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BRITISH
FLOWERING PLANTS
AND
MODERN SYSTEMATIC
METHODS

BEING THE REPORT OF THE
CONFERENCE
ON
THE STUDY OF CRITICAL BRITISH GROUPS
ARRANGED IN APRIL 1948, BY
THE BOTANICAL SOCIETY OF
THE BRITISH ISLES

EDITED BY
A. J. WILMOTT, M.A., F.L.S.

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Botany

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EDITORIAL NOTE

This volume explains itself. The success of the Conference which it records is indicative of the growing realisation of the fundamental importance of Systematics, an importance which has been too long overlooked in our Universities. 114 different people attended the Conference; 71 members and 43 guests, the average attendance at each session being between 80 and 90. The invitation extended to University students was well responded to, and not only by London colleges.

The Programme was carried out as arranged, with the addition of several more exhibits. For publication, however, it seemed desirable to put the items into a sequence more suitable for reading and reference, and this has therefore been done. The actual course of the proceedings has been indicated by reprinting the original Programme.

Thanks are here given for permission to reprint from *The Times* (fourth leader of April 10th). Those who enjoyed the Conference owe their pleasure largely to the energy of the Society's Honorary General Secretary, Miss M. S. Campbell, and to the work of the other officers and members who assisted her. The organisers wish to record their special indebtedness to the staff of the Royal Horticultural Society whose willing and helpful co-operation in all ways and at all times reduced difficulties to a minimum.

A. J. WILMOTT.

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1. *Viola Riviniana* Rehb. with adventitious shoots (Surrey).
2. *Viola Riviniana* Rehb. with adventitious shoots (cultivated in Durham).
3. Development of pollen in some pentaploid Canine Roses.
4. Development of megaspores in the ovules of a pentaploid Canine Rose.
5. *Galium debile* Desv. and *G. palustre* L. ; both $2n = 24$.
6. Ecovarieties of *Juncus articulatus* L.
7. *Juncus articulatus* L., *J. acutiflorus* Ehrh., the hybrid between them, and *Juncus* "large 80".
8. *Nasturtium officinale* R. Br.
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11. *Cardamine pratensis* L., $2n = 30$, with normal single flowers.
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15. *Cardamine pratensis* L. ; distribution map of the two types examined cytologically.
16. *Glyceria fluitans* (L.) R. Br., *G. declinata* Bréb., and *G. plicata* Fr. ; photograph of herbarium specimens.
17. Spikelets of British species of *Glyceria*.
18. Adaxial and abaxial views of the glumed and naked grains of the British species of *Glyceria*.

BOTANISTS TO-DAY

(From 'The Times', 10th April, 1948; fourth leader)

THE deceptive innocence and simplicity of wild flowers means that they are looked upon as suitable and easy for casual study. This is all to the good, but the request for the name of a good, simple book about English flowers has baffled many a naturalist. The subject is not simple. That great botanist George Bentham, who made the classic attempt at a work of this kind in the book now known as "Bentham and Hooker," produced what is perhaps the best attempt at an A.B.C. This book has been immensely valuable as an introduction, but even it demands serious application from the student, and he cannot apply himself to it seriously without very soon finding that it will not always fit the facts which he sees for himself in the plants. To consider the lilies of the field is an intricate business. Of that truth the conference of the newly renamed Botanical Society of the British Isles, which began yesterday under the presidency of Mr. J. S. L. Gilmour and goes on to-day, once again bears witness.

The steadily increasing complexity of the study of British flowering plants does not rest on the old quarrel between the "lumpers" and the "splitters" — between those who grouped as many forms as possible under a single name and those who elevated as many small variations as they could to named specific rank. It rests rather on the growth of scientific method, on the new tools of study which the botanist to-day has at his disposal. Chief of these, perhaps, is cytology, the study of the plant cell and especially of chromosomes, the bodies by which hereditary characters are contained and transmitted. By counting chromosomes it has often been possible to confirm specific differentiations previously only surmised. For instance, it is now known that there are two British species of watercress, differing only in small visible characters, but established as distinct by their different numbers of chromosomes. Yet, as Dr. E. F. Warburg said yesterday, the result of this kind of examination is not always to increase the number of acknowledged species. In the case of the little spring flowering whitlow grass, of which the French botanist Jordan thought there were 200 species, modern cytologists think there may perhaps be four.

There are also experimental studies of living plants, of which Dr. W. B. Turrill spoke, with such strange phenomena as apomixy — the production of seeds by vegetative growth without sexual fertilization, so that, among the dandelions, one plant may give rise to a whole generation whose evident distinguishing characteristics are those of one individual often repeated. The membership of the Botanical Society shows how the amateur and the professional can work together in these fields. The study of the British flora is going forward seriously and scientifically, and much will yet be found out about the nature and ways of life of familiar plants.

Patroness : H.R.H. The Princess Royal
President : J. S. L. Gilmour, Esq., M.A.
Vice-President : A. H. G. Alston, Esq., M.A.

The Botanical Society of the British Isles

CONFERENCE

The Study of Critical British Groups

PROGRAMME

(subject to slight alteration)

Lecture Room
Royal Horticultural Society's New Hall
Greycoat Street
Westminster, London, S.W.1

APRIL 9th and 10th
1948

FRIDAY, APRIL 9th

First Session

- 10.30 a.m. Introductory Talk
 The President : MR. J. S. L. GILMOUR
- 10.50 Cytology in Relation to Critical Groups
 DR. E. F. WARBURG
- 11.30 Experimental Studies on British Species of Plants
 DR. W. B. TURRILL
- 12.15 Ecology in Relation to Critical Groups
 PROF. A. R. CLAPHAM
- 1.00 p.m. Interval for Luncheon

Second Session

- 2.15 EXHIBITION MEETING
 The Exhibits will include :
- | | |
|--|--------------------------|
| <i>Epilobium</i> | Mr. G. M. Ash |
| Gramineae | Mr. C. E. Hubbard |
| Colour Plates | The Rev. W. Keble Martin |
| <i>Glyceria</i> | Dr. J. M. Lambert |
| “ The Importance of Cytology in
the Study of <i>Rumex</i> ” | Mr. J. E. Lousley |
| <i>Carex</i> | Mr. E. Nelmes |
| “ Variation and Ecology in the
British Watercresses ” | Mr. H. K. A. Shaw |
| <i>Bromus</i> | Prof. T. G. Tutin |
| | Miss E. Vachell |
| <i>Alchemilla</i> | Mr. S. M. Walters |
| <i>Rubus</i> | Mr. W. C. R. Watson |
- 4.30 Interval for Tea

Third Session

- 5.00 An Introduction to *Rubus* (illustrated)
 Mr. WM. C. R. WATSON
 (*followed by discussion*)
- 6.00 Vegetative and Cytological Variation in *Viola*
Riviniana *Rchb.* (illustrated)
 DR. D. H. VALENTINE
 (*followed by discussion*)
- 7.00 End of third session

SATURDAY, APRIL 10th

First Session

- 10.00 a.m. Intra-Specific Categories
MR. A. J. WILMOTT
(followed by discussion)
- 11.00 Chromosomes and Classification in the Genus *Rosa*
(illustrated)
DR. K. B. BLACKBURN
(followed by discussion)
- 12.00 Forms of *Valeriana officinalis* (illustrated)
DR. T. A. SPRAGUE
(followed by discussion)
- 12.55 Interval for Luncheon
- 2.00 p.m. (sharp)
ANNUAL GENERAL MEETING of the SOCIETY
(NOT open to visitors)

Second Session

- 2.45 Some Taxonomic Problems in *Galium* and *Juncus*
(illustrated)
PROF. A. R. CLAPHAM
(followed by discussion)
- 3.40 Some Problems of Water Buttercups (illustrated)
DR. R. W. BUTCHER
(followed by discussion)
- 4.40 Interval for Tea

Third Session

- 5.15 BRAINS TRUST—
Question Master—MR. J. S. L. GILMOUR
MISS M. S. CAMPBELL PROF. T. G. TUTIN
MR. J. E. LOUSLEY DR. E. F. WARBURG
PROF. C. E. RAVEN MR. A. J. WILMOTT
- 6.30 Closing Remarks by The President
- 7.00 End of Conference.

NOTES

TRANSPORT : The R.H.S. New Hall is in Greycoat Street, Westminster, which is close to the Army & Navy Stores. The nearest Main Line station is Victoria (circa 10 mins. walk). The nearest Underground Station is St. James Park, (District Line and Inner Circle), thence walk via Victoria Street, Artillery Row and Greycoat Place (circa 6 mins. walk).

Buses : Nos. 11, 24, 29, 76, 134 to Victoria Street, alight at Army & Navy Stores and thence via Artillery Row and Greycoat Place.

Green Line Coaches to Coach Station, Victoria (Buckingham Palace Road), thence by No. 11 Bus and proceed as above.

CATERING : Luncheon (4/-) is available each day in the Refreshment Room at the Hall (Licensed). Tea (from 1/6 plain tea, 2/- with supplementary dish) will also be available each day.

BRAINS TRUST : Questions for this should be handed in on April 9th at the Hall, or sent on a post card to the Hon. Assistant Secretary, 64 Elsworthy Road, London, N.W.3. to arrive not later than April 7th.

PUBLICATIONS : Samples of the Society's Publications will be on view and orders may be placed with the attendant in charge.

INFORMATION : Membership of the Botanical Society of the British Isles is open to all persons, whether amateur or professional, interested in British Botany. Subscriptions are : 1 guinea per annum for Ordinary Members ; 10s. 6d. per annum for Junior Members (under 21 years) ; 10s. 6d. per annum for Family Members. All enquiries should be addressed to the Honorary General Secretary (Miss M. S. Campbell), c/o Department of Botany, British Museum (Natural History), Cromwell Road, London, S.W.7.

TICKETS : Additional tickets can still be obtained (both for members and guests) from the Hon. General Secretary.

The Committee responsible for the arrangement of the Conference wish to thank all who have assisted them, and especially the Royal Horticultural Society and Mr. W. R. Price.

INTRODUCTORY REMARKS BY THE PRESIDENT

J. S. L. GILMOUR.

In the first place I would like to welcome all who are to-day attending this first Conference held by our Society, for the study of Critical British Groups—the first big function, in fact, sponsored by the Society under its new title—and especially the many younger students whom we have invited to help us in our deliberations.

A glance at the programme will show that nearly every aspect of our subject is being covered by one speaker or another. There are, however, two points on which I would like to touch.

Firstly, what is a critical group and how does it differ from other groups? Clearly, there is no sharp distinction between a comparatively uniform group like the genus *Pteridium*, on the one hand, and avowedly critical groups like our old friends *Rubus* and *Hieracium* on the other. For the time being, however, perhaps we can define a critical group as one whose members cannot be classified into sub-groups that are distinguishable by clear-cut and constant differences. This, I know, is too negative and too simple, but it will serve to be shot at and replaced by a better one. You notice that I do not mention the causes—genetical, cytological and ecological—which make a group critical; these are being fully covered by speakers in the main programme.

My second point is: what can we expect to get out of studying critical groups? The basic reason should, of course, be the same as that for carrying out any taxonomic work, namely to arrange individual organisms in the way that expresses most clearly and conveniently all the facts that we know about them. Why, then, study critical groups in particular? I think there are two reasons, a scientific and a psychological one. The scientific reason, namely that by such study we are able to learn a great deal about evolutionary methods (and especially the production of species and subspecies): I will not elaborate, but I would like to make the point that it is a mistake to regard the older, "static", type of purely morphological and distributional work as a waste of time. I think that even the most hardened "modern" taxonomist would agree that such work in the past has contributed an essential framework for his more dynamic researches.

The second reason is a more human one. There is a tremendous satisfaction in being an expert on something—whether that something is candlesticks, cigarette cards or eyebrights—and the study of a critical group gives this satisfaction to a very high degree. Further, in the process of becoming an expert, one has the pleasure of tackling a difficult job—the pleasure of the chase—the pleasure of a detective trying to solve an intricate mystery—pleasures by no means the least noble open to human enjoyment.

I hope, therefore, that this conference will confirm in your ways those of you who are hardened "critical groupers" and inspire others to tackle some of the many groups awaiting their attention. I need hardly add that the Society will endeavour to help you in any way that it can, by its publications, its field and other meetings and its panel of experts.

CYTOLOGY AND CRITICAL GROUPS

By E. F. WARBURG.

The President has already referred to the importance of modern methods in the taxonomy of higher plants. Of these methods, one of the most useful is cytology. The purpose of this talk is to give some introduction to the way in which cytology is used in taxonomy and in particular to critical groups, though some of the examples used will be taken from groups which are not ordinarily regarded as critical. I hope that this introduction will clear the ground for some of the speakers who are to follow. I should, however, emphasise that I have simplified (perhaps over-simplified) the subject as far as possible and that this talk is intended for those unacquainted with cytology and not for the professional botanist. I should like, also, to state that I speak as a taxonomist interested in cytology and not as a cytologist.

Cytology is literally the study of the cell, but it as come to mean more especially the study of the chromosomes. It is only in this sense that it has proved useful in taxonomy. It is closely linked with the kindred science of genetics and I shall, at times, have occasion to refer to the latter.

The chromosomes are the bearers of the hereditary characters or genes of an organism, and it is on this fact that their main importance depends. It has been shown that the genes are arranged in a linear series down the chromosome.

When a cell is at rest the chromosomes are very long and thread-like and are not, in general, individually distinguishable but appear to form a network inside the nucleus of the cell. When a cell divides (the process being known technically as 'mitosis'), the chromosomes become much wider and separate from each other. They arrange themselves on the equator of a spindle in the middle of the cell, divide longitudinally, one of the results of each longitudinal split passes to each end of the spindle and becomes included in one of the two daughter cells. During the process of mitosis the number of chromosomes present in the cell can be counted,

When reduction division (or meiosis), a process occurring during the formation of the pollen grains and embryo sac, takes place, the chromosomes instead of splitting arrange themselves in pairs on the spindle. In a normal (diploid) plant there is only one

chromosome which can pair with any other given chromosome. Pairing is intimate and during pairing an interchange of parts between chromosomes takes place so that there is a redistribution of genes within them. This leads to a recombination of characters in the progeny. Chromosomes capable of pairing with one another are known as 'homologous' and one member of each pair passes to each end of the spindle, becoming incorporated in the resulting pollen grain or megaspore. On sexual fusion taking place the chromosomes from the parent cells are incorporated in the resulting zygote without fusion so that the original number is restored.

Thus in a normal plant, if the chromosomes of the sexual cells are designated a, b, c, there will in the vegetative cells be 2a, 2b, 2c chromosomes, the two 'a' chromosomes being homologous (though probably not identical in their gene make-up). More conveniently the number in the sexual cells may be denoted by 'n' and that in the vegetative cells '2n'.

In any individual, therefore, the number of chromosomes in the vegetative cells is constant. In most cases, this is also true of a species, though in some species, strains with different chromosome numbers exist. This will become apparent later in the conference. As examples of the ways in which cytology can be used in taxonomy, the three following, which are perhaps the most important, may be given.

1. CHROMOSOME NUMBER

Though, as I have already stated, this is in general constant within a species, there is a considerable range of variation in the higher plants. Thus some species of *Crepis* have $2n = 6$ and, on the other hand, *Morus nigra* has $2n = 308$ and species of *Kalanchoë* about 500.

There are three main classes into which groups of allied plants may be divided when the relations of the chromosome numbers of the various members of a group to each other are considered.

- (a) Number constant throughout a comparatively large taxonomic unit e.g., *Ribes*, $2n = 16$; *Pinus* (and several allied genera), $2n = 24$. In such groups, cytological methods are generally of little use to taxonomists.
- (b) The numbers in a group of species are all multiples of the same 'basic' number (the basic number being denoted by x), and form a 'polyploid' series. The species with the lowest number, viz., $2x$, is called a diploid, $4x$ a tetraploid and so on. (It should be noted that confusion is possible between what are, in fact, two uses of the term 'diploid' (1) the number of chromosomes ($2n$) in the vegetative cells of a plant, whether $2n = 2x$ or $2n = 4x$ or any other number, as opposed to the haploid number, n , in the sexual cells, and (2) the number of chromosomes $2x$ as opposed to the tetraploid, etc., numbers $4x$, etc., in a polyploid

series. It is clear that in a 2x species the uses of the term 'diploid' are the same but that this is not true of the higher members of a series.) This multiple relation is perhaps the commonest type of relation met with and it is, on the whole, that in which difference in chromosome number is of most use to taxonomists. Some simple examples may be given. Each of the following three pairs of plants is regarded in our standard floras as constituting a single species, but in each case cytological researches have revealed or confirmed morphological differences between the two members of the pair. Professor Manton has shown that *Nasturtium officinale* consists of the diploid *N. officinale* ($2n = 32$) and the tetraploid *N. uniseriatum* ($2n = 64$) which may be distinguished from it by differences in the fruit and seed. Hagerup found that *Empetrum hermaphroditum* (which figures in the *Comital Flora*) is a tetraploid with $2n = 52$ and *E. nigrum* a diploid ($2n = 26$). In this country *E. hermaphroditum* appears to replace *E. nigrum* on the higher mountains. The third example (also due to Hagerup) is less known in this country. *Oxycoccus quadripetalus* is a tetraploid ($2n = 48$) with puberulous pedicels and leaves which start to taper to the apex from about the middle. *Oxycoccus microcarpus* (usually regarded by British botanists as a variety of *O. quadripetalus*) is a diploid ($2n = 24$) with glabrous pedicels and leaves tapering from near the base. It appears to be not infrequent in the Scottish Highlands.

In many critical genera the basic number is constant and the chromosome number is important as a character additional to morphological ones. Examples are: *Taraxacum* ($x = 8$, $2n = 16, 24, 32, 40, 48$), *Salix* ($x = 19$, $2n$ ranging from 38 to 152), where there is however one exception, a form of *S. triandra* having been found with $2n = 44$, and *Sorbus* ($x = 17$, $2n = 34, 51, 68$). The basic chromosome number (17) found in *Sorbus* appears to be constant throughout the subfamily *Pomoideae*. The subject of polyploidy will be returned to later.

- (c) The numbers of a group of species have no obvious simple relation to each other. As examples the following may be given: the genus *Carex*, the annual species of *Geranium* Sect. *Columbina* where *G. columbinum* has $2n = 18$, *G. dissectum* $2n = 22$ and *G. molle* and *G. rotundifolium* $2n = 26$, and the collective species *Erophila verna* where various numbers from $2n = 14$ to $2n = 64$ occur.

An interesting example where chromosome counts have helped to elucidate the relationships is in *Viola* Sect. *Melanium* where *V. arvensis* has $2n = 34$, *V. tricolor* (in the sense of the *Tricolores* of Drabble) $2n = 26$ and *V. lutea* $2n = 48$. *V. Curtisii* has the

same number as *V. tricolor* and should be subordinated to it and not to *V. lutea* as is done by Drabble. The perennial *V. saxatilis* also has $2n = 26$ and should be placed with *V. tricolor*. Several segregates of *V. arvensis* have also been examined by Fothergill and have been found to agree in chromosome number. In my opinion, these segregates should not be treated as species.

2. HYBRIDS

When two species hybridise, the diploid ($2n$) chromosome complement of the hybrid plant will be derived in part from each parent. If the chromosome numbers of the parents are different, it is clear that the complement of the hybrid will (except perhaps in very exceptional cases) consist of chromosomes not all of which are members of homologous pairs. This will mean that pairing at meiosis is incomplete. Even if the chromosome numbers are the same the chromosomes derived from the two parents will frequently not be homologous.

