der Beschreibung der *D. serotinus* (1805) hat sich dieser Artenname in der Literatur derart verbreitet, daß man alle Sandfedernelken, auch außerhalb des Karpatenbeckens (Mähren) für *D. serotinus* hielt (Neilreich, Hegi und viele andere).

Der Stengel von *D. arenarius* ssp. *borussicus* ist feiner, die Pflanze ist niedriger (25 bis 30 cm), grün (*D. serotinus* var. *arenosus* f. *viridis* Novák), ihre Blätter sind schmal, lineal und weicher als die der *D. serotinus*, sie sind aufwärts gerichtet und bilden mit dem Stengel einen spitzeren Winkel (Hegi III. Fig. 594a sub *D. serotinus*), der Stengel steht gerade aufwärts, mit wenigen Blüten (1 bis 3). Blütezeit von Mitte Juni bis Oktober.

D. serotinus ist grau bis graulich, der Stengel ist unten anfangs abliegend, dann aufrecht (35 bis 50 cm hoch), von der Mitte oder vom oberen Drittel sperrig-doldig verzweigend, mit vielen Blüten (7 bis 15). Die Nodi des Stengels sind stark angeschwollen, die Blätter spitz, steif, abstehend, der Kelch ist um etwa 2 mm länger als bei der vorigen Art. Blütezeit von Juli bis September.

Die weißen Blüten geben keine Anthocyanreaktion, die blütenbiologischen Eigenschaften sind ähnlich wie bei den vorigen Felsennelken. Andere Merkmale siehe Tabelle 1.

D. arenarius ssp. *borussicus* ist eine Reliktpflanze der Eiszeit, die während der Würm-Vereisung vom Baltikum nach Süden wanderte, einerseits über das Böhmisch-Mährische Becken in das Karpatenbecken, anderseits, gezwungen der Karpatenkette nach Südost auszuweichen, über Polen nach den Sandflächen der Ukraine; sie begleitete die *Pinus silvestris*-Wälder und ist in vielen Varietäten bekannt. Gemäß ihren ökologischen Ansprüchen wächst ssp. *borussicus* auf saurem oder schwach saurem Sand. In dem Marchfeld und in Niederösterreich ist sie eine Charakterart der Assoziationen *Corynephoretum canescentis* bzw. *Dianthus arenarius* ssp. *borussicus-Festuca Domini* (= *vaginata* f. *mucronata*) und in Ungarn in der geographischen Variante der gleichen Assoziationen (*Festuco-Corynephoretum arrabonicum* etc.).

Dagegen ist *D. serotinus* eine Charakterart der Assoziation *Festucetum vaginatae danubiale* zwischen Donau und Theiß und teilweise entlang der Donau auf kalkigem Sand.

Nach cytologischen Untersuchungen ist *D. arenarius* ssp. *borussicus* bei Fenyőfő tetraploid: $2n = 60$. Auf Grund florenhistorischer Erwägungen steht unzweifelhaft fest, daß an dieser Stelle zuerst *D. arenarius* resp. deren tetraploider Cytotyp verbreitet war, und aus dieser entstammte nach der Eiszeit, durch Vereinigung einer unreduzierten und einer reduzierten Gamete, die hexaploide *D. serotinus*. Ich bin der Meinung, daß ohne

die Anwesenheit der *D. arenarius*, *D. serotinus*, das letzte und am weitesten nach Süden verbreitete Glied der polyploiden Reihe (2x, 4x, 6x) der baltischen *D. arenarius*, nicht hätte entstehen können.

Hinsichtlich der cytologischen Merkmale sei erwähnt, daß in der Meiose der ssp. *borussicus* normale Bivalente zu sehen sind. Die hexaploide *D. serotinus* verhält sich gleich den hexaploiden Felsennelken (2 bis 3 Multivalenten) und ihr Pollen ist auch dementsprechend (Tabelle 1). Bis zu einer künftigen ausführlichen Analyse sehen wir keinen Grund zu glauben, daß beispielsweise *D. serotinus* zu den Felsennelken gehört; die vergleichende Untersuchung der einzelnen Glieder der polyploiden Reihe der *D. arenarius* wird aber auch eine Klärung der Abstammung der Felsenfedernelken herbeiführen.

Um die natürlichen Hybriden resynthetisieren zu können, habe ich die heimischen Vertreter der *Fimbriatus*-Sektion des Genus *Dianthus* im Glashaus und im Zuchtgarten gekreuzt (1970), wobei jede Kombination erfolgreich war, auch im Falle von verschiedenen Chromosomenzahlen (4x, 6x). Sie können auch in der Natur Hybriden bilden, wenn sie sich unter geeigneten Bedingungen treffen; die Sand- und Felsennelken kreuzen sich gleichfalls und bringen natürliche Hybriden zustande, worüber hier erstmalig berichtet wird.

Ein solcher Fall von Hybridisation geht auf dem Marchfeld vor sich, wo sich der Sand auch auf den westlichen Abhang der Kleinen Karpaten erstreckt, die Sandvegetation mit der Vegetation des Kalkfelsens in direkter Berührung steht und in beiden Nelken-Arten vorhanden ist. Hier hat J. Gayer eine Hybride von *D. arenarius* ssp. *borussicus* und *D. plumarius* ssp. *lumnitzeri* gefunden, hielt dieselbe aber für eine Sandvarietät von *lumnitzeri* und nannte sie f. *sabulicola*.

Ähnlich ist auch der andere beobachtete Fall: unter den gleichen orographischen und edaphischen Verhältnissen hatte sich in der Nähe von Budapest, auf dem Felsen Egyeskő (Berg Kisszénás), dessen Fuß auf der einen Seite mit Sand und Sandvegetation umgeben ist, die am Dolomitfelsen wachsende *D. plumarius* ssp. *regis-stephani* mit *D. serotinus* gekreuzt. Erstere Unterart blüht zwar früh, aber nach meinen Beobachtungen können die Regenfälle eine Nachblüte hervorrufen, wodurch die Hybridisation ermöglicht wird. Abb. 2f ist eine resynthetisierte (1969) ssp. *regis-stephani* × *serotinus*-F_1-Hybride, ein männlich steriler Nachkomme einer männlich sterilen Mutter. Über die natürlichen und künstlichen Hybriden wird an anderer Stelle berichtet.

ZUSAMMENFASSENDE BEMERKUNGEN

Die aus der pannonischen Flora dargestellten Repräsentanten des Genus *Dianthus* sectio *Fimbriatus* sind ökologisch differenzierte, nahe verwandte Taxa. Nach unseren bisherigen Erfahrungen ist zwischen den Populationen bzw. Arten ein freier Genaustausch möglich. Diese kleinen herausgegriffenen Beispiele der Artenentstehung zeigen, daß die Hybridisation ein ebenso wichtiger Faktor der Evolution sein kann, wie die Genommutation. In unserem Falle sehen wir in der Migration die auslösende Ursache der Evo-

lution, da zur Zeit der größeren Klimaveränderungen dieses Gebiet der lebhafte Wanderweg der Pflanzen in Mitteleuropa war, wo sie vom Norden nach Süden und wieder zurück wanderten, inzwischen aber sich geändert haben. Es ist bekannt, daß die gleichen Gene, die die morphologischen Merkmale bestimmen, auch die physiologisch-ökologischen Eigenschaften bedingen. Eine geringe ökologische Abweichung innerhalb der Art bedeutet eine Differenzierung, auch wenn ihre morphologischen Merkmale noch nicht klar sichtbar sind. Wie das Beispiel der Arten *Dianthus plumarius* L. s. l. und *Dianthus arenarius* L. zeigt, differenziert ihre Taxa eine Grundart im Laufe ihrer Entwicklungsgeschichte ihrer Autökologie gemäß in ökologische Serien, deren gegenwärtige Anzeiger die Pflanzengesellschaften sind, in denen die Taxa notwendigerweise leben.

SUMMARY

Dianthus plumarius L. s. l. is indigenous in the region of the Alps and on limestone rocks of the Carpathians. It splits into subspecies and, together with the feather pinks of sandy soils, belongs to the sectio *Fimbriatus*. The author conducted morphological, ecological, phytogeographical, and cytological investigations, as well as crossing experiments (1970) on the representatives of the section, and obtained the following results.

D. plumarius ssp. *lumnitzeri* (Wiesb.) Dom. arrived from the northwest, whereas ssp. *praecox* (Kit.) Pawl. from the northeast, at the time of the last glaciation into the lower montane-colline region of the Carpathian Basin, a refuge in that period. Along the line of meeting of the two microspecies (southwest from the Great Bend of the Danube to the southern end of Lake Balaton) the youngest member of *D. plumarius*, namely ssp. *regis-stephani* (Rapcs.) came into being by hybridization on dolomite substrate. Hybridization and the impoverishment and disappearance of the parental populations are also shown by the conditions of the present populations; in numerous points of the research area (Fig. 1) the plants (var. *soói* Jáv.) approach one of the parents, ssp. *lumnitzeri*, exhibiting introgression.

All the *D. plumarius* subspecies are hexaploid ($2n=90$), crossable reciprocally. They cross with the cultivar *D. gratianopolitanus* Vill. also in natural population, given the necessary conditions. The natural populations consist of relatively few plants, they contain 25% male-sterile plants and variability is maintained by outcrossing. The feather pinks on sandy substrate differ morphologically and ecologically from those of rocky sites. *D. arenarius* L. ssp. *borussicus* (Vierh.) Kleop. inhabiting acid sands, is also a glacial relict, often confused with the extremely similar *D. serotinus* W. et K. of calcareous sands. This latter taxon is an endemic plant distributing between the Danube and Tisza, and locally along the Danube. The ssp. *borussicus* is tetraploid ($2n=60$), its meiosis is normal; *D. serotinus* is a hexaploid, $2n=90$, in meiosis it shows 2–3 multivalents. Despite the difference in chromosome numbers the two species can be crossed reciprocally; the chromosome number of progeny is $2n=75$.

The Hungarian representatives of the section *Fimbriatus* can be successfully crossed in every direction with one another. Besides the hybrids listed

in the literature, some natural hybrids are also known between *D. arenarius* ssp. *borussicus* and *D. plumarius* ssp. *lumnitzeri* (e.g. from the Moravian Plain), where limestone rocks and sandy areas meet. Furthermore, hybridization occurs occasionally between *D. plumarius* ssp. *regis-stephani* and *D. serotinus*, not far from Budapest, where the dolomite cliffs meet sandy vegetation at one locality. All these features explain the close relationship between the taxonomically extremely complicated group and the relatively recent stage of specific differentiation.

LITERATUR

Anderson, E. (1953): Introgressive hybridization. *Biol. Rev.* **28** 280–307

Aszód, L. (1936): Adatok a nyírségi homoki vegetáció ökológiájához és szociológiájához (Beiträge zur Ökologie und Soziologie der Sandvegetation des Nírség) (ung). *Acta geobot. Acad. Sci. hung.* **1** 98–9

Baksay, L. In Soó: *Synopsis systematico-geobotanica florae vegetationisque Hungariae* IV. Akadémiai Kiadó, Budapest 1970

Borbás, V. (1889): Hazai szegfüveink mint kerti virágok (Die Nelken Ungarns als Gartenblumen) (ung.). *Természetrajzi füzetek* **12** 210–24

Blackburn, K. B. and Morton, J. K. (1957): The incidence of polyploidy in the *Caryophyllaceae* of Britain and of Portugal. *New Phytologist* **56** 344–51

Borhidi, A. (1956): Die Steppen und Wiesen im Sandgebiet der Kleinen Ungarischen Tiefebene. *Acta bot. Acad. Sci. Hung.* **2** 241–72

Borhidi, A. (1968): Karyological studies on Southeast European plant species. I. *Acta bot. Acad. Sci. hung.* **14** 253–60

Buell, K. (1953): Developmental morphology in *Dianthus*. III. Seed failure following interspecific crosses. *Amer. J. Bot.* **40** 116

Carolin, R. C. (1957): Cytological and hybridization studies in the genus *Dianthus*. *New Phytologist* **56** 81–97

Degen, Á., Gayer, J. und Scheffer, J. (1923): Ungarische Moorstudien I. Die Flora des Detrekőcsütörtöker Moores und des östlichen Teiles des Marchfeldes. *Magy. Bot. Lapok* **22** 15–82

Gayer, J. (1917): Supplementum Florae Posoniensis. *Magy. Bot. Lapok* **16** 57

Gentscheff, G. (1937): Experimental and karyological investigation of the relationships among the species of the genus *Dianthus* (*Dissert. Univ. Sofia*, ex Borhidi 1968)

Grant, F. W. (1960): Categories of classical and experimental taxonomy and the species concept. *Rev. Canad. Biol.* **19** 241–62

Győrffy, I. (1924): Über die Variabilität des *Dianthus hungaricus* Pers. in der Hohen Tatra und über *Dianthus Generichii* hybr. nov. *Magy. Bot. Lapok* **23** 65–71

Hegi, G. (1911): *Illustrierte Flora von Mitteleuropa*. Bd. III, 338–41

Heywood, V. H. (1963): Flora Europaea Notulae Systematicae No 2. *Feddes Repert.* **68** 190

Jain, S. K. (1959): Male sterility in flowering plants. *Bibliographia Genetica* **18** 101–66

Jávorka, S. (1925): *Magyar Flóra* (Ungarische Flora). Budapest

Kiss, M. (1938): Az Északi Kárpátok endemikus növényfajai (Die endemischen Pflanzenarten der Nordkarpaten) (ung.). *Acta geobot. Acad. Sci. hung.* **1** 98–9

Klika, J. (1934): Studien über die xerotherme Vegetation Mitteleuropas. III. Die Pflanzengesellschaften auf Sandböden des Marchfeldes in der Slowakei. *Beih. Bot. Zbl.* **52B** 1–16

Krippel, E. (1954): Die Pflanzengesellschaften auf Flugsandböden des slowakischen Teiles des Marchfeldes. *Aichinger Festschrift* **1** 632–9

Lewis, D. (1941): Male sterility in natural population of hermaphrodite plants. *New Phytologist* **40** 56–63

Löve, A. and Löve, D. (1961): Chromosome numbers of Central and Northwest European plant species. *Opera Botanica Soc. Bot. Lundensi, Stockholm* **5**

Melquist, G. (1945): Inheritance in the Carnation. V. Tetraploid Carnations from interspecific hybridizations. *Proc. Amer. Soc. Hort. Sci.* **44** 397

Novák, A. F. (1915): *Dianthus arenarius* in Böhmen. *Österr. Bot. Zschr.* **10–12** 324

Novák, A. F. (1923): Monografická studie o *Dianthus plumarius* (L.). *Vestnik Kral. společ. Nauk Tr.* **II** 1–42
Novák, A. F. (1927a): Monografická studie evropských druhů rodu *Dianthus* ze skupiny *Dianthi fimbriati*. *Publ. de la Faculté des Sci. de l'Université Charles à Prague* **76** 1–60
Novák, A. F. (1927b): Monografická studie o postglacialných druzích rodu *Dianthus* ze sekce *Plumaria*. *Vestnik Král. Česk. Spol. Nauk Tr.* **II** 1–88
Novák, A. F. (1928): *Dianthi fimbriati* europaei I. *Feddes Repert.* **25** 38–47, parte II: 204–8. Ibidem parte III (1929): **26** 219–28. Parte IV: 280–5
Pawlowski, B. (1956): *Flora Tatr I.* 249, Warszawa
Rapaics, R. (1922): A növénytársadalom úttörői a sziklán (Die Pioniere der Pflanzenwelt auf den Felsen) (ung.). *Term. Tud. Közlem.* **54** 291
Rohweder, H. (1934): Beiträge zur Systematik und Phylogenie des Genus *Dianthus* unter Berücksichtigung der karyologischen Verhältnisse. *Bot. Jahrb.* **66** 249–368
Stebbins, L. G. (1958): The inviability, weakness and sterility of interspecific hybrids. *Adv. in Genetics* **9** 147–203
Stebbins, L. G. (1959): The role of hybridization in evolution. *Proc. Amer. Philosoph. Soc.* **103** 231–51
Tutin, T. G. et al. (1964): *Flora Europaea I.* 197–8, Cambridge
Valentine, D. H. and Love, A. (1958): Taxonomic and biosystematic categories. *Brittonia* **10** 153–66
Vierhapper, F. (1901): Zur systematischen Stellung des *Dianthus caesius* Sm. *Österr. W Bot. Zschr.* **51** 408–17
aldstein et Kitaibel (1805): *Descriptiones et Icones Plant. Rar. Hung. II. t.* **172**
Wiesbaur, J. (1870): Beiträge zur Flora von Preßburg. *Verh. Verein Natur-Heilkunde. N. F.* **1** 52
Wiesbaur, J. (1886): Prioritätszweifel über *Dianthus Lumnitzeri* und *Viola Wiesbauriana*. *Bot. Zbl.* **26** 83, 116, 165

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EVOLUTIONARY PROBLEMS OF THE EUROPEAN *KOELERIAS*

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How many approaches are there to solve correctly the same complex problem? Could investigations conducted from diverse points of view and by different methods both arrive at correct results? In my opinion they could. Indeed, results free from error can be obtained only in this way. These propositions inspired me in elaborating this survey.

I perceived it more and more clearly that herbarial systematics, locality, areal-geographical, paleobotanical, and genetical investigations, or even the modern taxonomic approaches, will present a picture only in accordance with their scope of the evolution in the plant kingdom — an evolution independent of systematizing man. I attempted therefore to make my studies as many-sided as possible, in order to prevent the predominance of any one of the special branches of study in the reconstruction of the way of evolution.

Accordingly, the investigator faces a twofold set of requirements: (1) he should be as versed in the special fields of study as to be able to select and apply the most appropriate one; (2) he should possess the critical acumen to evaluate objectively the results obtained by the diverse means of investigation.

My own evolutional view emerged from taxonomic investigations and experience, now looking back to several decades, on the European species of *Koeleria*, *Sesleria* and *Lotus*.

In the course of the monographic elaboration of *Seslerias*, it was proved already ten years ago that heterophylly is much more common in *Gramineae* than was hitherto believed (e.g. in the case of *Festuca heterophylla* Lam.). The basal leaves of the vegetative shoot, the so-called senile leaves, are invariably wider, more expanding, and their epidermal structure is characteristic of the species, whereas the so-called juvenile leaves, developing from their innovations, are narrower, their epiderm may lose the specific character and becomes uniformized. In species growing in xerotherm sites, only the vagina develops, and linear blades form from the juvenile leaves. This modification, arising probably through hormonic actions, clothes with similar appearance species which have no common origin. In the genus *Sesleria*, M. Deyl's *turma rigida*, as well as his *Sesleria rigida* Heuff., are members of certain polyploid level of several distinct series. A similar case has been found in some members of *Festuca* and *Brachypodium* (Ujhelyi 1962).

The same recognition proved to be valid also in my *Koeleria* studies (Ujhelyi 1961–1970).

My method, suitable for the study of the entire epidermis of a leaf,

allowed to make many thousands of photographs of identical magnification (Ujhelyi 1954). In my experimental garden, I studied more than a thousand living plants and made ontogenetic observations. These studies have been completed by cytotaxonomic and chromosome investigations.

Herbarium researches, conducted concurrently with habitat observations, gave information on the ecological and sociological characteristics of the species. In certain cases, knowledge of geographical surface alterations (mountains, seas) of certain regions permitted inferences concerning the approximate age of species. The final conclusions were drawn by a synoptic consideration of all these data.

The known connection between the dimensions and degree of polyploidy of plants was not reflected in the previous systems of *Koeleria*. Relationship should be sought for in the polyploid series of the several evolutionary lines. This suggestion was supported by the cytological investigation of living material rich in species.

I have found the related members of the polyploid series frequently in unsuspected or incorrectly assigned places of the system. They were treated under the name of some other species, often as synonyms or as some infraspecific taxa. On the other hand, closely related species sometimes had to be sought in remote places of the system. In most cases I succeeded in identifying the herbarium types with living material.

Owing to secondary habitat conditions or to the disturbed state of the plant community, the morphological features of the plants may change. Because of human influences especially in the last two centuries, deforestations and extensive grazing ascending to the subalpine regions, most of the habitats of the European *Koeleria*s are more or less secondary. Consequently, species originally adapted to diverse ecological habitats and distinct communities now live not only in their original habitat, but often mixed up with other species. This is particularly true for the situation in the area between the Danube and the Tisza in Hungary. Owing to the sinking of the ground water level by draining, there coexist in certain places *Koeleria javorkae* Ujh. of the moore with *Koeleria cristata* (L.) Pers. em. Borb. as relic of the former forest, and *Koeleria majoriflora* (Borb.) Borb. of the steppe. In regions free of such large-scale human interference, each one of these three species inhabit only their characteristic community. It is correspondingly evident that in such secondary, disturbed sites, their characters, leaf dimensions, panicle structure, rhizome formation, etc. will all suffer alterations.

The diverse taxa has usually been described on the basis of herbarium materials, but the dead plant in itself is insufficient for an evolutionary consideration. This resulted, besides the incognizance of ploidy, in the description of many infraspecific taxa, transitus, unprovable hybrids, and in the establishment of several unjustified hierarchies. A unilateral evaluation of the features is nothing but artificial systematization.

At the turn of the century, K. Domin (1907) erected his *Koeleria* system with a phylogenetical approach, but he overestimated the significance of life-forms. He regarded explicitly convergent phenomena as proofs of relationship. He considered the species an abstract idea and not an objective reality. It often occurred that Domin placed two members of the same polyploid series into different sections of his system.

Certain obsolete provisions of the recent codex of nomenclature also strongly support, even today, artificial systematization disregarding the phylogenetical past.

Let me illustrate these statements with a few examples. (Plate I.)

The species of the series *Penzesii* Ujh. range in the southern part of the Balkan Peninsula. While the diploid species *Koeleria penzesii* Ujh. lives in submontane grasslands somewhat richer in humus and of a continental character, the tetraploid species *Koeleria mitrushii* Ujh. inhabits warm and dry rocky places of a Mediterranean character, and the hexaploid species *Koeleria paparistoi* Ujh. grows in montane grasslands of rocky soils.

The diploid species is loosely cespitose, its base is not enlarged, hence it was hitherto accepted under the name *Koeleria glaucovirens* Dom. in the sectio *Caespitosae* Dom. On the other hand, the other two species have, owing to their xerothermous habitat, a rather dwarf stature with enlarged, bulbous base, erect leaves and thus they were regarded as *Koeleria splendens* Presl. *species collectiva* var. *typica* Dom., or some other variety to the sectio *Bulbosae*. Specimens of *Koeleria mitrushii* Ujh. growing in less devastated habitats in Albania and Makedonia, display pubescent leaves and less bulbous bases; Domin published these specimens first as *Koeleria glaucovirens* Dom. var. *macedonica Dom.*, later as *Koeleria splendens* var. *macedonica* Dom.

If seeds are sown from each of these plants regarded by Domin as members of different sections, the descendants grown under similar conditions show no significant differences, considering the natural variability present within the frame of all species.

The epidermal structure of all three species constituting the series *Penzesii* Ujh. show close relationship. The epidermal structure of the tetraploid *Koeleria mitrushii* Ujh. agrees with that of *Koeleria penzesii* Ujh., except the cellular dimensions which are bigger. This holds even more for the hexaploid *Koeleria paparistoi* Ujh. Either H. Prat's or C. R. Metcalfe's index would give the same picture.

These species are not simple autopolyploids, since besides other anatomico-morphological features, their ecological requirements, sociological position, and climatical adaptations are also different.

Within certain series, diploid taxa are brought together [e.g. *Koeleria rodriguezii* Ujh., and *Koeleria filifolia* (Dom). Ujh., in the series *Caudatae* Ujh]. These, of course, have not originated by polyploidy.

That the two sections, accepted even today, reflect wholly artificial and convergent phenomena, is revealed by a further analysis of the collective species *Koeleria splendens*. Domin described 15 varieties and many subvarieties within this 'species'. A part of them comes from the Mediterranean region, one from the Pyrenees, one from the Italian Alps, one from Transylvania, one from Northern Bulgaria, and one from the Crimean Peninsula.

It was proven that the higher polyploid members of *Koeleria splendens* Presl., hitherto considered a single species, represent several distinct species of a high polyploid level in the fifteen phylogenetical series described up to now. Their diploid or tetraploid progenitors were listed as members of the series *Caespitosae*.

Besides their homologous morphological structure, the species of the

series *Subcaudatae* Ujh. differ also in dimensions. The hexaploid *Koeleria splendens* Presl. is the biggest, the tetraploid *Koeleria borbasii* Ujh. is smaller, and the diploid *Koeleria subcaudata* (A. et Gr). Ujh. is the smallest. The anatomical structure of the three species displays the same fact (Plate II).

This does not hold, however, if the anatomical picture of *Koeleria splendens* is compared with that of *Koeleria paparistoi* Ujh. (Plate III). The situation is even more striking if a comparison is made with the members of the series *Pseudoglaucae* Ujh. Here, the biggest-sized *Koeleria csatoi* Ujh. has hitherto been regarded as *Koeleria splendens* Presl. The anatomical structure of the Transylvanian diploid *Koeleria schurii* Ujh. and the tetraploid *Koeleria fenzliana* Schur exhibits their relationship. Domin discussed these latter two species as *Koeleria gracilis* Pers. species *collectiva* var. *typica*, or as one of its varieties. The highest ploidy grade member of the series *Degenii* Ujh. ranging in the Pontus, namely *Koeleria skorpilii* (Podp.) Ujh. was also known as *Koeleria splendens* Presl. Geographically, the example of the series *Glaucae* Ujh. is the most striking. Its biggest member, the decaploid *Koeleria callierii* (Dom.) Ujh. was also listed as *Koeleria splendens* Presl., whereas its microscopic epidermal picture shows the structure of *Koeleria glauca* (Schk.) DC. (Plates IV–VI.)

The areas of the series taken as examples support these contentions in every respect. The series *Splendentes* inhabits only the Western Mediterranean, the series *Penzesii* Ujh. the southern part of the Balkan, the series *Pseudoglaucae* Ujh. Bulgaria and Transylvania, the series *Degenii* Ujh. Dobrogea and Ukraine. The area of the series *Glaucae* Ujh. is the greatest, comprising also the Crimea, inhabited by *Koeleria callierii* (Dom.) Ujh.

Similar surprises can be encountered when studying anyone of the collective species of the European *Koelerias*, even if recent literature waives the term 'collective species' and lists them as simple species.

The establishing of the series mentioned above is not tantamount to the traditional classificatory work. From places of the most diverse rank in the heretofore valid but undoubtedly artificial *Koeleria* system I singled out taxa I considered coequal and interrelated despite contrary contentions even today. Thus, allied species, shown as such by a diversity of methods, were placed to the same series.