Non-homology of chromosomes leads to imperfect pollen and eggs and varying degrees of sterility and is the most important cause of the sterility of hybrids. The irregularity of meiosis can be seen by microscopical examination and the suspected hybridity thus often confirmed.

As an example of a completely sterile hybrid between two species with the same chromosome number and a small degree of morphological difference, that between *Veronica Anagallis-aquatica* and *V. aquatica* which was first noticed in this country by I. A. Williams, may be given. It has since been synthesised on the continent. The two plants must be regarded as distinct species.

It is now known that hybridisation plays an important part in the origin of new species and in particular in the formation of polyploids. The first example to be discovered was the garden plant *Primula kewensis*. A completely sterile hybrid between *P. floribunda* and *P. verticillata* produced a fertile branch. This bore seed and reproduced itself more or less true to type in the same manner as a wild species. On cytological examination of the progeny they were found to be tetraploid ($2n = 36$) whereas both the sterile hybrid and the two parents were diploid ($2n = 18$).

Since then a number of other species have been shown to have originated in a similar way, though the mechanism of doubling may differ. It may, for example, take place by the fusion of two gametes produced after failure of reduction division instead of by somatic doubling. Many further species are strongly suspected of having originated thus.

The following examples may be given as certain or reasonably so.

Galeopsis Tetrahit ($2n = 32$) has been synthesised from *G. speciosa* ($2n = 16$) and *G. pubescens* ($2n = 16$) by a series of hybridisations. This is the first example found of an already known wild species being made artificially.

Spartina Townsendii ($2n = 126$) arose spontaneously in Southampton Water following hybridisation between the native *S. stricta* ($2n = 56$) and the introduced American *S. alterniflora* ($2n = 70$).

Prunus domestica ($2n = 48$) almost certainly arose in the distant past by hybridisation between *P. spinosa* ($2n = 32$) and *P. cerasifera* ($2n = 16$). Among garden plants, not known wild, the pink horse-chestnut, *Aesculus carnea*, and the loganberry, *Rubus loganobaccus*, originated in a similar way.

It should be noted that in all these cases there are only two sets of completely homologous chromosomes, that pairing is normal and that the plants behave in every respect in the same way as many other wild polyploid species whose origin is unknown. From a taxonomic point of view, therefore, it may be emphasised that their names should be written without the hybrid sign (thus *Spartina Townsendii* and not \times *Spartina Townsendii*). Plants of this type (i.e. polyploids with only 2 sets of homologous chromosomes) are known as 'allopolyploids.' There is no doubt that this process of hybridisation followed by polyploidy has played a large part in the formation of species in many critical genera.

The second type of polyploidy—autopolyploidy—has no relation to hybridisation but arises (in the autotetraploid) by the doubling of chromosomes in a non-hybrid plant. The result is a plant with four sets of homologous chromosomes so that pairing is often irregular (as four chromosomes may try to pair) and fertility incomplete. Normally no morphological difference (except, frequently, size) is involved and it is often impossible to separate such plants except by microscopical examination, though they may have different habitats or geographical ranges. Usually an immediate sterility barrier is set up, as hybridisation between a diploid and its autotetraploid gives rise to an autotriploid with three sets of homologous chromosomes. Thus three chromosomes try to pair resulting in very irregular meiosis and usually in complete or almost complete sterility. It is uncertain how far autopolyploidy has been significant in species formation.

3. APOMIXIS

This phenomenon is widespread in flowering plants. It is the name given to reproduction by seed where the embryo is produced from a diploid cell of the female parent without either reduction division or fertilisation having occurred. In externals it, therefore, resembles normal sexual reproduction but in essentials vegetative reproduction, the female parent being reproduced exactly.

For some reason, incompletely understood, but presumably associated with irregular pairing, apomixis is much commoner in polyploids than in diploids (the same is true, also, of vivipary). It is particularly common in odd-numbered polyploids (triploids, pentaploids, etc.) which if they are to reproduce themselves effect-

ively at all, must do so apomictically (or vegetatively). If a triploid, for example, produces uniform progeny from seed it may be assumed to be an apomict.

The vast majority of 'species' in *Rubus*, *Hieracium*, *Alchemilla*, *Sorbus*, etc., are apomicts and this combined (at least in *Rubus*) with occasional sexual reproduction is the prime reason for the difficulty of classification in these genera.

Apomicts are often very restricted in geographical range. Thus in *Sorbus*, the diploid sexual species *S. Aria*, *S. Aucuparia* and *S. torminalis* are widespread but the triploid apomicts *S. minima* and *S. bristoliensis* are each restricted to a small area of carboniferous limestone. It may be remarked that it is not at present known whether such tetraploid species as *S. rupicola* are apomictic or not.

I hope I have made it clear that cytological investigation can contribute considerably to the elucidation of taxonomic difficulties though I am afraid it must be admitted that it sometimes makes two species grow where one grew before.

EXPERIMENTAL STUDIES ON BRITISH SPECIES

By W. B. TURRILL.

In considering some aspects of experimental methods in plant taxonomy, mainly with reference to British species, it is to be emphasized most strongly that no disparagement of other methods is intended. Historically, plant taxonomy is based on external morphology and the continued importance of accurate, full, and comparative descriptions of structure is obvious both for practical determination and for theories of classification. Further, it is fully acknowledged that plant distribution, anatomy, biochemistry, ecology, cytology, and even physiology in the narrower sense, have much to contribute to taxonomy. The synthetic attack, not only on "critical species" but on all taxonomic problems, can alone lead to stable solutions.

Nevertheless, experimental methods have certain advantages over observational methods. They also have certain disadvantages and dangers. Disadvantages include the often greater consumption of time—not only in total amount but in tying one down at definite periods—, the need for an experimental ground or grounds and laboratory accommodation, and the cost of apparatus and labour. These disadvantages can, however, be reduced to a minimum and excellent research be still carried out. The greatest danger in experimental research with organisms is in drawing conclusions from results obtained under artificial conditions and extending those results to what happens in nature without taking essential precautions and checking "against nature" at every stage. This danger exists even in the experiments to be discussed later but is

extreme in some experiments in the realm of pure physiology. The greater the degree of control, the greater is the artificiality of the conditions and the less reliable are the results as applied to what happens in nature. To isolate the action of one factor is an important experimental method. Factors, however, not only interact but their reactions are variously intensified, reduced, or deflected in a most complicated manner by changing even one condition.

The advantages of experimental taxonomy more than outweigh its disadvantages and risks. One studies the living plants, often as large families of known wild origin. The same plants can be interviewed more or less continuously all through their lives, at every season and at every stage of growth. Any reasonable number of herbarium sheets can be made for future comparisons or for distribution. Physiological characters, in the broadest sense, can be recorded. Correlations between form and behaviour can be worked out comparatively. The opportunity is given for well-planned team-work.

In experimental taxonomy as part of a synthetic scheme one "gets inside" the species (or other taxonomic unit) instead of viewing it as a bundle of specimens to be pigeon-holed after determination. The species becomes a population of living, changing, fighting, winning, losing, reproducing, and dying individuals. Consideration of the relationship between the characters of an individual and the characters of other individuals leads to concepts of individual and population characters. The population is found to be dynamic, enlarging, increasing in complexity, or becoming reduced, decreasing in complexity—at any rate, fluctuating or changing, sometimes segregating, sometimes amalgamating, at least locally, with other populations. It is, by the way, advisable to define very precisely the term "population" in any piece of research. In working experimentally with living plants one soon realizes the importance of physiological characters in the broad sense and often one wishes that physiologists would take up some of the problems the experimental taxonomist has to leave on one side. What would appear to be a particularly open field for investigation is the death of plants in the wild and in culture, treated not merely statistically but also causally. Another is flowering and fruiting investigated not by extensive phenological statistics, of which there are most serious criticisms to be made, but intensively and by experiments. It is suggested that these are among the subjects about which we are very ignorant but which probably have taxonomic and evolutionary significance.

Two practical points are interpolated here. All so-called "negative results" should be recorded and published. For example, that two species cannot be crossed, even reciprocally, may be a negative fact but may also be of considerable taxonomic and cytogenetical importance, apart from immediately raising questions as to how the non-fertility is caused. Secondly, mutations should be saved and perpetuated, not so much because they are interesting

in themselves as that by using them in experiments they may throw light on the more usual structures and functions. The normal can often only be understood by contrast with the abnormal. In genetics one must have allelomorphs for analysis of genoms. In simpler terms, to study the heritable make-up involved in the production of characters one must have opposite characters also. The genetical cause of many-flowered inflorescences or many-fruited infructescences in *Solanum Dulcamara* could only be investigated when a variant with one-flowered inflorescences was discovered, found to breed true for this character, and then crossed with the common variant.

Let us turn now to actual experimental methods as illustrated by examples. A rough but practical classification of methods will serve to prevent undue lingering if the ground is to be covered in outline.

1. SIMPLE CULTURAL TRIALS.

No taxonomist should be without an area of ground on which he can grow series of plants under his own immediate and constant supervision. It may not be practical politics to study, say, the British elms by this method but all terrestrial herbs and many shrubs present no great difficulties. The one great rule is: "Take the utmost care with labels, entries, and scoring".

Two kinds of experiments come under this heading. First, growing numerous stocks near together, for ease in comparative scoring, under conditions as uniform as possible. This often, though not always, enables one to suggest that two stocks which in the field looked different are only phenotypes of one genotype, or, conversely, gives a strong suggestion that they are different genotypes. The evidence may be so definite as to amount to reasonable proof. Several stocks of *Scilla non-scripta* var. *bracteata* have retained for eight years the character of long bracts often overtopping the inflorescence and vegetative propagules show the same character. Certain dwarfed forms of *Plantago Coronopus*, on the other hand, quickly grew to normal-sized individuals.

Secondly, there is the test of inheritance: that a given character reappears, or fails to reappear, in offspring produced from seed. A great many botanists, including Linnaeus, have acknowledged the taxonomic importance of such a test. It is, of course, understandable, with our present knowledge of genetics, that a negative result is not conclusive unless the seed be pure bred, since a recessive gene will not express itself phenotypically in the presence of a dominant gene. However, quite impressive results are sometimes obtained. *Cytisus scoparius* var. *prostratus* and *C. scoparius* var. *genuinus* both come true in their differential characters from seed. A remarkable large and broad- and thick-leaved variant of *Plantago Coronopus* from Skokholm and Grassholm, originally sent to Kew by Dr. Julian Huxley, not only retained its characters under cultivation, as did also wild seedlings grown to the adult stage,

but the next generation plants have also the distinctive features. My colleague, Mr. Milne-Redhead, discovered a large-headed *Lapsana* in Bedfordshire which retained its marked characters, including perennial habit and late diurnal closing of the capitula, under cultivation and they reappeared *in toto* in the next generation from seed. The pale-flowered variant of *Lapsana communis* from Wiltshire also "comes true from seed."

2. TRANSPLANTS GROWN UNDER A RANGE OF ENVIRONMENTS.

Experiments designed to test plasticity under a range of known, and sometimes artificially controlled, conditions are naturally more costly than simple cultural experiments, but they open up an enormous and important field of research. One can conveniently classify the environmental factors as climatic, edaphic, or biotic in so far as they can be disentangled. The first are very complicated and have been little studied by transplant methods in this country. Biotic factors are probably in many ways the most interesting, and their experimental investigation may be recommended to our younger naturalist members. The most intensive transplant experiments with British plants are those of the British Ecological Society's Transplant Experiments at Potterne, Wiltshire. Reference to the series of reports published in the *Journal of Ecology* 1930-45 must be made for details. Here only an outline of the methods employed with a very few of the results can be given. The experiments were carefully planned and standardized to give information on the reaction of a dozen species and paramorphs of wild British plants to different "soils": sand, calcareous sand, clay, chalky clay, Potterne Upper Greensand soil, and Kew garden soil (the last at Kew under a somewhat different climate). It was found that every species reacted differently from every other, though a classification of reactions is possible if any class be diagnosed by a certain range of conditions. *Centaurea nemoralis* survived well on all soils, showed no marked morphological changes on any, but did best on sand, the poorest of the soils to all other species and, as one would judge, from the chemical analysis. As a contrast, two different variants of *Plantago major* showed the greatest and most rapid changes. In less than two years phenotypes were produced from ramets of a single clone, which agree with the descriptions of supposed distinct varieties and subspecies of *P. major* in Pilger's 1922 monograph of the species (Pilger in Fedde, *Repert.* 18, 257 : 1922). On the other hand, with pairs of congeners : *Silene Cucubalus* and *Silene maritima*, and *Phleum pratense* and *Phleum nodosum*, there was no approximation, on any soil, of one species to the diagnostic characters of the other. *Phleum* showed slow cumulative changes, largely parallel in the two species, on different soils, not the rapid reactions shown by *Plantago major*. Many of the species showed differential death-rates, varied behaviour of seedlings, and some more or less significant variations in flowering and fruiting times on the different soils.

Enough has, perhaps, been said to indicate the taxonomic as well as the ecological importance of such closely controlled transplanting. It is to be regretted that they had to be discontinued at the end of 1940.

3. THE STUDY OF APOMICTS.

Experience has suggested that, in some groups, plasticity increases, probably within limits, with increase in heterozygosity. This may be due simply to a heterozygote having a greater number of genes than a homozygote of the same group. However this may be, many apomicts are certainly or probably hybrids and many are very plastic. Hence, in the study of apomictic groups, experimental methods are essential for sound results. Our British *Taraxaca*, so far as at present tested and examined, are all apomictic and triploid ($3n = 24$). Sexually reproducing dandelions are known and two (one from Japan and one from Russia) have been grown at Kew. If any member finds such in the British flora please send it to Kew for cultivation and study in the Herbarium Experimental Ground. It should have good anthers with plenty of well-formed and no shrunken pollen-grains and should fail to set seed after semi-decapitation.

While *Taraxacum* plants are extremely plastic, and this alone makes their proper detailed taxonomic study impossible from wild collected material alone without experimental testing, even more striking is the behaviour of different stocks when grown in rows side-by-side in an environment as nearly uniform as possible on an experimental ground scale. The rule at Kew has been "one head to one row" in the experimental plots, with castration and fruit setting carried out in an insect proof greenhouse. Differences can be detected from row to row and the greatest possible similarity, with very few exceptions, is seen within the rows, as soon as growth starts in the spring, throughout the spring, summer, and autumn, and even in the winter. The differences between stocks are more obvious than easy to describe precisely. How far names should be given to the different biotypes and even to the proved apomicts is controversial. That there are numerous different biotypes and, that these, except for rare mutations, breed true is beyond doubt. Moreover, some of these biotypes have different geographical ranges and some are edaphic ecotypes.

It is worth while here to call attention to the need for a taxonomic revaluation of the contents of some apomictic groups by a reference to Turesson's recently published account of "Variation in the apomictic microspecies of *Alchemilla vulgaris* L." (*Bot. Not.* 1943, 413-427). In most of the microspecies studied as clones and from seeds a remarkable genetic variation was revealed. The so-called microspecies were genetically heterogeneous and built up of a number of apomicts which themselves showed no segregation from seed.

Lastly, under this heading, attention may be called to the partially or casually apomictic species. These may be very numerous. Marsden-Jones and Turrill found rather less than 1% apomixis in a stock of *Ranunculus acris* they were using for breeding purposes. It was impossible to interpret the results obtained till apomixis gave the clue. Apomixis is more frequent, so far as is known, in *R. Ficaria*. The warning is necessary that taxonomic uniformity in a family grown from seeds does not necessarily indicate homozygosity.

4. GENETICAL EXPERIMENTS.

Time will not allow details to be given of experiments which are throwing much light on the constitution of some British species. Two groups of experiments are desirable and can be carried on concurrently: by selfing and crossing to investigate the genetic make-up of British stocks and by crossing with exotic stocks to trace relationships of the British plants to as many as possible of other stocks within the range of the species or other group. Probably the best example is the work on bladder champions published in the *Kew Bulletin* from 1928 onwards. Rather more than half the researches have now appeared in print in 26 papers. Four more have been sent to press and others are in various stages of preparation. The comprehensive programme outlined in the first paper is nearing completion and the general picture is already clearly outlined for British plants. The equivalent of about 20 pairs of characters have been investigated genetically and to a considerable extent in wild populations from many localities in both *Silene Cucubalus* and *S. maritima*. Some hundreds of families have been raised from crossings and selfings and thousands of plants have been scored for all the characters studied. Conclusions regarding taxonomy and nomenclature will only be attempted when the working out of the experimental results is complete. Meantime the *alpha* taxonomy is used with devices to avoid complicating the nomenclature any further.

Work on the British knapweeds has been almost as extensive except that foreign stocks have not been used and it is hoped to publish the bulk of the results together. Other breeding work at Potterne and Kew has been with *Anthyllis*, *Geum*, *Saxifraga*, *Ranunculus*, *Primula*, and *Anagallis*.

Very briefly to sum up the broad generalizations of such researches it may be said:

- (1) The experiments have revealed an hitherto unsuspected range of genetic variations in common species—variations not or inadequately described in floras.
- (2) They have proved how very differently different species are constituted in relation to their ranges and their local environments.

- (3) They have thrown light on the relationships of species one to another.
- (4) They have given valuable information on the causes of speciation which are much more diverse than is sometimes suggested.
- (5) They have shown some of the possibilities of evolution through mutation, through hybridization, and through polyploidy, and, on the other hand, some of the limitations of these causes of variation as evolutionary mechanisms.
- (6) They have furnished examples of natural selection and of what happens in its absence.
- (7) They are enabling more and more complete descriptions of the structure and behaviour of the species to be prepared as populations of living organisms.
- (8) Most important of all, the researches are stimulating other, younger botanists to carry out synthetic investigations with a systematic bias in various genera and are thus playing a part in the rejuvenation of taxonomy.

As a last example of recent work of a synthetic type the attention of British botanists may be called to Winge's researches on *Erophila*. Jordan (1873 : *Congr. Assoc. franç. Avanc. des Sci.*, Lyon), stated that he grew about 200 species of *Erophila* every year from seed. Winge (1940 : *Compt. Rend. Trav. Lab. Carlsberg*, 23, No. 3, 41-78) divides *E. verna* into four species on the basis of his experimental and cytological studies. There is no doubt of the interest of Winge's researches though one could have wished that much more British material had been investigated. The contrast between Jordan and Winge is here used to illustrate the fact that modern synthetic investigations can lead to a considerable reduction in the number of accepted species, to suggest that British botanists might check and add to Winge's results, and to urge that critical consideration be given to the theoretical basis of the taxonomic and nomenclatural conclusions reached by him.

In conclusion, it is repeated that experimental methods in taxonomy must be used in addition to the older methods of observation and comparison and of herbarium techniques, not to replace them, and in collaboration not in competition with ecology and cytology. The British flora is now relatively well-known in its broad taxonomic outline and the time has come to deepen our factual knowledge of intra-specific structure and behaviour. Expansion of the scope of our subject by the introduction of experimental and other methods and techniques must stimulate all of us and will encourage many young students with a modern training either to become taxonomists or so to direct their researches that they provide us with reliable needed data. At the present time the future of systematic botany is brighter than it has been for decades. It is your duty and privilege to turn optimism into such sound scientific results that taxonomy regains and retains its rightful position as the focus of all branches of botany.

ECOLOGY AND CRITICAL GROUPS

By A. R. CLAPHAM.

Critical groups I take to be those in which the distinction between species is difficult, either because the differences, though constant, are difficult to observe ; or because ranges of variation overlap considerably ; or because there are at least some populations in which there is more or less continuous gradation between the extremes, so that no dividing lines can be drawn.

I propose in this hurriedly prepared and sketchy talk to consider the ecological relations of the constituents of such critical groups. If the groups in question really consist of two or more separable species they must be isolated in some sense ; for I take it that the two ideas of specific distinctness and isolation are closely connected, in the sense at least that distinctions of a kind a taxonomist would call specific cannot be maintained without barriers to free interbreeding. What then I wish to ask is first, " Are the constituents of such critical groups ecologically differentiated ? ", and, secondly, " If there is ecological differentiation does it constitute the effective mode of isolation ? " I am supposing that *ecologically differentiated* means something different from *having different geographical ranges*. The distinction is, of course, not a clear one, but it is useful nevertheless. For examples we may turn to the native dactyloorchids : *Orchis purpurella*, *O. occidentalis* and *O. praetermissa* are geographically differentiated, but *O. Fuchsii* and *O. ericetorum* are ecologically differentiated, the former occurring on base-rich peat and mineral soil, the latter on acid peat and raw humus, often within the same small area and occasionally intermingled.

In the British Isles certain kinds of habitat are confined to certain parts of the country, for reasons of topography and geology. When this is so the distinction between ecological and geographical differentiation becomes difficult. But broadly speaking geographical differentiation arises from climatic and historical causes (e.g., *Primula scotica* and *P. farinosa*) ; ecological differentiation refers to habitat differences within the same climatic area, and it is to the latter that I shall attempt to confine myself.

There are many familiar examples of ecological differentiation of related species in critical groups. Sir Edward Salisbury gave some in his paper " Ecological Aspects of Plant Taxonomy " in *The New Systematics*, published in 1940. He instanced amongst others the series of *Salicornia* species found in the different zones of a salt-marsh, *S. herbacea* (on mud) or *S. ramosissima* (on sand) in the lowest zone being replaced by *S. gracillima* and *S. disarticulata* at successively higher levels, and the series of *Limonium* species, with *L. humile* succeeded by *L. vulgare* and then by *L. vulgare* var. *pyramidale*.

Many other examples come readily to mind. During the past summer I examined some sand dunes and salt marshes on the west coast of Anglesey and was interested to see the ecological differentiation of three species of *Centaureum*: *C. pulchellum* was confined to the drier parts of the sandy salt marshes, in the zones dominated by *Armeria*, *Juncus maritimus* and *Festuca arenaria*; *C. littorale* was in dune slacks, and *C. umbellatum* on the drier dune sand.

The two wood violets, *V. Riviniana* and *V. Reichenbachiana*, are more or less differentiated ecologically, and so are the marsh bedstraws, *Galium palustre* agg. and *G. uliginosum*, the constituents of the *Glyceria fluitans* aggregate, the Water Crowfoots, the annual species of *Sagina*, etc.

Mention of *Sagina* draws attention to one of the difficulties confronting the taxonomist studying ecological differentiation. Many plants, and not least the species of *Sagina*, are very plastic in the sense of assuming very different habits and statures in different environments. It may not be possible to determine with certainty whether two specimens do or do not belong to the same species in a critical group until they have been grown side by side in various habitats. We still do not know whether *Sagina Reuteri* is really worthy of specific distinction from *S. ciliata*. That it resembles *S. ciliata* very closely when grown side by side with it in a good garden soil does not give the whole of the evidence required. We need also to know that *S. ciliata* resembles it closely when grown in its normal habitat, or, more precisely, that they are indistinguishable in all habitats. The same kind of gap in the evidence persists in *Plantago Coronopus* var. *pygmaea**. And when the necessary evidence from growing together in different habitats has become available, we need still to know whether the observed differences justify specific distinction—but that is a matter we are not concerned with at the moment.

We find then, many examples of ecological differentiation in the sense that closely related species show ecological differences, more or less clear-cut, which emphasize the distinctions based on morphological and perhaps phenological characters. It should be noted in passing that these ecological differences are not to be used as primary diagnostic characters. We cannot yet define similarities and differences in habitats, from the standpoint of the plant, in any precise way, and indeed we are often left with the unsatisfactory alternative of defining the habitat in terms of the plants growing in it. And to say in effect, as often is said, that *Orchis Fuchsii* and *O. ericetorum* grow respectively in *O. Fuchsii* and *O. ericetorum* habitats is not to add appreciably to the precision of a diagnosis.

But there is no denying that closely related species often do grow in different habitats within the same climatic area. When they do so, however, it is often found that there is also some dif-

* But see Dr. Turrill's article, p. 16.

ference in chromosome number between the ecologically differentiated species. *Orchis Fuchsii* and *O. ericetorum*, *Viola Riviniana* and *V. Reichenbachiana*, *Oxycoccus quadripetalus* and *O. microcarpus*, *Empetrum nigrum* and *E. hermaphroditum*, *Juncus articulatus* and *J. acutiflorus*, *Galium palustre* and *G. uliginosum*, all show this cytological differentiation. In other words we find that ecological differentiation is not the only isolating factor. From a casual consideration of these examples, without knowledge of chromosome numbers, we might suppose that ecological specialization of two or more parts of a once single species has led to morphological and genetical isolation and so to ecological speciation, the separate units becoming more or less cut off from intercrossing. But a moment's reflection will show how improbable this must be. Generally speaking ecological differentiation cannot be sufficiently complete to allow of the development of specific distinctions. Where a single widespread and abundant species shows some ecological differentiation it is usually of the kind found in *Juncus articulatus*, where the various eco-varieties, clearly distinct in the centres of their range, grade in the intermediate and bounding habitats, and can certainly not be treated as separate species or even subspecies. But differences in chromosome number constitute an isolating mechanism sufficiently powerful to permit full specific distinctions to develop. During their evolution there is likely to be an intensification of any initial ecological differentiation through the selective effect of competition.

When cytological differences are lacking between closely related species which show ecological but not geographical differentiation there is often a strong presumptive probability that the original distinctions arose as a result of geographical isolation. When such species are brought together through climatic, topographic or man-made changes, they may or may not be found to be sufficiently isolated physiologically, phenologically or morphologically to enable them to maintain their distinctness. *Galium palustre* and *G. debile* have apparently acquired an isolating mechanism; but *Silene maritima* and *S. Cucubalus* have not, though they hybridize sufficiently infrequently, because of their rather distinct habitats, to remain effectively separated species. *Geum urbanum* and *G. rivale* are in much the same condition, though hybrid populations are more extensive than in *Silene*. *Crataegus monogyna* and *C. oxyacanthoides*, about which we heard in an interesting paper at the last meeting of the British Ecological Society, form a still more extensive series of hybrid types and help us to understand how deforestation and the bringing together of species formerly isolated has led to the recent development in North America of a most difficult complex of hawthorns. It should be noted in passing that in days before man had made much impression on the natural vegetation of north-west Europe, when plant communities covered great unbroken areas, ecological and geographical differentiation may have been much more nearly synonymous than they are to-day.

A more puzzling situation is found in the genera *Sagina* and *Cerastium*, several of whose annual species may be found growing side-by-side although their chromosome numbers are identical. There is some ecological differentiation (e.g., *S. maritima* and *C. tetrandrum*) but I think the specific differences have probably arisen through past geographical isolation and have been maintained because of prevalent self-pollination. The species of the *Euphrasia officinalis* aggregate may preserve their identity in the same way. Some of the species are clearly products of geographical isolation, but there are others living in the same geographical area and showing incomplete ecological isolation. Their chromosome numbers appear to be the same, though more work must be done on them, and the maintenance of specific distinctions seems likely again to arise from the prevalence of self-pollination.

I have said nothing so far about the really difficult genera: *Rubus*, *Rosa*, *Taraxacum*, *Hieracium*. I know none of these genera intimately, but from the standpoint of ecological relations three features are conspicuous. First, many species, often very closely related, may be found growing side-by-side in the same meadow, neglected pasture or wood-margin, the same limestone scar or tract of riverside boulders. In other words ecological differentiation is conspicuously lacking. This may be a temporary phenomenon, characteristic of a successional phase when competition is ineffective, but it is none the less striking that these closely related forms do grow side-by-side without breakdown of the distinctions between them.

Secondly, however, many closely related forms show different geographical ranges, although their ecological requirements appear to be similar. Thus hawkweeds of the section *Cerinthoidea* Pugsl. may grow together as do *H. anglicum* and *H. iricum* in Upper Teesdale, or may be geographically vicarious, like the Hebridean endemics, related to *H. anglicum*, described by Pugsley. There are dozens of these strictly local hawkweeds, as there are also of dandelions and brambles.

Thirdly, the main sections of these critical genera tend to be geographically though often also ecologically differentiated.

Now these highly critical genera are all of complex cytogenetic behaviour and all at least facultatively apomictic. The present bewildering taxonomic situation must be in part a consequence of recent changes in climate and vegetation which have disrupted once continuous distributions and have later brought together species formerly isolated with resultant hybridization, polyploidy and apomixis. Isolation was originally geographical, but the acquisition of the apomictic habit in plants of open habitats with little inter-specific competition has resulted in minimal ecological differentiation.

We have found then that ecological differentiation between closely related species is a frequent but certainly not an invariable feature of critical groups. When such differentiation is lacking the

operative isolating factors are commonly differences in chromosome number, the prevalence of self-pollination, or apomixis. But even where ecological differentiation is found it is rarely the effective isolating factor, there being usually cytological differences as well. And when ecological isolation is effective (as in *Silene maritima* and *S. Cucubalus*), there are commonly good reasons for believing that the specific distinction arose originally from geographical isolation.

This was discussed by Dr. Baker, Dr. Valentine, and Mr. Wilmott.

MR. WILMOTT mentioned that ecological relationships of species could be obscured by bad systematics: the *Salicornias* mentioned, e.g., *S. ramosissima*, were in his opinion not always the same species. He also noted that *Limonium humile* was not always in the low zones of salt marshes, in which he had seen it at Scolt Head. The last time he met it he found it growing in some abundance in a high zone (above the *Spartina*) about high-water-mark below the bank at North Hayling.

DR. CLAPHAM said he had never seen *Limonium humile* in such a habitat.

DR. BAKER considered that *Limonium vulgare* var. *pyramidale* was probably only a habitat form, although *L. humile* was a distinct and not closely related species.

DR. CLAPHAM agreed that this might be so.

DR. VALENTINE suggested that the ecological differences shown by subspecies might indicate that ecological conditions could act as a stimulus to evolutionary development.

DR. CLAPHAM replied that the ecotypes of *Juncus articulatus* are good examples of the incomplete separation brought about by mere habitat differences. Such a situation might conceivably lead to specific fission, but probably only if climatic and other changes first converted ecological into geographical differentiation.

MR. WILMOTT mentioned that Prof. Thoday had long ago told him that in South Africa species (of *Passerina*) seemed to have differentiated along ecological rather than geographical lines.

INTRASPECIFIC CATEGORIES OF VARIATION

By A. J. WILMOTT.

Critical groups are those in which the variation is so complicated that the relations between varying individuals can only be understood after long and critical study, which may involve experiment. Individuals vary, and the question soon arises: Do these individuals belong to one group or more than one, and if more than one, how many, and what are their *differentiae*, i.e., constant characteristics, by which they can be distinguished?

We know that in man individuals are all different: it is rare to find oneself mistaken for anybody else, and such mistakes are never made by those who have critical knowledge, i.e., one's friends, or perhaps one's enemies. I once recognised a Chinaman I had met some half-dozen times in my father's house by half of the back of his head seen in a corridor of a train near Magdeburg. At first I distrusted my senses, but surely enough I found him in the next coach and travelled back to Cambridge with him. The shepherd is said to know his sheep individually. I do not suppose that any botanist ever claimed to recognise many individuals of any species, but there is no doubt that it is possible to recognise *some* of the individuals, so it may be possible that even in plants individuals are all different.

But individual differences do not justify the separation of *groups*. We do not group men (women included) by the colour of their eyes, or hair, or any other obvious differences. It is only when a lot of differences are correlated—or go together—that we recognise different groups—Bushmen, Japanese, Negroes, and others normally distinguished as “races”. This should be remembered by British botanists who are given to naming as varieties individuals differing only in one or two characters, just as if we should group together men with blue eyes and knobbly knees, or even moustaches. Variations of this nature are not worthy of distinction by name, and a large number of the varieties in the British Plant List need to be struck out as being of this kind. They are worthy of investigation in the study of variation in general, but not in the systematic study of groups, which is the province of systematics, except insofar as may be required to determine whether correlation of characters exists or not.

It is only when characters are correlated that *natural* groups, as apart from those invented by man which are mere artefacts, exist and are worthy of separate names as systematic units. Even so, some correlation can exist in single groups. It may be that there is genetic linkage of characters, which arises from genes being in some way connected in the chromosomes. I put it in this way because I do not think that the real nature of such linkages is yet known. Why some parts of chromosomes should behave as units and not permit normal segregation during meiosis can at present

only be guessed at, I believe, but such linkages do produce certain correlations of characters within single groups, and this kind of correlation needs to be distinguished from that which occurs in the characters of Bushmen, Japanese, Negroes, etc., until it is proven, should it ever be, that it does play its part in the production of such races. And how are we to distinguish the correlation which justifies the separation of a natural group ?

The real test of the existence of a distinct natural group is its possession of a *distribution* different from that of other allied groups. It is not sufficiently realised—is indeed often quite unrealised—that natural groups are primarily distinguished not by their differentiae, i.e., “characters”, but by the *distribution* of the characters. Systematists talk of “good characters” and “bad characters”,—the latter indeed the “bad characters” of systematics, doing much mischief—without thinking what they mean by a “bad” character. What they mean is that the character in question does not have the same *distribution* as that of the “good” characters, but occurs indiscriminately among the individuals of allied groups—groups recognisable because they *have* distinct distributions, geographical or ecological. The “good” characters are those which are correlated with the different distributions, the “bad” are not, and it is the *distribution* test that is fundamental, not the characters selected as *agreeing* with the distinct distributions. I believe that we may truly say that *specific difference is that in which we find correlation of characters coupled with distinct distributions*. It is probable that these distinct distributions are due to the real distinctness of the groups which, being distinct, have had different histories since their origins, whatever these may have been, and have acquired their different distributions during their different histories. This is the natural interpretation. Indeed, I would go further and say that all intellectual studies of man are studies of the *distribution* of phenomena in space and time: if phenomena have distinct distributions, there is something to be recognised and named, whereas if they occur indiscriminately, there is only the indiscriminate nature of the distribution to be studied. I emphasise this fundamental position of distribution because it is not generally realised in systematics.

But we do not in these days call all the really different groups “species”. In early days the term species included such things as mere white-flowered variations, but although the concept of species has been much developed there is still no agreement as to what the term should mean. It certainly means groups differing in accordance with my definition of specific difference, but there are many different kinds of groups which thus agree, and the only factual definition to-day of the term is that it is a group which has a “binary”, “binominal”, or what I prefer to call “biverbal”, scientific name, i.e. a generic name plus a specific epithet. Some give these names to big groups, some to small, which causes much

trouble and argument. (Even yesterday, one speaker thought that one kind of group was a species and another thought not.)

Discussions of this problem are always complicated by diverse usages of the word species, some using it in the nomenclatural sense and others for various sized natural groups. I find it impossible to produce a clear discussion and use the same word with different meanings, and I therefore propose here to use the term species for the natural groups, and to use a completely different term for the nomenclatural taxonomic species. Both uses are unfortunately so completely ingrained that the rejection of either is sure to produce some demur, but it cannot be helped if we are to get clear thinking. So the word *biverbum*—a thing with two words—will be used for the nomenclatural species, with *triverbum* for what are variously called subspecies and races. Admittedly, in botanical nomenclature we insert a fourth word—subspecies, variety, or something else—between the second and third words, but in zoology this is not done, so *triverbum* may be permitted. And we are now free to consider whether the supraspecies, ordinary species, or microspecies, shall be a *biverbum*, and whether a microspecies, race, or variety, shall be a *triverbum*. I hope this may produce a little more transparency in a very opaque subject. What is required is to determine what actual kinds of natural group exist, and then to decide which kind shall be given biverbal names, for, as I have already said, groups of various kinds and sizes are specific in their nature.

What kinds of groups, therefore, *can* we recognise smaller than the biggest groups that are sometimes called species? That is, what intraspecific groups exist and what terms shall we use to indicate the different kinds? A very large number of terms have been proposed for different kinds of variation and the Systematics Association is at present interested in their definition and codification. It is of fundamental importance in the study of critical groups, because until a terminology and form of nomenclature is devised which will indicate definitely the nature of a named group, the study cannot progress satisfactorily. One man's species is another's subspecies or variety, another's variety is someone else's subvariety or forma, and so on. And what, we may ask, is a microgène, a paramorph, an ecad, an ecotype, a cytovar., and so on through a long series of terms? We *must* start by trying to discriminate how many kinds of variation we can find in Nature, and then try to agree on some means of indicating each kind. The second task would then be to agree on how the real groups should be named.

The simplest kind of variation is that which is a mere response of changes in the conditions of life. *Sparganium simplex* reaches typical development on river banks or in ditches; *Sagittaria sagittifolia* does it in still or very slowly moving water. But in the slowly flowing water of the river Cam at Cambridge both may be found in midstream, unflowering and with very long ribbon-shaped leaves,

those of the *Sparganium* floating on the surface, those of the *Sagittaria*, which are somewhat broader, keeping just below the surface. If the roots producing such plants were removed to normal habitats they would produce typical flowering plants. The so-called "var. *longissimum*" of *Sparganium simplex* is a mere product of the environment and not a natural group at all. This kind of variation was called a *forma* by Moss, as opposed to a variety which he restricted to variation dependent on genetic differences. It is the ecad of Clements, the modificatio, somation, ecophen, morpha, topomorph, paravariation, of various other systematists, with equivalent translated terms in other languages. Personally I doubt if these should be given names at all: I prefer to denote them by elisory phrases indicating the conditions which produce them, e.g., "forma in fluviatilibus", i.e., locis fluviatilibus,—or "forma in currentibus" i.e., aquis currentibus, the verb collecta, reperta, crescens, or what you will, being omitted. Similarly *Plantago Coronopus* var. *pygmaea* Lange would be *Plantago Coronopus* forma in arenosis siccis. It may be objected that we so often lack the experimental evidence that a variation is such a forma, and this is true. I therefore prefer to keep the term *varietas* for variation of unknown nature, to be replaced by some definite term when from scientific evidence we know the nature of the variation. If we use the term *varietas* in any other sense we shall be forced to coin a new—and obviously less appropriate—term for use in this sense. Indeed, "paramorph" has been proposed, but it must be emphasised that such terms are too lightly coined by those who are not systematists, who do not seem to appreciate that terms should be in latin if they are to be suitable for use in systematics, and paramorph is not suitable. The term *varietas* has been used with so many diverse connotations that it is now not really suitable for use in one restricted sense, and it is so obviously the right term merely to connote variation—of unknown unspecified nature.

There are other kinds of variation which are not based on constitutional, i.e., genetic, differences. Some stages of individual development in insects—instars, the forms of the insect between each moult—have been described as different species before their real relations were discovered, and this was natural where such stages were able to reproduce themselves before undergoing further development, a phenomenon known as paedogenesis. Something similar to this occurs in lower plants in which the sporophyte of a species can reproduce itself asexually before producing the different-looking gametophyte. But such stages are not distinct groups requiring distinct names, any more than the group "baby" requires a name different from that of "man". Their existence complicates systematic study, that is all; there are no different-distributions corresponding with such characters.