I was the most amazed that the species of the series forming in this way constituted polyploid series already known to me in some other genera. It happened after this that I began to search deliberately after the governing factors of the polyploid series emphasized so much in the previous discussion. In the evaluation of species of which I could not obtain living material till now, experiences gained from the study of the rest of the rich living material helped extensively; further investigations will hardly alter their relegation — they may at most increase the number of series.

Whether my coequal taxa are species or not is a taxonomical problem. The result of the evolutional investigations is that plants assigned to the same series belong together and not those which had been relegated hitherto beside or below one another.

The examples outlined above also indicate that there is no irreconcilable antagonism in every case between Linneus' tenet on the constancy of species and the idea of evolution, if the former is not as rigidly interpreted

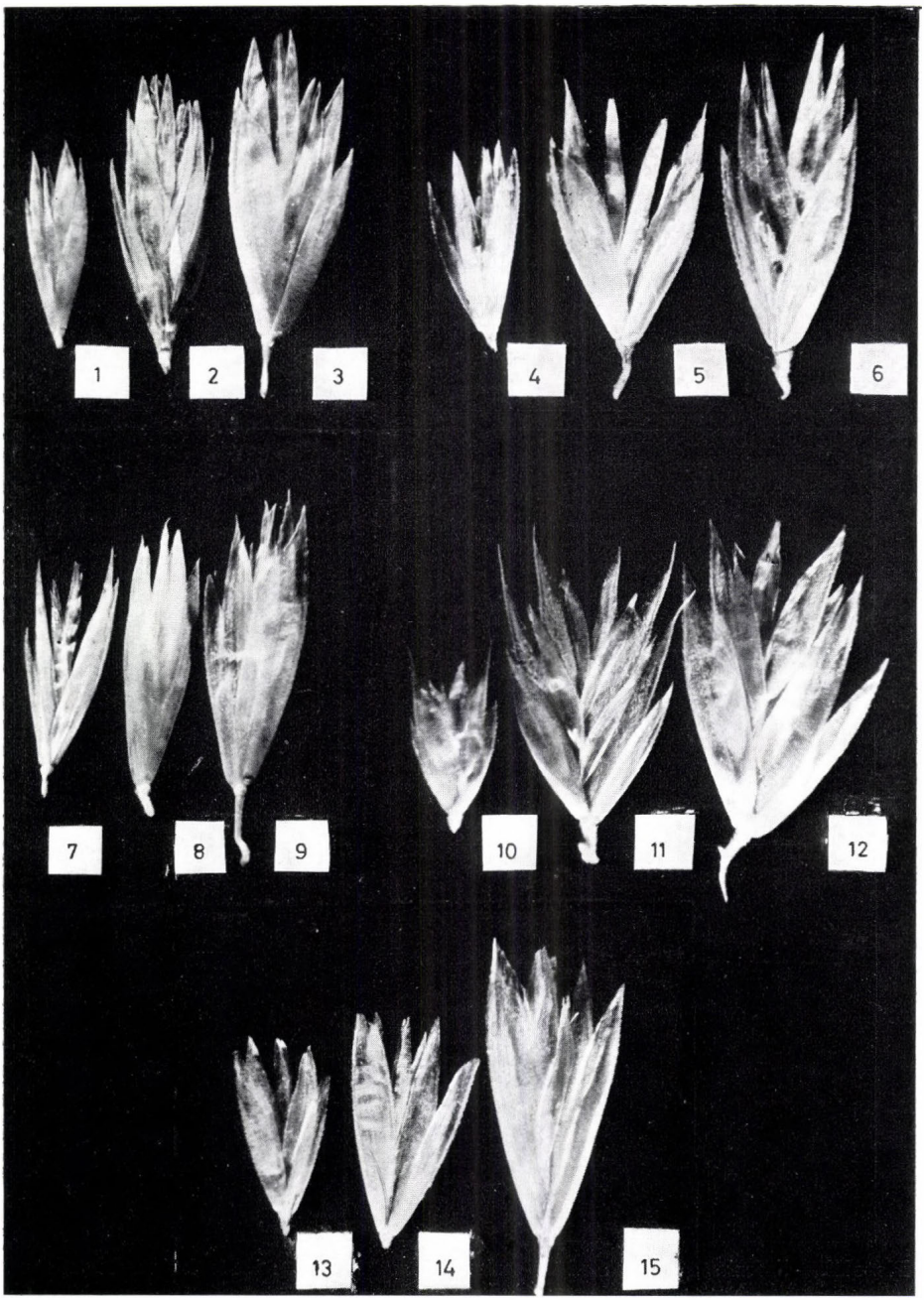

Plate I. — Spikelets of the series *Subcaudatae* Ujh.: 1. Koeleria subcaudata (A. et Gr.) Ujh.; 2. Koeleria borbasii Ujh.; 3. Koeleria splendens Presl. Spikelets of the series *Penzesii* Ujh.; 4. Koeleria penzesii Ujh.; 5. Koeleria mitrushii Ujh.; 6. Koeleria paparistoi Ujh. — Spikelets of the series *Pseudoglaucae* Ujh.; 7. Koeleria schurii Ujh.; 8. Koeleria fenzliana Schur; 9. Koeleria csatoi Ujh. — Spikelets of the series *Degenii* Ujh.; 10. Koeleria crassa Ujh.; 11. Koeleria degenii Dom.; 12. Koeleria skorpilii (Podp.) Ujh. — Spikelets of the series *Glaucae* Ujh.; 13. Koeleria glauca (Schk.) DC.; 14. Koeleria rochelii Schur; 15. Koeleria callierii (Dom.) Ujh.— × 5½

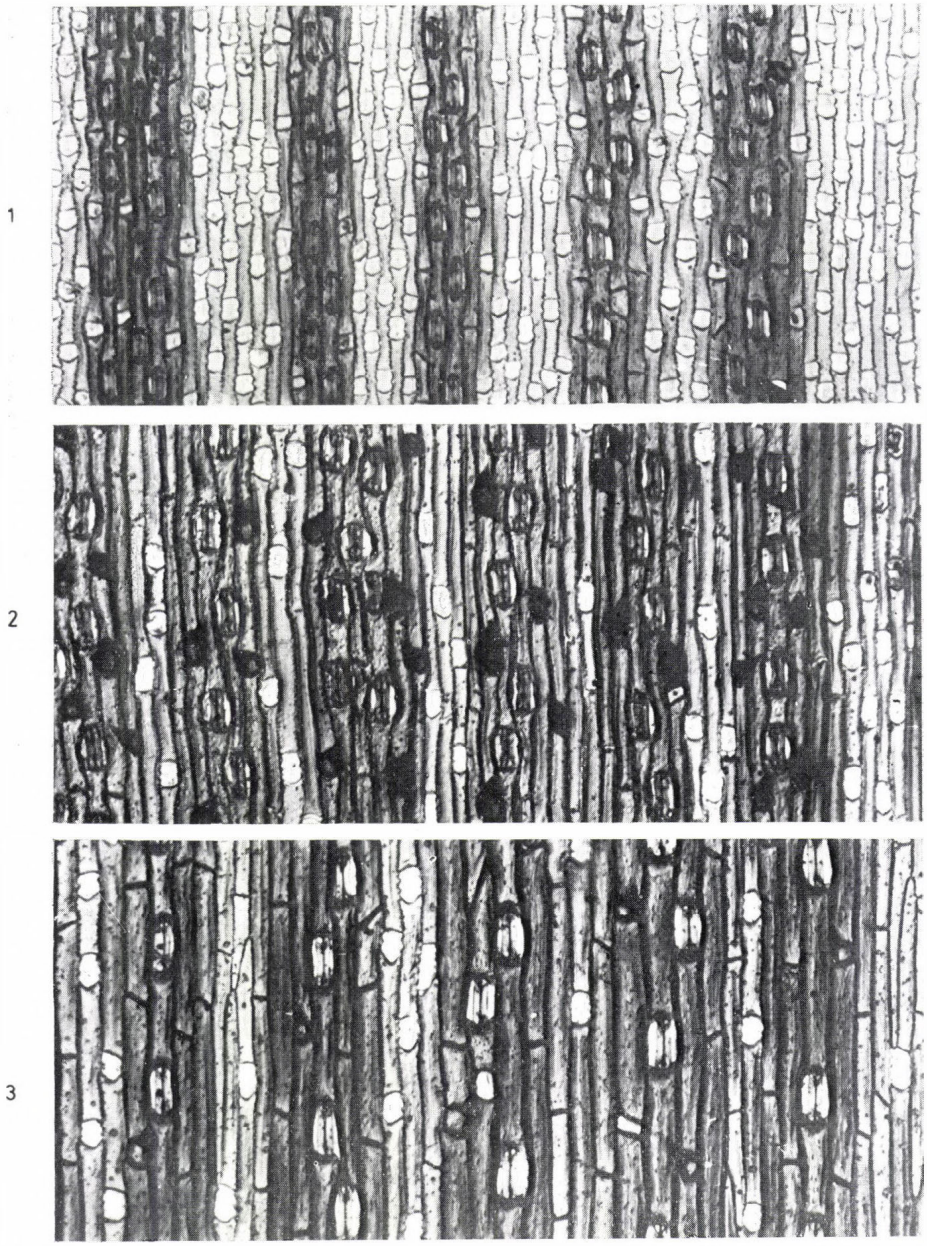

Plate II. — Inferior epidermis of the series *Subcaudatae* Ujh.: 1. Koeleria subcaudata (A. et Gr.) Ujh.; 2. Koeleria borbasii Ujh.; 3. Koeleria splendens Presl. — × 160

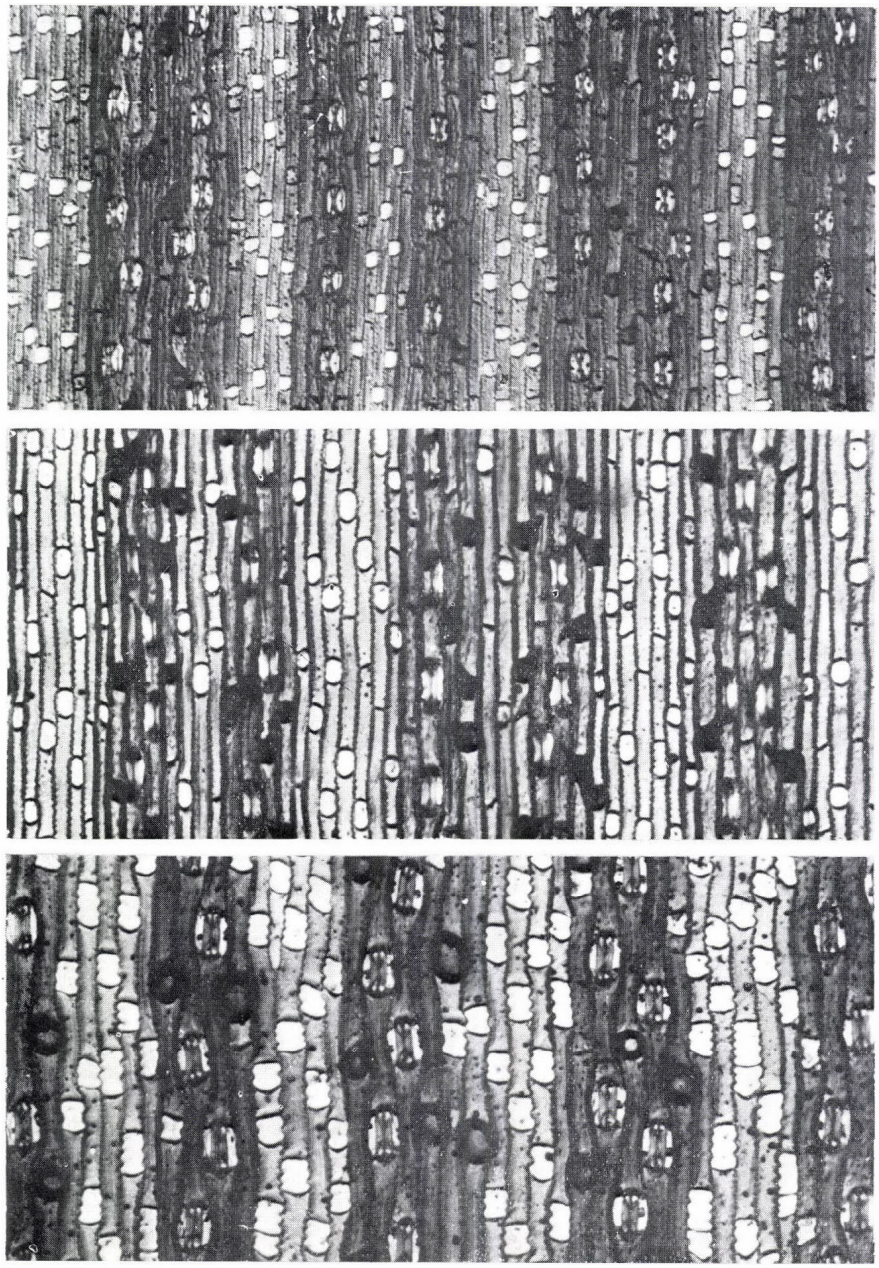

Plate III.— Inferior epidermis of the series *Penzesii* Ujh.: 1. Koeleria penzesii Ujh.; 2. Koeleria mitrushii Ujh.; 3. Koeleria paparistoi Ujh.— × 160

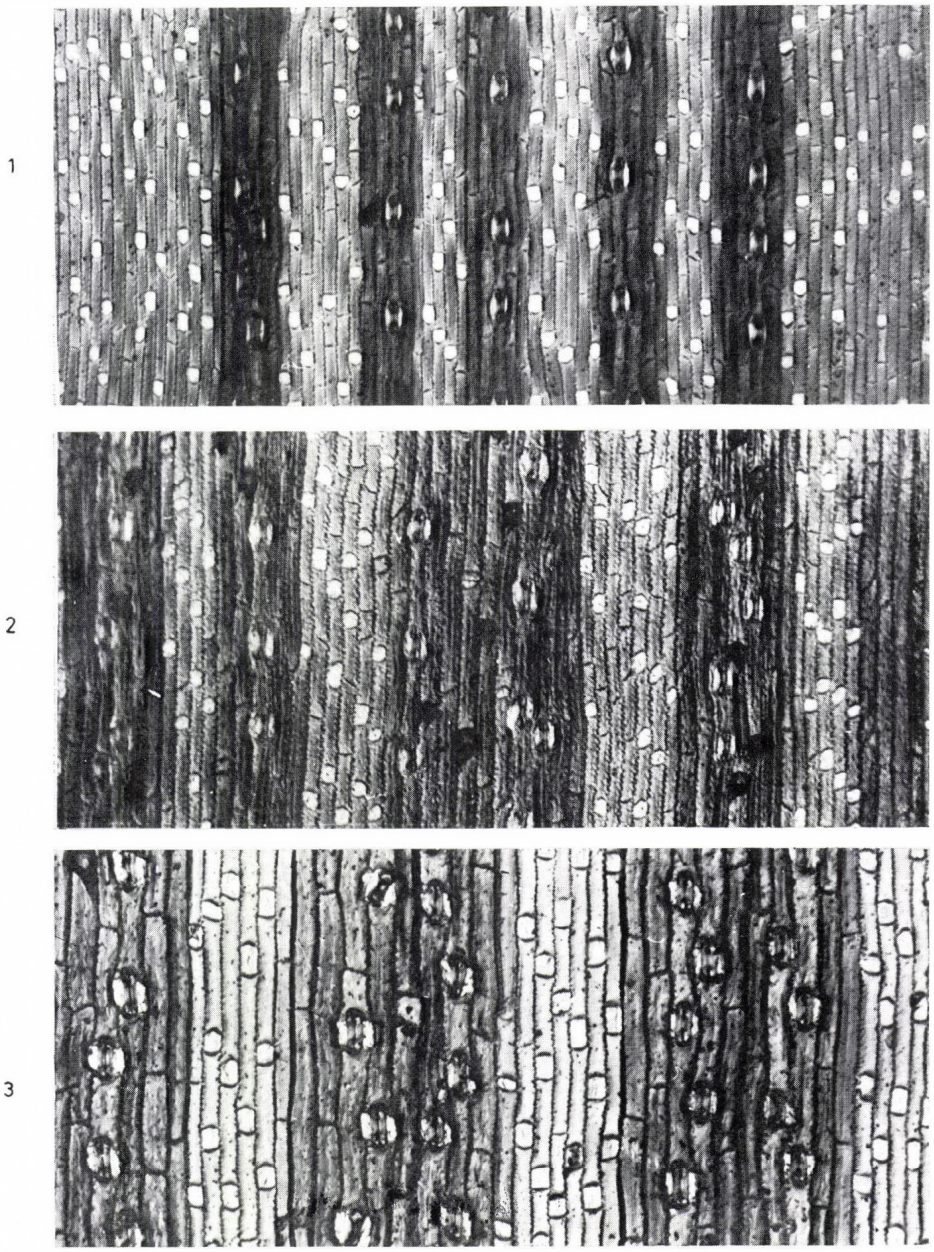

Plate IV.— Inferior epidermis of the series *Pseudoglaucae* Ujh.: 1. Koeleria schurii Ujh.; 2. Koeleria fenzliana Schur; 3. Koeleria csatoi Ujh.— × 160

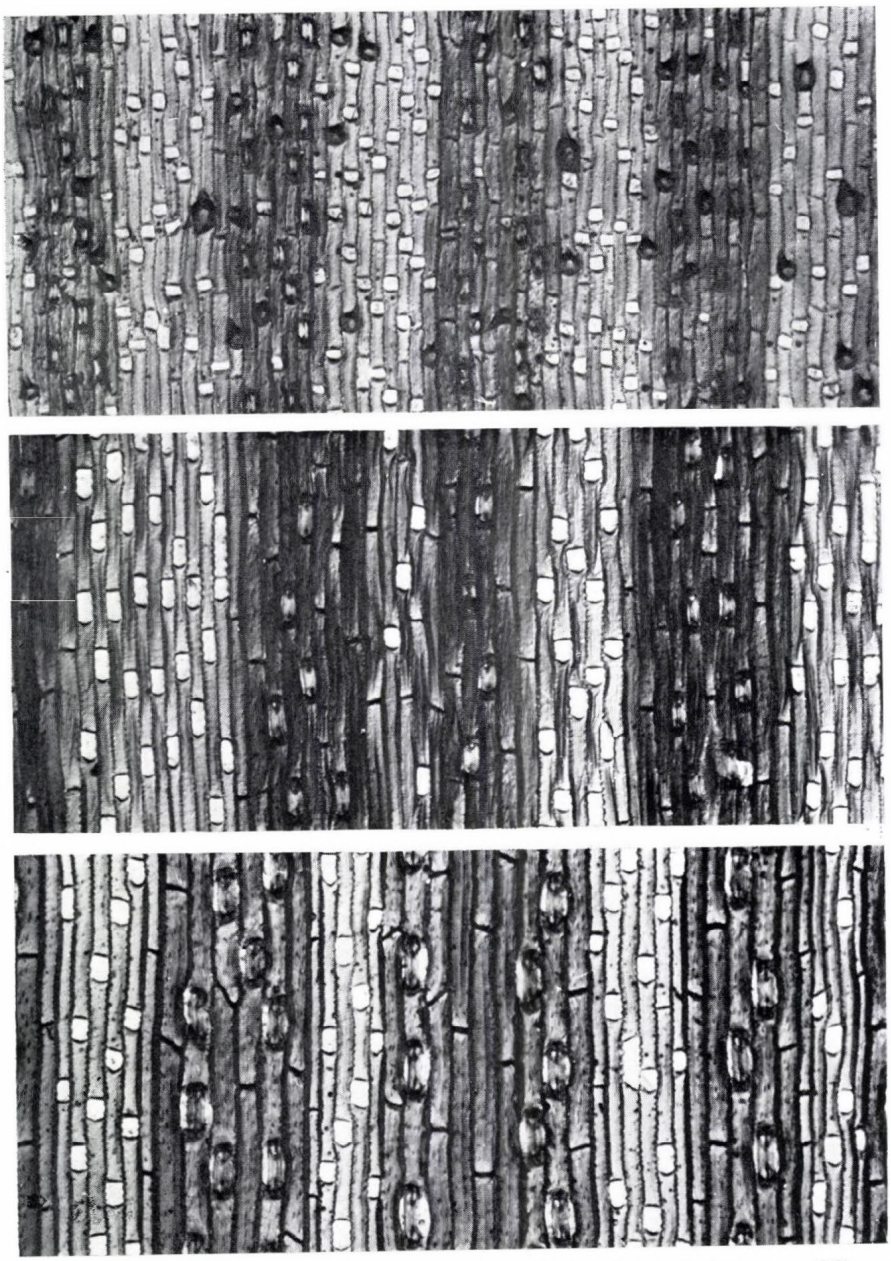

Plate V. — Inferior epidermis of the series *Degeni* Ujh.: 1. Koeleria crassa Ujh.; 2. Koeleria degeni Dom.; 3. Koeleria skorpilii (Podp.) Ujh. — ×160

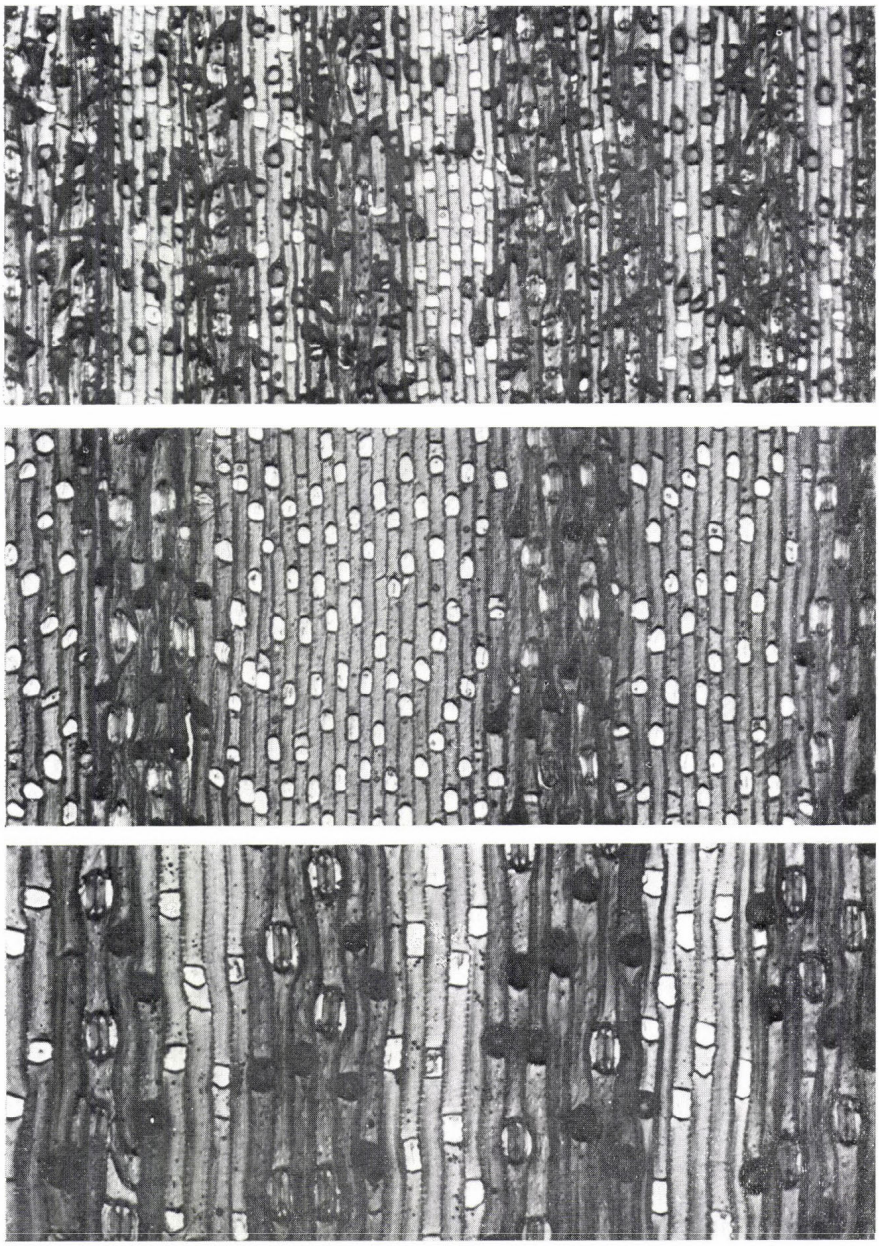

Plate VI. — Inferior epidermis of the series *Glaucae* Ujh.: 1. Koeleria glauca (Schk.) DC.; 2. Koeleria rochelii Schur; 3. Koeleria callierii (Dom.) Ujh. — × 160

as before. Species having survived all vicissitudes of their past still exist unchanged, coexisting with their descendants, evolved from and now belonging to the same genus as they.

Beside the *Koelerias* there are similar experiences in genera now under investigation, namely *Molinia, Phleum, Typha, Corydalis, Lithospermum, Anthericum* (Milkovits, Valko ined.).

Finally, I should like to call attention to the species of the same polyploid level of the same series. Their relationships should be clarified by cytogenetical methods.

The results of the evolutionary studies clarified by the methods and points of view outlined above imply that the biosystematic investigations continue with every hope of success. I am convinced that by such or similar experimental proofs we can obtain information on the evolution of the taxa.

Under such circumstances, the results of the traditional taxonomy will gain a new meaning, since its taxa will be identifiable. Herbarial material will thus also become invaluable — not as a dead bulk of pressed plants, but one in which the past and present of a species will come to life again, in the wake of the valuable data entered on the sheets and the concurrent locality knowledge of the investigator. Subsequent to such complex researches, the species concept of the geneticist and taxonomist will also converge.

The large-scale occurrence of hybrids and apomicts (usually in disturbed and secondary sites) cannot, in my belief, be regarded in every case as straight lines in evolution. Their mass occurrence is rather caused by indirect anthropogenous effects. I am convinced that these factors had had nothing to do with the appearance, migration, or disappearance of the scores of species, formed by the impact of the changes in environmental conditions during the geological past.

APPENDIX

1. Series *Glaucae* Ujh.

Koeleria glauca (Schk.) DC. (K. glauca sp. coll. ssp. K. glauca [DC.] Dom.)	$2n = 14$	Eurasia
Koeleria rochelii Schur (K. glauca sp. coll. ssp. K. glauca [DC.] Dom. var. dactyloides [Roch.] Dom.)	$2n = 28$	Europa orientalis
Koeleria callierii (Dom.) Ujh. (K. splendens Presl var. callierii Dom.)		Tauria

2. Series *Caudatae* Ujh.

Koeleria rodriguezii Ujh. (K. caudata [Link] Steud. var. typica Dom.)	$2n = 14$	Marocco, Iberia
Koeleria filifolia [Dom.] Ujh. (K. caudata [Link] Steud. var. filifolia Dom.)		Iberia meridionalis
Koeleria caudata [Link] Dom.	$2n = 28$	Marocco, Iberia
Koeleria dasyphylla Willk.		Iberia

3. Series *Arenariae* Ujh.

Koeleria arenaria Dom. (K. albescens sp. coll. ssp. albescens DC. var. glabra DC.)	$2n = 14$	In maritimis Europae occidentalis

Koeleria britannica (Dom.) Druce (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. britannica Dom.)	$2n = 28$	Britannia
Koeleria albescens DC. (K. albescens sp. coll. ssp. K. albescens DC. var. typica Dom.)	$2n = 14$	In maritimis Europae occidentalis et Gallia
Koeleria maritima Lge (K. albescens sp. coll. ssp. K. albescens var. maritima [Lge] Dom.)		In maritimis Iberie occidentalis
Koeleria pyrenaica (Dom.) Ujh. (K. eriostachya spec. coll. ssp. K. Schroeteriana Dom. var. pyrenaica Dom.)		Pyreneus occidentalis

4. Series *Hirsutae* Ujh.

Koeleria brevifolia Reut.		Alpes meridionales
Koeleria hirsuta (Lam. et DC.) Gaud. (K. hirsuta [Gaud.] Dom. sensu ampl. ssp. K. hirsuta Gaud.)		Alpes centrales

5. Series *Setaceae* Ujh.

Koeleria andreanszkyi Ujh. (K. vallesiana Bertol. sensu ampl. ssp. K. vallesiana [All.] Bertol. var. typica Dom.)	$2n = 14$	Mediterraneum occidentale
Koeleria castellana Boiss. et Reut. (K. vallesiana Bertol. sens. ampl. ssp. K. castellana [Boiss. et Reut.] Dom.)	$2n = 14$	Hispania centralis
Koeleria pauneroi Ujh. (K. vallesiana Bertol. sensu ampl. ssp. K. vallesiana [All.] Bertol. var. typica Dom. p. p.)	$2n = 28$	Mediterraneum occidentale (Britannia meridionalis)
Koeleria vallesiana (Honck.) Bertol. (K. vallesiana Bertol. sensu ampl. ssp. K. vallesiana [All.] Bertol. var. typica Dom.)	$2n = 42$	Mediterraneum occidentale et Alpes centrales
Koeleria linkii Kunth (K. vallesiana Bertol. sensu ampl. ssp. K. vallesiana [All.] Bertol. var. alpicola [Gren. et Godr.] Dom.)	$2n = 42$	Montes Alpium occidentalium

6. Series *Subcaudatae* Ujh.

Koeleria subcaudata (A. et Gr.) Ujh. (K. splendens Presl var. subcaudata [Aschers. et Gr.] Dom.)		Mediterraneum occidentale
Koeleria borbasii Ujh. (K. splendens Presl var. typica Dom.)		Mediterraneum occidentale
Koeleria splendens Presl (K. splendens Presl var. typica Dom.)	$2n = 42$	Mediterraneum occidentale

7. Series *Pseudoglaucae* Ujh.

Koeleria schurii Ujh. (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. gracilis [Pers.] Dom.)		Transsylvania, Bulgaria
Koeleria fenzliana Schur (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. gracilis [Pers.] Dom. var. glabra [Janka] Dom. subvar. Fenzliana [Schur] Dom.)		Transsylvania, Bulgaria
Koeleria csatoi Ujh. (K. splendens Presl var. rigidula [Simk.] Dom.)		Transsylvania

8. Series *Transsilvanicae* Ujh.

Koeleria transsilvanica Schur (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. transsilvanica [Schur] Dom.)		Transsylvania
Koeleria tenuipes (Schur) Ujh. (K. gracilis [Pers.] Dom. sensu ampl. ssp. transsilvanica [Schur] Dom. var. tenuipes [Schur] Dom. f. discolor Deg.)		Transsylvania

9. Series *Javorkae* Ujh.

Koeleria javorkae Ujh. (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. gracilis [Pers.] Dom. var. typica Dom.)	$2n = 28$	Hungaria et Transsylvania
Koeleria jankae Ujh. (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. gracilis [Pers.] Dom var. glabra [Janka] Dom.)		Transsylvania
Koeleria nyaradyi Ujh. (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. gracilis [Pers.] Dom. var. typica Dom.)		Transsylvania

10. Series *Degeni* Ujh.

Koeleria crassa Ujh. (K. Degeni Dom.)		Pontus
Koeleria degeni Dom.		Pontus, Ucraina
Koeleria skorpilii (Podp.) Ujh. (K. splendens Presl var. pseudorigidula [Dom.] Dom.)		Pontus

11. Series *Nitidulae* Ujh.

Koeleria nitidula Vel.	$2n = 14$	Peninsula balcanica orientalis et Anatolia occidentalis
Koeleria rhodopea Ujh. (K. nitidula Vel. var. obscura [Vel.] Dom. p. p.)		Bulgaria meridionalis

12. Series *Glaucovirentes* Ujh.

Koeleria pilatii Ujh. (K. glaucovirens Dom. p. p.)		Peninsula balcanica orientalis et Anatolia
Koeleria kurdica Ujh. (K. glaucovirens Dom. var. longiflora Dom.)		Kurdistania et Armenia turcica

13. Series *Penzesii* Ujh.

Koeleria penzesii Ujh. (K. glaucovirens Dom. p. p.)		Peninsula balcanica media et orientalia
Koeleria mitrushii Ujh. (K. splendens Presl var. typica Dom.)	$2n = 28$	Peninsula balcanica media
Koeleria paparistoi Ujh. (K. splendens Presl var. typica Dom.)		Peninsula balcanica media et meridionalis

14. Series *Gracilescentes* Ujh.

Koeleria cristata (L.) Pers. em. Borb. (K. gracilis [Pers.] Dom. sensu ampl. ssp. K. gracilis [Pers.] Dom. var. typica Dom.)	$2n = 14$	Eurasia
Koeleria majoriflora (Borb.) Borb.	$2n = 28$	Europa

(K. gracilis [Pers.] Dom. sensu ampl. ssp.
K. gracilis [Pers.] Dom. var. pusztarum Dom.)
Koeleria mollis Mann — $2n = 70$ — Europa
(K. pyramidata spec. coll. ssp. K. pyramidata
[Lam.] Dom. p. p.)

15. Series *Ciliatae* Ujh.

Koeleria montana (Hausm.) Dalla Torre — Alpes centrales
(K. pyramidata spec. coll. ssp. K. montana
[Hausm.] Dalla Torre)
Koeleria kernerii Ujh. — Alpes centrales
(K. pyramidata spec. coll. ssp. K. pyramidata
[Lam.] Dom. var. ciliata [Kern.] Dom.)
Koeleria lamarckii. Ujh. — Alpes centrales
(K. pyramidata spec. coll. ssp. K. pyramidata
[Lam.] Dom. p. p)

REFERENCES

Domin, K. (1907): Monographie der Gattung Koeleria. *Bibl. Bot. (Stuttgart)*, **65** 354

Ujhelyi, J. (1954a): Újabb eljárás a szálaslevelű *Egyszikűek, különösen a Gramineae*-család epidermisz-szövettani vizsgálatához (Neues Verfahren zur epidermis-histologischen Untersuchung der faserblättrigen *Monocotyledonen*, insbesondere der *Gramineae*-Familie). *Bot. Közl.* **45** 227–30

Ujhelyi, J. (1954b): Taxonomical evolution of linear leaves in the family *Gramineae*. *Acta Biol. Acad. Sci. Hung.* Suppl. **4** 17

Ujhelyi, J. (1961): Data to the systematics of the subsectio *Glaucae* of sectio *Bulbosae* of the genus *Koeleria*. *I. Ann. Hist.-nat. Mus. Nat. Hung.* **53** 207–24

Ujhelyi, J. (1962): Data to the systematics of the sectio *Bulbosae* of the genus *Koeleria*. *II.* Ann. Hist.-nat. *Mus. Nat. Hung.* **54** 199–220

Ujhelyi, J. (1963): Data to the systematics of the sectio *Bulbosae* of the genus *Koeleria*. III. *Ann. Hist.-nat. Mus. Nat. Hung.* **55** 187–214

Ujhelyi, J. (1964): Data to the systematics of the sectio *Bulbosae* of the genus *Koeleria*. *IV. Ann. Hist.-nat. Mus. Nat. Hung.* **56** 195–214

Ujhelyi, J. (1965): Data to the sectio *Bulbosae* and sectio *Caespitosae* of the genus *Koeleria*. *V. Ann. Hist.-nat. Mus. Nat. Hung.* **57** 179–202

Ujhelyi, J. (1966): Data to the systematics of the sectio *Bulbosae* and sectio *Caespitosae* of the genus *Koeleria*. *VI. Ann. Hist.-nat. Mus. Nat. Hung.* **58** 177–96

Ujhelyi, J. (1968): Data to the systematics of the sections *Bulbosae* and *Caespitosae* of the genus *Koeleria*. VII. *Ann. Hist.-nat. Mus. Nat. Hung.* **60** 79–107

Ujhelyi, J. (1969): Data to the systematics of the sections *Bulbosae* and *Caespitosae* of the genus *Koeleria*. VIII. *Ann. Hist.-nat. Mus. Nat. Hung.* **61** 165–88

Ujhelyi, J. (1970): Data to the systematics of the sections *Bulbosae* and *Caespitosae* of the genus *Koeleria*. IX. *Ann. Hist.-nat. Mus. Nat. Hung.* **62**

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PROBLEMS IN BIOSYSTEMATIC STUDIES OF HUNGARIAN *FESTUCA OVINA* (SENSU LATO) REPRESENTATIVES

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INTRODUCTION

Members of the *Festuca ovina* group have always been problematical taxa. This fact is reflected in the confused nomenclature as well as in the considerable disagreement concerning the rank of almost every taxon of this group. Very little is known about the relationships and the kind and degree of genetic isolation between these taxa. Their genomic composition, the importance and frequency of natural hybridization, the possibility and degree of introgression, a number of problems connected with breeding systems (e.g. frequency of auto- and allogamy in natural populations, population dynamic role of self-incompatibility systems) and the origin of polyploid taxa, etc. are all to be studied. The main goal of our long-term research programme is to study these questions. By this, we hope to solve partly evolutionary genetical, and partly taxonomic problems.

We started our investigations on the widespread Hungarian taxa of the group in question, but an extension to species of neighbouring countries will obviously be necessary in many cases. The collection of living samples from different natural populations started in 1968. We report now on the results of preliminary investigations and also on some of the possible methods to be used. In the discussion a scheme of our working hypothesis for further studies is given.

PROBLEMS OF IDENTIFICATION

Since the time to deal with the complicated nomenclature has not yet arrived for convenience, we have temporarily kept the names most commonly used in the Hungarian literature (Soó and Jávorka 1951). Similarly the use of specific epithets in this paper is provisional, so it does not always reflect our opinion regarding the proper taxonomic rank.

On the basis of the data assembled so far we cannot, by characters other than chromosome number, tell with certainty the different cytotypes from each other within a 'species'. This may be explained by the fact that cytologically controlled populations were compared in an insufficient number. It is not yet clear how efficient the barrier is that exists between populations of different polyploidy level.

For the characterization of taxa of the *F. ovina* group the pattern and distribution of different tissues in cross-sections of leaves are often applied in identification keys and diagnoses. The appearance of the sclerenchyma

tissue in the cross-section can be classified into three types: (a) continuous (ring-shaped) sclerenchyma; (b) three-banded sclerenchyma; (c) intermediate sclerenchyma (with seven or more bands or a discontinuous ring).

This character seems to be fairly stable and reliable. The pattern may slightly change only under very humid greenhouse conditions. Results comparable for identification can be obtained from midpart sections of the basal leaves of adult plants.

Continuous, ring-shaped sclerenchyma is characteristic of plants belonging to *Festuca vaginata* W. et K. and *F. glauca* Lam. Three-banded sclerenchyma is typical of *F. sulcata* (Hack.) Nym., *F. valesiaca* Schleich. and *F. pseudovina* Hack. ap. Wiesb. Leaves of *F. pseudodalmatica-Krajina*, *F. stricta* Host. and *F. wagneri* have an intermediate sclerenchyma pattern.

Quantitative characters of the inflorescence (those of the panicle, spikelet, gluma, lemma, etc.) are also used for identification. Their usability, however, is very limited on account of considerable overlapping between different taxa, as well as ecological flexibility and enormous intraindividual variability. Nevertheless, the latter error can be eliminated by localized sampling (Horánszky 1970), e.g. by measuring for a comparison between the lengths of glumes, etc. of equivalent sites of spikelets. Measurements from random samplings do not give a symmetrical distribution curve. Although after rearrangement it can be treated as a symmetric one, there is rarely such problem in localized samplings that can be applied for conventional statistical significance tests without difficulty (Horánszky 1970).

RELIABILITY OF PREVIOUS DATA ON DISTRIBUTION AND HABITAT

Geographical distribution data concerning species with continuous sclerenchyma type are usually acceptable in spite of the difficulty in separation of *F. glauca* and *F. vaginata* at the vegetative stage. Their habitats are markedly different. *F. vaginata* grows always on sandy steppes, while *F. glauca* prefers pioneer communities of limestone and dolomite (sometimes also volcanic) rocks. The distribution of diploid and tetraploid cytotypes of *F. glauca* in Hungary is not yet completely known. The tetraploid seems to be the common cytotype, the diploid one being abundant in north-eastern Hungary (Bükk, Torna) only.

Among the species with three sclerenchyma bands in leaf sections *F. pseudovina* is characteristic of alkaline soils, where it can be a dominant grass in certain communities. The presence of the same species in pastures of colline regions (mainly on loessic soil) is, however, disputable and requires further studies. It is not impossible that the grass in such places is a variety of *F. valesiaca*, which is a common species of the oakwood region (up to 500 m) usually on the tetraploid level. The few records of the diploid *F. valesiaca* refers to habitats on relatively dry rendzina soil (Baksay, personal communication).

Critical revision is necessary to evaluate the distribution and ecology of *F. sulcata* in Hungary. This species was formerly reported as a dominant grass on the sandy soil of the Great Hungarian Plain (cf. Soó 1964 pp. 205–6 and many cenological tables of associations published in Hungary before 1960). However, after more careful investigations they proved to be *F.*

wagneri in most if not all localities. The real *F. sulcata* is abundant in the hilly region, but also present on the loessic soils of the lowland.

The other species of intermediate sclerenchyma type are *F. pseudodalmatica* and *F. stricta*. Their distributions are by no means well known. Investigations of the leaf cross-sections of a small sample can easily be misleading, for some of the leaves may be of three-banded sclerenchyma type, while some leaves of the three-banded species may have a tendency to form five-banded (intermediate) sclerenchyma patterns. The primary origin (by differentiation) or the secondary one (by hybridization) of this overlapping in sclerenchyma pattern is not yet understood.

HYBRIDIZATION

Natural hybrids in numerous combinations have been reported in various floras. None of them has been controlled by resynthesis. Spontaneous hybridization is very likely between certain species where different populations have come into contact. In order to demonstrate the possibility of natural hybridization, transplantation experiments were started in 1969; 60 plants of diploid *F. glauca* have been planted into populations of *F. vaginata* (2x), which are under investigation.

Artificial pollination in the same combination in our greenhouse yielded 27 hybrids in 1968, which have since been propagated vegetatively (making 3–5 clones of each F_1 plants). In 1970 similar clones were also made of the parents, and the plants were grown in uniform conditions. Nine quantitative characters of these plants were investigated (see Tables 1–3). The measurements of pollen were also extended to those population samples present in the experimental garden, from which the two parental plants (*F. glauca* and *F. vaginata*) originated. The parental samples show very significant differences in all nine characters studied. The variation of the F_1 hybrid population is greater, often exceeding both parents (Table 1). The fertility of spikelets and the stainability of pollen grains also show wide variations (Tables 2 and 3). It was impossible to find a correlation between male and

Table 1

Quantitative changes in panicle and spikelet of Festuca glauca and F. vaginata parent plants and in their hybrids (means and standard deviations)

Character	*F. glauca*	*F. vaginata*	Hybrids
Panicle internode number	7·20 ± 1·30	8·20 ± 0·84	7·75 ± 1·26
Number of terminal spikelets of panicle	6·40 ± 1·34	5·40 ± 0·17	6·42 ± 1·09
Florets per spikelet	5·60 ± 0·69	3·40 ± 0·68	6·23 ± 1·35
First glume length, mm	2·57 ± 0·21	1·95 ± 0·13	2·36 ± 0·29
Second glume length, mm	3·75 ± 0·24	2·94 ± 0·11	3·28 ± 0·26
Lemma length, 2nd flower, mm	5·11 ± 0·07	4·07 ± 0·13	4·64 ± 0·33
Palea length, 2nd flower, mm	4·83 ± 0·13	3·81 ± 0·23	4·27 ± 0·34
Lemma length, 3rd flower, mm	5·01 ± 0·06	3·80 ± 0·18	4·53 ± 0·34
Palea length, 3rd flower, mm	4·79 ± 0·07	3·52 ± 0·22	4·20 ± 0·25
Awn length, 2nd flower, mm	0·36 ± 0·05	0·19 ± 0·06	0·26 ± 0·14
Awn length, 3rd flower, mm	0·30 ± 0·02	0·19 ± 0·03	0·24 ± 0·13

Table 2

Female fertility in Festuca glauca and F. vaginata parent plants and in their hybrids (means and standard deviations)

Character	*F. glauca*	*F. vaginata*	Hybrids
Number of spikelets per panicle	47·60 ± 7·60	60·22 ± 5·45	45·56 ± 12·86
Number of grains per spikelet	3·67 ± 0·36	2·66 ± 0·36	2·49 ± 1·19

Table 3

Quality and size of pollen grains in Festuca glauca and F. vaginata population samples and in their hybrids (means and standard deviations)

Character	*F. glauca*	*F. vaginata*	Hybrids
Number of investigated plants	8	10	27
Unstained pollen, per cent	14·5 ± 3·71	11·2 ± 4·98	14·8 ± 45·8
Pollen diameter, μ	35·24 ± 2·23	35·94 ± 2·41	34·89 ± 4·92

female sterility. The sizes of pollen grains were not uniform. The parental species (*F. glauca* 2x and *F. vaginata*) do not differ significantly in this respect. Diameters of the pollen of F_1 plants range between very wide limits (25μ–44μ, for instance, in a single plant). At the same time these pollen grains are often sterile (Table 3). These are obvious consequences of meiotic irregularities, which are, however, not effective enough to cause total sterility in the hybrid.

DISCUSSION

The importance of proper sampling for identification and other studies in populations of the *Festuca ovina* group cannot be overemphasized. For cytological and morphological investigations the sample ought to contain a minimum of 20–30 plants. In order to study morphological variations a culture at least six months old is necessary in uniform conditions so that the diversity of phenotypic modifications may be minimized.

The next step will be to clarify the simplest evolutionary relationships in the *F. ovina* group. Our working hypothesis, which is based mainly on morphological and chromosome number observations, is outlined in Fig. 1. Having dealt with polyploid complexes, the primitive progenitors ought to be sought among the diploid taxa. Such cytotypes have been found both in the three-banded (*F. pseudovina*) and continuous sclerenchyma types (*F. vaginata*, *F. glauca*). It cannot be excluded, however, that at least some of the polyploid taxa may also have incorporated other diploids, which do not grow in Hungary.

The continuous sclerenchyma type *F. vaginata* is known on diploid level only. *F. glauca* (rocky habitats), on the other hand, consists of two cytotypes

in Hungary. The diploid has a more restricted submontane-montane distribution, while the tetraploid is much more common, particularly in the colline region. The same species with higher polyploid level has been reported from the Alps (Bidault 1966). The ecological superiority and the regular meiosis (without multivalents) of the tetraploid cytotypes do not seem to refer to simple autopolyploidy. On the other hand, the close morphological similarity of the 2x and 4x cytotypes does not support a genomic allopolyploidy. It is probably a segmental alloploid (sensu Stebbins 1950).

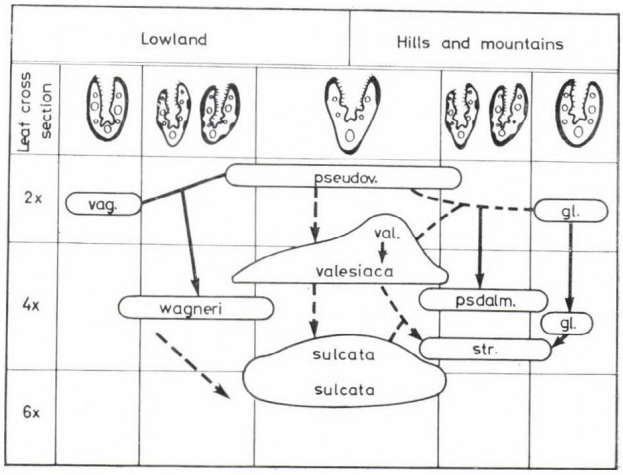

Fig. 1. Hypothetical interrelations and origin of the investigated taxa of the *Festuca ovina* group. The taxa are arranged according to their polyploidy level, habitat preference and leaf anatomy; vag. = *F. vaginata;* pseudov. = *F. pseudovina;* gl. = *F. glauca;* val. = *F. valesiaca;* psdalm. = *F. pseudodalmatica;* str. = *F. stricta.* (Sclerenchyma in the leaf cross-section is in black)

The origin of polyploids in the taxa with discontinuous sclerenchyma is even more complicated. In Hungary among the diploid taxa of this type, we know *F. pseudovina* of sodic soils, *F. capillata* and *F. ovina s. str.* growing on acidic soils. The 2x *F. valesica* mentioned above has been reported from dry rendzina soil.

Most problems arise about the three-banded polyploids: *F. valesiaca* and *F. sulcata*. They grow often in the same plant community without obvious signs of any intergradation. We assume that they are built up from at least partly different genomes.

The intermediate sclerenchyma type is probably polyphyletic in origin. *F. wagneri* of the sandy soils of the lowland is very probably an allotetraploid between *F. vaginata* and *F. pseudovina*. The colline and montane representatives of this group exhibit two taxa: *F. pseudodalmatica* and *F. stricta*. *F. pseudodalmatica* is a common vigorous 'species' predominantly on volcanic rocks. It seems reasonable to suppose that this is an allotetraploid of *F. glauca* 2x and another diploid with three-banded sclerenchyma (like *F. pseudovina*). The other 'species', *F. stricta*, is less vital and occurs sporadically. This could be a hybrid of tetraploid *F. glauca* and one of the three-banded tetraploids (*F. sulcata* or *F. valesiaca*). Owing to the probable segmental alloploid origin of at least one of its parents (*F. glauca* 4x), this hybrid has only partly homologous (homoeologous) chromosomes at meiosis, which will cause reduced fertility and consequently decreased evolutionary success.

It has been pointed out (Tables 2 and 3) that the reproductive isolation is not complete between certain diploid species (*F. vaginata* and *F. glauca*

2x). Therefore, there is even more possibility for hybridization and probably for introgression at the polyploid level. Differences in chromosome number do not represent a strong genetic barrier (cf. Zohary and Nur 1959). There are many ways in this group to obscure taxonomic differences making almost insoluble problems for the taxonomist.

By selecting several problems outlined above, we have attempted to illustrate the complicated taxonomic and evolutionary situation of the *F. ovina* group. We realize that our moderate opportunities are not enough to solve the whole problem. We are convinced that the questions on the evolution of this group could be answered much sooner and more properly in an international co-operation, in which we are ready to participate.

REFERENCES

Bidault, M. (1966): Remarques sur les *Festuca ovina* L. var. *duriuscula* et var. *glauca* des Alpes-Maritimes. *Bull. Soc. bot. Fr.* **113** 173–83

Horánszky, A. (1970): Festuca-tanulmányok. II (Festuca studies. II). *Bot. Közlem.* **57** 207–15

Soó, R. (1964): *A magyar flóra és vegetáció rendszertani-növényföldrajzi kézikönyve* (Synopsis Systematico-geobotanica Florae Vegetationisque Hungariae), Vol. 1. Akadémiai Kiadó, Budapest

Soó, R. and Jávorka, S. (1951): *A magyar növényvilág kézikönyve* (Handbook of the Hungarian flora), Vol. 2. Budapest, Akadémiai Kiadó

Stebbins, G. L. (1950): *Variation and evolution in plants.* New York, Columbia University Press

Zohary, D. and Nur, U. (1959): Natural triploids in the orchard grass, *Dactylis glomerata* L., polyploid complex and their significance for gene flow from diploid to tetraploid levels. *Evolution* **13** 311–7

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EVOLUTION OF THE CULTIVATED POTATO *SOLANUM TUBEROSUM* L.

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The cultivated potato, *Solanum tuberosum* L., originated in South America and was brought to Europe during the latter half of the sixteenth century. At first it was treated as a botanical curiosity, and it was not until the mid eighteenth century that it became widely cultivated outside South America. Like most other plants of ancient domestication its early history as a cultivated plant is obscure. Nevertheless, from the techniques pioneered by de Candolle (1882), Vavilov (1926, 1930, 1951, etc.) and others we can reconstruct the main outlines of its evolution as a cultivated plant and point with some degree of confidence to the wild species from which it was derived.

Much of the nineteenth century thought on the origin of the potato was invalidated because of an insufficient knowledge of the species and its relatives in South America itself. Only after the pioneer collecting expeditions of Vavilov, together with the Russian potato specialists Juzepczuk and Bukasov (1929, Bukasov 1930, 1933, etc.) was it possible to understand the botanical and genetical basis of the origin of the potato. These investigators further showed that we should not merely speak of the origin of a single species, *S. tuberosum*, but of a polyploid series of species with diploid ($2n = 24$), triploid ($2n = 36$) and pentaploid ($2n = 60$) species as well as the tetraploid *S. tuberosum* ($2n = 48$). These were well distributed in the high Andes of South America at altitudes of 2000 m to 3500 m or even higher, and were cultivated from Venezuela southwards to Argentina. Potatoes were also grown in the temperate coastal regions of southern Chile. Most were fairly resistant to cool growing conditions whilst several species and varieties were actually resistant to sub-zero temperatures (*S. juzepczukii*, *S. curtilobum*, *S. ajanhuiri*). Another species, *S. phureja*, was grown in the subtropical medium altitudes and showed no dormancy in its tubers. The variation in tuber form, colour, taste and texture was shown by the Russian investigators to be immense in comparison with the potatoes then grown in Europe, and it was confidently predicted that the primitive cultivated species would form a useful genetic basis for twentieth century potato breeding. Not all these hopes have been realized, and in fact the wild species have been found to be rather more promising than the cultivated ones. Even so, the genetic reservoir of the primitive cultivated species has not yet been fully evaluated and much remains to be done.

Opinions on the species boundaries in cultivated potatoes differ widely. At the one extreme Juzepczuk and Bukasov have tended to split the total variability into a rather large number of narrowly defined species. On the other, Dodds (in Correll 1962) has included them all under the one species,

S. tuberosum. I have tended to take the middle course (Hawkes 1963), recognizing the following species:

1. *S. stenotomum* ($2n = 24$). A very 'primitive' looking species with many variants hardly distinguishable from wild species; cultivated in the high Andes of Bolivia and Peru and incorporating frost-resistant clones. (*S. goniocalyx* can be regarded as a northern subspecies in central Peru).