Other kinds of asexual reproduction also complicate systematic study. In *Mentha*, *Salix*, and other genera, fragments of one

individual may be broken off and start life as a new plant. Fragments of a stream-side *Salix* hybrid, or of a *Potamogeton* hybrid, can be carried down stream, take root and grow, become distributed over a considerable area and look like a species. Such fragments of a single individual are together known as a clone, each fragment a "ramet", but together they make the "major individual" of Pallas. Very similar may be the result of grafting. All Victoria Plums are the result of grafting from a single original plant, but the results are so widespread and of such interest to man that he does, in this and other similar cases, find it desirable to name as a group, albeit an artificial one, all fragments of a single kind, and according to the International Rules of Botanical Nomenclature the name is *Prunus domestica* var. *Victoria*. It is not, however, a varietas, but a major individual, and a special term is required. Again, "clone" is not suitable, not being suited to the latin required in nomenclature. Further, the greek κλων means a branch, twig, or slip, and really corresponds to the term ramet, not to the major individual. The required term should indicate that the name applies to a single individual, albeit much subdivided, or that the group is a mere asexual multiplication. The best latin word I can find which would make a suitable term is *divisum*, a something divided. If clone is latinised to *clonus*, its abbreviation would be confused with that of *cline*, to which we come later, but it may be that *clonus* will be preferred to *divisum**

Another kind of asexual multiplication occurs when organisms reproduce themselves apogamously or parthenogenetically, the two phenomena being together termed apomictic, i.e., resulting from apomixis, meaning "without fertilisation". Apomicts occur in insects and are widespread in such plant genera as *Hieracium*, *Taraxacum*, *Alchemilla*, and others, forming some of the most critical of systematic groups. In this, as explained yesterday, the cytological reduction division which normally precedes fertilisation is omitted, and one of the unreduced somatic cells divides as if it were a fertilised egg-cell to produce a structure just like what would have been formed from a fertilised egg. This is therefore a form of asexual reproduction except for the fact that the bud produces a structure just like a fruit. The products form a sort of major individual, but because of the greater powers of dispersal afforded by these asexual fruits, the pseudo-individual can acquire a distribution of exactly the same kind as that of species or subspecies. Since there is correlation of differentiae spread throughout the plant, coupled with a distinct distribution, they have to be treated as one of the kinds of species, and are the agamospecies of Turesson.

The majority of natural groups are, however, formed as a result of isolation of one part of a group from the rest of it. At first the isolated parts would be interfertile, capable of inter-

* As *divisio* (a part of a *divisum*) is already in use for one of the major groups, *confractum* (each part a *fragmentum*) is substituted.—A.J.W.

breeding if they were able to meet. The sum of such potentially interbreeding individuals has been called a syngameon by Lotsy, and a commiscuum by Danser, but the significance of these terms is philosophical rather than systematic: they are theoretical groups rather than actual ones.

Distributions are never really continuous, for each species has its own ecological requirements, and the various fragments of each species are to a greater or less extent isolated, forming local populations, which Gilmour has termed topodemes. The variation shown by these topodemes will depend partly on the genetic constitution of the individuals which originally invaded the area, and partly on any natural selection due to the environment. Such fragments of species will not become distinct natural groups so long as they are within the dispersal areas of neighbouring topodemes. But major earth changes, such as glacial periods or other enduring changes, force species to migrate or to survive *in situ*. Turesson has found that many isolated populations presumed to have survived as relicts of a former widespread distribution, show slight differences which remain constant in cultivation. Such relict or otherwise ecologically produced topodemes he calls ecotypes. Although it is possible that the original populations were slightly different *ab initio*, it is more probable that the differences in relicts are, at least in part, due to natural selection, which would eliminate all genetic differences antagonistic to the chances of survival, with the production of a group specially suited to the particular environment. When—or if—conditions later returned to something like what they were originally, such ecotypes might well lack the normal variation of the species as a whole, and thus be insufficiently adaptable to spread from their relict area. There are many species with such restricted areas surrounded by apparently suitable habitats into which they do not spread: such non-spreading topodemes must be presumed to be ecotypic in nature, even if we cannot find any morphological differentiae; the ecotyposis may be physiological. Such topodemes must be presumed to be relicts, of great value for the unravelling of the past history of the country. But they can only be treated as systematic groups when they show morphological differentiae. Except for the small extent and critical nature of their differentiae they are essentially specific in nature, with correlated differentiae and distributions. The amount of difference in such topographically isolated fragments will vary from more or less nothing at their origin, to considerable in course of time, and to great when, after long intervals of time, they have developed along different lines to become quite distinct species and sometimes, later, even more isolated groups of higher rank than species. Where are we to draw the line between the slight ecotype and the full species? And what terms are required, if any, to denote the degree of difference? The only fixed line may prove to be where the changes have gone so far that the two fragments can no longer interbreed, or can only do so with formation of completely

sterile offspring. Even here we must hedge somewhat, for it might be possible that something similar to what occurs in strains of fungi might occur, and that A might be genetically isolated from C, but that both could cross with B with partial fertility, and thus again produce a commiscuum. But in general it would be possible to draw a fixed line here, where in fact most zoological systematists do draw it, and treat all groups capable of fertile interbreeding as intraspecific groups. On the other hand, in botany it would be very impracticable, and would involve uniting many groups universally recognised as distinct species, and further, botanists know inter-generic hybrids which are fertile and also self-sterility in individual species, as in *Reseda*. It seems probable that we cannot in botany draw any such hard-and-fast line. There exist very distinct non-critical "monotypic" species which are presumably comparatively old, and less distinct critical species resulting from a more recent breaking up of a widespread variable species. If the differentiae between these groups are absolute, i.e., if every individual can be referred to one or other without any doubt, then each group is really a species, from a philosophical point of view. Whether each of them should be a biverb may be a matter for debate, for some consider that there are some advantages in using 'large' biverbs, so that there are fewer of them and therefore there is more chance for the general naturalist to have some idea of what the organisms denoted by each of them are like. Personally I think we must regard as species all groups that are absolutely discrete. In this sense we shall have large species ("macrospecies") and small species ("microspecies"), those very distinct and those which are critical. There is no reason that I can see to demand that our "species" shall be approximately of the same size. Families are not of the same size, nor are genera, and there is no reason to expect that species should be of the same size. If the groups are quite distinct there is little or no philosophical reason for "lumping" any of them together, though possibly there may be a practical one. The "collective species", "coenospecies", "supraspecies", and all such aggregates, are theoretical concepts rather than real species.

I have long expressed the view that species are of different kinds, and have made the following analogy between the so-called "tree" of evolution and an actual tree. Some species are like leaves, of limited growth and short duration, whereas others are like shoots, which have greater capacities and themselves give rise to more leaves and shoots. These latter are polymorphic species, which occur in all organic classes, and are commonly surrounded systematically by a number of less variable or fixed, less widely distributed, small species. The small species are probably often short lived because when conditions change they lack the wide variability necessary to enable them to adapt themselves easily to the change, though there seem to be some fairly fixed species which have no close relatives and are probably older and more long lived, just as some leaves last for several years. The polymorphic species

are more vigorous ; they spread, possibly because of their wider variability, and can give rise by isolation and fragmentation to the next series of small species analogous to leaves, as well as in part retaining their polymorphic nature like shoots. I was interested to hear Mr. Hubbard say yesterday that after all the segregate species had been removed from *Poa pratensis*, that species remained almost as polymorphic as ever. It may be that it will always remain so ! If sufficient individuals are examined, one can often find in the more fixed small species occasional variants which show the continued existence in them of characters frequent in the polymorphic species, or in allied small species, which in the polymorphic species have never become fixed through selection or any other way. The polymorphic species can usually be recognised by the length of their synonymy. This is because systematists have attempted to subdivide them on the basis of characters which are specific for the small allied species, not realising that in the polymorphic species these characters are *not* fixed and are therefore systematically worthless. And in this way a large number of "bad" biverbs are continually being created in attempts to subdivide the polymorphic species by such characters, attempts which, if systematists realised the different nature of the polymorphic species, they would know were probably foredoomed to failure. These "bad species" get sunk and add to the synonyms of the polymorphic species. It is curious that the universality of this phenomenon has not been generally recognised by systematists, who do not seem to realise that characters specific in some members of a species-group can be worthless in others, which should be obvious if the implications of Mendelian segregation are considered. For some lineages may well be homozygous (or, more often, nearly so) in the presence or absence of a character, while others nearly allied may easily be heterozygous. And the polymorphic species are probably heterozygous in many of the characters which have become nearly or quite fixed in their small allies. It must be recognised in the study of critical groups that no character is universally good or bad ; they are like the curate's egg, good in parts. That at least is the conclusion to which my studies have led me. Huxley distinguishes between polymorphic species, in which differentiated or sharply contrasted forms co-exist, and polytypic species, in which the differentiated forms show geographical or ecological replacement although transition forms or regions may exist. The latter seem to me to be aggregations of small species, whereas the true polymorphic species are single groups.

Sometimes, however, the differentiation of the parts of a fragmented old species has not gone so far that all of them are absolutely distinct. In the *Onosma echioides* series of species, most of the topographically isolated groups are quite distinct, some of them with very restricted ranges, such as the one that only occurs in one Alpine valley, and others with wider ranges. One of them grows in the neighbourhood of Trieste, another above Naples, and

although the French, Sicilian, Greek, Cretan, Danubian, and other small species are completely distinct, I found it impossible to say without seeing the labels whether some specimens were from Trieste or from Naples. About 90% could be distinguished, but about 10% seemed to me to be inseparable owing to the overlapping ranges of variation. These two are what I would call subspecies, for unless we have one name to include both of them it would be impossible to give a scientific name to some specimens if their origin were unknown, and in systematics this can not be permitted: it must be possible to give an accurate scientific name to every specimen on morphological grounds. It may be, or course, that another student may find some absolute means of distinguishing the two, but until this is done, it seems preferable to call them subspecies, this term indicating that the stock has actually branched but the parts are not yet discrete. As an analogy one may cite the anatomy of the stem of a vascular plant. Just above the branching of the vascular strand at the base of a branch there is a region where the two strands are still enclosed in a single cortex. But anyone familiar with anatomical structure would know that the stem had in fact branched and that a little higher up a section would show each strand surrounded by its own cortex. There is, however, no fundamental difference between such subspecies that are nearly species and those which have had a similar history but are now quite distinct.

It seems possible that all these geographically isolated fragments of the *Onosma echioides* series—or supraspecies—may be of the same age and from that point of view are equivalent. Are we to use different terms for those which are discrete and those which are not? Some systematists would call them geographical races, others subspecies, and yet others would term the discrete fragments micro-species. The term used does not matter to zoologists, for they treat them as triverba regardless of the term used, and I must say that I think this simpler than the botanical practice.

Some systematists try to make a hierarchy of these intraspecific groups, using terms such as race, subrace, natio, subnatio, but the definitions given to these generally depend on an imagined—even if it may be correct—history of their evolutionary development rather than on the factual differences between the groups, other than size. Systematically it seems desirable—to me at least—to classify on the actual differences and to treat all these groups as biverbs and triverbs of different kinds, adding, in parenthesis, if desired, some indication of their kinds—big or small, geographical or cytological, etc., rather than using different terms to denote them in nomenclature. It should be noted that if groups are to be distinguished as races, the term for them in nomenclature is the latin “proles”, and not the diverse equivalents in different languages. As the Rules of Nomenclature put it: “Nomenclature is in Latin for all groups”; and this should include the terms as well

as the epithets, for to use a series of words for the same thing—race, Rasse, or the equivalents in Swedish, Russian, Japanese, and so on,—is surely undesirable.

From the standpoint of systematic method, it seems to me impossible satisfactorily to subordinate different kinds of species or of races to one another, and the Zoological Rules of Nomenclature, which treat species and subspecies—as they term races—as coordinate in nomenclature, again seem based on sound and better principles than the Botanical Rules which set out a hierarchy of intraspecific groups, in which one and the same group could be designated by a different valid epithet according to the rank given to it by different systematists, which is nomenclaturally an absurdity.

The isolation which leads to fragmentation of a species is not always geographical. In Fungi we find what are called “host-races”, which are small physiological races, or microspecies. It may be that further study will show that something of the same kind exists in hemiparasites such as *Euphrasia*, *Rhinanthus*, etc. But I do not see that the different nature of the isolation should prevent the use of the same term for such groups. I have been told that in South Africa the differentiation of species has tended to be ecological rather than geographical, allied species being restricted to different kinds of soil. Such ecological isolation might produce ecological subspecies and species, though I agree with what Prof. Clapham said yesterday, that in this part of the world it is difficult to find examples, although the case of the two *Crataegus* species cited may be one. It seems more likely that the isolation was originally of some other kind, which may later have been ecologically developed. I am one of those who think that plants grow where they do because they are what they are and find these or those conditions suited to them, rather than that they are what they are because of the conditions in which they grow. But to use such terms as eco-species or eco-subspecies seems to me undesirable; it is better, as I have said, to add some indication of the kind of species or race in parenthesis. The nature of the kind of isolating factor seems to me to concern the study of evolution rather than systematics.

A very different kind of natural group is that which is due to the doubling of the chromosome number. We need not consider how this happens; it is the result that is important. Here we get the sudden origin of a new group. Morphologically the differentiae of the new group vary from very slight to considerable, but genetically we find that the new group, when crossed with that from which it sprang, commonly produces a sterile hybrid. It is, in fact, a distinct species, whether a small one very similar to its parent or a bigger one with many differences. It is a cytological species or, if the differentiae are not absolute, a cytological subspecies. The sterile triploid may undergo doubling of chromosome number and produce

another group, a hexaploid. Or the tetraploid may again double and produce an octoploid, and so on. But from a systematic standpoint, these should also be treated merely as species and subspecies on morphological grounds, the cytological nature of the isolation being the concern of evolution and not systematics. And other more complicated cytological species, or subspecies, are now known (see Dr. Valentine's paper).

We have now dealt with the most obvious intraspecific groups, the races or microspecies, often called subspecies, of various kinds. The various terms such as Jordanon, microgène, elementary species, etc., mostly indicate species of different kinds and sizes. We must now consider some features of variations which, although not really concerned with natural groups, do complicate the study of the critical groups.

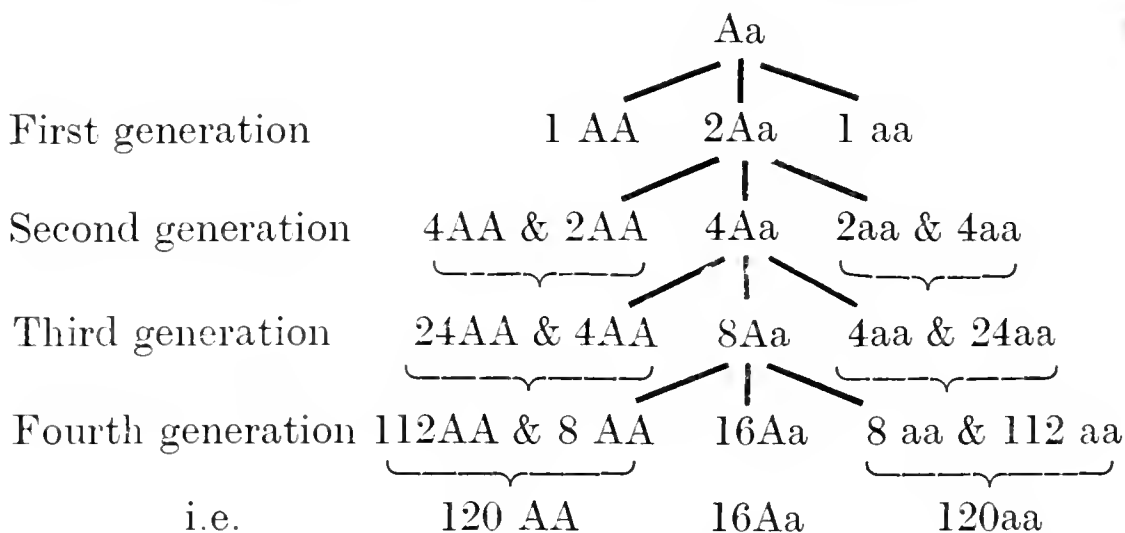
The first is what I call "differential variation", by which I denote cases where the proportions of variations vary in different areas without forming different groups. In Britain *Anagallis arvensis* is mostly scarlet-flowered and rarely blue; in Macedonia it is mostly blue and much less commonly scarlet. In western Europe *Trifolium fragiferum* has glabrous peduncles; in south-eastern Europe the peduncles are very often pilose. It is clear that mutations which arise in one area will take time to spread, and may never do so over the whole of the range of the species, and presumably differential variation arises in this way, or partly so at least. If it occurs to any great extent in a widespread species broken into fragments by some major earth change, it may form the basis of ready-made microspecies different from the beginning. Sometimes there is said to be a gradual transition in characters from one part of the area of a species to another, and the term "cline" has been proposed by Huxley for this phenomenon. How far such "clines" exist needs careful examination: they have been said to exist in *Plantago maritima*, but my own experience with this variable species in the field does not bear this out: I find in north-west Scotland great variation in the populations actually growing together. The line between clines and the existence of different small groups growing together needs careful study: intercrossing between small species and races where they meet might lead to the appearance of a cline. But a cline is not a true natural group. Study of such phenomena is concerned with the study of individual genes and their distributions more than with systematic groups. As I said at the outset, we cannot make a systematic group by selecting men with blue eyes and knobbly knees: we can only study the distributions of these separate characters. The term genotype, indicating individuals with certain genetic characters, does not indicate a natural group, and should not be named as if it were one. It is the genes—or rather, the "phenes" or characters to which they give rise—that should be named and studied. Until these different studies are carefully separated, although they are so closely interlinked, progress in each will be impeded and difficulties

of nomenclature will be unnecessarily increased. And again it must be pointed out that the word "cline", not being latin, is not really suitable for a term proposed for use in systematics. There seems to be no latin word indicating merely a slope. The Romans were a practical people who thought in terms of action, and to them a slope up was quite a different thing from a slope down, and so they had a different word for each. The best latin word for the "cline" would appear to be "transitio", which may be considered suitable if a latin term is needed. Although it is not a separate group and should therefore not have an epithetal designation, a latin term suitable for use in nomenclature may be desirable. It is suggested that where such transitions are considerable and continuous, they should be designated by a formula consisting of the epithets denoting the two end-series, connected by a dash where in the formula of a hybrid there is a \times . This certainly seems to provide a satisfactory way of indicating them. It is also suggested that in both triverba and transitiones ("clines") their nature should be indicated by a capital letter placed before the epithet (or formula), G. for geographical, E (or OE) for ecological, and C. for cytological; and I would add A. for apomict and P. for physiological, though Kiriakoff in developing the system treats the last-named as ecological. Kiriakoff's complicated system (1948: *The Lepidopterist's News*, p. 15; example by Rimington on p. 16) appeared since this paper was drafted: he suggests a means of indicating the various relations between allied groups, embodying not only Huxley's suggestions for using capital letters as suggested, but other features to indicate supraspecies and degrees of inter-fertility. While such taxonomic indications may be helpful to students, they are part of classification rather than nomenclature. But they certainly seem preferable to the creation of a hierarchy in nomenclature. The use of a capital M to indicate the small species (the "microspecies"), and of a lower-case m to indicate a smaller one (the "race"), and even a small italicised *m* for a smaller "ecotype", might also help to remove any objection to treating all these groups as triverba. It seems to me undesirable that the name itself should consist of a string of words indicating a classification. A single extra epithet is all that is required in nomenclature to indicate the exact intraspecific group referred to. But I expect that many such hybrid schemes between classification and nomenclature will be produced.