2. *S. ajanhuiri* ($2n = 24$). Frost resistant. High Andes of the Lake Titicaca basin. Probably close to, if not specifically identical with *S. stenotomum*, or possibly of hibrid origin.

3. S. *phureja* ($2n = 24$). Widely distributed from Venezuela to north Bolivia at lower altitudes than the other species and showing no tuber dormancy.

4. S. *chaucha* ($2n = 36$). High Andes of Peru and Bolivia. The name has been applied to triploid hybrids between diploid and tetraploid cultivated species which are maintained by clonal propagation and no doubt are being continually re-formed.

5. *S. juzepczukii* ($2n = 36$). This is a natural triploid hybrid between the wild frost-resistant tetraploid species, *S. acaule*, and the cultivated diploid, *S. stenotomum* (Hawkes 1962). It is grown at very high altitudes ($\pm$3800 m) and is highly frost resistant.

6. *S. tuberosum* ($2n = 48$). I have included all the tetraploid cultivars under this species (Hawkes 1956), distinguishing the Andean forms as subspecies *andigena* and the Chilean ones as subspecies *tuberosum*. Juzepczuk and Bukasov, however, considered that these were two distinct species, each with separate origins. Subspecies *andigena* is grown from Venezuela to northern Argentina and is especially variable from central Peru to central Bolivia. It is also grown in Guatemala and Mexico but was probably taken to those countries by the Spaniards after the conquest. Subspecies *tuberosum* is cultivated in southern Chile. The 'European'* varieties also belong here.

7. *S. curtilobum* ($2n = 60$). This interesting pentaploid species is grown in Peru and Bolivia and is derived from natural crosses between *S. juzepczukii* and *S. tuberosum* ssp. *andigena* (Hawkes 1962). It is frost resistant and occurs at high altitudes.

It will be seen from the above very brief account of cultivated potato species that there is a considerable concentration of specific diversity in the central Andes from central Peru southwards to central Bolivia. Apart from ssp. *tuberosum* all the species and subspecies are grown in that region. In addition, genetic diversity is particularly high there, and especially in the Lake Titicaca basin on the borders of Peru and Bolivia. Here are found extreme shapes, colours and colour patterns in the tubers, with a wide range of flower colour and leaf type.

Vavilov's well-known method for determining the centre of origin of a cultivated plant by identifying the centre of diversity and comparing that with the distribution of related wild species would lead us to consider therefore that the central Andes of Peru and Bolivia are the centre of origin of the potato. The Russians considered that the potato had two centres of origin, one in the Andes, as I have just mentioned, and the other in southern

* By 'European' are meant in this context all the tetraploid potatoes grown throughout the world and derived from European sources in the first place.

Chile. I shall return to a discussion of this Chilean origin later. Apart from that, the potato seems to fit ideally with Vavilov's thesis, even to the extent of showing a concentration of dominant alleles at the centre of diversity and recessive ones at the periphery, providing that we consider the Chilean forms to be at the periphery of the primitive distribution area rather than in the centre of another one.

Archaeological evidence is not very strong but does not actually contradict the hypothesis of Andean origin. There are plenty of records of ancient civilizations in Peru and Bolivia but the spectacular archaeological remains of the Inca, Tiahuanaco, Nazca and Mochica cultures are unfortunately comparatively recent, dating from not earlier than about 500 BC. (2500 before present). However, recent work by Engel (1970) gives radiocarbon dating of 10 500–8 000 BP for certain tuber remains, which is the earliest yet found; there is some doubt in fact as to whether they are genuinely cultivated, and it is probable that these are the remains of early gathered materials before the advent of potato domestication. Apart from this, cultivated potatoes have been tentatively identified from levels dated at 2 400 BP but 1000 AD is the oldest level from which they are known with certainty (see Towle 1961; Hawkes 1967).

Let us now examine current theories on the origins of the various potato species I have just described.

Because of its 'primitive' appearance, that is to say, its similarity in the above-ground parts to many wild species, *S. stenotomum* is generally considered to be closest to the ancestral form of all the cultivated potatoes. It is particularly similar to the wild species *S. leptophyes* and *S. canasense* which occur in the same area, but further work, especially biochemical and serological, is needed to verify this relationship more exactly. The other diploid species (*S. phureja* and *S. ajanhuiri*)* are considered to have been derived from *S. stenotomum* by mutation and selection.

We have already seen that the triploid species *S. chaucha* and *S. juzepczukii* are hybridogenic and are maintained and propagated vegetatively. The origin of *S. juzepczukii* and *S. curtilobum* was verified by synthesizing them from the parental species and comparing the synthetics morphologically and cytologically with the naturally occurring species (Hawkes 1962).

S. tuberosum still presents many problems. It will be remembered that Juzepczuk and Bukasov considered that there were two tetraploid species, *S. andigena*** and *S. tuberosum*, each with its separate origin in the Andes and Chile, respectively. Salaman (1946, 1954) pointed out that there were really no essential differences between the two species, but Hawkes (1956) and Simmonds (1966) demonstrated clear differences between them, even though not of specific rank. Hawkes showed that there were no genetic barriers between these Andean and Chilean tetraploids visible from F_2 progeny tests and that the morphological and photoperiodic differences were better regarded as characterizing two subspecies rather than two species.

It would seem that the tetraploid complex originated in the central

* There is some evidence that *S. ajanhuiri* is also hybridogenic, derived from *S. stenotomum* × *S. megistacrolobum* crosses. This hypothesis is now being investigated.

** They used the spelling *S. andigenum*.

Andes and was disseminated by Man to the north and south. The northward spread was stopped in Colombia by the lowlands of Central America, but to the south potatoes were taken into the temperate lowlands of southern Chile where they became modified by the new day-length conditions. The Chilean forms were separated from their sources in Peru and Bolivia by the Atacama desert and the high dry mountain barriers of northern Chile and Argentina.

Juzepczuk and Bukasov (1929) postulated an origin of the Chilean tetraploids from the 'wild' species, *S. molinae* and *S. leptostigma*. However, it is more likely that these represent escapes from cultivation that have become naturalized here and there. In Chile there are no diploid wild species (apart from the unrelated *S. maglia*, which in any case is generally triploid) from which the tetraploid might have been derived. On the other hand, in Peru and Bolivia there is a great wealth of wild and cultivated diploid forms. The related Chilean tetraploids, *S. leptostigma* and *S. molinae* demonstrate no genetic breakdown in the F_2 of crosses with *S. tuberosum* and even show a red tuber pigment mutation which is everywhere else confined to cultivated potato varieties. This evidence seems to me to point towards a *single* origin for tetraploid potatoes rather than a dual one.

The search for a tetraploid *wild* ancestor of *S. tuberosum* ssp. *andigena* in the Andes has not been successful and those forms which have been found look, again, as though they were escapes from cultivation. It therefore seems highly likely that *S. tuberosum* has no wild ancestor at all in the strict sense, but has probably been derived from a diploid cultivated potato such as *S. stenotomum*.

It has generally been assumed that *S. tuberosum* is an autotetraploid species since in its cytological behaviour it compares closely with autotetraploid tomatoes and with autotetraploids of diploid cultivated potatoes (Swaminathan 1954). Cadman (1942, 1943) demonstrated tetrasomic inheritance in it also. On morphological grounds the derivation of *S. tuberosum* from *S. stenotomum* alone does not seem very likely and I have suggested on various occasions that it might perhaps be an amphiploid of *S. stenotomum* and a wild or weed species. The widespread weed, *S. sparsipilum*, bears many morphological similarities to *S. tuberosum* and we are at present trying in my laboratory to verify this hypothesis. In addition to morphological and cytological techniques we are using various biochemical tests and raising synthetic hybrids of the sort postulated for the naturally occurring tetraploid. We are also attempting to raise polyhaploids from ssp. *andigena*, using the methods devised by Hougas and Peloquin (1957, 1958). These will be crossed and selected for extreme characters to see how far it may be possible to recreate the original diploid ancestors. The results so far are promising, and it seems very likely that naturally occurring hybrids between two distinct species which were genomically very similar could have given rise to tetraploids under cultivation which behaved cytologically like autotetraploids, and where the chromosomes were so similar as to associate as multivalents in enough cases to show tetrasomic inheritance of a number of characters. Although the genomic situation is different it will be appreciated that this process is similar in many ways to that in which the hexaploid wheat species were formed by crosses of *Triticum dicoccum* × *Aegilops squarrosa*.

Finally, how was the potato first brought into cultivation? We can suppose that Andean peoples at the hunting and gathering, pre-agricultural stage began to eat the tubers of wild potatoes and also stored them for further use. Potatoes possess weedy tendencies and are nitrophiles. Hence, they would automatically colonize the rich disturbed soils round Man's dwellings. After many generations the process of gathering gradually would have turned into harvesting. Finally, the process of planting was discovered, that is, all the tubers were harvested and some were kept for re-planting.

Even now, remnants of an early stage exist in remote parts of the northern Andes of Colombia and Venezuela, where I have found cycles of gathering over several years before new plantings were made. In one area I found evidence of continual harvesting, with no planting having taken place within living memory. This surely must be a remnant of a very early stage in potato domestication.

When planting and harvesting have been incorporated as regular processes, then other selection pressures act on the plants under cultivation. For instance, short stolons are selected for unconsciously, since tubers borne on long stolons will not be gathered because they are too far away from the parent plant. Thus short stolons, which are eliminated in the wild because the daughter plants will compete too strongly with each other in the same place, are of positive advantage under cultivation. Possibly also, brightly coloured skin pigments may also help towards efficient harvesting, whilst the dull brown colours of wild species may be overlooked. Thus, again selection pressure for bright colours and distinctive shapes and colour pattern will result in quite different evolutionary end points in the cultivated potatoes as compared with the wild ones.

In this brief review of the evolution of cultivated potatoes we have had no time to deal with the evolutionary history of *S. tuberosum* in Europe. There has been some controversy about the source of the European potato and the subspecies introduced. However, one can say that the European potato is at present an amalgam of germ-plasm from both subspecies, whilst many of the newer varieties incorporate genetic material from wild species, such as the Mexican *S. demissum* and *S. stoloniferum*, the Andean *S. acaule* and the Argentine *S. vernei*. Thus to the processes of natural evolution plant breeders have added a new dimension, that of synthetic or artificial evolution.

REFERENCES

Bukasov, S. M. (1930): The cultivated plants of Mexico, Guatemala and Colombia. *Bull. Appl. Bot. Genet. and Plant Breed. Suppl.* **47** Chapter 14, 141–226

Bukasov, S. M. (1933): The potatoes of South America and their breeding possibilities. *Bull. Appl. Bot. Genet. Pl.-Breed. suppl.* **58** 192

Cadman, G. H. (1942): Autotetraploid inheritance in the potato: some new evidence. *J.Genet.* **44** 33–52

Cadman, G. H. (1943): Nature of tetraploidy in cultivated European potatoes. *Nature (Lond.)* **152** 103–4

Candolle, de, A. (1882): *Origine des Plantes Cultivées.* Paris

Correll, D. S. (1962): The potato and its wild relatives. *Texas Res. Found. Bot. Studies,* **4** 606 pp.

Engel, F. (1970): Exploration of the Chilca Canyon, Peru. Research Report. *Current Anthropol.* **11** 55–8

Hawkes, J. G. (1956): Taxonomic studies on the tuber-bearing Solanums. I. *Solanum tuberosum* and the tetraploid species complex. *Proc. Linn. Soc. (Lond.)* **166** 97–144
Hawkes, J. G. (1962): The origin of *Solanum juzepczukii* Buk. and *S. curtilobum* Juz. et Buk. *Z. Pflanzenz.* **47** 1–14
Hawkes, J. G. (1963): A revision of the tuber-bearing Solanums (2nd ed.) *Rec. Scott. Pl. Breed. Stn.* 76–181
Hawkes, J. G. (1967): Masters Memorial Lecture, 1966. The history of the potato. *J. Roy. Hort. Soc.* **91** 207–24; 249–62; 288–302; 364–65
Hougas, R. W. and Peloquin, S. J. (1957): A haploid plant of the potato variety Katahdin. *Nature (Lond.)* **180** 1209–10
Hougas, R. W. and Peloquin, S. J. (1958): The potential of potato haploids in breeding and genetic research. *Amer. Potato J.* **35** 701–7
Juzepczuk, S. W. and Bukasov, S. M. (1929): A contribution to the question of the origin of the potato. *Proc. USSR Congr. Genet. Pl. and Animal Breed.* **3** 593–611
Salaman, R. N. (1946): The early European potato: its character and place of origin. *J. Linn. Soc.* (Bot.) **53** 1–27
Salaman, R. N. (1954): The origin of the early European potato. *J. Linn. Soc.* (Bot.) **55** 185–90
Simmonds, N. W. (1966): Studies of the tetraploid potatoes. III. Progress in the experimental re-creation of the Tuberosum Group. *J. Linn. Soc.* (Bot.) **59** 279–88
Swaminathan, M. S. (1954): Nature of polyploidy in some 48-chromosome species of the genus Solanum, section *Tuberarium*. *Genetics*, **39** 59–76
Towle, Margaret A. (1961): *The ethnobotany of pre-Columbian Peru.* Aldine Publ. Co. New York, 1961
Vavilov, N. I. (1926): Studies on the origin of cultivated plants. *Bull. Appl. Bot. Pl. Breed.* **16** 1–248
Vavilov, N. I. (1930): The problems of the origin of cultivated plants and domestic animals, as conceived at the present time. *Proc. USSR Congr. Genet. Plant- and Animal Breed.* **2** 5–18
Vavilov, N. I. (1951): The origin, variation, immunity and breeding of cultivated plants. *Chron. Bot.* **13** 1–6, 1–366

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CYTOLOGICAL AND HYBRIDIZATION STUDIES IN THE GENUS *SYMPHYTUM*

by

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According to Wickens, who recently revised the Turkish species, the genus *Symphytum* contains 33 species. Relatively little attention had previously been paid to the genus, and, therefore, the revival of interest not only from the side of the herbarium taxonomist, but also of the experimentalist, is of great interest for the elucidation of the numerous taxonomic problems.

Also on behalf of my colleague, Mr. E. Kliphuis, I should like to show you some of the very complicated relationships that exist between the species (i) *Symphytum officinale*, (ii) *Symphytum uliginosum* and (iii) *Symphytum asperum*. The investigations were carried out at Utrecht, the Netherlands, during several years. We are fully aware of the fact that we have not found an answer to all questions and are of the opinion that the help of geneticists is badly needed in order to permit more definite conclusions.

Since 1963 we have collected many plants in various parts of Western and Central Europe. For final conclusions, however, a comparison of these plants with those of Eastern Europe, more specifically from Southern Russia, the Caucasus and the Balcan Peninsula, is absolutely necessary. One of the reasons why Mr. Kliphuis and I decided to participate in this Symposium is the fact that we have a fine opportunity now to add a sample of living plants collected in Hungary to the already existing collection, which consists of more than 1600 living specimens.

The three species to which this survey is limited are ecologically differentiated and differ also in their geographical distribution. *S. uliginosum*, which occurs in Southern Russia, Hungary and Romania, is partially sympatric with *S. officinale* and completely allopatric with *S. asperum*. *S. officinale* and *S. asperum* are allopatric according to Kuznetsov (1910), who studied the distribution of both species in the Caucasus and adjacent regions. *Symphytum asperum* prefers higher altitudes than *Symphytum officinale* and occurs in *Picea* forests and by streams from 800–2000 m. *S. officinale* and *S. uliginosum*, on the other hand, are lowland species, the former rarely exceeding 1000 m level, the latter preferring regions that are regularly flooded.

Symphytum officinale inhabits a larger part of Europe and lives in damp places, rich in nitrogen, i.e. in orchards, osier-beds, on dikes, by roadsides, in hedgerows, along rivulets, and at the edges of forests, but does not seem to be salt-tolerant and avoids much shade.

Since *Symphytum officinale* and *Symphytum asperum* are morphologically quite distinct and eco-geographically isolated, at first sight the relationship between these two species does not seem to be very interesting from the


24
40
48
32
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biosystematic point of view, whereas the opposite proves to be true. By the influence of man many puzzling forms of *Symphytum* arose, presenting interesting problems to both experimentalists and herbarium taxonomists.

To introduce the main themes of our *Symphytum* studies, let us first look at the variation of the individual species and secondly at their breeding relationships.

(i)–(ii) *Symphytum officinale* is a variable species. Not only the height of the plants and the indument of the stems and leaves vary considerably, but also the most conspicuous character, the colour of the flowers. In some populations all plants are white-flowered, in others purple-flowered, but also mixed populations are met with in various parts of Europe. According to Tutin (1956) most plants in Western Europe are white-flowered, whereas according to Steven (1851) and Popov (1953) no white-flowered individuals have been reported from Russia.

Studies of many Linnean species have shown that different individuals may have different chromosome numbers. Also in *Symphytum officinale* this is the case and the plants studied may be divided into three main groups (Gadella and Kliphuis 1967), viz. (a) plants with chromosome number $2n = 24$ (diploid plants); (b) plants with chromosome number $2n = 48$ (tetraploid plants); (c) plants with chromosome number $2n = 40$.

These groups will be treated in more detail (Fig. 1).

(a) *Diploid plants.*—These are white- or creamy-flowered. Diploid plants are probably not as common as tetraploid plants. They have been reported from the Netherlands (where they are very rare), Czechoslovakia, Great Britain, G. D. R., Italy, and Hungary (near Dabas). In the Dutch and Italian plants some B-chromosomes (1–4) are present.

(b) *Tetraploid plants.*—These have white, creamy, purple, or red flowers. The populations sometimes consist entirely of white-flowered or of purple-flowered individuals but mixed populations are also often found, in which white- and purple-flowered individuals occur in various proportions. Tetraploid plants seem to be the most common in various regions of Europe. They have been found in Austria, Belgium, Czechoslovakia, France, G. F. R., Great Britain, the Netherlands, Romania and Yugoslavia. In three localities in the Netherlands diploid and tetraploid plants grow together. A very close examination of the diploid and tetraploid white-flowered individuals in these mixed populations did not reveal the existence of clear cut morphological differences. From one of these localities 46 plants were cytologically studied, 12 of which were purple-flowered and 34 white-flowered. All purple-flowered plants proved to be tetraploid, while the white-flowered plants turned out to be diploid (16 individuals) or tetraploid (18 individuals). Not a single triploid plant ($2n = 36$) was met with.

(c) *Plants with chromosome number* $2n = 40$. These nearly always have purple flowers, it was only exceptional that white-flowered plants were

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Fig. 1. Chromosome number and colour of the flower in various populations of *Symphytum officinale*. 24. *Symphytum officinale* subsp. *officinalis*. 40. *S. officinale* subsp. *uliginosum*. 48. *S. officinale* subsp. *officinale*. 32. *S. asperum*. 36. *S. "asperum", garden origin* Hybrid?; 36. *S.* × *uplandicum* (artificial hybrid); 36. *S.* × *uplandicum* (nature: Ireland) 40. *S.* × *uplandicum* (artificial hybrid); 40. *S.* × *uplandicum* (nature: Belgium)

Table 1

Chromosome number	Number of populations	Number of plants	Colour of the flowers	
			white or cream	purple
$2n = 24$	12	75	75	0
$2n = 48$	35	198	75	123
$2n = 40$	26	149	5	144
			usually mixed in the same population	

met with. The leaves, which are extremely rough and provided with prickly hairs, with a tubercular base, are usually not as strongly decurrent as in the diploid and tetraploid types. Also the calyx is often purple, sometimes green, and the indument of the long free part of the sepals differs from that of diploids and tetraploids (Fig. 2). This cytotype occurs abundantly

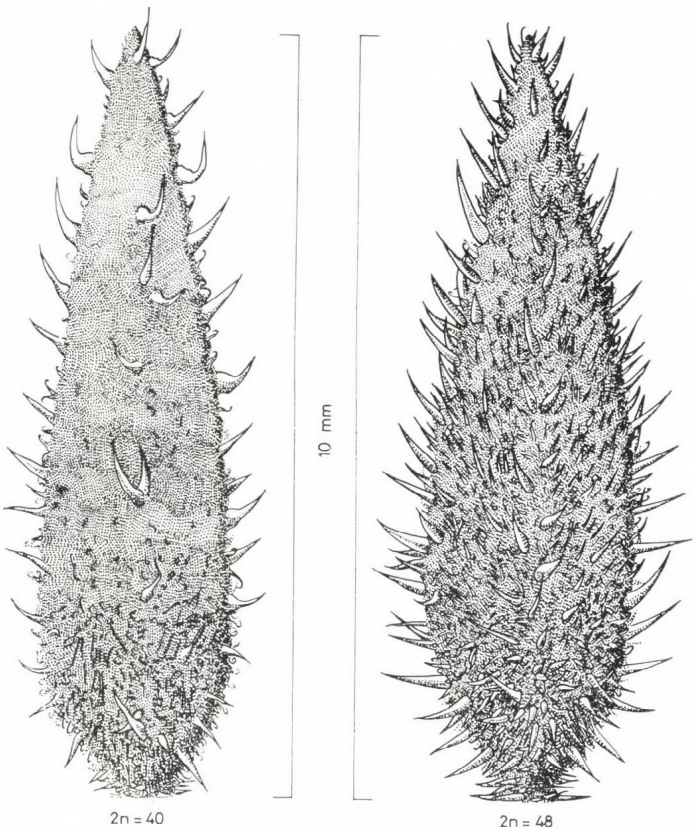

Fig. 2. Indument of the sepals of *Symphytum officinale* L. Sepals of diploid ($2n = 24$) and tetraploid ($2n = 48$) plants are not separable on morphological basis

in the Netherlands, but has so far not been found elsewhere. It always grows on peaty soil under very moist conditions. The plants are especially very common on so-called 'legakkers, (a Dutch word denoting the longitudinal remnants of the original peat-bog) but also along ditches and on shores of lakes in the lowmoor peat-bog regions of the Netherlands. The plants largely agree with Kerner's (1863) description of *Symphytum uliginosum*. This species is, however, restricted to Hungary and Southern Russia, according to Bucknall (1913). Transitional forms to *S. officinale*, which were recorded by Soó (1926) from Hungary, may obscure the differences between these two taxa. As *S. uliginosum* had not been reported from Western Europe before, Mr. Kliphuis and I doubted whether our material was identical with *Symphytum uliginosum*. A comparison with the descriptions by Kerner and Bucknall, the plate in the flora of Romania, and herbarium material collected by Kerner in the type locality led us to the conclusion that the Dutch plants closely but not entirely match *S. uliginosum*. Be this as it may, a close examination of Hungarian material of *S. uliginosum* and a morphological and cytological comparison between Hungarian and Dutch materials are highly desirable.

The view that *S. officinale* was introduced as a medicinal and fodder plant from the Pontic region into Western Europe (Gams in Hegi 1927) is contradicted by the fact that at present two of its cytotypes occur under different ecological conditions. In my opinion it is rather impossible that both cytotypes, $2n = 40$ and $2n = 48$, have been introduced independently of each other and occupy at present very different habitats. The distribution of the various cytotypes in the Netherlands is shown in Fig. 3.

The evidence about the status of the three cytotypes described is at present inadequate. Therefore, we tried to make artificial hybrids, which might provide a better insight into their breeding and taxonomic relationships. *S. officinale* is a regular outbreeder; this holds true for all cytotypes. Self-pollination never resulted in the formation of mature and viable nutlets. Despite this fact all flower buds were emasculated in order to avoid any possibility of self-fertilization. The following results were obtained (Fig 4).

The cytotypes 40 and 48 are interfertile and give rise to hybrids with 44 chromosomes, which are fertile and may be successfully back-crossed with either parent, resulting in hybrids with 42 and 46 chromosomes, respectively. By further back-crosses all numbers between 40 and 48 could be obtained. At least in three different localities in the Netherlands plants with the numbers $2n = 40$ and $2n = 48$ interbreed, resulting in highly variable hybrid swarms, with all possible chromosome numbers between 40 and 48. The two cytotypes, which do not grow intermingled for ecological reasons, were mixed as a result of man's activities in modifying natural communities and breaking down the natural ecological barriers (e.g. by road construction). Clearly this represents a case of introgressive hybridization. Anderson (1949), who was the first to describe this phenomenon, mentioned some interesting cases, all of which have in common that the chromosome numbers of the participating taxa are the same or in one case nearly the same. Consequently, all hybrid individuals have the same chromosome number as that of their parents, but in *Symphytum officinale* both parents differ widely in their chromosome numbers. This implies that both taxa, *S. uliginosum* and *officinale*, are very well suited for experi-

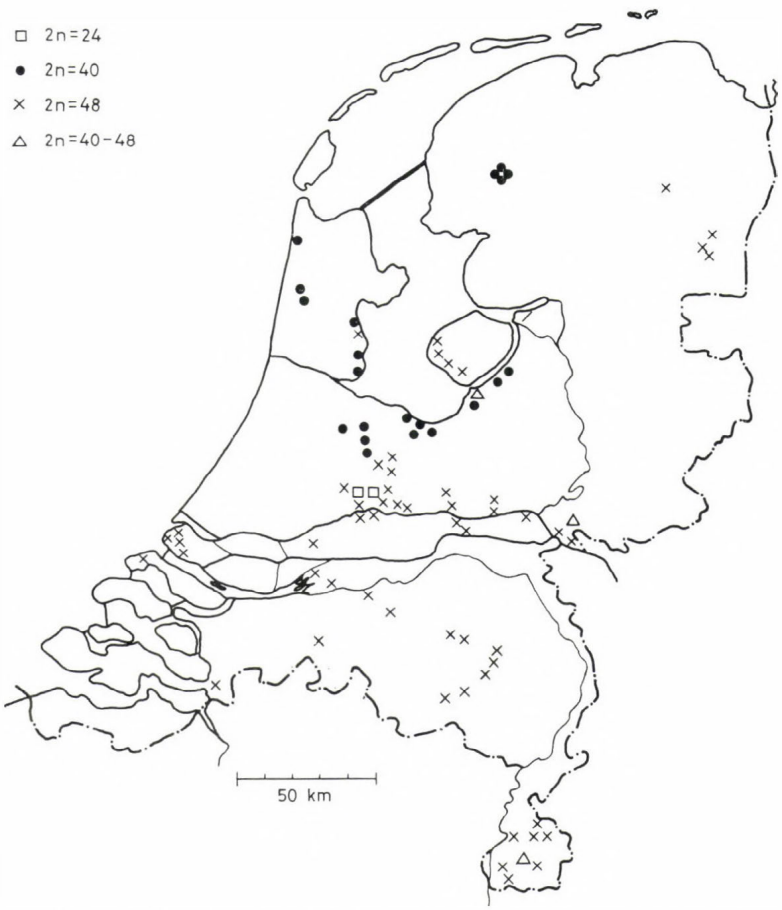

Fig. 3. Distribution of the cytotypes of *Symphytum officinale* in the Netherlands

mental research of introgressive hybridization. Introduction of one or a few plants into a pure population of the other cytotype may give a better insight in the way in which introgression takes its course in nature. Studies on this problem are in progress.