I have also sought a suitable latin term to replace "topodeme", should it be required in nomenclature. But it is a curious thing that names of groups have in systematic nomenclature suffered a kind of inversion in size relations. The word genus is cognate with gens, meaning a lineage or sort of race. The tribus is systematically bigger than a genus, but a tribe is smaller than a race. And the familia is systematically bigger still, though the family is again smaller than the tribe. If the topodeme is systematically differentiated, it is, in the scheme here proposed, a small race, but if, as

is usually the case, it is only an example of local differential variation, it would probably be better that it should not have a special epithetal designation as if it were a race. If a latin designation is required, I suggest the use of a noun in the plural—either *incolae*, i.e., inhabitants, or *paganae*, i.e., countrymen, with a word ending in *-enses* indicating the locality; slightly variable fish inhabiting Lake Ladoga would then be called “*incolae ladogenses*”, if they were but an example of differential variation, but would be a small *triverbum* if they formed a completely differentiated local group.

Another complication in the study of critical groups may occur when a species is normally self-pollinated. Let us consider what would happen if a topodeme started with an individual heterozygous in a gene A, i.e., was Aa, and that AA, Aa, and aa were equally viable. The proportions of each in successive generations can be seen from the following table, in which I have supposed that each individual produced four offspring each generation.



It is clear that in a few generations the heterozygote will tend to disappear, leaving what may be called semi-pure-breeding strains. It seems to me probable that what appear to be small subspecies in such plants as *Senecio vulgaris*, and possibly also *Erophila*, may be merely temporary phenomena arising in this way, which will be upset whenever cross-fertilisation occurs. Whether such temporary groups are of importance in systematics needs further study before sound judgment can be made. Trow grew several such groups of *Senecio vulgaris*, one of them being his var. *lanuginosa*, much covered with woolly hair. But whether such *lanuginosa* plants in different places agree in other characters also needs investigation. On the Sussex coast I once came across a large number of *Senecio vulgaris* which looked uniform in all characters but the wool, and about half of the plants were “*lanuginosa*” and the other half quite glabrous. Presumably the original invader of the habitat was heterozygous in this character. This made me very suspicious as to the existence of a real group to which the epithet *lanuginosa* could be given merely because plants were similarly lanuginose. These strains, or whatever we may call them, seem to be what are often called “pure lines”, although they do not correspond exactly to

Johansson's definition of that term. The only really pure lines may be the newly formed tetraploids or other groups with recently doubled number of chromosomes, and apomicts which are genetically really uniform. The so-called pure lines are of importance to man in the cultivation of some crops, but they may only be artificial groups. How far they are natural groups, real tiny microspecies, is a matter for study: it is certainly at times a matter for much argument! The "agrotype" (and "agro-ecotype") of Gregor—the "field crop unit"—is again, to my mind, scarcely a natural systematic group: certainly it has no distinct natural distribution. And it would be impossible to make a classification to cover all the products of a normally self-pollinated variable species. Studies of such variation is a study of genes and their distributions, not of groups.

Another kind of variation is that which Rothschild and Jordan, working on insects, called "forma alicujus loci", i.e., a form special to a restricted area. These are presumably the product of a local mutation which has not yet spread. They occur *with* the normal form and their existence as a group therefore depends on selection by man. It has been said that they are "museum populations" rather than natural groups. They are genotypes which, when occasional, sporadic, and well-marked, are sometimes termed *aberratio*. The *lusus* (sport) is usually only an extreme example of such individual variation: it is sometimes defined as something that cannot reproduce itself, but some of the peculiar sports of *Digitalis* with peculiar peloric flowers do reproduce themselves. Possibly many sports owe their origin to hybridisation, but they are little understood.

Genotypes should not be given epithetal designations or form part of the normal system of nomenclature. A system of using different letters for the different genes (or phenes) has been adopted by Dr. Turrill in his work on *Silene* which he mentioned yesterday, and this seems the best way for dealing with genotypes. When it is necessary to refer to an individual genotype, the system of such letters could be preceded by capital GT after the name, to fit in with the system already mentioned. A similar system, using PT, i.e., phenotype, and letters, could be used to deal with variations presumed to be genotypic as the results of morphological study only. It is most desirable to distinguish between known fact following experiment, and guesses, however right such guesses may prove later to be. However it is done, we must have some method of harmonising systematics with genetical, cytological, and ecological knowledge.

A few words must be added about hybrids, although they are not intraspecific groups but interspecific ones. When the product of hybridisation is sterile, and vegetative multiplication can occur, as in the triploid resulting from *Nasturtium officinale* crossed with *N. uniseriatum*, we get a widespread plant which can, except for

its sterility, look like a species and obtain a distinct distribution. It must be treated as a separate systematic group with a distinctive pseudospecific name. But when a hybrid is fertile and segregation occurs we get a "hybrid swarm", in which no two individuals are exactly alike, as when *Linaria repens* crosses with *Linaria vulgaris*. Such an assemblage is not a distinct natural group; it should be designated by the hybrid formula and not given a pseudospecific name. Such swarms are commonly of temporary duration. How far they may affect the variation of the parent species by back-crossing is yet unknown: by some means the parents seem to retain their characters, though why they should not be affected is not clear to me. Apart from these points, hybrids do not really come within the scope of our title.

Here we must also consider what is called an aneuploid series, in which the chromosome number is very variable, sometimes almost continuously. *Viola arvensis* has eight more chromosomes than *Viola tricolor*, as mentioned yesterday (Dr. Warburg's paper). If these cross, it is possible that the chromosomes of the *Viola tricolor* element may pair with the same number of *Viola arvensis* chromosomes, but there are four left over. If these could pair among themselves we could get a new group which would breed true, but normally these four behave independently, and may wander in meiosis to one or other pole, maybe three to one and one to the other. In this way can arise plants with all sorts of chromosome number and gene content, and this is what some populations of pansies in some fields look like. We may find that in a given locality the majority of plants show a certain degree of uniformity, but that mixed with them are all sorts of plants which do not fit into any of the recognised groups. They will probably not reproduce their own kind, and indeed it may be impossible to find a method of systematising all individuals connected with an aneuploid series, which is a sort of delayed hybrid swarm of peculiar origin. There is a similar aneuploid series in *Cochlearia*, which may well explain the difficulty of finding any satisfactory classification of the plants collected. When I first saw the so-called *C. micacea* above Glen Doll it seemed to me that there were two forms there, and not one, for some had white flowers while others were tinged with purple. And Crane and Gairdner later found that plants from that place had two different chromosome numbers. It will need an enormous amount of cytological work counting chromosome numbers of large numbers of plants of *Cochlearia* from different places and correlating the results with morphological characters, before we can begin to know how many distinct groups there are and what their characters are. Certainly aneuploid series may form the worst critical groups.

The term cytotype has been suggested as suitable for indicating intraspecific units depending on chromosome differences. They are, however, of different kinds, as already indicated, some being one of the kinds of species, such as various polyploids. Some are

individuals of aneuploid series analogous to hybrid swarms, and will need some special kind of designation. Some are mere individuals, like the sterile diploid *Viola Reichenbachiana* x *Riviniiana* which Dr. Valentine obtained from the triploid hybrid. How we shall ultimately manage to deal with all the peculiar kinds of variation which are being brought to light as genetics and cytology develop I do not know. I suppose that systematists have got to deal with them somehow.

I have deliberately excluded from consideration here the special difficulties of geologists. They have troubles in an extra dimension—time—which do not, except theoretically, trouble the field naturalist. Our groups are but sections of lineages, and thin sections at that, for except for specimens from Egyptian tombs and the like, our oldest herbarium specimens are a mere three or four centuries old, and most of them less than two centuries. Yet it is the lineages that are the more real entities, and the sections are mere temporary phenomena. The problems of the geologist are somewhat different and it seemed better today to ignore them, except to remark that many of their species are short lengths of lineage rather than thin sections like ours. For them the term *palaeospecies* could be used.

I must now try to sum up what I have said. It would seem that from a systematic point of view we can recognise:—

(A) Distinct groups :

- (1) species, of various kinds, origins, and sizes : G,C,E,A,P ; M,m, and possibly *m* ; some of which we may prefer to call microspecies, races, ecotypes, and the like.

(B) Incompletely differentiated groups and their transitions.

- (2) subspecies ; incompletely differentiated microspecies. I am not sure whether these are what was intended by the term semi-species (Huxley), defined as “ on the borderline between subspecies (i.e., races ?) and species ”.
- (3) transitio (eline) : a transitional assemblage between two normally differentiated groups ; geographical or ecological, and possibly others.

(C) Genotypes and other individual variations : assemblages or individuals differing in gene content.

- (4) segregates : of the blue-eye knobbly-knee type ; “ museum populations ”.
- (5) differential variation, due to local distribution of genes, including the “ forma alicujus loci ”.

(D) Variationes non satis notae.

- (6) varietas : a variation of unknown nature which nevertheless seems reasonably referable to some known taxonomic species.

(E) Variations due to environment.

(7) forma. Possibly, as the word "form" is so often used in an untechnical sense, some other term would be preferable.

(F) Mere local populations ; topodemes.

The difficulty in systematics is to decide, in the absence of the really necessary cultural, transplant, genetical and cytological evidence, what is the nature of the variation with which we are dealing. Long field experience may enable us to make shrewd guesses concerning the effects of environment, for we can often observe the probable effects of the environment in the field. But we may be wrong when we only have herbarium material ; there are, for instance, genetical dwarfs and ecological dwarfs, and both genetical difference and conditions of growth affect such things as leaf shape, indumentum, and other characters. Observation of variation in the field—or even in the herbarium if sufficiently long series are available—may enable us to feel sure that there is no correlation between certain characters, but in other cases we are unable to feel sure. And sometimes cytological investigation of chromosomes is urgently needed.

We must therefore, as I have said, keep a taxonomic category for variation of unknown kind, and this is particularly needed in purely herbarium studies when we are dealing with few specimens without the possibility of further field work. My own view is that it is very undesirable to confuse more or less well-known species or other groups by referring to them by mere guesswork specimens outside their known ranges of variation. I would rather describe all uncertain specimens as new species than do that. My opinion is that the first rule of systematics should be : No specimen or group should ever be subordinated to another group without definite evidence, from cultural, genetical, cytological, or intensive field study, which makes it almost certain that the group will never again be raised from its subordinate position. If this rule were universally adopted, classification would begin to settle into a fixed position because, although we should at first have larger numbers of separate groups, they would gradually be reduced to their fixed positions. Whereas at present systematics tends to be like a quaking bog in which different parts go up and down according to the existence of systematists working on different parts of it. The material seen by the different systematists is different, the proportions of material of different groups and from different places is different, and naturally the conclusions reached by the various systematists are different.

And if all this may seem to you "to make things too complicated", as E. S. Marshall once complained to C. E. Moss, I will offer you Moss's reply to Marshall :—"Good Lord, Marshall, do you think that *I* made Nature complicated ?"

(It was hoped that examples of the proposed methods might be

added, but the knowledge of our plants does not readily offer an example as complete as that supplied by Rimington (for a critical group of American *Papilio* butterflies) as an appendix to Kiriakoff's paper, and this example must serve until a good series can be provided from plants.)

DR. WARBURG welcomed this paper as giving a very clear picture of ideas many of which he and others would have felt to be correct but had not been able to put into words. He suggested that the time had come when botanists, like zoologists, should adopt "triverba" for subspecies without any qualifying word, or where desirable with the suggested qualifying capital letter. He asked whether such capital letters might not be confused with capital letters used as abbreviations of generic names.

MR. WILMOTT replied that confusion would not occur because the suggested qualifying capital letters are separated from the generic name (or capital) by the specific epithet, which they follow in brackets.

SOME PROBLEMS OF THE WATER BUTTERCUPS

By R. W. BUTCHER

In spite of all the taxonomic work that has been done on the Batrachian *Ranunculi* by Felix (1913), Glück (1924), Pearsall (1928) and others, there are still many problems concerning them that need elucidation.

It has already been shown (Butcher, 1940) that the form of the plants is easily changed by depth of water and by exposure to air. Terrestrial forms and those with elongate pedicels are evanescent and are not worthy of special naming.

Linnaeus gave the name *Ranunculus aquatilis* to cover “*R. foliis submersis capillaceis, emersis peltatis*” and the specimens in his herbarium appear to be the plant which British botanists describe as *R. heterophyllus*. On the other hand continental workers attach the Linnaean name to what we call *R. peltatus* while apparently our *R. heterophyllus* is put partly under *R. aquatilis* and partly under *R. radians*.

The river forms, of which there are several more than the books describe, present many interesting features. *R. fluitans* is well marked and the variety *Bachii* is simply a small form of the plant. Floating leaved forms of it are very rare and many of the records refer to other species.

The calcareous streams are often filled with a well marked form with large flowers, peduncles not exceeding the leaves, and receptacle hairy, which is usually referred to as *R. pseudo-fluitans* Baker and Foggitt. It appears, however, that Baker and Foggitt's form, which is also referred to by Newbould, Babington and others by the same name, was a plant which developed floating leaves and which is the dominant plant in Irish and Welsh rivers. The plant of the calcareous streams does not develop floating leaves and appears to be distinct, though there is not enough information to permit decision as to its exact status, so it is here called the “chalk-stream plant”.

In addition to typical *R. fluitans*, other puzzling river forms—all with floating leaves—are to be found in Britain. In New Forest streams there is a plant which seems to be simply a running-water form of *R. peltatus* and is the var. *penicillatus* of Dumortier. In the south of England there is also an unusually robust form which has flowers 30 mm. in diameter and large leaves.

The distributions of *R. fluitans* and the “chalk-stream” plant in certain rivers is of interest. The latter is abundant in the upper reaches while it is replaced by the former in the lower reaches and there appears to be little or no overlap of the two.

The form, nature, and development of the floating leaf is also a problem in the pond forms. Nobody has as yet shown what are the

causal factors of their development, though they seem to be principally nutritional ones, and the tendency to repress or develop these leaves varies in different species. *R. circinatus* never develops them, *R. peltatus* almost always does so from May to September. *R. trichophyllus* is said by some authors never to produce floating leaves, but others hold the view that *R. radians* is its floating-leaved form and that *R. submersus* is a form of *R. heterophyllus* without floating leaves. These two opposite arrangements of type and variety appear very inconsistent and need further research.

Numerous other puzzling points, such as the supposed hybrids, the relations of the still-water and running-water forms, the real systematic value of the leaf-segments collapsing or not when taken out of water, the shape of the carpels and characters of the receptacle, all need elucidation. It is clear that in this group there are physiological, ecological, and taxonomic problems which would give ample scope for research to anyone who is looking for an interesting problem to tackle.

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The paper was discussed by Dr. Sprague and Mr. Wilmott. Mr. WILMOTT said that whether leaf-segments collapsed or not depended on whether the segments were or were not rigid enough to resist the force of the surface tension of the water film on them, and that in some streams deposits on the segments made them thicker and more rigid and therefore less liable to collapse, so that the character might not always be dependent on the nature of the plant itself.

VEGETATIVE AND CYTOLOGICAL VARIATION IN *VIOLA RIVINIANA* RCHB.

By D. H. VALENTINE.

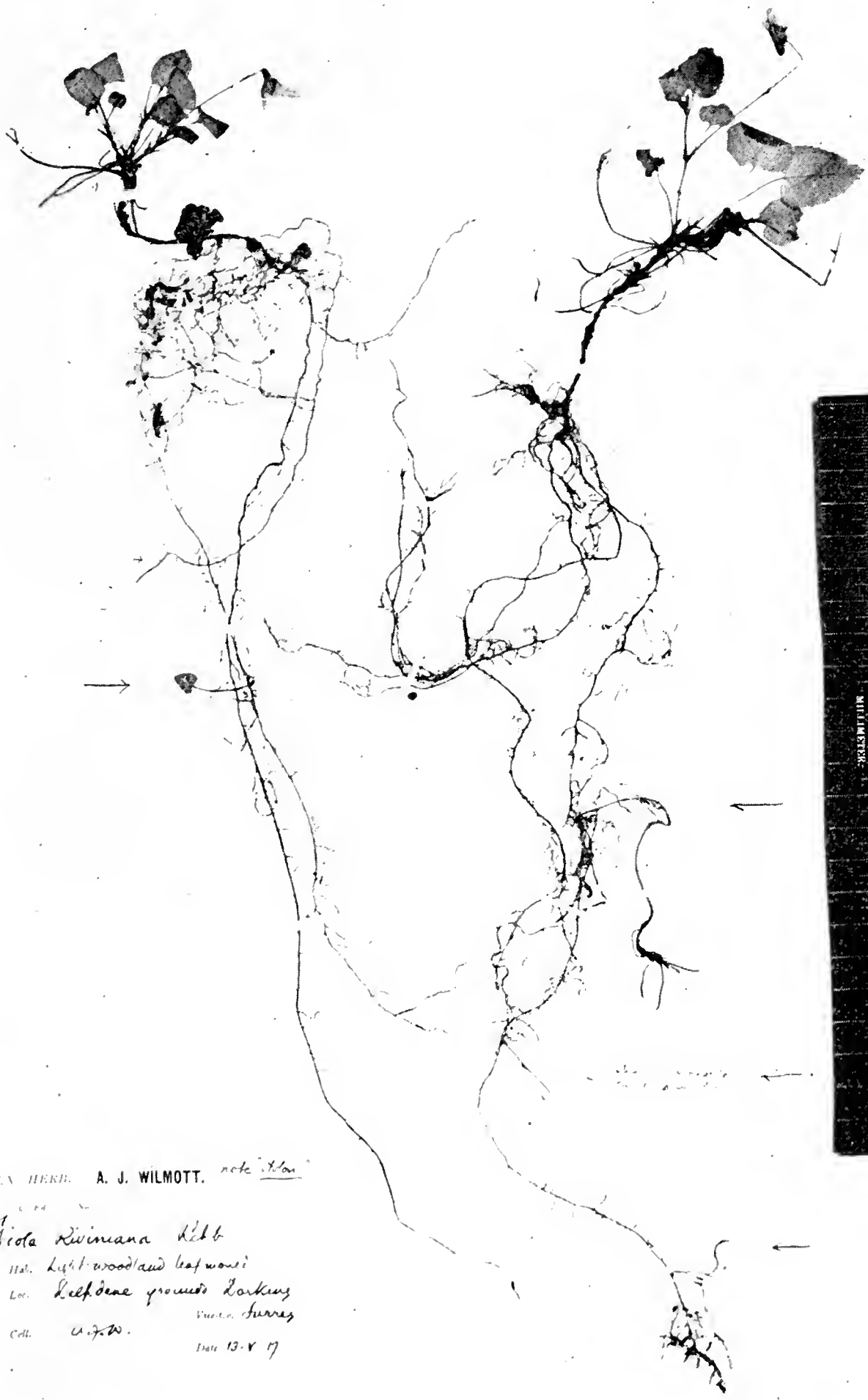
Viola Riviniana is the commonest British dog-violet and also the most variable ; an account of its variation has been published (Valentine, 1941). The formation of adventitious shoots on the roots is a character of certain plants of the species ; it has been noted previously by Wilmott (British material : plate 1) and Gershoy (1934 : Danish material). Cultivation experiments have shown that plants are constant for presence or absence of the character : breeding experiments are still in progress, but it is clear that the character is heritable, and it is probably dominant. Scoring is not easy, as, even in potted plants, adventitious shoots are not formed at once (sometimes not until 12 months after potting).

TABLE 1.