Crosses between the cytotypes $2n = 24$ and $2n = 40$ on the one hand, and between $2n = 24$ and $2n = 48$ on the other, always failed, with two exceptions. In both cases the pollen of a white-flowered individual of the cytotypes $2n = 40$ and $2n = 48$ was needed; the cross always failed if the pollen originated from a purple-flowered individual. Of a potential number of nutlets of 1224 in the cross between the cytotypes $2n = 24$ and $2n = 40$ only one hybrid was obtained, i.e. 0·08 %. In the cross between the cytotypes $2n = 24$ and $2n = 48$ two hybrids were formed, i.e. 0·1 % of the potential number of nutlets.

Purple- and white-flowered tetraploid plants could be readily crossed. The same holds true to the cytotype $2n = 40$.

From these morphological, cytological, and hybridization studies the following conclusions may be drawn. (a) Morphologically very similar plants of the cytotypes 24 and 48 are crossable only potentially and with great difficulty, and they do not hybridize actually, in so far as is known up till now. This makes it possible for these cytotypes to grow in company and yet remain distinct. It does not seem advisable to assign the diploid plants to a special taxon since they are indistinguishable from tetraploid white-flowered plants. (b) Morphologically separable plants of the cytotypes $2n = 40$ and $2n = 48$ are potentially and actually crossable with great ease. In nature the cross is prevented by differences in habitat preferences of the two types, but in some localities fertile hybrid swarms arose under the influence of man; they show a remarkable range of variation. This led us to the conclusion that probably the best solution is to treat the two cytotypes as subspecies. We assign the tetraploids to the subspecies *officinale* and, provisionally, the plants with the number $2n = 40$ to the subspecies *uliginosum*. The diploids are also considered to belong to subspecies *officinale*, as they are indistinguishable from the tetraploids. (c) Biosystematically the cytotypes $2n = 40$, and $2n = 48$ belong to the same biospecies, the cytotypes $2n = 24$ and $2n = 40$ to different biospecies. The same holds true for the cytotypes $2n = 24$ and $2n = 48$. In the classical taxonomic sense the two types $2n = 24$ and $2n = 48$ belong to the same taxon, as opposed to the type $2n = 40$. We agree with Davis and Heywood (1963) that in cases of conflicting evidence preference should be given to morphological data over hybridization experiments. (d) Many crossing experiments had to be performed (more than 8000 flowers were involved) before we could arrive at the foregoing conclusions.

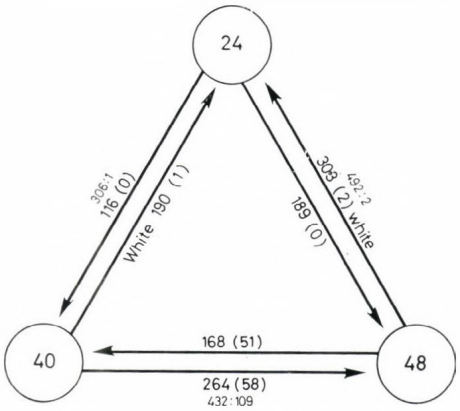

Fig. 4. Crossing relationships between the three cytotypes of *Symphytum officinale* ($2n = 24$, $2n = 48$, $2n = 40$). The direction of arrows corresponds to that of pollination. The number of F_1 plants obtained are in brackets, the other figures refer to the number of emasculated flowers

(iii) The third species studied, *Symphytum asperum*, is variable according to Wickens (1969), but owing to lack of material we had to confine ourselves to one strain collected in the wild in the Caucasus. Contrary to the results obtained by Strey (1931) and Britton (1951), who counted $2n = 36$ and $2n = 40$, respectively, Gadella and Kliphuis (1969) found $2n = 32$ and confirmed the results obtained by Grau (1968). *S. asperum* and *S. officinale* are morphologically quite distinct. In *S. officinale* the leaves are decurrent, the calyx is large, the nutlets are smooth, and the flowers are white, purple or red, whereas in *S. asperum* the leaves are not decurrent, the calyx is small, the nutlets are strongly areolate and granulate, and the flowers are

skyblue. Also the shape of the corolla differs. In spite of the absence of natural hybrids between these taxa, the opinion is held by many taxonomists that both species are crossable and that their hybrid is widespread in Europe. In Britain the hybrid is called Prickly Comfrey and was described by Nyman (1878–82) as *S.* × *uplandicum* Nym. Most authors (Gams in Hegi 1927; Faegri 1931; Tutin 1956) agree that. *S.* × *uplandicum* is a hybrid between *S. asperum* and *S. officinale*. In their opinion the hybrid was introduced as a fodder plant into Western and Central Europe. Since it escaped from cultivation and established itself in many localities, backcrossing with *S. officinale* cannot be excluded. Other authors, e.g. Bucknall (1913), regard the putative hybrid as a true species in view of its true breeding and assign it to *Symphytum peregrinum*. Kuznetsov (1910), however, regarded *S. peregrinum* as a good species of the Transcaucasian province Talysh, which is not at all identical with *S.* × *uplandicum* and which was placed by Wickens very close to *S. asperum*. It is clear that this true-breeding is not in accordance with its presumed hybrid nature. Since hybridization experiments are lacking, an experimental approach to the problem appeared to be absolutely necessary.

Crossing experiments gave the following results (Fig. 5). Both cytotypes

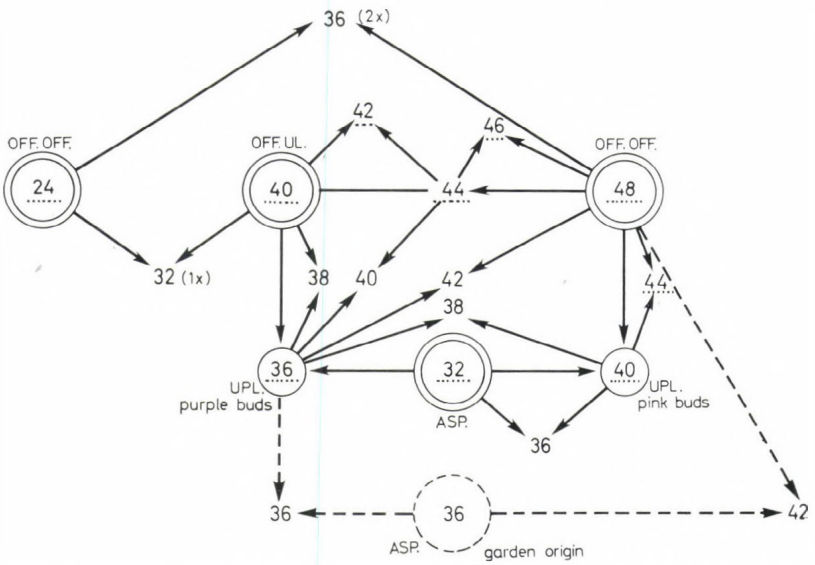

Fig. 5. Crossing experiments between *Symphytum officinale*, *Symphytum asperum* and *Symphytum* × *uplandicum*. Double circles indicate pure species or subsp., single circles the two types of *Symphytum* × *uplandicum;* also the results of (repeated) back-crosses have been included; OFF. OFF. = *Symphytum officinale* subsp. *officinale*; OFF. UL. = *Symphytum officinale* subsp. *uliginosum*- UPL. purple buds = *Symphytum* × *uplandicum* with purple flower buds; UPL. pink buds = *idem*, but with pink buds; ASP. = *Symphytum asperum;* ASP. garden origin = *Symphytum 'asperum'*, $2n = 36$, originating from some European botanical gardens [these plants resemble *Symphytum asperum* to a certain extent; probably they are identical with the hybrid *Symphytum asperum* ($2n = 32$) × *Symphytum* × *uplandicum* ($2n = 40$)]

$2n = 40$ and $2n = 48$ of *S. officinale* can be crossed with great ease with *S. asperum*, giving rise to hybrids with 36 and 40 chromosomes, respectively. Both hybrids very clearly show the characters of *S.* × *uplandicum*, but they are not identical. Perring (verbal communication) showed us some populations of *S.* × *uplandicum* near Cambridge and drew our attention to the fact that some *S.* × *uplandicum* plants have purple flower buds, others pink ones. These and other plants were cytologically analysed. The plants with purple flower buds have chromosome number $2n = 36$, those with pink buds $2n = 40$. The same holds true for our experimental hybrids; the pink-budded form $2n = 40$, the purple-budded $2n = 36$. This implies that *S.* × *uplandicum* is a collective name covering a series of hybrids between *S. officinale* and *S. asperum*. The story, however, has not yet come to an end. Both experimental hybrids are fertile and produce many viable nutlets, at least as many as pure *S. officinale* and *S. asperum*. Wade (1958) grew a large number of plants from nutlets collected in a uniform hybrid population and observed that these plants did not deviate from the parent plants. The absence of segregation led Bucknall (1913) to the conclusion that *S.* × *uplandicum* is a good species. *S.* × *uplandicum* may be a fixed hybrid, but before we can arrive at more definite conclusions more data on the absence of segregation must be available. Mixed populations of *S.* × *uplandicum* hybrids with 36 and 40 chromosomes have not yet been found. In the experimental plot artificial hybrids have been made between the two *S.* × *uplandicum* types, but these plants ($2n = 38$) have not flowered so far.

Other combinations made are: (a) the backcrosses of *S.* × *uplandicum* $2n = 40$ to both parents; (b) the backcross of *S.* × *uplandicum* $2n = 36$ with the *S. officinale* parent; (c) the cross *S.* × *uplandicum* 36 and the hybrid *S. uliginosum*/*officinale* 44; (d) the cross *S.* × *uplandicum* 40 and the hybrid *S. uliginosum*/*officinale* 44.

Many of these hybrids have not flowered so far, but they may be identical with a number of putative natural hybrids with the chromosome numbers 36, 38, 40, 42, 44 (see also Fig. 5).

This picture gives a certain impression of the complicated series of relationships between the three taxa. In spite of the very effective eco-geographical isolation of *S. asperum* and of *S. officinale*, the introduction of the former into Western Europe resulted in a remarkable and complicated series of hybrids and back-crosses. From the biosystematic point of view *S. asperum*, *S. uliginosum* and *S. officinale* (with the exception of the white-flowered diploids) constitute one biospecies, from the classical point of view *S. asperum* and *S. officinale* are distinct species (Fig. 6).

The production of a fertile hybrid is a result of great interest, as it illustrates very well the way in which two related species, which presumably diverged a long time ago, are able to reunite and produce a new type with new evolutionary potentialities. The fact that hybridization is so extensive is mainly due to the breakdown of both geographical and ecological isolation between originally allopatric species. The breakdown of the sympatric but ecologically isolated subspecies *officinale* and *uliginosum* is largely a result of man's activities in modifying natural communities and the ecological barriers.

Extension of this problem, i.e. covering a wider range of species, especially those of the Caucasus and adjacent regions, is clearly needed. Moreover, a

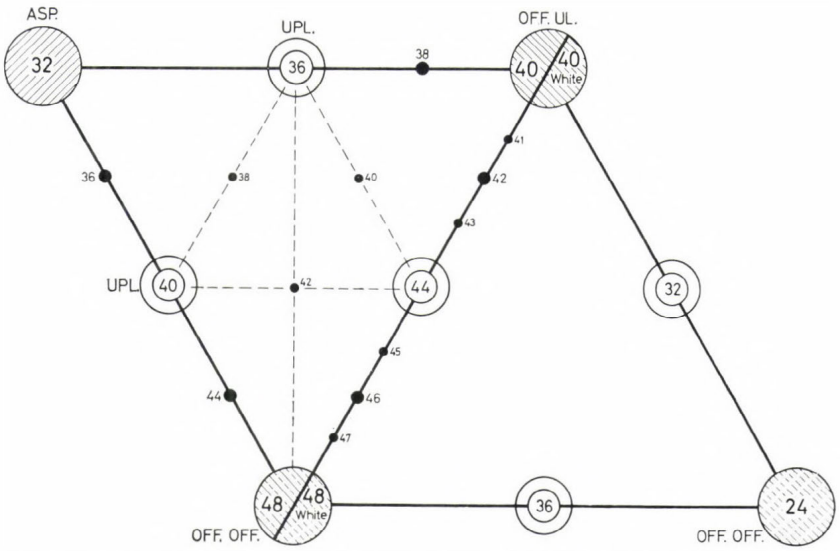

Fig. 6. Relationships between *Symphytum asperum* (= ASP.), *Symphytum officinale* subsp. *uliginosum* (= OFF. UL.) and *Symphytum officinale* subsp. *officinale* (= OFF. OFF.); double circles indicate hybrids between these species and subspecies, black dots represent back-crosses (with the chromosome numbers indicated), e.g. *Symphytum* × *uplandicum* $2n = 40$ (= UPL. 40) × *Symphytum officinale* subsp. *officinale* $2n = 48$ (= OFF. OFF. 48) ⟶ hybrid $2n = 44$ (= black dot 44)

study of meiosis of the various species and hybrids is planned, in order to permit more definite conclusions concerning the basic chromosome number(s).

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REFERENCES

Anderson, E. (1949): *Introgressive Hybridization*. New York

Britton, D. M. (1951): Cytogenetic studies in the *Boraginaceae*. *Brittonia* **7** 233–66

Bucknall, C. (1913): A revision of the genus *Symphytum*. *Jour. Linn. Soc. Bot. (London)* **41** 491–556

Davis, P. H. and Heywood, V. H. (1963): *Principles of Angiosperm Taxonomy*. Edinburgh and London

Faegri, K. (1931): Über die in Skandinavien gefundenen *Symphytum*-Arten. *Bergens Mus. Arbok* **4** 1–47

Gadella, Th. W. J. and Kliphuis, E. (1967): Cytotaxonomic studies in the genus *Symphytum*. I. *Symphytum officinale* L. in the Netherlands. *Proc. Roy. Neth. Acad. Sci. ser. C* **70** 378–91

Gadella, Th. W. J. and Kliphuis, E. (1969): Cytotaxonomic studies in the genus *Symphytum*. II. Crossing experiments between *Symphytum officinale* L. and *Symphytum asperum* Lepech. *Acta Bot. Neerl.* **18** (**4**) 544–9

Gams, H. in Hegi, G. (1927): *Illustrierte Flora von Mittel Europa*. V–3, 2220–9
Grau, J. (1968): Cytologische Untersuchungen an *Boraginaceen*. I. *Mitt. Bot. (München)* **7** 277–94
Kerner, A. (1863): *Österr. Bot. Zeitschr.* **13** 227–8
Kuznetsov, N. (1910): Kavkazskie vidy roda *Symphytum* (Tourn.) L. *Mém. Acad. Imp. Sci. St.-Pétersbourg, ser. 8, Phys.-Math.*, **25** (**5**) 1–94
Nyman, C. F. (1878–82): *Conspecitus Florae Europaeae*. Örebrö
Popov, M. (1953): *Boraginaceae in Flora S.S.R.* Moscow—Leningrad
Soó, R. (1926): Diagnoses plantarum novarum et revisio formarum specierum nonnularum. *Rep. Spec. Nov. Regn. Veg.* **22** 316–22
Steven, C. (1851): Observationes in *Asperifolias taurico-caucasicas*. *Bull. Soc. Imp. Mosc.* **24** 577–80
Strey, M. (1931): Karyologische Untersuchungen an *Boraginoideae*. *Planta* **14** 683–730
Tutin, T. G. (1956): The genus *Symphytum* in Britain. *Watsonia* **3** 280–1
Wade, A. E. (1958): The history of *Symphytum asperum* Lepech. and *Symphytum* × *uplandicum* Nyman in Britain. *Watsonia* **4** 117–8
Wickens, G. E. (1969): A revision of *Symhytum* in Turkey and adjacent areas. *Proc. Roy. Bot. Gard. Edinburgh* **XXIX** 157-80

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NUMERICAL CHEMOTAXONOMY OF THE *BETULA CAERULEA* COMPLEX*

by

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INTRODUCTION

In a private publication called 'Betula', W. H. Blanchard (1904a) first reported the discovery in southern Vermont of two new white birch species, which he called blue birches because of a bluish tint to their foliage. *Betula caerulea-grandis* Blanchard was described as a tree larger than *B. caerulea* Blanchard though in bark and foliage they resembled one another. In a subsequent publication (one week later!) Blanchard (1904b) considered *B. caerulea-grandis* as a variety of *B. caerulea* rather than a distinct species in that the former was merely larger than the latter. However, on the bottom of a copy of this article which he sent to the Gray Herbarium he reaffirmed his original conclusion, namely, that "I believe these are two good species". The subsequent history of these taxa has been complex and has been reviewed by Guerriero et al. (1970).

Briefly, *B. caerulea* and *B. caerulea-grandis* were considered to be hybrids between *B. papyrifera* and *B. populifolia* (Sargent 1922), but Fernald (1950) and Little (1953) considered *B. caerulea-grandis* to be a good species and only *B. caerulea* to be a hybrid. In 1960, Erskine suggested that *B. caerulea-grandis* was of hybrid origin and Brayshaw (1966) reaffirmed Sargent's opinion that both *B. caerulea* and *B. caerulea-grandis* were hybrids between *B. papyrifera* and *B. populifolia*. Brittain and Grant (1967) reported that seedlings of artificial crosses between *B. papyrifera* and *B. populifolia* did not resemble *B. caerulea-grandis* and suggested that *B. cordifolia* should be considered as a putative parent. In an analysis of these taxa from Grand Manan Island, New Brunswick, Brittain and Grant (1969) presented data to show that plants of *B. caerulea* and *B. caerulea-grandis* were hybrids and/or backcross progeny between *B. populifolia* and *B. cordifolia*. Since *B. caerulea*, *B. caerulea-grandis*, *B. cordifolia* and *B. populifolia* all possess the same chromosome number a chemotaxonomic study was undertaken in order to assess the species relationships by another experimental means and the results are reported here.

MATERIALS AND METHODS

The study was carried out using fresh leaves from birch seedlings growing in a nursery in the Morgan Arboretum of Macdonald College. The plants originated from seed collected by Dr W. H. Brittain from Grand Manan Island, New Brunswick (Brittain and Grant 1969). Altogether leaves from

* Paper presented by W. F. Grant at the Symposium.

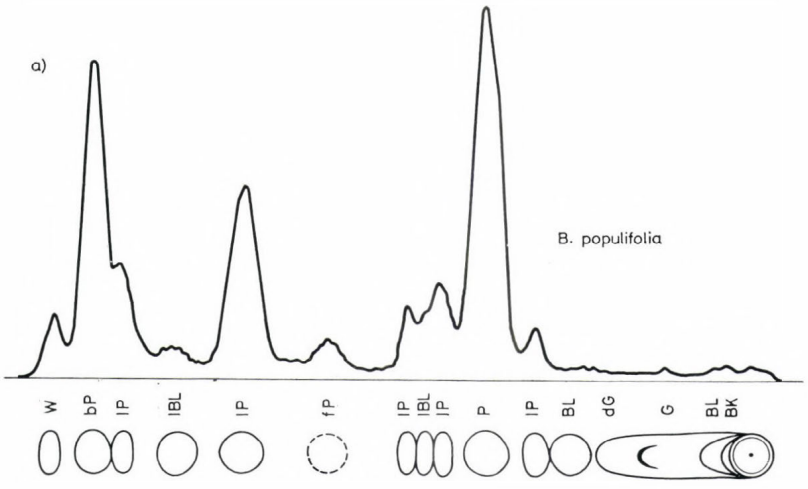
plants of 81 accessions representing five taxa were used [*B. caerulea* Blanch. (1 accession, 6 plants), *B. caerulea-grandis* Blanch. (7 accessions), *B. populifolia* Marsh. (15 accessions), *B. cordifolia* Regel (39 accessions) and *B. papyrifera* Marsh. (19 accessions)].

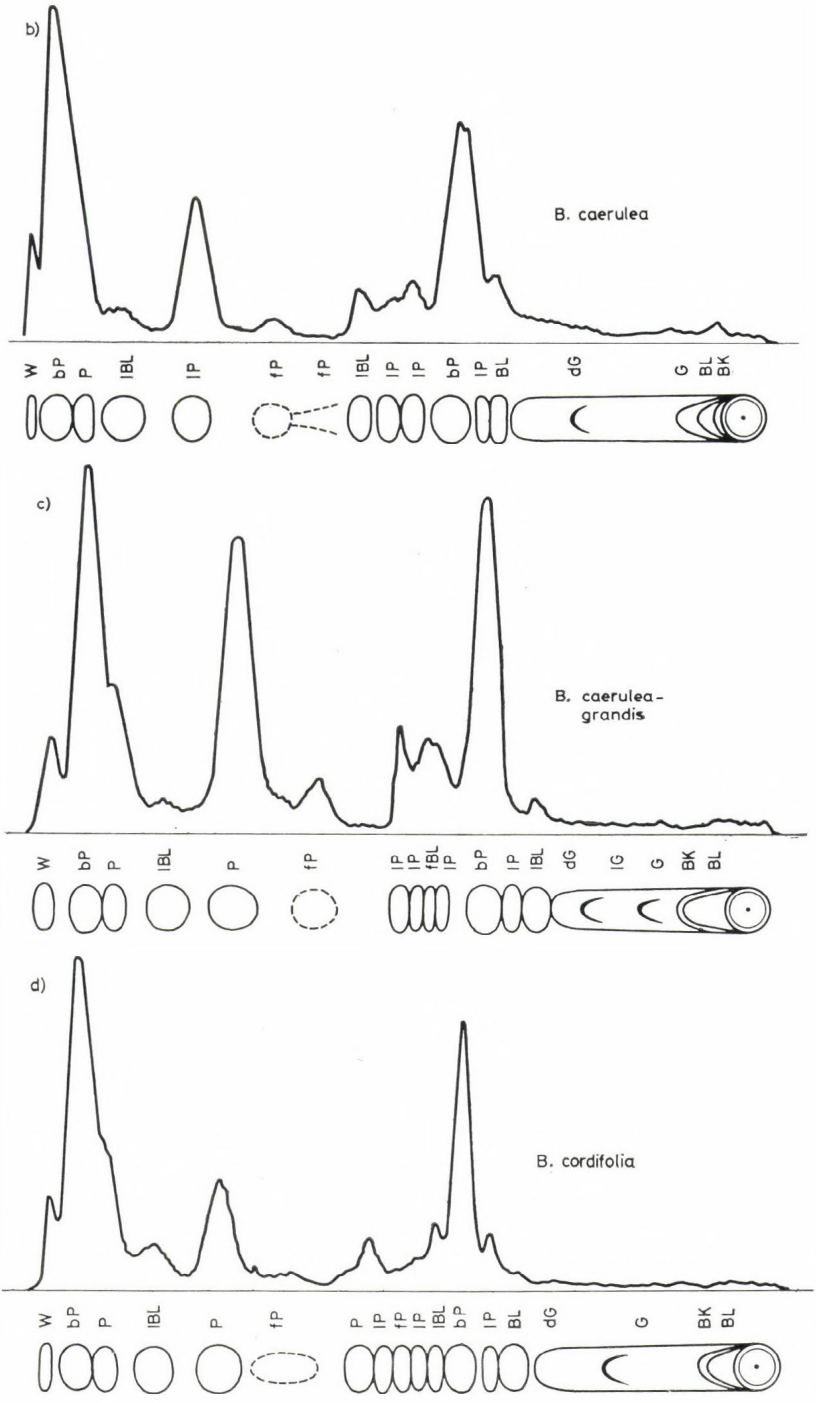
For each sample, 0·08 g of fresh leaves were air dried for 24 hrs in an oven at 70° C. The extracts were prepared by adding 0·5 ml of 1·0% HCl in methanol to each leaf sample and storing the vials in the dark at room temperature. Plates were coated with silica gel G (250 μ thickness) and heated to 100° C for 5 minutes before use. A 5 μl extract was applied for each run and extracts for two or more taxa were run in duplicate on each plate. The experimental procedure followed was a one-dimensional multiple pass development system (Grant and Whetter 1966). The solvent systems used were cyclohexane–ethyl acetate (1 : 1) and methanol–chloroform (30 : 70). The first solvent system was allowed to run up the layer twice to 14 cm and the second system twice to 7 cm. The plates were air dried by means of a hair drier. To increase the number of spots as well as the intensity of the fluorescence, the upper half of the plate (R_f 0·5 to 1·0) was sprayed with concentrated sulphuric acid and then heated for 5 min at 110° C after which the lower half of the plate (R_f 0·0 to 0·5) was sprayed with a 50% solution of aqueous morpholine. To obtain evidence on the variability of the experimental system the extract was stored at room temperature for 1 and 8 days in the first trial and 7, 14 and 21 days in a second trial. For each of the selected days the extract was run on fresh plates and the fluorescence recorded. On one set of plates the fluorescence was recorded, the plates were stored in the dark at room temperature for seven days and then the fluorescence was recorded from these same plates to ascertain the degree of decay of fluorescence upon storage of the plates. A graphical representation of the fluorescent spot pattern was obtained by means of a Zeiss chromatogram spectrophotometer using a wavelength of 655 mμ in conjunction with a recorder (Grant and Whetter 1970). The total intensity of the fluorescence pattern for a taxon was estimated by weighing the area under the curve and also by means of an integrator disc on the recorder. The patterns of the fluorescent compounds as they appeared under long wave ultraviolet light were recorded by mapping the spots on paper to the same scale and also by photographing the plates.

The relationships of the species have been shown diagrammatically on the basis of their coefficients of association calculated in the manner previously described (Grant and Zandstra 1968). Each distinct color at any particular R_f value was regarded as a separate character and the total number of characters for a species was the total number of spots occurring for the species. The simple matching coefficient of association, $S_{SM} = m/n = m/(m + u)$, in which matched and unmatched pairs are equally weighed was used to measure the association between each pair of species (Sokal and Sneath 1963). The relationships of the species have been shown also in the form of a dendogram prepared from a cluster analysis of the coefficients using the criterion of Sokal and Michener (Sokal and Sneath 1963).