ADVENTITIOUS SHOOTS ON THE ROOTS OF <i>VIOLA RIVINIANA</i>			
Number of localities for plants which have <i>not</i> produced advent- itious shoots.		Number of localities for plants which have produced advent- itious shoots.	
Cambs.	5	Cambs.	2
Essex	4	Hunts	1
Suffolk	1	Lancs.	1
Hants.	1		
Glos.	2		
Surrey	2	Surrey	3
Durham	4	Durham.	9
Glamorgan.	1	Glamorgan	1
Pembrokeshire	3		
Cairngorms.	1		

Table 1 shows the distribution in Britain of plants which have so far been tested for adventitious shoots ; the character, which we term *AS*, is clearly widespread. No obvious correlation with type of habitat or soil has yet been noted. From three localities plants with and without *AS* have been collected : it is intended to investigate the distribution of the character in one of these populations. Scoring in the field is often difficult, as the underground connections between parts of a clone are easily broken. Recent observations in Durham have shown that clones formed by the production of adventitious shoots may be two feet across, and they may well prove to be much more extensive.

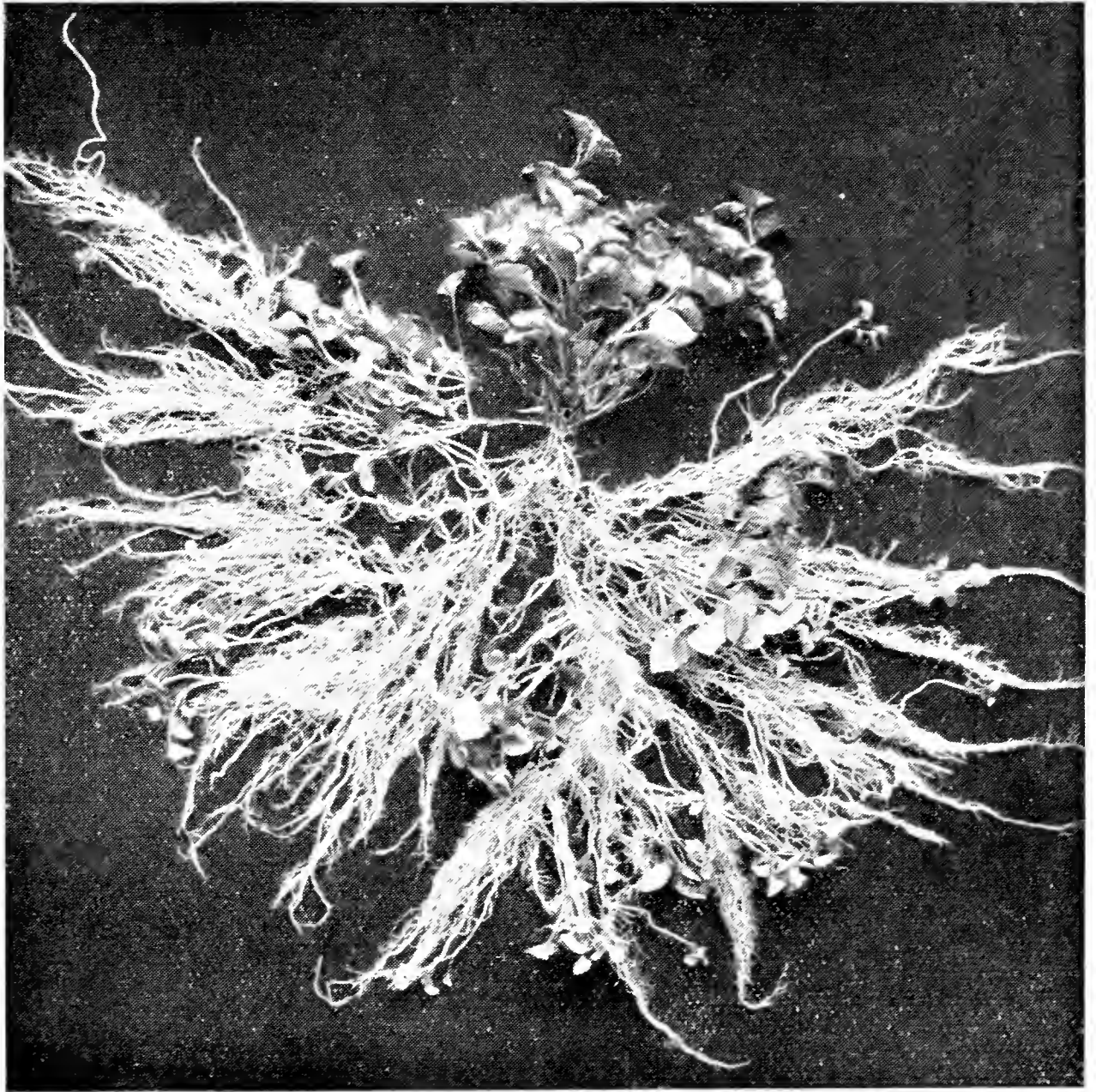
The only closely related species in which *AS* is certainly known is *V. stagnina* Kit. : it is a constant character of this species, which is for this reason described as soboliferous. *AS* can be transmitted from *V. Riviniana* to its hybrids with other species ; sterile hybrids showing *AS* have been made artificially with *V. Reichenbachiana* Jord. and *V. canina* L., and the former hybrid, with *AS*, has been observed in the field.



EX HERB. A. J. WILMOTT. note Ston

781
Viola Riviniana Rehb
 Hab. Light woodland leaf-moss
 Loc. Halfdene grounds, Hooking
 coll. A. J. W. Vernon, Surrey
Date 13-V-17

Viola Riviniana Rehb., with adventitious shoots (Surrey).



V. *Reichenbachiana* ($2n = 20$) \times *Viola Riviniana* ($2n = 45$), a single sterile plant. The *Riviniana* parent had adventitious shoots on the roots: sister plants of the hybrid shown had $2n = 33, 34$. The specimen, which was grown in good soil in the Durham garden for a year, was washed and spread out to show the adventitious shoots (of various ages) which arise from the roots. The vigour of the hybrid is characteristic and is reflected in the large number of adventitious shoots, which in this plant have about 55 places of origin. About $\frac{1}{4}$ natural size.

AS does not appear to be linked to any other morphological character of *V. Riviniana*, and it appears in both subsp. *nemorosa* and subsp. *minor*. It may, however, be linked with the presence of extra chromosomes; an account of these follows.

Clausen (1927) first examined the chromosomes of *V. Riviniana*; he found $2n = 40$, but he mentions certain plants which showed some irregularities at meiosis. Subsequent determinations are given in Table 2.

TABLE 2.

CHROMOSOME NUMBERS OF *V. RIVINIANA*.

Without extra chromosomes, $2n = 40$	With extra chromosomes.
Clausen (1927) - Denmark.	Valentine - Cambs.; Little Widg-
West (1930) - London.	ham Wood; $2n = 46$.
Gershoy (1934) - Denmark.	Durham; Croxdale; $2n = 35$.
Fothergill (1944) - Durham; Gibside.	$2n = 46$.
Valentine - Surrey; The Nower (Dorking).	Surrey; Godalming. $2n = 47$.
	Pembr.; St. Ann's Head.
	Durham; Widdybank Fell.

It will be seen that up to the present extra chromosomes have been observed in plants from three localities. The extra chromosomes are markedly smaller than those of the normal complement. Observations of meiosis show that in plants with $2n = 45$ or 46 , some of the extra chromosomes may fail to pair. They appear as univalents at the first meiotic division, and may also be seen at anaphase, where they sometimes divide near the equator of the plate, having lagged behind the bivalents. Judging from his account, it is likely that Clausen, in 1927, saw *V. Riviniana* of this type in Denmark; he thought it might be of hybrid origin, but we do not think that our plants are. All the likely interspecific hybrids with *V. Riviniana* are practically sterile, and their meiosis is quite different from that described. Our plants with extra chromosomes are all typical of the pure species and fully fertile; and it may be observed that extra (or supernumerary) chromosomes have been recorded in many "good" species; a list is given in Darlington (1937).

Chromosome numbers of some artificial hybrids with *V. Reichenbachiana* are given in Table 3. In these, *Riviniana* gametes have carried either 3 or 4 of the extra chromosomes; because of their somewhat irregular behaviour at meiosis, this variability in the numbers reaching the gametes is not unexpected.

TABLE 3.

CHROMOSOME NUMBERS OF *V. REICHENBACHIANA* × *V. RIVINIANA*.

- (a) Female parent of cross, *V. Riviniana*, Widgham, Cambs.,
 $2n = 46$. Hybrid had $2n = 33$.
- (b) Female parent of cross, *V. Riviniana*, Croxdale, Durham,
 not counted, but from same population as other Croxdale
 plants which have $2n = 45, 46$. Hybrid had $2n = 34$.
- (c) Female parent of cross, *V. Riviniana*, Howe Wood,
 Essex, not counted. Hybrid had $2n = 30$.
- (d) Female parent of cross, *V. Riviniana*, Dorking, not
 counted, but from same population as other Dorking
 plant with $2n = 40$. Hybrid had $2n = 30$.

It is remarkable that the three stocks in which extra chromosomes have been described all have *AS*; and it is possible that the correlation is invariable, though there is clearly not enough evidence yet to establish it. Support has been obtained from examination of a population on Widdy Bank Fell, Durham, which is the only British locality for *V. rupestris* Schmidt. *V. Riviniana* subsp. *minor* occurs here; the two species, which are closely related, occupy distinct areas, and their habitats are, to some extent, ecologically distinguishable. Gregory (1917) refers to "intermediates" between the species which have been found here, but proven hybrids have not been described though they are known on the Continent. In 1947, two large groups of apparent hybrids were discovered; these were very uniform in their characters, and intermediate in many respects between the supposed parents. Three plants were collected; they were found to be self-sterile and to have bad pollen; and the somatic chromosome numbers of the plants were 33, 33, and 34. *V. rupestris* is diploid, with $2n = 20$; we may infer that these plants are indeed hybrids, one of the parents being *V. Riviniana* with extra chromosomes, probably with $2n = 46$. The analogy with the hybrids with *V. Reichenbachiana* (Table 3) is clear. Further, by April 1948, all three hybrids had produced adventitious shoots from the roots. There is thus confirmation here for the correlation between *AS* and extra chromosomes.

It should be noted that Clausen (1931) found stocks of *V. canina* in Denmark with somatic numbers of $2n = 47$. From his account, some of the plants he described seem to us to have been hybrids (*V. canina* × *V. Riviniana*) but at least one was probably pure *V. canina*. The somatic number of this plant was not reported, but the behaviour of its chromosomes at meiosis agrees closely with that of our plants of *V. Riviniana* with extra chromosomes. It would be of great interest to find such a stock of *V. canina* in Britain, and to discover if it has *AS*. A footnote in Gregory (1912) suggests that a plant of *V. canina* with *AS* has been recorded; more information is being collected, and the author would be very glad to receive living plants or seed of *V. canina* for investigation.

It is of interest to note that in many other plants in which they have been described, extra chromosomes appear to be genetically inert. If in *V. Riviniana* they carry the genes for *AS*, we can account for their persistence and spread in populations of the species; for *AS* presumably provides the plant with powers of vegetative reproduction which it otherwise does not possess, and thus gives it a selective advantage.

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ACKNOWLEDGMENTS.

My thanks are due to Mr. J. S. Redhead for assistance with the cytological preparations, and to the Council of the Durham Colleges for a grant in aid of the work.

The paper was discussed by MR. Milne-Redhead, Mr. Wilmott, and Dr. Warburg.

MR. MILNE-REDHEAD said he was very interested by Dr. Valentine's paper, especially by his remarks about the formation of adventitious shoots on the roots of *V. Riviniana* and its hybrids. In May 1935 he saw a cliff slope near Port Eynon on the Gower Peninsula coloured blue by a very lovely violet which on examination seemed to be a hybrid between *V. lactea* and *V. Riviniana*. Both the supposed parents were present, but in small quantity compared with the supposed "hybrid". Living plants of all three violets were brought back and planted in his garden at Petersham, Surrey. All grew satisfactorily, but the "hybrid" showed a character not present in the supposed parents, namely, the abundant production of fresh plants from adventitious buds on the roots. In a few years the "hybrid" occupied a square yard or more whilst the plants of

V. lactea and *V. Riviniana* nearby had increased little in size. The "hybrid" set no seed in spite of the plentiful production of both normal and cleistogamic flowers. Unfortunately the plants were not examined cytologically, and this is no longer possible as they were all lost during the war years.

MR. WILMOTT described his discovery of the soboles of *V. Riviniana* near Dorking [in 1917], which were exhibited and described at a Tea Party at the Natural History Museum [in 1924]. He started, one Sunday afternoon, to get up a complete plant of *V. Riviniana* growing in light woodland leaf mould, but was surprised, after getting up the main root system, to find some fine but slightly tougher roots extending horizontally away from the plant about two inches beneath the ground surface. The disentanglement of these from the decaying twigs, especially bramble stems, was a difficult business, but ultimately they were found to run for nearly two feet, sending up younger and younger shoots at intervals, the last of which were quite tiny and not yet reaching the surface. [Further specimens were collected for him by Mr. I. A. Williams, who sought for such development on *V. Reichenbachiana* without success.] *V. canina (ericetorum)* was dug out of a sandhill at Arbroath, but showed nothing but a greatly elongated normal root-system. One specimen of *V. canina* was collected later which seemed to show about an inch of stoutish horizontal root connecting two "plants". Two plants of *V. lactea* were found about nine inches apart on a stony hillside in Brittany. An attempt to get these up completely with the only digger available—a piece of flat stone—ended in failure, as although a horizontal root was found going in the direction of the smaller plant, it was accidentally broken off about two inches from the second plant, and all attempts to find the broken root-end in the soil of similar colour were fruitless. The observations were never published as it was hoped that an opportunity would occur of further examination of the root system of *V. lactea*.

DR. WARBURG said that he was much interested in what both Dr. Valentine and Mr. Milne-Redhead had said about the hybrid violets reproducing by adventitious shoots. As the hybrids are sterile, this would seem to be their only effective method of reproduction, and it might result in the persistence of hybrids which would otherwise soon die out. In the pure species its advantage would be less. One would therefore expect that a much larger percentage of hybrids would have such root systems (and hence also have the extra chromosomes) than of species.

DR. VALENTINE replied that Dr. Warburg had made an interesting point which was worth further investigation. Mr. Milne-Redhead's plant was probably a hybrid between *V. lactea* and *V. Riviniana* with adventitious shoots: its persistence and spread in the garden illustrates Dr. Warburg's point and was paralleled by garden observations on other hybrids. He was interested to hear from Mr. Wilmott

that plants of *V. lactea* might have adventitious shoots ; the few plants of *V. lactea* that he had cultivated had not produced them so far. He would be grateful for living plants, particularly of *V. canina* and *V. lactea*, from specified habitats, which could be grown and examined.

CHROMOSOMES AND CLASSIFICATION IN ROSA

By KATHLEEN B. BLACKBURN

Crépin, perhaps the greatest authority on roses in the last century, wrote in 1896—" the genus *Rosa* has the singular fortune of having been studied more than any other genus and having had its species become more obscure and less recognizable as the work upon them has multiplied, so that today the study of the genus is dreaded by the majority of botanists "

In 1934 Erlanson writes in a much more hopeful and constructive vein of these same plants : she says—" the lack of good distinguishing morphological characteristics among the vast number of rose species and the ease with which interspecific hybrids are obtained are indications that the genus has been in a rapid evolutionary phase, probably since the Pleistocene, and that most of the species are genetically not distantly related"—" Parallel series of variations of the polymorphic species provide further evidence for the assumption that the species of the *Cinnamomeae* and the *Caninae* at least are closely allied to one another "

These writers clearly have in mind the multiplicity of micro-species with which we are all so familiar in our hedges and which Crépin himself thought possible to sort into larger Linnean species, but in practice found so difficult. It is however in the broader aspects of taxonomy that the modern study of cytology has proved of most service in this genus and to make this clear we must take a brief look at the history of the classification of the genus, so admirably outlined by Herring.

Roses were known from the earliest of times : Theophrastus described the Provence or Cabbage Rose as far back as the third century B.C. Some two thousand years later in the 17th century we find Gerarde illustrating it and writing—" the rose doth deserve the chief and prime place among all flowers whatsoever ". He and other writers about that time described and figured a number of different types of roses but it was not till the early nineteenth century (1818) that de Candolle produced what could be called a natural classification. Here we can already recognize familiar-sounding sections ; *Synstylae*, *Rubigineae*, *Cinnamomeae*, *Pimpinellifoliae*, *Villosae*, *Centifoliae*, *Caninae*, etc., but the arrangement is unfamiliar and we find curiously heterogeneous elements in the groups, as for example *R. montana* in the *Rubigineae* and *R. rubrifolia* in the *Cinnamomeae*.

In 1820 Lindley gave a classification in which he used more characters in defining the sections (styles, stipules, bracts, disk, sepals and armature) and succeeded in arranging them better and putting species in their natural groups without doing too much violence to the agreement with sectional characters.

Other classifications about this time were less happy because they were based on single characters : Dumortier's using the nature of the disk, that of Dr. W. Koch paying attention to whether the ovary was stalked or sessile, and that of Godet using the armature. These failed because their use disarranged natural groups.

An increasing interest in and knowledge of European roses became evident in the 1860's. In Déséglise's classification of the roses of France the sections differed little from those of de Candolle, but in 1869 Crépin introduced several novel ideas in his classification of European roses : he split off the *Stylosae* from the *Synstylae*, he picked out a group of plants we now know to be hybrids, under the name *Sabinae*, he separated *Tomentosae* from *Villosae* and also changed the position of a number of species from one section to another. The classification of Christ in 1873 shows a definite step forward in that the *Caninae* there constitute but one section with subsections *Caninae*, *Rubigineae*, etc., and this new idea was recognized at once as a sound one.

The classification now most generally used is that of Crépin in 1889 and on it is based Wolley-Dod's arrangement of the roses of Britain. Although in general this is considered satisfactory there still remain a number of questions which have been raised by other authors such as :—

- (a) Is the *Stylosae* a good section and well placed ?
- (b) Does the Persian *R. elymaitica* really belong to the *Caninae* ?

Such questions as these, added to the major outstanding problems of why the *Caninae* and the *Cinnamomeae* are so difficult to divide into Linnean species and why they have such an infinite number of microspecies, prompted an attack on more modern lines.

Täckholm for all the roses and Professor Harrison and myself for the British roses set on foot studies on the cytology, and later Hurst and also Erlanson took up the tale of the chromosome as well as breeding experiments. More recently Gustafsson and Håkansson have again considered the chromosomes in relation to a series of artificial hybrids.

From the work of these various authors we can pick out the most salient cytological characteristics. The basic number of chromosomes for the roses in general is 7. The Field Rose (*R. arvensis*), the Japanese Rose (*R. rugosa*) and many others have 7 chromosomes in the reproductive cells and 14 in the vegetative cells, and are referred to as diploid species. The Burnet Rose (*R. pimpinellifolia*) and the Provence Rose (*R. damascena*) have 14

and 28, as also have a number of the American members of the *Cinnamomeae*. In America also we have *R. nutkana* and *R. acicularis* with the numbers 21 and 42 ; and lastly some *R. acicularis* have 28 and 56. All these species behave in a perfectly normal way in the reduction divisions and with regard to them we must conclude with Erlanson that—"Chromosome number has proved to be no more than another important diagnostic characteristic". To take an example, the chromosome number may tip the scale in identification between a choice of two species if these are known to have different numbers ; indeed, you may not actually have to count the chromosomes because their tally may be indicated by the size of the pollen grain on your herbarium sheet.