RESULTS AND DISCUSSION

An examination of the chromatograms showed that the different taxa may be identified by their individual characteristic pattern of spots and colors. A drawing of the pattern of the spots characteristic of each taxon and a tracing of the intensity of the fluorescence of one individual for each taxon is shown in Fig. 1. The major changes in the chromatogram spot patterns which differentiated the taxa were between 0 and 0·6 R_f. The highest peaks on the fluorescent tracing were produced by the pink spots which were the brightest. The colors of the spots observed in the fluorescent tracing and their presence and absence in the different taxa and the number of plants examined are given in Table 1. It may be seen that the majority of the spots did not differ between plants from different accessions, but in some cases one or more plants differed from the reaction observed for the majority of the individuals. For example, spot number 5 (light blue) was missing (not observed) in one plant of *B. cordifolia*. Likewise, with the exception of *B. caerulea* for which the plants were all from one accession number, spot number 8 (faint pink) was not observed in two plants of each of the other taxa. It will be noted that the spots which were observed to have the opposite reaction from the majority of the plants in most cases were the faint and light pinks and blues. It is considered that these spots may have been present and that the fluorescence had decayed in some instances by the time the observation had been made (within 30 minutes) but that in the majority of cases, these fainter colors were masked by the pinks which emitted a greater fluorescence. Since color differences were noted for plants which all originated from the same accession number as in the case of *B. caerulea* (Table 1), it is considered that these spots for which the fluorescence decays rapidly, or which are very faint, are not reliable characters for making taxonomic decisions. At the same time it indicates the importance of studying a sufficient number of individuals before one tries to draw a taxonomic conclusion.




b)
B. caerulea
W bP P IBL IP fP fP IBL IP IP bP IP BL dG G BL BK
c)
B. caerulea-grandis
W bP P IBL P fP IP IP fBL IP bP IP IBL dG IG G BK BL
a)
B. cordifolia
W bP P IBL P fP P IP fP IP IBL bP IP BL dG G BK BL

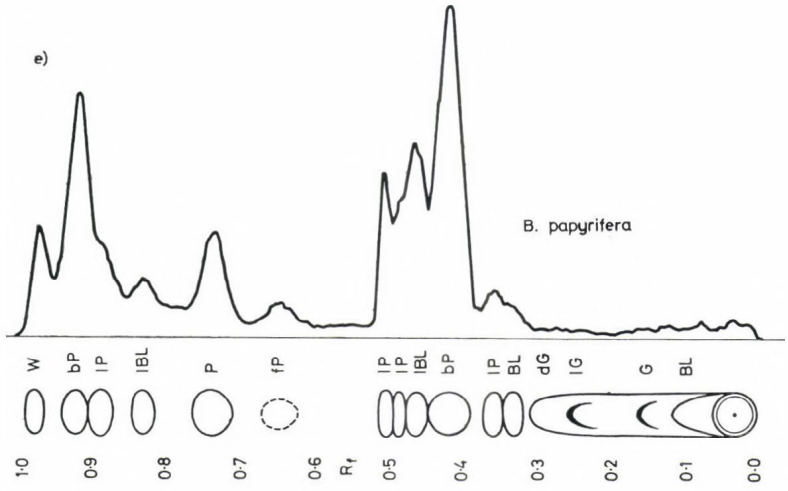


Fig. 1. Chromatographic patterns, fluorescent spot colors and fluorescent tracings of taxa of the *B. caerulea* complex. BL, blue; BK, black; G, green; P, pink; W, white; b, bright; d, dark; f, faint; l, light

The highest coefficient of association, 81·48, was between *B. populifolia* and *B. caerulea* (Fig. 2), and disregarding *B. papyrifera*, the second highest coefficient of association of 70·37 was between *B. cordifolia* and *B. caerulea-grandis*. The result of this analysis of the relationship of these four taxa using thin-layer chromatography bore out our earlier conclusion of the relationship of these taxa based on pictorialized scatter diagrams and hybrid indices (Guerriero et al. 1970), namely, that plants which have been designated *B. caerulea* were more closely related to *B. populifolia* than to *B. cordifolia* and likewise, those of *B. caerulea-grandis* were more closely related to *B. cordifolia* than to *B. populifolia*. In regard to the relationship between *B. papyrifera* and *B. cordifolia*, morphological and cytological evidence have shown these two taxa to be distinct

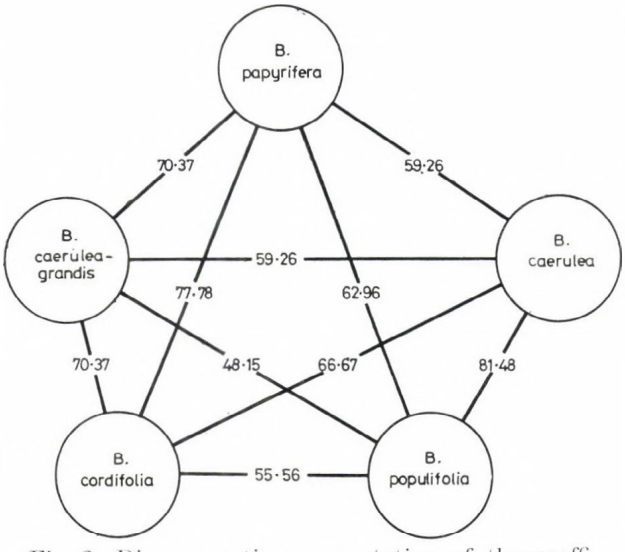


Fig. 2. Diagrammatic representation of the coefficients of association of taxa in the *B. caerulea* complex

Table 1

Summary of fluorescent spots occurring in five taxa of Betula. Fluorescent spot present (+), absent (—). Numbers indicate number of plants examined. With the exception of B. caerulea which represents 6 plants from one accession number, the remaining numbers represent one plant for different accession numbers

Spot no.	Color	*B. populifolia*		*B. caerulea*		*B. caerulea-grandis*		*B. cordifolia*		*B. papyrifera*	
		+	—	+	—	+	—	+	—	+	—
1.	white	15	0	6	0	7	0	39	0	19	0
2.	b. pink	15	0	6	0	7	0	39	0	19	0
3.	pink	0	15	6	0	7	0	39	0	0	19
4.	l. pink	15	0	0	6	0	7	0	39	19	0
5.	l. blue	15	0	6	0	7	0	38	1	19	0
6.	pink	0	15	0	6	7	0	39	0	19	0
7.	l. pink	15	0	6	0	0	7	0	39	0	19
8.	f. pink	13	2	6	0	5	2	37	2	17	2
9.	pink	0	15	0	6	0	7	39	0	0	19
10.	l. pink	15	0	6	0	7	0	38	1	19	0
11.	f. pink	0	15	0	6	0	7	20	19	0	19
12.	l. pink	0	15	0	6	7	0	22	17	18	1
13.	f. blue	0	15	0	6	3	4	0	39	0	19
14.	l. blue	15	0	5	1	0	7	30	9	13	6
15.	l. pink	15	0	6	0	3	4	0	39	0	19
16.	l. pink	0	15	4	2	0	7	0	39	0	19
17.	b. pink	15	0	6	0	7	0	39	0	19	0
18.	l. pink	14	1	6	0	5	2	26	13	15	4
19.	blue	14	1	5	1	0	7	39	0	17	2
20.	l. blue	0	15	0	6	6	1	0	39	0	19
21.	d. green	15	0	6	0	7	0	39	0	19	0
22.	l. green	0	15	0	6	7	0	0	39	19	0
23.	green	15	0	6	0	0	7	39	0	19	0
24.	blue	15	0	6	0	0	7	0	39	0	19
25.	black	15	0	6	0	3	4	36	3	0	19
26.	blue	0	15	0	6	5	2	35	4	19	0

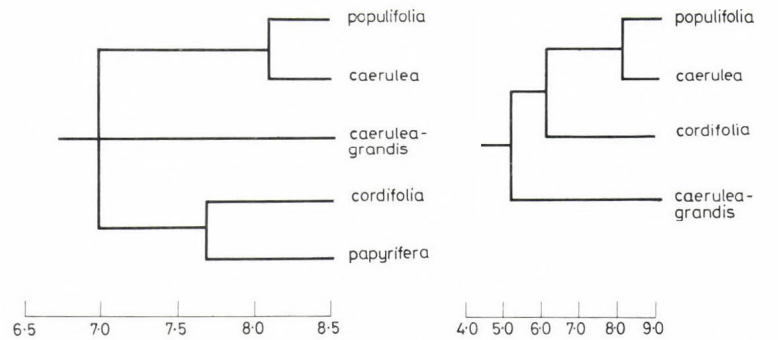


Fig. 3. Dendograms of *Betula* taxa based on their coefficients of association. The horizontal lines indicate the levels of association at which taxa are linked. The vertical lines represent taxa showing closest coefficient of association

(Brittain and Grant 1969), however, the data here in which there is a coefficient of association of 77·78 between these two taxa indicate that many of the fluorescent spots are similar between these two taxa. At the same time the coefficient of association here is not as great as that between *B. populifolia* and *B. caerulea* (81·48) indicating that there are differences between these two taxa. The relationships between these species have been shown in the form of dendograms in Fig. 3, in which *B. papyrifera* has been included and excluded in the comparison.

An analysis was also carried out for these same taxa employing paper chromatography by Mr. G. S. Reh as a fourth year project in Agricultural Chemistry. As may be seen in Fig. 4, chromatograms A (*B. populifolia*) and B (*B. caerulea*) were very similar and those between C (*B. cordifolia*) and D (*B. caerulea-grandis*) were likewise very similar confirming the close relationship between these taxa. The paper chromatogram for *B. papyrifera* (Fig. 4, E) emphasized the difference between these taxa to a greater extent than that found for the chromatograms run on thin-layer.

The total fluorescence was calculated for each chromatogram to establish what use this information might play in determining species relationships by means of thin-layer chromatography. Several aspects were considered for which the data are given in Tables 2 and 3.

A comparison of the results of the two methods used to quantitatively determine the total fluorescence from the spots showed that the more laborious and time consuming method of cutting out with scissors and weighing the area of the graph paper below the peaks of the curve representing the amount of fluorescence for each spot, differed very little from the disc integrator method and so the former method was dropped (Table 2).

A considerable amount of variation was noted in the total amount of fluorescence and the age of extract, that is, the time the extract was stored before being applied to a thin-layer plate, and the development of the chromatogram in the solvent systems. As may be seen in Table 2, there was in general an increase in total fluorescence with an increase in age of the extract. Using *B. caerulea* (C) as an

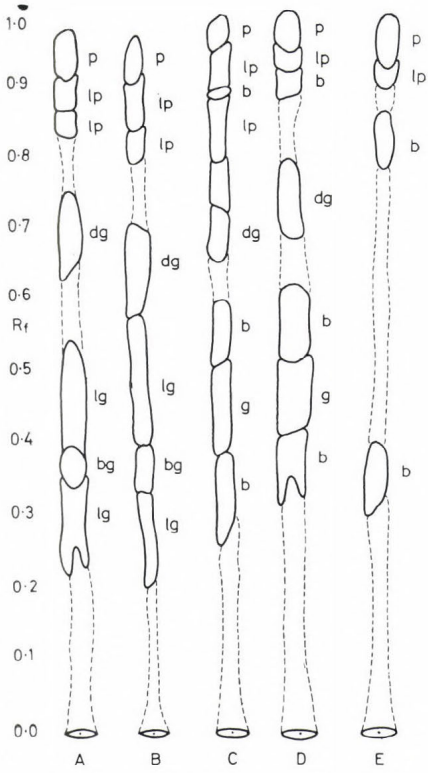


Fig. 4. Paper chromatographic pattern from methanol extract run in Forestal solvent by descending chromatography. Letters indicate the fluorescent spot colors. A, *B. populifolia* (Acc. No. 950); B, *B. caerulea* (Acc. No. 924); C, *B. cordifolia* (Acc. No. 160); D, *B. caerulea-grandis* (Acc. No. 7VI); E, *B. papyrifera* (Acc. No. 19). b, blue; g, green; p, pink, lp, light pink; bg, bright green; dg, dark green; lg, light green

Table 2

Total fluorescence of individual chromatograms as determined by weight of area under curve (for eight samples) and a disc integrator (all samples). A comparison of the intensity of fluorescence has been made between sprayed and unsprayed plates and the loss of fluorescence determined from plates stored in the dark for one week

Taxon	Acc. No.	Age of extract (days)		Weight (g)	Disc integrator units (days)			
		First trial	Second trial		1*	1*	7**	7**
B. populifolia	468	1	—	0·30	289	—	216	—
		8	—	—	436	334	340	236
		—	7	—	304	—	—	—
		—	14	—	395	—	—	—
		—	21	—	415	—	—	—
	470	1	—	0·31	313	—	202	—
		—	7	—	298	—	—	—
		—	14	—	345	—	—	—
		—	21	—	416	—	—	—
B. caerulea	420 (C)	1	—	0·22	208	—	146	—
		8	—	—	465	409	372	261
		—	7	—	444	—	—	—
		—	14	—	479	—	—	—
		—	21	—	490	—	—	—
	420 (A)	1	—	0·29	261	—	155	—
		—	7	—	341	—	—	—
		—	14	—	401	—	—	—
B. cordifolia	449	1	—	0·24	240	—	191	—
		8	—	—	318	249	228	135
		—	7	—	317	—	—	—
		—	14	—	379	—	—	—
		—	21	—	426	—	—	—
	535	1	—	0·25	238	—	154	—
		—	7	—	281	—	—	—
		—	14	—	325	—	—	—
B. caerulea-grandis	461	1	—	0·33	325	—	273	—
		8	—	—	470	362	366	180
		—	7	—	388	—	—	—
		—	14	—	408	—	—	—
		—	21	—	443	—	—	—
	443	1	—	0·37	361	—	296	—
		—	7	—	402	—	—	—
		—	14	—	458	—	—	—
		—	21	—	497	—	—	—

* Comparison of total fluorescence between duplicate chromatograms one sprayed (day 1, first column: upper half of plate sprayed with concentrated H_2SO_4, lower half, 50% aqueous morpholine) and one unsprayed (day 1, second column).

** Fluorescence recorded 7 days later from same plate recorded on day 1 (see text).

Table 3

Average total fluorescence in arbitrary units

Age of extract (days)	*B. cordifolia*	*B. caerulea-grandis*	*B. caerulea*	*B. populifolia*
1	239	343	235	301
7	299	395	393	301
8	318	470	465	436
14	352	433	440	370
21	426	465	513	415
8*	249	362	409	334

* Unsprayed plate

example, an extract of 1 and 8 days of age had spots which gave a total fluorescence of 208 and 465 units, respectively. In a second trial using extracts of 7, 14 and 21 days of age, the total fluorescence for all spots was 444, 479 and 490 units, respectively. It was considered that an extract stored longer than one week did not have any effect on the number or arrangement of spots but merely increased the peaks, primarily those of the pink spots.

A quantitative comparison of the total amount of fluorescence was made between chromatograms after normal development in the solvent systems without post treatment spraying (unsprayed plates) and those receiving a post treatment spraying (sprayed plates).

It was observed that spots of chromatograms on sprayed plates were more definitive after spraying and that the spots emitted a greater intensity of total fluorescence. For example, a chromatogram on a sprayed plate of *B. populifolia* (468) gave a total fluorescence of 436 (Table 2, day 1, first column), whereas on an unsprayed plate for a duplicate run of extract a chromatogram gave only 334 units of fluorescence (Table 2, day 1, second column). After plates had been developed there was a gradual decay of fluorescence of both sprayed and unsprayed chromatograms and even when the plates were stored in the dark. As may be seen in Table 2 for *B. populifolia* (468) after a sprayed plate had been stored for one week, the fluorescence dropped from 436 units to 340 and the fluorescence of a chromatogram on an unsprayed plate dropped from 334 units to 236.

The average total fluorescence calculated from the chromatograms was considered to be of little value in delineating the relationships of these taxa (Table 3). Chromatograms of *B. cordifolia* gave the lowest fluorescent values whereas those of *B. caerulea-grandis* consistently gave higher values than both *B. cordifolia* and *B. populifolia*, and with the exception of the extract of one day of age, chromatograms of *B. caerulea*, likewise, showed greater fluorescence. Since, both *B. caerulea* and *B. caerulea-grandis* are considered hybrids of *B. cordifolia* and *B. populifolia*, the higher fluorescent values for these two taxa may be considered a heterotic effect. In general, three pink spots which were in common to all four taxa accounted for the major total fluorescence from the chromatograms (Fig. 1). These spots varied considerably in the intensity of their fluorescence and are considered to

account for the considerable total fluctuation in fluorescence between chromatographic runs even for the same accession number.

Since the taxa under study are very closely related [*B. caerulea* and *B. caerulea-grandis* both considered hybrids and/or backcross hybrids (introgressants) between *B. cordifolia* and *B. populifolia* = *B.* × *caerulea*, see Guerriero, Grant and Brittain 1970] it is considered that the use of the average total fluorescence for the delineation of taxa would be of greater value when the taxa are more distantly related.

ACKNOWLEDGEMENTS

The results of the taxa analyzed by paper chromatography were kindly supplied by Mr G. S. Reh who undertook this aspect of the study as a fourth year project in the Department of Agricultural Chemistry. The cooperation of Dr R. H. Common of this Department is gratefully acknowledged. Certain aspects of the research have been supported by a grant to Dr W. H. Brittain from the National Research Council of Canada and a grant to Dr W. F. Grant from the Canada Department of Fisheries and Forestry. The Zeiss Chromatogram Spectrophotometer was purchased through a major equipment grant to Dr W. F. Grant from the National Research Council of Canada which is gratefully acknowledged.

SUMMARY

A thin-layer chromatographic study of fluorescent compounds present in the leaves from plants of 81 accessions representing five taxa of *Betula* (*B. caerulea* Blanch., *B. caerulea-grandis* Blanch., *B. cordifolia* Regel, *B. papyrifera* Marsh. and *B. populifolia* Marsh.) has been carried out and their relationships have been determined on the basis of coefficients of these compounds. The analysis supported the general taxonomic relationships of the species based on a previous morphological study. The highest coefficients of association were between *B. caerulea* and *B. populifolia* (81·48) and *B. caerulea-grandis* and *B. cordifolia* (70·37). Whereas morphological and cytological evidence have shown *B. cordifolia* and *B. papyrifera* to be distinct, the high coefficient of association of 77·78 between these two taxa indicated that they share a number of fluorescent compounds in common.

A paper chromatographic study of these same five taxa confirmed the close relationship of these taxa, but paper chromatography emphasized the difference between *B. papyrifera* and the other taxa to a greater extent than that shown through thin-layer chromatography. An increase in the total intensity of fluorescence of thin-layer chromatograms was obtained by increasing the age of the extract from one to three weeks before development of the chromatograms in the solvent systems. Representative fluorescent tracings of chromatograms of the different taxa have been presented.

REFERENCES

Blanchard, W. H. (1904a): New white birches. *Betula* **1** (1) 1

Blanchard, W. H. (1904b): A new white birch. *Betula* **1** (**2**) 1–2

Brayshaw, T. C. (1966): What are the blue birches? *Can. Field-Naturalist* **80** 187–94

Brittain, W. H. and Grant, W. F. (1967): Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. IV. *B. caerule-agrandis* and hybrids. *Can. Field-Naturalist* **81** 116–27

Brittain, W. H. and Grant, W. F. (1969): Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. VIII. *Betula* from Grand Manan Island, New Brunswick. *Can. Field-Naturalist* **83** 361–83

Erskine, D. S. (1960): *Betulaceae*, pp. 128–31. In *The Plants of Prince Edward Island.* Canada Department of Agriculture Publ. No. 1088

Fernald, M. L. (1950): *Gray's Manual of Botany.* 8th ed., American Book Co., New York

Grant, W. F. and Whetter, J. M. (1966): The cytogenetics of *Lotus*. XI. The use of thin-layer chromatography in the separation of secondary phenolic compounds in *Lotus* (Leguminosae). *J. Chromatog.* **21** 247–56

Grant, W. F. and Whetter, J. M. (1970): The use of thin-layer chromatography in the separation of fluorescent compounds in *Avena*. *Phyton* **27** 1–5

Grant, W. F. and Zandstra, I. I. (1968): The biosystematics of the genus *Lotus* (Leguminosae) in Canada. II. Numerical chemotaxonomy. *Can. J. Bot.* **46** 585–89

Guerriero, A. G., Grant, W. F. and Brittain, W. H. (1970): Observations on Canadian birch (*Betula*) collections from Valcartier, Quebec. *Can. J. Bot.* **48** 2241–47

Little, E. D., Jr. (1953): Check list of native and naturalized trees of the United States (including Alaska). *Agriculture Handbook No.* 41. U.S. Forest Service, Washington, D.C.

Sargent, C. S. (1922): *Manual of the Trees of North America.* Vol. I. Houghton Mifflin Co., New York. (Reprinted, 1961. Dover Publications Inc., New York)

Sokal, R. R. and Sneath, P. H. A. (1963): *Principles of Numerical Taxonomy.* W.H. Freeman and Company, San Francisco, 359 pp.

Symp. Biol. Hung. 12, pp. 213–225 (1972)

EINIGE BETRACHTUNGEN ÜBER DIE ENTWICKLUNG UND PHYLOGENIE DER GRÜNALGEN UND IHRE BEDEUTUNG INNERHALB DES ALLGEMEINEN PFLANZENSYSTEMS

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ALLGEMEINE, EINLEITENDE BETRACHTUNGEN

Im Pflanzensystem kennen wir bei den Thallophyten und Kormophyten einige Gruppen, die durch ihre Bedeutung beim Studium der verschiedenen taxonomischen und phylogenetischen Probleme Aufmerksamkeit erregt haben.

Unter diesen haben die Chlorophyceen, die auf der Linie der Autotrophie den Hauptentwicklungszweig darstellen, die Forscher ganz besonders beschäftigt.

Die Grünalgen treten durch die außerordentlich große Variabilität ihres Thallus hervor und sind durch einen hohen Grad von Polymorphismus und Metamorphismus gekennzeichnet. Sie bilden eine heterogene Gruppe, die infolge ihrer großen ökologischen und geographischen Amplitude eine vielfältige, den verschiedenen Entwicklungsstufen entsprechende Organisation ihrer vegetativen und reproduktiven Apparate aufweisen.

Es kann angenommen werden, daß die Amplitude der Variabilität dieser Pflanzen viel größer ist als diejenige der anderen Thallophyten sowie auch der Kormophyten überhaupt. Dies ist eine Folge ihrer geschichtlichen Entwicklung, die mit fortlaufenden Spaltungen und Differenzierungen (Primitivität, Fortbildungen, Rückbildungen) einherging.

Die komplexen Forschungen auf dem Gebiet der Entwicklung sowie die phylogenetischen Darstellungen sind Äußerungen der modernen Taxonomie.

Die Grünalgen bevölkern sämtliche Lebensmedien und weisen charakteristischerweise die meisten Formen von Aerophyten auf. Die Analyse des eingesammelten Materials und die Auslegung der Ergebnisse im Lichte der biosystematischen Kenntnisse haben die Erarbeitung einer Forschungsmethodik ermöglicht, die zu wertvollen Beiträgen zu der Evolution und Phylogenie der Grünalgen geführt hat.

Die elektronenmikroskopischen, biochemischen und physiologischen Forschungen haben zur Aufklärung einiger Probleme der Mikroevolution und dadurch zu einer eingehenderen Kenntnis der Taxonomie und Phylogenie der Grünalgen und deren Bedeutung im allgemeinen Pflanzenreich beigetragen.

Die Zahl der taxonomischen Merkmale dieser Pflanzen ist immer größer und vielfältiger geworden. Aus diesem Grunde hat der Umfang, die Umgrenzung und Eingliederung der Chlorophyceen im Laufe der Zeit in den verschiedenen Systemen Schwankungen gezeigt.

Die Aufklärung des Entwicklungsprozesses der Grünalgen, aus denen sich allmählich nicht nur verschiedene Gruppen anderer Thallophyten, sondern höchstwahrscheinlich auch die Vorläufer der niederen Kormophyten *(Pteri-*

dophyta) entwickelt haben, gestattet auf Grund zahlreicher Kriterien deren Einreihung in ein natürliches phylogenetisches System.

Obwohl in manchen Fragen noch Meinungsverschiedenheit herrscht, wie z. B. in bezug auf den Primordialtyp der gegeißelten oder der plasmodialen Formen, oder die Primordialität der Autotrophie oder Heterotrophie, sind Forschungen dieser Art dennoch notwendig, weil sie für die Probleme der Genese, Entwicklung und Taxonomie von Interesse sind.

Die in letzter Zeit gemachte Entdeckung von neuen aerophyten Chlorophyceen-Gattungen und die Kenntnisse über deren Organisation, Ökologie und Verbreitung gestatten uns, über die Entwicklung und Phylogenie der Grünalgen Betrachtungen anzustellen und neue Fragen aufzuwerfen.

Im vorliegenden Beitrag werden wir nur einige allgemeine, mit neuen Elementen belegte Aspekte des Aufbaus und Entwicklungsvorganges der Grünalgen, begleitet von einigen neuen taxonomischen Bemerkungen, hervorheben, zusätzlich zu den Feststellungen von Pascher, Oltmanns, Smith, Fott, Beger, Zimmermann, Dangeard, Fritsch, Printz, Pringsheim, Chadefaud, Greguss u. a.

Vor allem werden wir die Thallustypen, Rhizoidensysteme, Ernährung und Entwicklungsrichtungen untersuchen, und zwar im Zusammenhang mit phylogenetischen, ökologischen, geographischen u. a. Betrachtungen, nicht nur innerhalb der Grünalgen, sondern auch im Rahmen des allgemeinen Pflanzensystems.

Aus diesem Grunde werden wir unsere Forschungen nicht ausschließlich auf die Chlorophyceen beschränken, sondern in gewissem Maße auch auf einige Typen von *Chrysophyta*, *Charophyta*, *Phaeophyta*, *Rhodophyta*, *Bryophyta*, *Pteridophyta* und *Spermatophyta* eingehen.

ORGANISATIONSGRAD UND ENTWICKLUNG DES THALLUS

Bei den Grünalgen sehen wir im Aufbau des Thallus in bezug auf die Mikro- und Makroevolution eine ständige Differenzierung vom primitiven Thallus (Archethallus) über den entwickelten, auf unterschiedlichen Organisationsstufen stehenden, abgeleiteten Thallus (Prothallus) bis zum hochentwickelten heterotrichen Thallus.

Über die Grundtypen des Thallus in seinen Evolutionsetappen haben in der letzten Zeit H. Beger (1954), B. Fott (1959), W. Zimmermann (1959) u. a. schon eingehende Betrachtungen angestellt. Bei der Ausbildung der Entwicklungszyklen sehen wir haploide und diploide Typen.

Nach Ansicht der meisten Verfasser (W. Zimmermann u. a.) ist der heterotriche Thallus morphologisch, physiologisch, progressiv und adaptativ der am meisten differenzierte Thallus. F. Fritsch u. a. betrachten ihn jedoch zu Unrecht als primitiven Typ.

Bei den Grünalgen nimmt schon A. Pascher in bezug auf ihre Evolution eine parallele, monophyletische Entwicklung in mehreren Serien an.