In contrast to this straightforward cytology we find something quite different when we consider the section *Caninae*, to which most of our native roses belong. Here the vegetative parts of the plants may have 28, 35 or 42 chromosomes but one and all behave in an irregular manner in the reduction divisions : you could not expect a plant with 35 chromosomes to behave normally, but the others behave in a similar style.

In producing the pollen, (plate 3), 7 pairs of chromosomes appear on the equator of the first spindle, surrounded by the remainder of the chromosomes unpaired (univalents). The pairs of chromosomes separate first and move to the poles, followed by halves of the univalents. This behaviour is rather like that of the classic hybrid sundew, described by Rosenberg, but there the plant is completely sterile and most wild roses produce perfectly good hips full of fruits. If these roses are hybrids, how is it that seed is produced ?

The first suggestion was that seed arose by apomixis or the production of seed without fertilization. By cutting off the top of the bud and obtaining seed, apomixis was demonstrated in some cases, but this could not always be because wild plants, obviously hybrids between two Canine species, were found, and required explanation.

The mystery was solved by examining the reduction division on the female side. Taking as an example a rose with 35 chromosomes it was found that in the first reduction division all the 21 univalents remained at one pole of the spindle and were presently joined by 7 chromosomes from the bivalents to form a nucleus from which ultimately the egg cell was derived (plate 4). The egg therefore had $35 - 7 = 28$ chromosomes. Looking more carefully on the male side and counting the chromosomes in the good-looking developing pollen, it was noticed that this always contains about 7 chromosomes. Apparently pollen with more (or less) chromosomes does not survive.

Considering then fertilization, we have the chromosome set of the fertilized egg with $28 + 7$ chromosomes, which gives the parent number again. Thus, by the difference of behaviour in

pollen and ovules, plants, presumably upset by hybridity in their far back ancestry, are nevertheless able to continue to reproduce by a new and unique type of balance.

Hybrids between such species will be much more like the mother, as Gustafsson and Håkansson have lately proved, and so give rise to a false idea of a large occurrence of apomixis, whereas really both new and old hybrids within the *Caninae* normally reproduce by the method described. So it comes about that this group of roses has been able to spread and to produce in Europe as large and complex a group as is the *Cinnamomeae* of America which reproduces by the more orthodox method.

How then has cytology helped taxonomy here ?

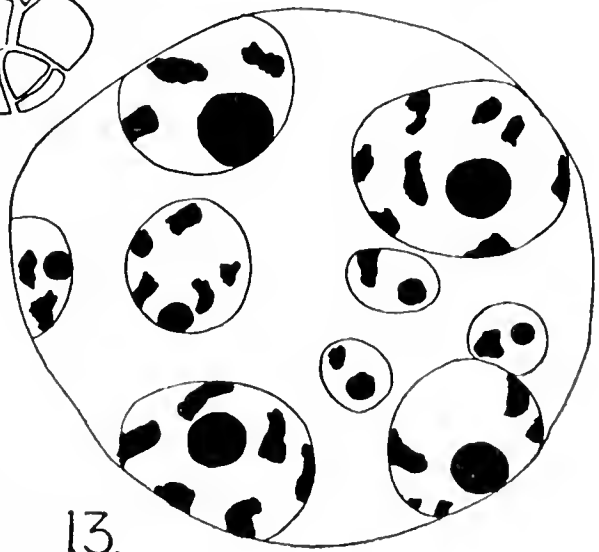
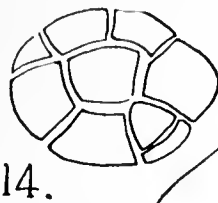
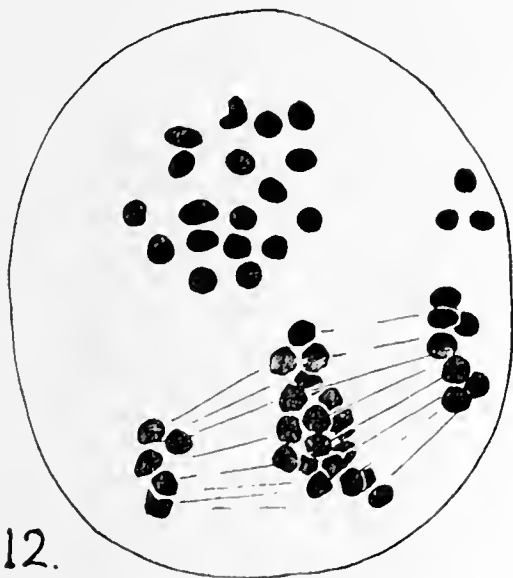
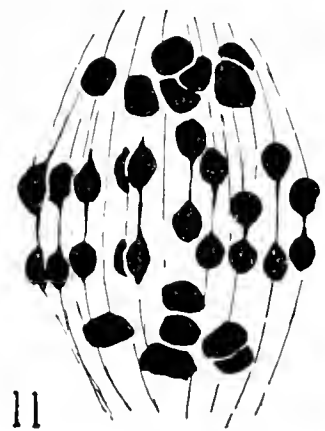
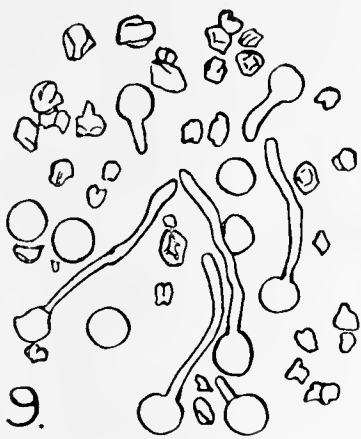
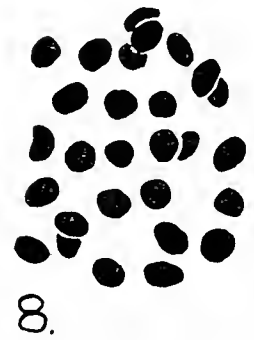
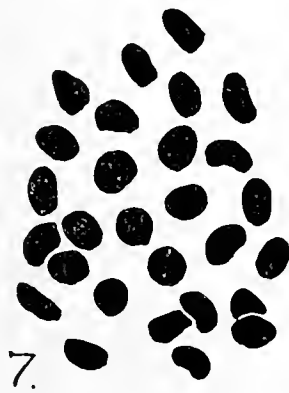
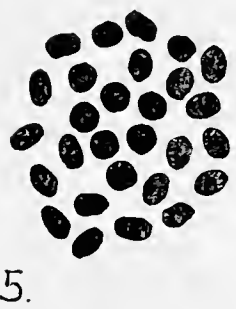
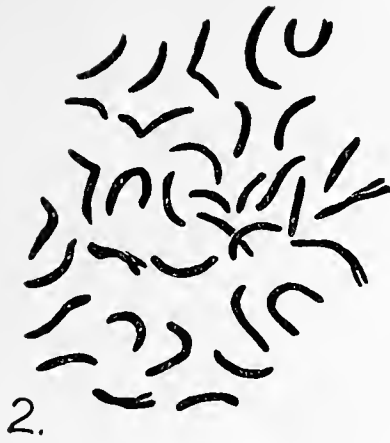
First we find that the *Caninae* is a homogeneous section marked off from the rest of the roses by its unique method of reproduction. It therefore follows that we can recognize whether a plant belongs to the *Caninae* or not. *Rosa elymaitica* has only 14 chromosomes, according to Täckholm, and must therefore be of normal type and be excluded from the *Caninae*.

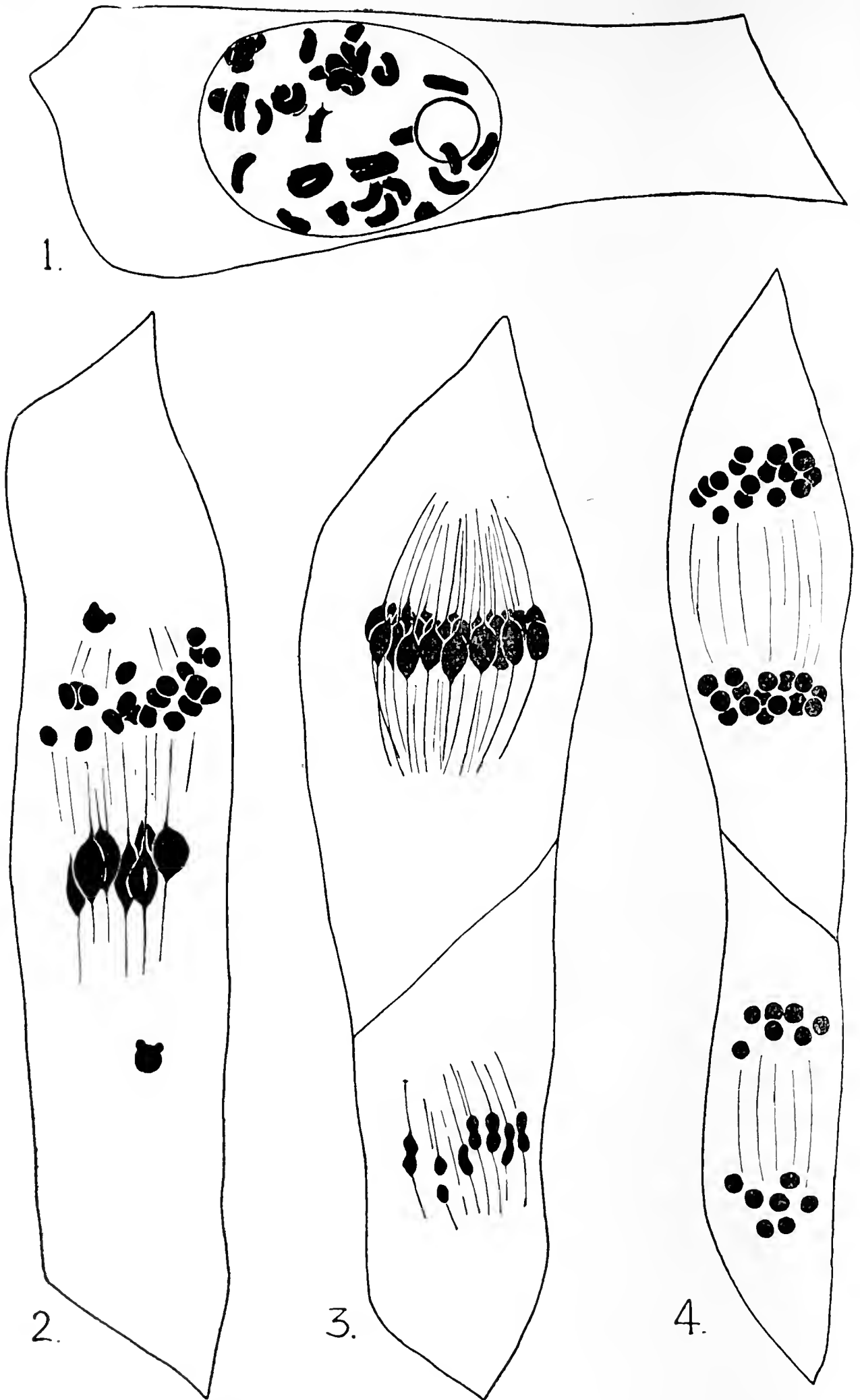
On the other hand *Rosa stylosa*, to some extent intermediate in character between *Synstylae* and *Caninae*, reveals a chromosome number of 35 or 42 and a Canine type of behaviour and therefore should be put as a subsection of *Caninae*, rather than within the *Synstylae* after Déséglise, or in a Section next to *Synstylae* as Crépin has it.

Development of Pollen in some Pentaploid Canine Roses

(Figs. 1, 5, 10, 12-14 from *Rosa tomentosa* var. *Richardsoniana* Harrison ; 2, 6 and 9 from *R. rubiginosa* L. ; 3, 7 and 11 from *R. canina* L. x *R. caesia* Sm. ; 4 and 8 from *R. Afzeliana* var. *berniciensis* Blackburn).

- 1-4 The vegetative set of 35 chromosomes of the above pentaploid roses.
- 5-8 Chromosome plates of these roses at the pollen mother-cell division, showing 7 pairs of chromosomes in the centre and 21 unpaired ones round them.
- 10 "Diakinesis", an earlier stage in division, showing the paired chromosomes more clearly.
- 11 Side view of the spindle : paired chromosomes have separated and are travelling to the poles followed by halves of the unpaired chromosomes.
- 12-14 At the second division the chromosomes are again in two sets and behave in a very irregular manner. Nuclei are of various sizes, as are the pollen grains which later form round them.
- 9 Good and bad pollen grown on sugar agar. The good grains are described as containing about 7 chromosomes, probably derived from the original paired chromosomes.





Development of Megaspores in the Ovule of a Pentaploid Canine Rose

1. Spore mother cell at diakinesis showing 7 pairs of chromosomes and 21 unpaired. (*Rosa tomentosa* var. *Richardsoniana* Harrison).
2. The unpaired chromosomes remain at one pole of the spindle and become incorporated in the upper nucleus with seven derived from the pairs.
- 3 & 4. Stages of the second division, a larger number of chromosomes passing to the uppermost cell. The figures do not show the full number of chromosomes which for embryo sac and egg is 35-7-28.

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The paper was discussed by Dr. Warburg and Dr. Young.

DR. WARBURG asked : (1) What is the present position of apomixis in *Rosa* ? Early workers believed it was usual but recent Scandinavian workers deny its existence. From field observations he thought it probable that it occurred. (2) What is the chromosome number (or numbers) in *R. Sherardi*, for which various numbers have been reported ? Is chromosome number of any value in separating *R. Sherardi* from allied species ?

DR. BLACKBURN replied that she thought the Scandinavian statements concerning apomixis were too sweeping, a great deal more work would need to be done before all the earlier experimental results could be judged erroneous. With regard to *R. Sherardi* she was at present re-examining some of the forms reported as tetraploid and hoped to know the answers to the questions at an early date.

DR. YOUNG pointed out that the undoubted hybrids mentioned by the lecturer could not possibly have been formed except by sexual crossing, and enquired whether it was possible that the roses could reproduce both apomictically and sexually.

DR. BLACKBURN replied : Yes, possibly, as in *Rubus*.

AN INTRODUCTION TO THE STUDY OF RUBUS

By W. C. R. WATSON

The genus extends over the five continents. With the exception of *R. saxatilis* all the primary Eurasian-Arctic species are found also, with variations, in N. America ; but apart from this no close relation is traceable between the species in Europe and those in America. A very few British species are known to occur, with allied species, in N. Africa, Madeira and the Canary Isles.

Some of the species that gave rise to the present British species are no doubt extinct, but some primitive progenitor-species still exist, and others may be recognized in time to come in Britain or on the continent. As will be seen from *R. caesius* it is not necessary that a progenitor should have been a diploid, or even a pure 'sexual' species.

It may be useful to state certain results of investigations so far as they have a bearing on the mode of origin of new forms, or on what may be observed taking place naturally in the field.

- (i) The diploid 'sexual' *R. ulmifolius* is found to be very largely self-sterile. Necessary intraspecific cross-fertilisation opens the door to recombination of characters, explaining the variation observable in *R. ulmifolius*, and is also liable to lead to reduced pollen fertility.
- (ii) The diploids *R. ulmifolius* and *R. idaeus* have not been successfully crossed together.
- (iii) The tetraploids are not autonomous apomicts. The prevention of all pollination has the effect of preventing the formation of fruits and seeds ; but as a result of self-pollination or cross-pollination, by the same species or by a different species, fruit and seeds will develop, yielding in the case of cross-pollination by a different species either (a) true hybrids, showing that sexual reproduction has ensued, or (b) offspring all identical with the mother plant, showing that induced apomixis (pseudogamy) has occurred, or (c) offspring, of which some agree with the mother plant, and some show characters of both parents.
- (iv) *R. caesius* when pollinated from a different species uniformly gives *R. caesius* as offspring ; but when any *Morifer* (see below) is pollinated by *R. caesius*, the offspring are hybrids.

It will be instructive summarily to review the characters of the extant primary European species, since they afford examples of the origin of tetraploids, noting what characters and tendencies have descended to our present-day British species.

Circumpolar. Prickles Wanting.

R. arcticus L. ($2n = 14$: pollen pure). Arctic-alpine. Silicicole. Woods, pastures. Hermaphrodite (ssp. *acaulis* Michx., in Canada, is dwarf and dioecious). Stem short, annual, from the creeping root, with simple and 3(-5)-nate leaves. Stipules broad, cauline. Flowers terminal and, sometimes, axillary. Receptacle rounded convex. Fruit blackish purple. Closely allied forms in Central Asia.

R. Chamaemorus L. ($2n = 56$). Arctic-alpine. Boggy ground. Dioecious. Stem short, erect, annual, from the creeping root. Leaves simple. Stipules broad, cauline. One solitary, terminal flower. Fruit crimson-orange.

Eurasian. Prickles present. Hermaphrodite.

R. saxatilis L. ($2n = 28$: pollen pure). Arctic-alpine. Calciphile. Woods and rocks. Barren shoot slender, procumbent, rooting at the tip in autumn, then dying back to the base. Flowering shoot from the base of the barren shoot. Leaves 3-nate. Stipules cauline-petiolar. Occasionally the procumbent shoot bears axillary flowers. Flowers small. Petals narrow, white, erect, glabrous. Fruit red. (The hybrid with *R. arcticus* is fertile.)

R. idaeus L. ($2n = 14$: pollen pure). Arctic-alpine. Lowland. Silicicole. Woods. Stem strong, erect. Suckers from the creeping roots. Leaves pinnate, usually felted beneath. Stipules petiolar, filiform. Flowers drooping in bud. Petals small, narrow, white, glabrous. Fruit red or amber, finely felted. Var. *denudatus* Schimp. & Spenn. has leaves green and subglabrous beneath. Related species in N. America.

R. caesius L. ($2n = 28$: pollen pure). Lowland. Calciphile. Watersides, damp woods. Stem trailing, strongly pruinose, terete, freely branching and rooting at the tips in autumn. Leaves 3-nate, lateral leaflets subsessile. Stipules petiolar, narrow-linear at the base expanding into an ovate blade. Flower buds erect. Fruit black, pruinose. *R. caesius* does not enter the polar circle, but is limited at a considerably lower altitude than the foregoing four species.

All the above species flower in May, both in northern latitudes and in Britain. The fruit is highly flavoured and fragrant. The leaves are shed in autumn. The floral disc secretes nectar, is closed over by the erect stamens in *R. arcticus* and *R. idaeus*, but is exposed and accessible from above in the rest.

In *R. arcticus* the shoot has, exceptionally, leafy axillary branches, bearing more than one flower : the petals may be entire, or notched at the apex or along the sides : the flowers open widely ; petals, stamens and styles are all purple (entomophilous !). *R. arcticus* is fertile only in a restricted latitudinal belt, 62° — 65° in Finland, 60° — 64° in Russia, but flowers regularly both north and south of those limits.

R. arcticus and *R. Chamaemorus* frequently have flowers with supernumerary petals (7, 8 or 10).

R. caesius and *R. idaeus* have a biennial stem, with bark disrumpent after the stem dies.

R. caesius and *R. saxatilis* have one fruit or a few principal fruits of 14—20 drupelets and the rest of the fruits of 1—6 drupelets.

R. arcticus is normally eglandular, but var. *pseudoarcticus* O. Kuntze has pedicels and calyces glandular, as is the case in *R. caesius*.

Certain varieties of both *R. caesius* and *R. saxatilis* are copiously glandular in the panicle.

R. idaeus is visited by night-flying moths, which alight on the flowers. Occasionally plants with male flowers only are produced, having, as secondary sexual characters, blunt leaflets and blunt sepals. The hermaphrodite plants have acuminate leaflets and sepals.