Es sei erwähnt, daß sich der heterotriche Thallus sowohl im Süßwasser als auch besonders bei manchen aerophyten Typen (*Fritschiella*, *Oedocladium* u. a.) morphologisch und physiologisch in zwei unterschiedlichen Regionen differenziert hat (unter- und oberirdischer Teil). Wir sind der Ansicht, daß die Evolution des heterotrichen Thallus der Grünalgen ökolo-

gisch in folgenden zwei Richtungen abgelaufen ist: (a) heterotrich, in Süßwasser differenziert, mit höher ausgebildetem reproduktivem Apparat *(Coleochaete)*; (b) heterotrich, als Aerophyten differenziert, mit einem unterirdischen rhizoiden Thallus und mit einem oberirdischen Thallus, häufig mit scheinbar quirlförmigen Verzweigungen (*Fritschiella*, *Oedocladium* u. a.), also mit höher organisiertem vegetativem Apparat.

Bei der Erklärung der Thallusentwicklung ist auch der Wachstumsrichtung des Thallus zum Substrat Rechnung zu tragen. Aufrechtes Wachstum hat zu höher differenzierten Typen geführt (*Bryopsis*, *Dasycladus*, *Caulerpa*, *Chara* u. a.).

Der Gliederungsgrad des Thallus sowie auch die quirlförmigen Verzweigungen sind ebenfalls Kennzeichen höherer Entwicklung (*Draparnaldiopsis*, *Draparnaldia*, *Charophyta* u. a.).

Die Evolution des höher entwickelten Thallus der Grünalgen verlief in Abhängigkeit von der Haftungsweise, Natur des Substrates und von der Wachstumsrichtung im Wasser und auf dem Boden, und zwar vom horizontalen zum aufrechten Thallus und von der dorsiventralen zur radialen Symmetrie.

DIE RHIZOIDEN UND IHRE ROLLE

Die Rhizoiden dienen der Haftung und manchmal auch der Absorption. Ihre morphologisch-physiologische Entwicklung im Pflanzenreich kann ökologisch (Wasser, Boden) und in Abhängigkeit von der Unterlage (hart = Stein, Holz; weich = Schlamm, Sand usw.) erklärt werden.

Bei einigen Bodenformen der Gattung *Vaucheria* (*V. terrestris*, *V. sessilis* u. a.) beobachtet man als vorübergehende Anpassung eine gelegentliche Ausbildung von Rhizoiden entweder einfach *(Protosiphon)* oder verzweigt *(Botrydium)* (Abb. 1a–c). Bei *Stigeoclonium terrestris* entsteht bei der Keimung der Zoosporen ein Prothallium mit morphologisch-physiologisch differenzierten rhizoidalen Verzweigungen. Bei den Arten der Gattung *Prasiola* (*P. crispa*, *P. stipitata* u. a.) differenziert der ursprünglich einreihige Zellfaden einen monostromatischen Thallus mit oder ohne Rhizoiden im Boden.

Die höchstentwickelten Typen der aerophytischen Chlorophyceen mit gut diffe-

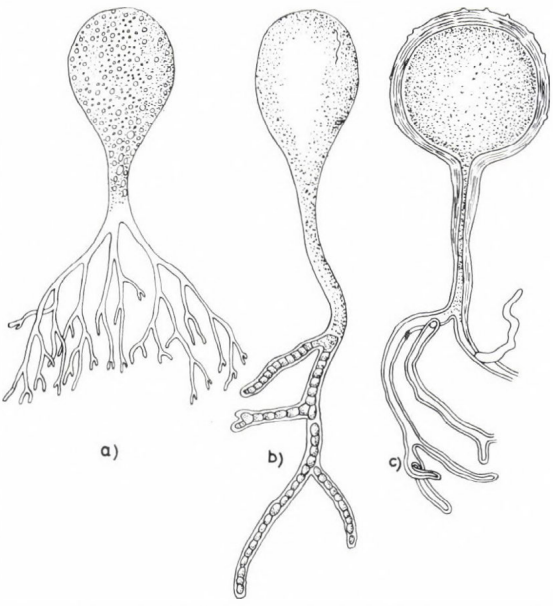

Abb. 1. (a), (b) *Botrydium vulgare;* (c) *B. wallrothi*, mit verzweigten Rhizoiden (nach Pascher, Fig. 96)

renziertem vegetativem Apparat finden sich bei *Fritschiella tuberosa* (Abb. 2) und *Oliveria terrestris (Chaetophorales)* sowie auch bei *Oedocladium protonema* (Abb. 3) *(Oedogoniales)*, bei denen sich unterirdisch ein komplexes Rhizoidalsystem entwickelt.

Die Grünalgen, welche in Salz- *(Caulerpaceae)* (Abb. 4) und Süßwasserbiotopen *(Characeae)* (Abb. 5) weitverbreitete Populationen bilden, tragen Rhizoidformationen, die für die weiche und an organischen Stoffen reiche Unterlage (Sand, Schlamm) charakteristisch sind.

Bei den Bodenformen einiger Lebermoose *(Riccia fluitans, Ricciocarpus natans)* läßt sich die Differenzierung zahlreicher Rhizoiden beobachten. Bei anderen *(Anthoceros, Dendroceros)* bilden die Sporophyten ein System rhizoidaler Papillen (Haustoren), die manchmal in den Boden dringen, die Sporophyten hier festhalten und bis zu ihrer völligen Reife »ernähren« *(Anthoceros fusiformis)*.

Bei manchen primitiven Typen der Laubmoose (*Haplomitrium* und *Calobryum*) bilden sich keine Rhizoiden, sondern rhizomförmige Verzweigungen, die etwa den rhizoidförmigen Verzweigungen von *Rhynia (Psilophytopsida)* ähnlich sind.

Gleichzeitig mit der Anpassung der Laubmoose an die Luftverhältnisse differenzieren die Gametophyten ein unterirdisches basales Rhizoidalsystem, das sowohl eine Haft- als auch eine ± Absorptionsrolle zu erfüllen hat, und ein oberirdisches (auf den Stengelchen und bei einigen sogar auf den Blättchen vorkommendes) Rhizoidalsystem mit ökologischer Rolle. Bei den mit

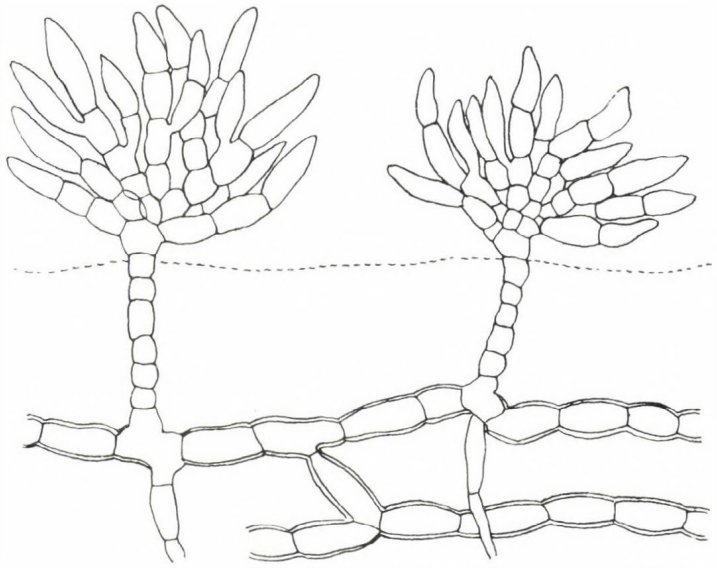

Abb. 2. *Fritschiella tuberosa:* vegetativer Thallus mit hochorganisiertem unterirdischem Rhizoidalsystem und oberirdischem assimilierendem Thallus (aus Fott, Fig. 161)

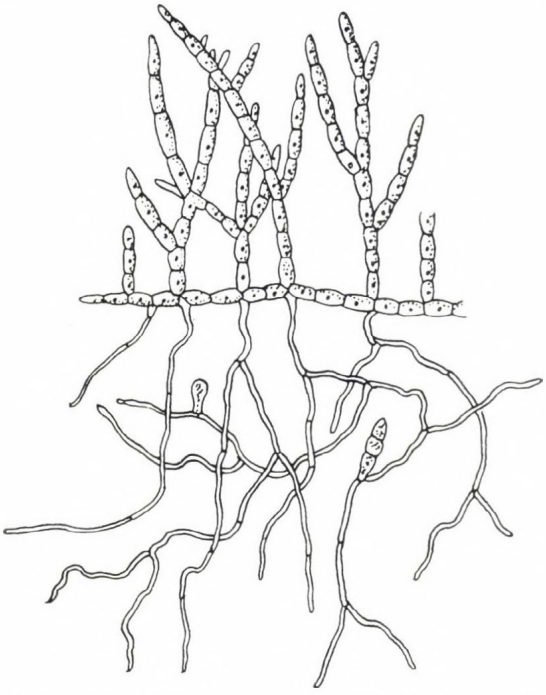

Abb. 3. *Oedocladium protonema:* Thallusfragment mit unterirdischen Rhizoidalverzweigungen und oberirdischem assimilierendem Thallus (nach Oltmanns, Fig. 219)

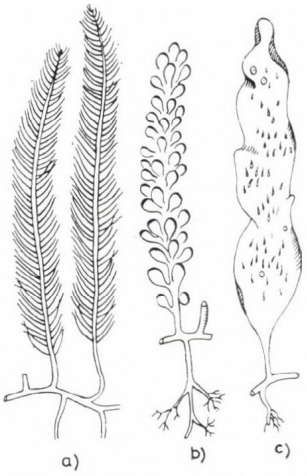

Abb. 4. *Caulerpa*-Arten: a) *C. sertularioides;* b) *C. racemosa;* c) *C. proligera,* mit verschiedenartigen Rhizoiden (nach Wettstein, Chadefaud u. a.)

besonderer Anpassung für Torfbiotopen versehenen *Sphagnales* bilden sich Rhizoiden nur auf dem Protonema.

Bei den Pteridophyten finden sich Rhizoiden nur auf dem Gametophyten und werden im Laufe der ontogenetischen und phylogenetischen Entwicklung während der morphologischen und physiologischen Abhängigkeit vom Sporophyten beibehalten.

Unter amphibischen Lebensverhältnissen differenzieren die primitiven Pteridophyten *(Rhynia, Horneophyton)* Rhizoiden sowohl im Stadium des Gametophyten (Prothallus) als auch in dem des Sporophyten (unterirdischer Stamm).

Die Anwesenheit von Rhizoiden läßt sich in Wasserbiotopen auch bei einigen Angiospermen beobachten, wo sie auf deren unterirdischen Haftorganen (im Schlamm, Sand) auftreten, wie z. B. bei *Utricularia neglecta, Ceratophyllum* sp. u. a., während *Ranunculus fluitans* eine den Algen ähnliche Haftungsart entwickelt. Die durch Parasitismus bewirkte Rückbildung des Cormus bei *Rafflesia* hat zu dessen Umformung in rhizoidale Organe geführt (ähnlich den Myzelfäden).

Aus allen diesen Beispielen geht hervor, daß die verschiedenen Rhizoidtypen sowohl bei Grünalgen als auch im allgemeinen in der Entwicklung

der Pflanzen nicht nur ein Freiwerden vom Wassermilieu und anschließend daran eine Anpassung an die Bodenverhältnisse ermöglicht, sondern auch zur Herstellung der morphologisch-funktionellen Beziehung zwischen Pflanze und Substrat verholfen haben. Diese Beziehung ist in der Entwicklung mancher Thallophyten und insbesondere der Kormophyten immer deutlicher zu sehen.

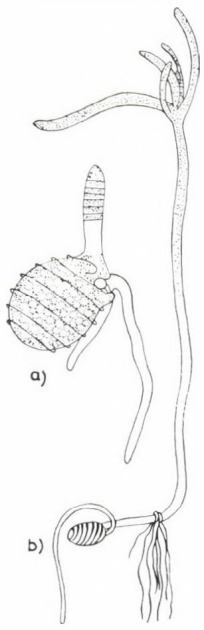

Abb. 5. Zygote, Keimungsstadien bei *Toplypella glomerata*, mit Rhizoiden, Stämmchen und Verzweigungen; a) nach Fritsch, Fig. 152 B; b) nach Pringsheim aus Fott, Fig. 201

PHYSIOLOGISCHE BETRACHTUNGEN ÜBER DIE ERNÄHRUNGSVORGÄNGE

Der Entwicklungsgang der spezifischen Ernährungsweise der Grünalgen erstreckt sich über eine sehr lange Zeitdauer. Die anfänglich langsame Autotrophie zahlreicher Süßwasserchlorophyceen hat sich mit der Zeit in Biotopen mit reichen organischen Substanzen mit einer saprophylen Lebensweise vereint, wodurch eine gemischte autotroph-saprophyle Ernährung entstanden war. Die Chromatophoren haben infolge fortschreitender Metamorphose und Wanderung im Zellinneren — unter gewissen neuen Belichtungsverhältnissen — eine Intensivierung der Photosynthese hervorgerufen. Im Laufe der Entwicklung haben selbst die systematisch höchststehenden Pflanzen auf einen gewissen Grad von Saprophytismus nicht verzichtet, sei es auch nur die Aufnahme von organischen Säuren. Der ausgeprägte Heterotrophismus ist gewissen sekundär abgeleiteten Typen eigentümlich und ist also aus autotrophen Typen hervorgegangen.

Bei den Chlorophyceen sind also in bezug auf die Ernährungsweise verschiedene Typen festzustellen: Autotrophie verschiedener Intensitäten, autotroph-saprophyle Mischernährung und manchmal Übergang zum Parasitismus. Es ist auch erklärlich, daß eben bei einer solchen Pflanzengruppe wie die der Chlorophyceen eine so große Mannigfaltigkeit im Stoffwechsel in Erscheinung tritt.

Zwischen der autotrophen, photosynthetischen Ernährung und der Absorption von Mineralstoffen ergibt sich eine Abhängigkeitsbeziehung. Dies ist eine Folge der Ausbildung des Rhizoidalsystems mit absorbtiver Funktion in Wasser und im allgemeinen bei aerophyten, auf weicher Unterlage wachsenden Formen.

Anscheinend erfolgt (Topacevski 1953) die Entwicklung des Ernährungsprozesses und der Nährstoffabsorption in mehreren Etappen.

Die Spezialisierung und die Verstärkung der Photosynthese führen im Laufe der Entwicklung allmählich zu einem Gleichgewicht zwischen der Photosynthese und der Mineralstoffaufnahme aus dem Boden. Dieser Prozeß bewirkte eine Reihe von Anpassungen und Progressionen, bei denen durch den Übergang der Pflanzen von der Lebensweise im Wasser zur Lebensweise auf dem Festland die Intensität der Photosynthese verstärkt wurde. Gleichzeitig mit diesem Vorgang sehen wir bei manchen noch im Wasser

lebenden Algen ein allmähliches Verschwinden einiger zusätzlicher Pigmentstoffe (Anpassungspigmente) und bei den Grünalgen das Fortbestehen nur jener Pigmentstoffe, die wir im allgemeinen auch bei den Kormophyten finden.

ÖKOLOGIE, BIOLOGIE UND GEOGRAPHISCHE VERBREITUNG

Infolge der Verschiedenheit des Lebensraumes (Wasser oder Festland) zeichnen sich die Chlorophyceen durch eine ökologische, physiologische und biologische Vielfalt aus. Manche Grünalgen weisen eine stark ausgeprägte ökologische Spezifität auf und sind durch Süßwasser- und Meerwasserformen vertreten.

Im Gegensatz zu Oltmanns Ansicht, wonach Algen keine Vorliebe für eine bestimmte Unterlage zeigen, sind wir der Meinung, daß für manche Algenarten aus gewissen Biotopen dennoch irgendeine Beständigkeit gegenüber bestimmten Unterlagen charakteristisch ist. Wenn auch diese Beständigkeit bei den auf fester Unterlage haftenden Meeresalgen nicht beobachtet werden kann, so ist sie für Wasserformen auf weicher Unterlage dennoch charakteristisch *(Caulerpaceae, Characeae)*. Dies gilt auch für einige Aerophyten (*Vaucheria, Protosiphon, Botrydium, Fritschiella, Oedocladium* u. a.), bei denen eine gewisse ökologische Spezifität gegenüber der physikalisch-chemischen Beschaffenheit der Unterlage zu bemerken ist.

Unter den Chlorophyceen kann man in bezug auf ihre Ökologie und Evolution auf Grund ihres Verhältnisses zum Biotop und zur Unterlage folgende Kategorien unterscheiden: I. Freie, nicht haftende, sich aktiv bewegende, geißelförmige oder amöboide Formen. II. Auf einer gewissen Unterlage fest haftende Formen: (a) Mechanisches Haften durch Rhizoiden (Sohle, Haftorgane), auf harter Unterlage (Felsen, Stein, Holz, Muscheln usw.). Diese Organe verkrusten und sterben ab. Diese Formen sind im allgemeinen für jene Meerwasserbiotopen bezeichnend, die starken Strömungen ausgesetzt sind. Die Rhizoiden haben keine absorptiven Aufgaben, es sei denn bei einigen Jugendformen. (b) Haften durch Rhizoiden (Rhizoidalsysteme) bei Süßwasserformen auf weicher Unterlage (Sand, Schlamm). Infolge ihres morphologisch-physiologischen Aufbaus erfüllen die Rhizoiden anscheinend auch eine schwache absorptive Funktion. Diese Algen entwickeln sich im allgemeinen in Gewässern mit schwacher Strömung. (c) Haften durch Rhizoidalsysteme bei aerophytisch-amphibischen und eigentlichen aerophyten Landformen, mit zahlreichen Typen eines höher entwickelten vegetativen Apparates. Unter den Ulotrichaceen sind uns in feuchten Standorten folgende aerophyte Formen bekannt: *Ulotrix oscillatoria, Hormidium dissectum, H. flaccidum, Gloeotila protogenica, Prasiola crispa, P. furfuracea* u. a.

Auf Grund von experimentellen Untersuchungen unterscheiden I. Grinţescu und St. Péterfi nach morphologisch-ökologischen Kriterien folgende zwei Arten in der Gattung *Stichococcus: St. minutus* als aerophyte Landform und *St. chlorelloides* als aerophyte Gesteinsform.

Die Wasser-, Land- und amphibischen Formen der Chlorophyceen vertragen das teilweise und zeitweilige Bedecktsein ihres Thallus mit Schlamm oder Sand und widerstehen ungünstigen Lebensbedingungen.

Bei den perennierenden aerophyten Landformen der Chlorophyceen verschwindet zu gewissen Zeitpunkten der obere vegetative, assimilierende und fruchtbare Teil, wobei sich das Plasma in das unterirdische Rhizoidalsystem zurückzieht; bei Wiedereinsetzen günstiger Lebensbedingungen wird der oberirdische Teil des Thallus wiederhergestellt [*Botrydium* (Abb. 1), *Protosiphon*, *Fritschiella* (Abb. 2), *Oedocladium* (Abb. 3) u.a.].

Die Arten der *Caulerpaceae* (Abb. 4) und *Characeae* (Abb. 5) bilden nach ihrem Absterben organische Stoffablagerungen, auf denen sich ausgedehnte benthonische, meist monospezifische und exklusive Populationen bilden.

Klimatisch und geographisch gesehen gedeihen die Chlorophyceen mit ihrem morphologisch-physiologisch gut differenzierten vegetativen Apparat (*Fritschiella*, *Oliviera* u.a.) unter warmen, feuchten Verhältnissen, besonders in Tropengebieten, seltener *(Oedocladium)* auch im gemäßigten Klima Europas.

Was ihre Verbreitung betrifft, sind die Grünalgen kosmopolitische Pflanzen mit großer ökologisch-geographischer Mannigfaltigkeit und verschiedene Faktoren sichern ihnen zahlreiche Verbreitungsmöglichkeiten. Ihre Verbreitungsgebiete sind nur zum Teil bekannt. Die bisherigen Forschungen gestatten nur einige vorläufige Betrachtungen.

Die Formen von *Protosiphon* sind vorwiegend tropisch. Die Gattung *Oedocladium* (7 Arten) ist in Europa, Indien und besonders in Nordamerika verbreitet. *Fritschiella* (1 Art) kommt in Indien und im Sudan vor, *Oliveria* (1 Art) in Afrika und Ägypten.

Unter den höher ausgebildeten Wasserformen ist die Gattung *Draparnaldia* (15 Arten) mit einigen kosmopolitischen Typen zu erwähnen, für gewisse Gebiete sind jedoch 9 Arten charakteristisch, die im Baikal in der UdSSR vorkommen. Die Gattung *Draparnaldiopsis* (4 Arten) ist in Nordamerika, Asien und Indien verbreitet.

Die Fragen der Herkunftsgebiete, der Wanderungen und der Verbreitungswege der Grünalgen sind nur zu einem geringen Teil gelöst. Ihr hohes Alter bietet auf jeden Fall eine Erklärung für ihre große geographische Verbreitung.

ÄHNLICHKEITEN ZWISCHEN DEN CHLOROPHYCEEN UND DEN TELOMOPHYTEN UND EINIGE PHYLOGENETISCHE BETRACHTUNGEN

Obwohl zwischen den Chlorophyceen und den Kormophyten große, im ontogenetischen Zyklus verschieden zum Ausdruck kommende Unterschiede bestehen, gibt es in bezug auf den Typ des heterotrichen Thallus mit quirlförmigen Verzweigungen dennoch gewisse Ähnlichkeiten und Berührungspunkte. Der höchstentwickelte Typ der Thallophyten *(Bryophyta)* und der niedere der Kormophyten *(Pteridophyta)* haben ihren gemeinsamen Ursprung wahrscheinlich in den höher organisierten Typen der Grünalgen (Abb. 6).

Die Abstammung ist teilweise durch folgende zytologische elektronenmikroskopische und biochemische Merkmale belegt: Ultrastruktur der Zellmembran, Kutikula, Kernteilung (Mitose und Meiose), Geißeln, Chromatophoren, Pigmentstoffe, Fermente, Reservesubstanzen u.a.

Die höheren Pflanzen haben die gleichen Assimilationspigmente, Fer-

mente und Reservesubstanzen wie die Grünalgen, von denen sie abstammen. Serodiagnostisch und biochemisch sind die Verbindungen zum Teil festgestellt.

Infolge des Organisationsgrades vollziehen sich bei der Evolution der Grünalgen physiologische Stoffwechselprozesse durch Spezialisierung und Anpassung und vor allem Autotrophie durch Photosynthese, ein Vorgang der sich bei den Aerophyten verstärkt und vervollkommnet *(Bryophyta, Kormophyta)*.

Die Art der vegetativen und geschlechtlichen Fortpflanzung bedingt bei den Chlorophyceen eine große Mannigfaltigkeit der ontogenetischen Entwicklungszyklen mit haplonten und diplonten Formen.

Die heterotrichen Thallustypen der rezenten Grünalgen *(Chaetophorales)* oder vielleicht auch andere, bereits verschwundene Typen gleicher Organisation können hypothetisch als Zentraltypen betrachtet werden, aus denen sich große Gruppen von Aerophyten entwickelt haben, und zwar die Bryophyten als thallomonobionte Formen und die Pteridophyten als kormodibionte Formen, die sich in den kormomonobionten *(Spermatophyta)* fortgesetzt haben (Bohlin 1901, Fritsch 1935, M. Guşuleac 1948, A. L. Takhtajan 1950, W. Zimmermann 1959, Tr. Ştefureac 1970 u. a.).

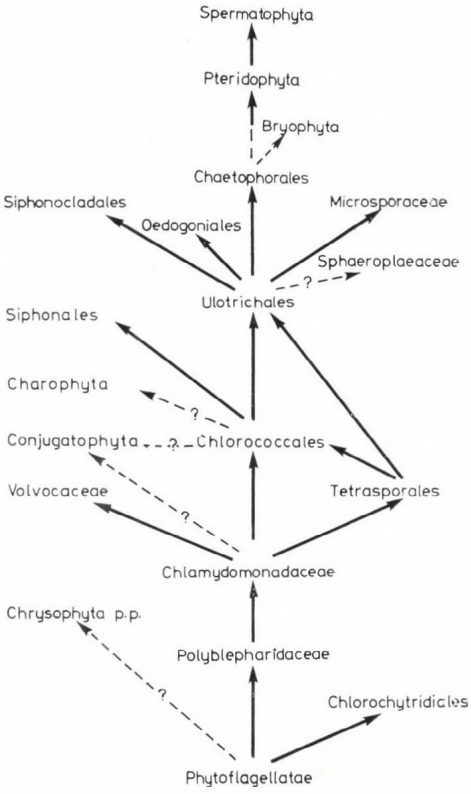

Abb. 6. Phylogenetisches Schema der Abteilung *Chlorophyta* mit den Hauptevolutionsetappen und Richtungen in aufsteigender Linie der Autotrophie der Algen und die Verbindung mit den Telomophyten (nach G. M. Smith 1955, B. Fott 1959, Tr. Ştefureac 1970)

Der schon im Paläozoikum verwirklichte höhere Organisationsgrad mancher Salz- (siphonaler Typ) und Süßwasserformen (heterotricher Typ) läßt uns vermuten, daß zur Zeit des Entwicklungsbeginns der Angiospermen die Chlorophyceen sich bereits in einem hohen Entwicklungsstadium befanden, aus dem sich dann Typen höherer Organisation im Pflanzenreich entwickelten. Es ist interessant festzustellen, daß sich die Chlorophyceen seither verhältnismäßig wenig weiterentwickelt haben. Dies beweisen die Reliktformen (*Dasycladaceae* u. a.).

Es kann jedoch angenommen werden, daß auf der Evolutionslinie des vegetativen Apparates bei einigen höher organisierten Formen der heterotrichen Chlorophyceen, auf weicher Unterlage, insbesondere in einigen Süßwasserbiotopen und in Übergangsbiotopen zur amphybischen Lebensweise, die Differenzierung und das Auftreten eines neuen Typs, eines morpho-

logisch und funktionell höher organisierten Thallus erfolgt war, desjenigen Thallustyps, den wir heute bei einigen aerophyten Bodenformen der Chlorophyceen kennen.

Die höhere Entwicklungsstufe einiger Chlorophyceen gestattet uns, die Grünalgen innerhalb einiger heutiger Systeme (Chadefaud, Capelletti, Fott u.a.) hinter die Rhodophyceen einzureihen.

Bei den hochentwickelten Chlorophyceen können folgende zwei Typen eines hochorganisierten Thallus festgestellt werden: 1. Heterotricher, monoenergider Thallustyp mit zwei Differenzierungsrichtungen in der Evolution: a) Höhere Organisation des reproduktiven Apparates (*Coleochaete* u.a.); b) höhere Differenzierung und Organisation des vegetativen Apparates *Fritschiella* (Abb. 2), *Oliveria, Oedocladium* (Abb. 3) u.a.; 2. siphonaler, polyenergider Thallustyp, spezialisiert und hochorganisiert für Lebensbedingungen im warmen Meerwasser, ohne daß hieraus Aerophyten entstanden sind.

Die Characeen mit ihrer polyenergiden Internodienzelle haben sich verhältnismäßig wenig umgewandelt und insbesondere in den Biotopen des Süß- und Brackwassers, seltener in jenen des Meerwassers (Lagunen) als Relikte erhalten; ausnahmsweise kommen aerobenthonische Formen vor (*Nitella mucronata*) (Migula 1897).

Die heterotrophen Pflanzengruppen waren polyphiletisch regressiv durch Anpassung einiger autotropher Grünalgen (*Flagellatae, Chlorophyta*) an Saprophytismus und Parasitismus entstanden, worunter auch einige Typen von *Heterosiphonales* (*Vaucheria* u.a.) nicht fehlen. Von letzteren stammen einige Phycomyceten (*Saprolegniaceae, Thraustotheca clavata*) ab. Aus den Rhodophyceen ist durch Herausbildung der Heterotrophie die Ordnung *Laboulbeniales* (*Ascomycetes*) entstanden.

PHYLOGENETISCHES SCHEMA DER ABTEILUNG CHLOROPHYTA UND IHRE VERBINDUNG MIT DEN TELOMOPHYTEN

In neuerer Zeit wurden von G. M. Smith (1955), B. Fott (1959) u.a. für Grünalgen mehrere phylogenetische Schemen vorgeschlagen.

In unserem Schema, dem wir indessen einen allgemeineren Charakter zuschreiben, bringen wir einige neue Berichtigungen sowohl über die taxonomischen Einheiten innerhalb der Abteilung *Chlorophyta* als auch über ihre möglichen Verbindungen mit den Kormophyten (Abb. 6).

Die Grundlagen des vorliegenden Schemas sind folgende: 1. Feststellung der hauptsächlichen Evolutionsetappen der Chlorophyceen (Abteilungen, Ordnungen, Familien) in aufsteigender Linie der Autotrophie und ihrer Verbindung mit den höheren Typen der Telomophyten. 2. Auf Grund der Geißeltheorie nehmen wir an, daß die Grünalgen von den autotrophen (niederen) Phytoflagellaten abstammen. 3. Die neuerlich erfolgte Einführung der Ordnung *Chlorochytridiales* in die Abteilung *Chlorophyta* betrachten wir als unnatürlich und provisorisch, weil diese Organismen einen kleinen Adaptationsabstammungszweig darstellen. Sie könnten zu den niederen Pilzen eingereiht werden, wodurch der polyphyletische Charakter der Pilze erweitert würde. 4. Zwecks Erklärung der differenzierten Entwicklung der Ordnung *Volvocales* erachten wir es als notwendig, die drei Familien getrennt

in das Schema einzureihen, und zwar die beiden ersten (*Polyblepharidaceae* und *Chlamydomonadaceae*) in direkter Linie, die dritte (*Volvocaceae*) seitlich abgezweigt (als Typen einer Kolonie von Einzelindividuen). 5. Die Konjugaten und Charophyten, haplonte Formen ohne Zoosporen, jedoch mit beträchtlichem und höher entwickeltem vegetativem und reproduktivem Apparat (*Charophyta*) betrachten wir als gesonderte und vermutlich abgeleitete Abteilungen (*Conjugatophyta* aus *Chlamydomonaceae* und *Charophyta* aus *Chlorococcales*). 6. Evolutions- und Differenzierungszentren der höher organisierten Chlorophyten sind die *Ulotrichales* und vor allem die *Chaetophorales*. Ihr heterotricher Thallus bildete die Grundlage der Entwicklung in Richtung der aerophyten Landtypen. 7. Von den *Chaetophorales* kann man auf Grund des hochorganisierten, heterotrichen Wasser- und Landthallus die Bryophyten als die höchstentwickelten Thallophyten (Thallomonobionten) ableiten sowie auch die Kormophyten mit ihren niederen sporiferen Typen (*Pteridophyta*—Kormodibionten) und ihre höheren spermatiferen Typen (*Spermatophyta*—Kormomonobionten), die gemeinsam die telomischen Pflanzen bilden (*Telomophyta, Cormobionta, Embryobionta*).

Die heterogene Abteilung *Chrysophyta* mit ihrer bedeutenden morphologischen Variabilität, mit einer Reihe von Konvergenzen und mit ungewissen taxonomischen Gruppen reihen wir in unserem Schema nur provisorisch ein, da es nach unseren gegenwärtigen Kenntnissen schwer ist, sie phylogenetisch zu betrachten. Durch ihre vielfachen Beziehungen zu den Flagellaten verdient diese Algengruppe in Zukunft eine ganz besondere Aufmerksamkeit. Es ist nicht ausgeschlossen, daß mit der Lösung der sich im Zusammenhang mit diesen Algen aufwerfenden Fragen auch solche Probleme besser geklärt werden, die sich auf die Entwicklung der Algen im allgemeinen beziehen.

LITERATUR

Algéus, S. (1946): Untersuchungen über die Ernährungsphysiologie der Chlorophyceen mit besonderer Berücksichtigung von Indolylessigsäure, Ascorbinsäure und Aneurin. *Bot. Notiser* Lund, 129–280 (also: Diss. Lund)

Beger, H. (1954): *Chlorophyta*. In A. Engler: *Syllabus*. 12. Aufl. Bd. I, Berlin, 86–109

Bohlin, K. (1901): *Zur Phylogenie der grünen Algen und der Archegoniaten* (schwedisch). Akad. Aufhandling. Uppsala

Brunthaler, Lemmermann, Pascher, Herring (1914–1921): *Chlorophyceae* II–IV. In A. Pascher: *Die Süßwasserflora Mitteleuropas* Nr. 5–7. Jena

Cappelletti, C. (1959): *Trattato di Botanica Sistematica*. Ed. I. Padova

Cejn, K. (1959): *Flora Č.S.R., Oomycetes I. B., vazeke*. Praha, 24–45, 280–5

Chadefaud, M. (1959): Sur le cycle sexuel des organismes eucaryotes et son evolution. *Les édit. de la Rev. scient.* **90** (**1**) 49–57

Chaudefaud, M. (1960): *Les végétaux non vasculaires (Cryptogamie). Traité de Botanique Systématique* par M. Chadefaud et L. Emberger, t. I. Masson, Paris, 305–419

Corillion, R. (1957): Les Charophycées de France et d'Europe Occidentale. *Bull. de la Soc. Scient. de Bretagne. Rennes*, **XXXII**, *fasc. hors série no. 1*, 1–499

Dangeard, P. (1933): *Traité d'Algologie*. Paris, 111–222

(Deduschenko-Schtschegolewa, N. T., A. M. Matwienko, L. A. Schkorbatow) Дедушенко-Щеголева, Н. Т., А. М. Матвиенко, Л. А. Шкорбатов (1959): Зеленые водоросли. Определители пресноводных водорослей. СССР. Москва—Ленинград, 8

Engler, A. (1954): *Syllabus der Pflanzenfamilien*. 12. Aufl. Bd. I. Berlin, 4–23

Feldmann, J. (1952): Les cycles de reproduction des Algues et leur rapports avec la phylogénie. *Rev. de cytolog. et de biol. végétale* **13**

Fott, B. (1959): *Algenkunde*. Jena, 1–482
Fritsch, F. E. (1954): Evolutionary trends among the Algae in relation to the origin of vascular plants. *8 Congrès internat. de Botanique, Paris, Section 5a*
Fritsch, F. E. (1961): *The structure and reproduction of the Algae*. Vol. I, Cambridge, 60–557
Gäumann, E. (1964): *Die Pilze*. Birkhäuser Verlag, Basel und Stuttgart, 9–492
Gessner, Fr. (1959): *Hydrobotanik*, Bd. II. Berlin, 2–11
Glück, H. (1936): Pteridophyten und Phanerogamen. In A. Pascher: *Die Süßwasserflora Mitteleuropas*, Nr. 15. Jena
Goebel, K. (1928): *Organographie der Pflanzen*. Erster Teil. III. Aufl. Jena, 57–66
Greguss, P. (1964): The phylogeny of sexuality and triphyletic evolution of the landplants. *Acta Univ. Szeged, Acta Biol. Bot.* **10** 1–51
Guşuleac, M. (1948): Sur la phylogénie des Cormophytes I. Leurs rapports avec les Bryophytes. *Bul. Grăd. Bot. şi Muz. Bot. Univ. Cluj* XXVIII, 251–67
Heering, W. (1914): *Chlorophyceae*. In A. Pascher: *Die Süßwasserflora Mitteleuropas*, Nr. 6. Jena, 1–244
Hindak, F. (1962): Beitrag zur Phylogenie und Systematik der *Ulotrichales*. *Biologia, Bratislava* **17**
Iyengar, M. O. P. (1932): *Fritschiella. New Phytologist* **31** 329–35
Lerche, W. (1937): Untersuchungen über Entwicklung und Fortpflanzung in der Gattung *Dunaliella*. *Arch. Protistenk.* **88**
(Meyer, A.) Мейер, А. (1961): О филогении зеленых водорослей *(Chlorophyta)*. Бот. журн. **46** 1073–86 (russ.)
Migula, W. (1897): Die Characeen Deutschlands, Österreichs und der Schweiz. In *Rabenhorst's Kryptogamen-Flora*. 2. Aufl. Bd. II, Leipzig 149–59
Migula, W. (1925): *Charophyta*. In A. Pascher: *Die Süßwasserflora Mitteleuropas*, Nr. 11. Jena, 1–19
Moreau, F. und Moreau, F. (1935): Remarques sur la systématique des Saprolegniaceae. *Bull. Soc. Bot. France* **82** 19, 354–8
Moreau, F. (1954): *Les Champignons*, vol. II. Paul Lechevalier, Paris, 2014–31
Oltmanns, Fr. (1922–1923): *Morphologie und Biologie der Algen*. 2. I–III. Aufl., Jena
Péterfi, Şt. (1937): Contribuţiuni la morfologia şi fiziologia algei verzi *Microthamnion Küetzingianum* Naeg. *Teză, Univ. Cluj*, **71**, 17–29
Péterfi, Şt. und Ştefureac, F. (1965): Concepţia despre specia la alge şi Briofite cu unele consideraţii asupra lucrărilor româneşti privitoare la aceste grupe. *Stud. şi Cercet. de Biologie S. Botanică* **17** Nr. **1**, 101–12
Péterfi, L. und Péterfi, Şt. (1965): Studies on the taxonomy and ecology of the Rumanian *Volvocales* I. Separately printed from *Nova Hedwigia* **X** 537–65
Pia, J. (1927): *Thallophyta*. In Hirmer: *Handbuch der Paleobotanik*. Bd. 1. München–Berlin, 31–136
Pringsheim, H. (1910): *Die Variabilität niederer Organismen*. Berlin
Pringsheim, E. G. (1963): *Farblose Algen*. Jena
Printz, H. (1923): *Chlorophyceae*. In A. Engler-Prantl: *Die natürlichen Pflanzenfamilien*. 2. Aufl. Bd. 3, Leipzig
Printz, H. (1927): *Chlorophyceae*. In A. Engler-Prantl: *Die natürlichen Pflanzenfamilien*. Bd. 3
Rothmaler, W. (1955): *Allgemeine Taxonomie und Chorologie der Pflanzen*. Jena, 1–120
Schelhorn, M. (1936): Zur Ökologie und Biologie der Erdalgen. In F. Boas: *Naturwissenschaft und Landwirtschaft* **18**
Schussnig, B. (1930): Generations- und Phasenwechsel bei den Chlorophyceen. *Österr. Bot. Zschr.* **79**
Singh, R. N. (1941): On some phases in the life history of the terrestrial alga *Fritschiella tuberosa* Iyeng. and its autecology. *New Phytologist* **40**
Singh, R. N. (1947): *Fritschiella tuberosa* Iyeng. *Ann. of Bot.* **11** no. **42**
Singh, R. N. (1954): *Fritschiella tuberosa* and the algal ancestry of higher plants. *8 Congrès internat. de Botanique, Paris, Section* 17
Smith, G. M. (1955): *Cryptogamic Botany*, vol. I. New York, Toronto, London, 1–345
Ştefureac, Tr. I. (1970): *Evoluţia plantelor reflectată in opere recente de botanică filogenetică*. Edit. Did. şi Pedag., 144–62
Strasburger, E. (1967): *Lehrbuch der Botanik*. 29. Aufl., Jena, 398–414
Тахтаджан, А. Л. (1950): Филогенетилеские основы систены высших растений. *Ботанилеский жсурнал* **35** 113–39

Teodoresco, E. C. (1906): Observations morphologiques et biologiques sur le genre Dunaliella. *Revue générale de Bot.* **18** 353–70, 409–27.
Vilhelm, J. (1923): Nouveau *Chara* d'eau thermale et radioactive des bains de Pistany en Slovaquie. *Bull. Int. Akad. Sci. Bohême*, 1–3
Vilhelm, J. (1931): *Archaiophyta und Algophyta* (tschech.). Praha, 1–355
Wettstein, R. (1935): *Handbuch der systematischen Botanik*. 4. Aufl. Leipzig und Wien, 160–91
Willy, N. (1897): *Chlorophyceae*. In A. Engler-Prantl: *Die natürlichen Pflanzenfamilien*, I. Teil, 2. Abt, 21–101
Wood, R. D. and Imahori, K. (1965): *Monograph of the Characeae*, vol. I, Verlag von J. Cramer, Weinheim, 1–34
Zimmermann, W. (1959): *Die Phylogenie der Pflanzen*. 1. Aufl. 1930; 2. Aufl. 1959, Stuttgart, 52–73

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REMARKS ON THE EVOLUTION OF MAJOR PLANT GROUPS

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The co-operation in a well-known textbook recently has given me the opportunity to elaborate some general ideas on the evolution and phylogeny of major plant groups (D. Denffer et al. 1971; cf. the same also for literature citations). I hope that these ideas, together with a new scheme of probable relationships (Fig. 1), will be of some interest within the framework of our Symposium.

The most ancient traces of life found on our earth evidently are more than 3000 million years old. It is generally believed that the atmosphere of that time contained practically no free oxygen. We can assume that such early organisms had already a cellular organization and were Bacteria-like P r o k a r y o t a which used organic compounds accumulated in the aquatic environment ('Ur-Suppe') for their metabolism; evidently, they were primarily heterotrophic and anoxybiontic. It is still quite uncertain whether forerunners of these 'Proto-Bacteria' on a molecular level of organization might have been Virus-like 'P r o b i o n t a'.

Increasing shortage of easily accessible organic compounds in the early biosphere forced ancient P r o k a r y o t a gradually to switch to facultative and later on to obligate autotrophy. This has led to the origin of anoxybiontic chemosynthesis and primitive forms of photosynthesis (using H_2S). Comparable metabolic types are still found among recent B a c t e r i o p h y t a. The decisive break-through to typical photosynthesis with H_2O fission and O_2 production then occurred in the prokaryotic C y a n o p h y t a (about 2000 million years ago). From that time on the increasing amount of oxygen in the biosphere made the development of oxybiontic metabolism and respiration possible much more 'economic' energy-wise compared with various forms of fermentation. The increase of autotrophic organisms in turn led to the differentiation of various forms of secondary heterotrophy: saprophytism and parasitism. These further developments also have taken place already at the prokaryotic level.

The next, most important evolutionary step was the origin of E u k a r y o t a (more than 1000 million years ago?). Their most primitive representatives are evidently flagellate and therefore mobile, unicellular, haplontic and photosynthetic algae. The transmission of their hereditary units localized in chromosomes became more precise through mitosis, and recombination was greatly enhanced through sexuality and meiosis (crossing-over!). These improvements evidently backed the origin of uni- and later on multicellular organisms with increasingly complex structures and functions.

The basic group of *Eukaryota* are the P r o t o b i o n t a. Their main differentiation concerns the form of nutrition; while algae remain photoautotrophic, fungi and animals, i.e. Protozoa and later on Metazoa = Z o o b i o n t a, became secondarily heterotrophic. Accordingly, algae elaborate their thallus towards light, fungi within their organic substrate. Both specialize on a sedentary way of life, growing towards their nutrition by extension of outer surfaces, i.e. 'extroversion'. In contrast, the development of animals is determined by mobility, hunting for nutrition, extension of inner surfaces, i.e. 'introversion'. These evolutionary trends towards secondary heterotrophy clearly have been parallel and convergent: fungi and animals are polyphyletic and only conventional taxa. All *Protobionta* form one closely interrelated and complex natural group.

Already from their most primitive mobile representatives the various lines of algae have differentiated particularly in regard to photosynthetic activity (pigmentation, products of assimilation, etc.). Further evolution of algal phyla is characterized by parallel developments, first at unicellular levels from naked monadal (single or colonial) either to rhizopodial, or further to mucilage enveloped capsal or cell wall surrounded coccal organization. This is continued on multicellular and/or multinuclear levels to filamentous and complex thallose, plectenchymatic or finally parenchymatic growth forms. These phyletic progressions are combined with a change from a mobile to an adnate life form, from a true aquatic to a littoral environment, and with a general increase in size, obviously related to the phenomenon of 'struggle for light' among photoautotrophs attached to the ground. In addition, 'division of labour' often leads to progressions from iso- to aniso- and oogamy (economy of fertilization!), to the origin of a ± regular sequence of generations with different forms of reproduction (sporo-and gametophytes) and to a shift of elaboration from haplo- towards diplophase (improved genetic versatility and homoeostasis!).

Comparable evolutionary progressions characterize the differentiation of fungi. Both groups probably have managed to occupy terrestrial habitats only to a rather limited degree before the origin of true land plants (*Cormobionta*). Only afterwards (i.e. since the Devonian) did sapro and parasitic fungi find a great array of new niches for further evolution. As obvious adaptations to terrestrial life we can refer to progressions from oogamy to gametangio- and somatogamy, or from zoospores to drought-resistant spores and conidia. In extreme habitats the development of symbiontic algae and fungi as lichens has been particularly successful.

Most important in the history of organismic life on our earth has been the origin of true land plants: C o r m o b i o n t a. Probably in the Upper Silurian, about 400 million years ago, we can postulate the origin of P s i l o p h y t a (= *Rhyniophyta*) from some unknown amphibious *Chlorophyta* with complex parenchymatic thalli, and with a characteristic sequence of (probably rather similar and independent?) gameto- and sporophytes. Root hairs, cuticula, epidermis, stomata, gametangia with a sterile outer cell layer (antheridia and archegonia), and drought-resistant spores with walls containing sporopollenine made *Psilophyta* particularly qualified to pioneer higher terrestrial plant life.

From *Psilophyta* we can follow an early but less successfull line: B r y o p h y t a (liverworts and mosses), where elaboration is manifest particularly

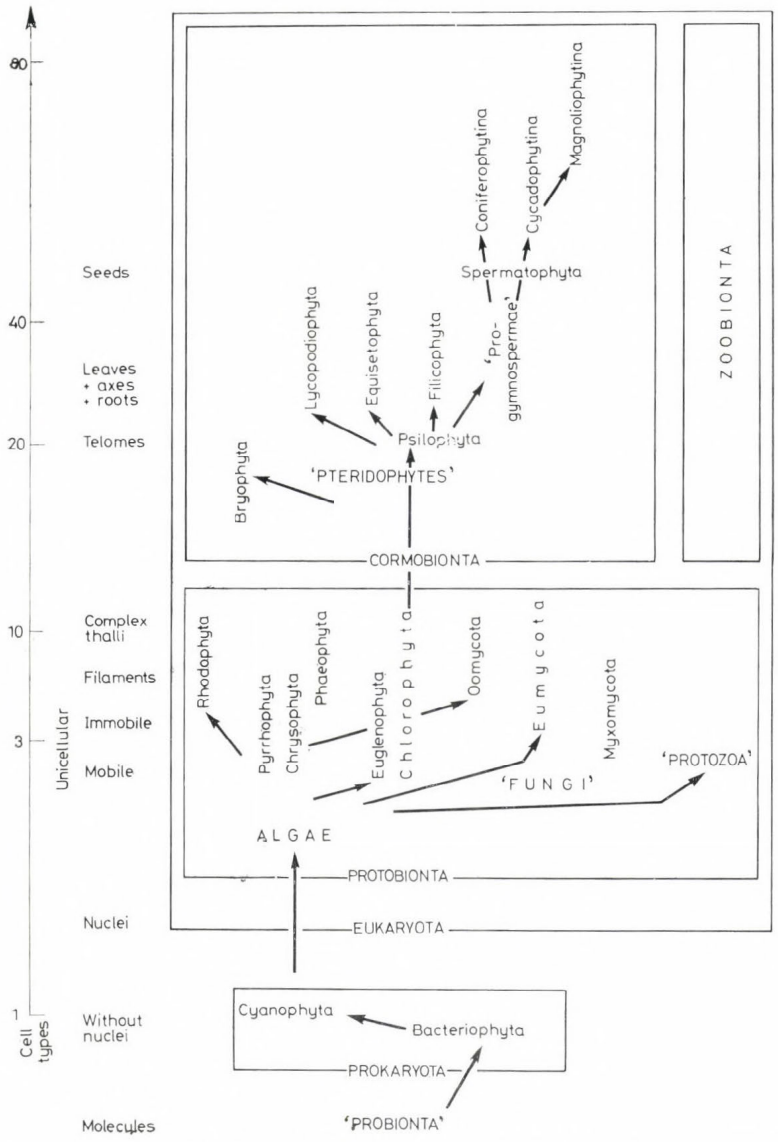

Fig. 1. Scheme of probable phylogenetic relationships between major groups of organisms, particularly plants. General references to organizational level and number of cell types (for plants) on the left margin.

in the haploid gametophyte, which supports the dependent sporophyte. In contrast, the stress of differentiation from *Psilophyta* towards the various Pteridophytic lines effected the diploid sporophyte: Under the selective drive of increasing size (again: 'struggle for light'!) the telomic (i.e. relatively undifferentiated) sporophytes of *Psilophyta* underwent a 'division of labour' and differentiated into roots and shoots with axes (caulomes) and leaves (phyllomes), while the more water dependent and drought susceptible gametophytes remained thallophytic and were progressively reduced (reduction of risk!). It is beyond doubt today that these progressions have occurred parallel in Lycopodiophyta, Equisetophyta and Filicophyta (= *Polypodiophyta*), because telomic systems of very different size and complexity have been incorporated into their phyllomes (i.e. trophophylls, sporophylls, sporangiophores). Further size increase has led to woody and arboreal life forms in all the Pteridophyte groups (cf. Carboniferous forests!). In all of these groups the stress for further reduction of gametophytes has led to the differentiation of male and female gametophytes. This has extended back onto the spores, and resulted in progressions from iso- to heterospory with micro- and megaspores.

Dependence on fertilization of archegonia by sperms in the presence of atmospheric water and on self-supporting megaprothallia remained a limiting factor for nearly all Pteridophytes. This structural and functional bottleneck was successfully overcome only by the true seed plants, viz. *Spermatophyta*, where development of megaprothallia and fertilization of eggs occur on the mother plant. *Spermatophyta* appear between the Upper Devonian and lower Carboniferous (about 350 million years ago) in the fossil record. They are nearly simultaneously represented by primitive members of their two drastically different subphyla. *Coniferophytina* (with simple dichotomous structure of trophophylls, single pollen sac groups as microsporophylls and single ovules as 'megasporophylls') and *Cycadophytina* (with complex pinnate structure of trophophylls, numerous pollen sac groups incorporated into microsporophylls and numerous ovules combined into megasporophylls).

It had been a long-standing unsolved problem, what ancestors these primitive *Spermatophyta* had, and how their relationships could be interpreted. Clarification is now promoted by the recent discovery of an array of (Lower?) Middle to Upper Devonian (Lower Carboniferous) fossils which combine the type of secondary growth and wood structure of seed plants with iso- to heterospory, and which partly have shoots not yet clearly differentiated into phyllomes and caulomes. They are provisionally called '*Progymnospermae*' and demonstrate firstly that early *Spermatophyta* were not derived from *Filicophyta* but developed ± directly and parallel from *Psilophyta* to *Coniferophytina* and *Cycadophytina*. This means in morphological terms that the different vegetative and fertile phyllomes of *Coniferophytina* and *Cycadophytina* are the result of parallel differentiation from simple or complex telomic systems of '*Progymnospermae*' and therefore not strictly homologous.

Within *Coniferophytina* evolution seems to have followed two main lines, viz. *Pinatae*, with the oldest *Cordaitidae* and the later *Pinidae* and *Taxidae*, and *Ginkgoatae*. In *Cycadophytina Lyginopteridatae* (= *Pteridospermae*) evidently are the oldest basic group; from them *Cycadatae* and *Bennetitatae*

are later offshoots, and *Gnetatae* possibly relic recent survivors. It probably was not only reproduction by seed but also a superior anatomical structure (water conducting system!) which made gymnospermous *Spermatophyta* groups dominant within the biosphere since the Upper Permian.

Another, still unsettled major phylogenetic problem is the origin of the third and largest Spermatophyta group, the Angiosperms: *Magnoliophytina*. It is evident that they are only related to *Cycadophytina*, but none of the mesozoic groups truly qualifies as ancestral. This leaves us with the hypothesis that Angiosperms are probably more ancient than the fossil record would suggest and that they are somehow connected with Pteridosperms. It seems evident today that their enclosed, sheltered ovules and typically hermaphrodite flowers with perianth are primarily adaptations for pollination by animals (zoophily).

The sudden appearance of Magnoliophytina in the Cretaceous (about 140 million years ago) and their quickly dominant role in the biosphere is paralleled by a remarkable plasticity and adaptability in respect to life and growth form, pollination, seed and fruit dispersal and partly extreme acceleration of ontogeny (neoteny of vegetative organs, flowers, gametophytes etc.). Anyhow, Angiosperms brought about an unprecedented productivity of plant life on our earth; they have advanced the front lines of higher plant life very considerably into cold and drought deserts.

The evolution and phylogeny of plants can be characterized by progressions to successively higher levels of organization (see left margin in Fig. 1). Differentiation, limited first to the levels of molecules and cell organelles, later extends to cells, tissues, and finally to organs and organ complexes. Generally, an increase of 'units' of a lower organizational level is followed by a 'division of labour' between them, their new combination and finally their transformation into a complex 'unit' on the next higher level of organization. (As an example we may refer to the following series: single sporangium → group of sporangia → sterilization of marginal sporangia: integument, fertile central sporangium: nucellus = ovule.) On a large scale we can observe in plant phylogeny a successively improving capacity for regulation as a prerequisite for increasing independence from environmental fluctuations and extremes. This enables plant life to penetrate from stable (e.g. sea water) into more and more labile environments (e.g. terrestial habitats, semideserts), and to utilize available niches and supplies more effectively, i.e. with increasing productivity.

REFERENCE

Denffer, D., Schumacher, W., Mägdefrau, K. and Ehrendorfer, F. (1971): *Lehrbuch der Botanik*. 30th ed., G. Fischer Verlag, Stuttgart

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Proceedings of a Symposium held in Tihany, 2–4 September 1971

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