R. saxatilis and *R. caesius*, each with $2n = 28$, have unlike pairs of chromosome sets, and must therefore be of hybrid origin (allo-tetraploids). *R. saxatilis* is perhaps from *R. arcticus* \times *idaeus*: it has much the same range as those species. *R. caesius* is perhaps another later form of the same origin, closer to *R. idaeus*; or possibly is from *R. idaeus* \times *saxatilis*. It overlaps the distribution area of *R. saxatilis* and *R. idaeus* but is more southern than those species.

RUBI MORIFERI FOCKE

The older species that occupy the west, the east and the south of Europe, but not the high north and the western isles of the Atlantic, may now be considered. They all have perennial, non-suckering roots, and biennial or perennial stems not flowering in their first year. They have black fruits, devoid of pruina or permanent felt.

I. WESTERN AND SOUTH-WESTERN SPECIES.

R. ulmifolius Schott fil. ($2n = 14$; pollen usually pure: ssp. *heteromorphus* Rip., $2n = 28^*$; pollen pure). S. Europe, W. Asia, N.W. Africa, E. Atlantic Isles. Stem arcuate-procumbent, pruinose, finely stellulately downy. Prickles strong. Leaves rather small, subcoriaceous, closely white-felted beneath, persisting through winter. Panicle strongly developed and strongly armed. Petals roundish-cuneate, margin crisped, deep rose, as are also the filaments and styles. Entirely eglandular. Coming into flower, in Britain, after midsummer. Variable.

R. incanescens Bertol. ($2n = 14$: pollen sometimes pure). Italy, S. and N.E. France, E. Spain, N.W. Africa. Recalls *R. grandifolius* in its pyramidal elongate glandular panicle, but approaches *R. tomentosus* in the white-felted leaves, the densely felted-villose panicle and the mixed glands and acicles on stem and panicle.

* fide Miss Y. Massey in lit.

R. grandifolius Lowe. (Chromosomes and pollen not studied) Madeira. Stem glabrous, eglandular, prickles broad-based, hooked. Leaves very large, glabrous; terminal leaflet ovate-oblong, cordate, acuminate (like *R. macrophyllus*). Panicle pyramidal compound with intricate racemose branches, followed above by a simple racemose upper part, furnished with numerous weak long-stalked glands and, below, numerous minute pricklets. Flowers large, white, on long weak pedicels. Fruit elongate, a long time red before ripening, dryish. Sepals patent.

R. Arrhenii Lange. ($2n = 28$: pollen about 68% pure). England, Holland, N.W. Germany and Denmark. The *Sprengeliani*, to which *R. Arrhenii* belongs, form a natural group, with a distinctive Atlantic distribution, and are presumably descended from a common primitive ancestor. *R. Arrhenii* is a small, slender bramble, with small flowers, very short stamens, erect sepals, and concolorous leaves, which are retained throughout the winter.

II. EASTERN SPECIES

R. tomentosus Borkh. ($2n = 14$: pollen often almost pure, but also frequently only about half pure). S. Asia, S.-West and Central Europe. Stems of two kinds, one erect, not rooting, furrowed, glabrous, the other low-arching, more hairy, rooting. Leaves of a characteristic shape, the leaflets rhomboid, with unequal or rather compound shallow but rather coarse triangular blunt teeth, terminating in a callous point, not in a mucro. Petiole channelled. Leaf-fall in winter. Flowers white, yellowish white or pinkish. Fruit dryish, rather hard.

This diploid is extraordinarily variable. On different plants, stem and flowering branch may be (1) eglandular and without pricklets; or (2) slightly, or abundantly, glandular, aciculate, and aculeolate; or (3) the stem may be as in (1) whilst the flowering branch is as in (2). Then, in different plants, the leaves may be (4) glabrous above; or (5) closely stellately felted above. Each of these last two types may have the variations (1), (2) or (3).

R. tomentosus crosses with *R. ulmifolius*, but the stalked glands, acicles and pricklets rarely pass to the hybrids.

In the region of the Caucasus and Persia (to which *R. tomentosus* extends) there are other apparently primary species requiring brief notice.

R. persicus Boiss. (*R. Raddeanus* Focke). Pollen pure. Chromosomes? Related to *R. tomentosus* in its white felted leaves and yellowish-white petals; but according to Focke rather to *Suberecti*, which it resembles in its erect stems forming dense thickets and producing few-flowered racemes. Like them also it flowers in May.

R. moschus Juzepczuk. (*R. caucasicus* Focke). Pollen 91% pure. Probably $2n = 14$ (Gustafsson). Characters of *Glandulosi*. Stem strongly pruinose. Leaves large, white-felted beneath. Leaflets

serriculate. Petals small, narrow, erect, white, resembling those of *R. idaeus*.

R. hirtus W. & K. Pollen 80% pure. Chromosomes? Caucasus. Mountain chains of Europe, descending the Rhine Valley to Belgium and S.E. England. This is a typical member of the *Glandulosi*, which contains several other forms with pollen as good as in the known diploids.

CLASSIFICATION

The British blackberries are classified on phylogenetic lines, as far as possible, using form, phenology and distribution as a guide. Owing to the numerous cross affinities this results in only a partially natural arrangement, but certain groups that have been recognized and introduced seem to be in part of common ancestry, and natural.

It may be mentioned that all blackberries when in the seedling stage bear gland-tipped fine prickles and acicles, and only settle down in their second year to produce the armature characteristic of them.

The classification runs as follows :—

1. *Suberecti*. Derivatives of *R. idaeus* × *Silvatici* and *Sprengeliani*. The attention is attracted by the thicket of upright canes produced by the suckering of the roots. They begin to flower late in May or early in June, and lose their leaves in autumn. Leaves with seven leaflets are frequent. On peat, or siliceous heaths, or in woods, or beside running water. *R. nitidus* and *R. integribasis* incline to build up isolated bushes; *R. plicatus* to form tufts.

2. *Corylifolii*. Derivatives of *R. caesius* × *Moriferi*. Patent stem-prickles and subsessile basal leaflets, together with other partial likenesses to *R. caesius*, mark the group. Flowering from late May or early June, and intermittently until autumn. (Protracted flowering is a general mark of *Rubus* hybrids.)

Rubi Moriferi

3. *Sprengeliani*. Flowers usually small (< 2cm.), stamens short, habit low and slender. Apparently a primitive group, whose further distribution has been arrested by changed climatic conditions.

4. *Silvatici*. The *Virescentes* stand nearer to *Suberecti*, the *Discoloroides* nearer to *Discolores*. Stems biennial in some species, perennial in others. Those species with a low percentage of good pollen (*R. rhodanthus* 18%, *R. Questierii* 19%) seem to do as well, and to spread geographically as far, as those with a much higher proportion (*R. gratus* 81%, *R. Schlechtendalii* 82%, *R. danicus* 84%).

5. *Discolores*. Eglandular, with rare exceptions. Leaves more or less closely white-felted with stellulate hairs beneath. Flowering scarcely before midsummer. *R. Winteri* appears to be

the latest of all brambles to come into flower, producing excellent late fruit.

6. *Vestiti*. The usher-group of the *Heteracanthi*, groups 3, 4, and 5 being *Homalacanthi*. *R. vestitus*, *R. Boraeanus*, and *R. adscitus* are the central types of the group. The two former species show well the scattered stout pricklets on the stem, which recur in some of the more advanced groups. Although many of the species are furnished with a dense coat of hair, the criterion of the group is not this, but the possession of a fair number of stalked glands, acicles and sometimes pricklets.

7. *Rotundifolii*. The typical species are *R. mucronifer* and *R. rotundifolius*. Both have large, broad leaflets, with a rounded even outline, regularly toothed, and a good deal hairy. Rather long acicles, some gland-tipped, along with shorter stalked glands and acicles, are irregularly distributed on the panicle, and are almost absent from the lower part of the stem. There are no instances of red or reddish styles in the group.

8. *Radulae*. Equal prickles confined to the angles of the stem, and numerous short, subequal acicles and stalked glands—these are the characters of the group.

9. *Apiculati*. This group has stalked glands, acicles and pricklets rather longer and more unequal than in *Radulae*, and divides readily apart into well-defined smaller groups. Red-styled flowers are very frequent. Panicle usually rather equal and truncate.

10. *Grandifolii*. Pricklets mostly give place to unequal slender smaller prickles accompanying the ordinary large prickles. Panicle often much elongated and taking one of two forms, (a) pyramidal with protracted racemose apex (e.g., *R. festivus*), or (b) broad, lax, interrupted, pyramidal, with spreading cymose branches and abrupt apex (e.g., *R. Moylei*). The showiest and most luxuriant species are found in this group.

11 and 12. *Hystrices* and *Glandulosi*. Both groups have graded acicles, stalked glands and prickles, although sometimes the acicles or the stalked glands, or both, are neither very numerous (e.g., *R. Hartmani*), nor so very long (!). The *Hystrices* panicle has cymose middle branches, whilst the *Glandulosi* panicle has all branches racemose, i.e., with the fourth pedicel coming off the peduncle, not off one of the pedicels. Prickles are usually broad-based and strong in *Hystrices*, narrow-based and weak in *Glandulosi*. Petals often white and narrow in *Glandulosi*, broader and often pink or rose in *Hystrices*. *Glandulosi* are distinctly rare in England, still more so apparently in Scotland, Ireland and Wales.

DISTRIBUTION, ETC.

1. *Suberecti*. These appear to have arisen in Pliocene times and to have spread in a general S.E. direction into W. Europe from a centre in the neighbourhood of Iceland. They are confined to

W. and especially N.W. Europe.

2. *Corylifolii*. These are found all over the distribution area of *R. caesius*, and are especially numerous in the northern countries of Europe. Nine out of our 18 forms are endemic.

3. *Sprengeliani*. The group is chiefly Atlantic in distribution. *R. Sprengelii*, for instance, occurs in the Channel Islands, Cornish Peninsula, S. Ireland, Welsh coast to S.W. Scotland (Wigtown, North Ebudes), most of the unglaciated counties of S. England : on the Continent from the Channel Islands to N. France, Belgium, Holland, N. Germany, S. Sweden and Denmark, with outlying stations in Central France and E. Germany.

4. *Silvatici*. Of the 83 British species 28 are apparently endemic, 27 others Atlantic, and 8 others N. Atlantic. In other countries of Europe the proportion of *Silvatici* in the *Rubus* flora is much lower than in Britain. This points to a western origin for the British *Silvatici*. The very large flowers of *R. Banningii*, *R. dumnoniensis*, *R. rotundatus* and *R. gratus* (up to 3.5. cm.) recall those of species found in the East Atlantic isles.

5. *Discolores*. All our *Discolores* are found in France, with the exception of *R. Brittonii* in the *Candicantes*. As they have an Atlantic type of distribution in N. Europe, it seems probable that they came to western Britain from W. and N.W. France, before the English Channel was opened.

6. *Vestiti*. The distribution of the *Vestiti* is mixed, but is mainly western. There are few British endemics (5 only out of 29).

7. *Rotundifolii*. With one exception (*R. Mullerii* Lef.) all the British species are confined to N.W. Europe. Three are endemic in Ireland, three endemic in Great Britain, whilst four others are found also in low latitudes of N.W. Europe.

8. *Radulae*. *R. Radula* and *R. echinatoides* are markedly northern species, whilst *R. Genevierii* and *R. discerptus* are markedly southern (Portugal). An original distribution of already formed species from the west and north-west seems to be indicated. Seven of the species occur in Ireland. There are two endemics.

9. *Apiculati*. The position is similar to that shown by the *Silvatici*. Out of 73 British species 21 are endemic and 27 Atlantic : out of the 21 endemic, 14 are peculiar to the west of Britain. Instances of extension to the north, or from the north, are extremely rare : whilst, on the other hand, there are several instances, chiefly in *Scabri*, of the presence of a British species in the Pyrenees or the south of France. (It is not to be assumed that all "endemics" have necessarily originated here. They may have originated, for example, in land situated west of Ireland, or south-west of Cornwall. Or they may have arisen in the west of France, spread to this country, and become extinct in France).

10. *Grandifolii*. Of the 18 native species 11 are endemic and 4 Atlantic, apparently survivors and derivatives from types related to *R. grandifolius* in Madeira.

11. *Hystrices*. Six only of the 27 species are endemic; eight others are Atlantic, and a few of these may have come to us from France or the extreme N.W. of Germany. The rest seem to have come from Germany beyond the Rhine, or in part down the Rhine Valley itself; *R. pilocarpus*, for instance (with nearly perfect pollen), came probably from Switzerland. There are several significant examples of extremely discontinuous distribution, suggestive of ancient extension and long continued attrition.

12. *Glandulosi*. Of 16 species three only are endemic. These are local and western: *R. Durotrigum*, Dorset only; *R. aristisepalus*, Wales and the Welsh border; *R. pallidisetus*, Wales, Leicester and S.W. England. They line up with four others in the London Basin, which although found in Central or far Eastern Europe occur also in the Pyrenees or S. France, viz., *R. vepallidus*, *R. hylonomus*, *R. perplexus* (Caucasus and Pyrenees), and *R. purpuratus*. With these exceptions it seems that the *Glandulosi* entered across a land connection from the Continent which covered the southern part of the North Sea.

To summarize: some 330 species have been found in Great Britain and Ireland. Of these, 96 are endemic—though not necessarily of native origin—including four purely Irish, five purely Welsh, and 29 others western. Not one of these can be said to be a purely local form. Of the remaining 234, 105 have an Atlantic distribution, of which 14 range rather to the north. This leaves 129 which are found also further east in Europe, 48 of them with a certain western tendency, keeping to the west of the Weser and the Danube. From this progressive diminution in numbers going eastwards it must be concluded that the British bramble flora has, for the greater part, not spread from the east, but has survived *in situ* from Pliocene times. This conclusion is supported by the fact of the survival of numerous species with discontinuous range upon the higher-lying terrain in the London Basin that has not suffered appreciable down-grading by subaerial or marine agency since early Pliocene times.

(It may be mentioned that a Key to all the Sections and Series of British Rubi is appended to the *Rubus* list in the *Journal of Ecology*, vol. 33, "Check List").

The paper was discussed by Mr. Wilmott, Dr. Dony, and Dr. Warburg.

MR. WILMOTT asked whether some of the groups were not of the nature of "rubbish dumps" made up of species which could not be fitted into other groups.

MR. WATSON said that this was a weakness of the large group *Egregii* figuring in older classifications, which he had discarded.

He granted that the new Series *Incompositi* in the Section *Apiculati* was made up of miscellaneous species of *Apiculati* that did not fall into the other Series of that Section. No doubt it would have been possible to take out three or four minor groups from this residue (see the published diagnosis of *Incompositi*). But he thought it a more workable arrangement not to create separate Series for very few members. In his opinion most of the new, as well as the old Series freshly introduced into his List represented well-defined and fairly natural groups.

DR. DONY asked if Mr. Watson could explain the discontinuous distribution of some species. For example, *R. sulcatus* occurred in Bedfordshire and the nearest station to this was at Boar's Hill forty miles away and it apparently had one other station equally distant. Similar cases could be mentioned for other species.

MR. WATSON said that this was indeed true of *R. sulcatus*. It could be explained by glacial action; plants now thus dispersed were formerly of more continuous distribution but had been obliterated by the ice-sheet or by the outwash from the ice-front.

DR. DONY asked whether, arising from this reply, Mr. Watson would say that some species were more capable than others of extending their range, and whether the rarer brambles tended to be isolated bushes remaining fixed while every waste patch was eventually colonised by the more common brambles?

MR. WATSON said that the older species seemed to have been unsuccessful in many cases in establishing themselves in the areas affected by the later glacial stages, whereas the newer species had done so. He did not suppose that temperature and soil conditions had been the predominant factors governing distribution.

MR. WILMOTT mentioned that Mr. Rilstone had told him that one bramble which he had thought to be a local endemic in Cornwall had been found in another station far away in Devon. MR. Wilmott stated his opinion that apomixis was in some way connected with the re-distribution of species caused by the glacial periods, some species migrating after them into the areas where allied species had survived, whereby species formerly isolated came into contact. These might have been able to cross, but the hybrid may have been incapable of producing offspring by normal methods and yet with cytoplasm not completely incompatible. The well known apomictic genera, *Rubus*, *Alchemilla*, *Hieracium*, and possibly *Crataegus* in North America which he had not studied, produced their welter of forms in and around the glaciated areas but seemed to be represented by normally distinct species outside these areas.

MR. WATSON did not agree that the pseudogamous *Rubus* species seemed confined to, or to the neighbourhood of, the glaciated areas.

FORMS OF VALERIANA OFFICINALIS L.

By T. A. SPRAGUE

Valeriana officinalis, the medicinal Valerian, has diploid ($2n = 14$ chromosomes), tetraploid (28) and octoploid (56) forms, but the number of chromosomes is not *definitely* correlated with external morphological characters. Hence it seems best to treat it as a single polymorphic species. All three forms occur on the Continent of Europe, but in Britain only tetraploids and octoploids have been found.

Drabble (1933) distinguished three species in the *Valeriana officinalis* complex, namely, *V. sambucifolia* Mikan, *V. officinalis* L. sensu stricto, and *V. angustifolia* Host. The British forms named by him *V. sambucifolia* and *V. angustifolia* are not quite identical with the Continental forms described under these names, judging from the herbarium specimens and descriptions in Floras (Sprague, 1944). The principal diagnostic characters given by Drabble are :

1. *V. sambucifolia* : lateral leaflets 3—5 pairs, broadly lanceolate or ovate, toothed on both margins, terminal leaflet larger than the others and with very broadly rounded apex which bears large teeth of which the uppermost are often as long as, or nearly as long as, the apex, which is usually obtuse ; stolons long.

2. *V. officinalis* : lateral leaflets 7—8 pairs, ovate-lanceolate to linear-lanceolate, acute or acuminate, narrowed to the base, all toothed, usually more abundantly on the basiscopic margin, acroscopic margin sometimes entire, terminal leaflet not much larger than the others, often no larger, acute ; stolons usually short.

3. *V. angustifolia* : lateral leaflets 7—9 pairs, those of the lower leaves narrow, linear-oblong, parallel-sided, obtuse, entire, scarcely narrowed to the base, strongly decurrent, those of the stem-leaves narrowly linear-lanceolate, acute or subacute, entire (or rarely with a few teeth), narrowed at each end, sessile, decurrent, terminal leaflet little or not at all broader than the others ; stolons usually short or absent.

Study by the writer of living plants and of herbarium specimens of 200-300 separate plants from about forty different localities in the Cotswold Hills, Gloucestershire, led to the conclusion that, while certain plants agreed fairly well with Drabble's descriptions, the specimens, as a whole, formed *a more or less continuous series*, comprising many different forms. The differences between these appeared to be almost entirely vegetative. There were greater morphological differences between the Cotswold specimens corresponding to Drabble's *V. sambucifolia* and his *V. officinalis*, than between those corresponding to his *V. officinalis* and *V. angustifolia*. At the same time, extreme forms, in the absence of intermediate specimens, would certainly have been treated as distinct species in herbaria. As the extreme size and vigour of certain plants of Drab-

ble's *sambucifolia* type found at Sapperton suggested that they might be polyploids or higher polyploids, the collaboration of a cytologist Dr. Maria Skalińska, was obtained. Dr. Skalińska made two visits to the Cotswolds, and, in company with the writer, visited a selection of typical localities of the species, including those of some of the more peculiar forms, and collected a number of living plants for transplant experiments by her at Kew. These were supplemented by living plants sent to her subsequently by the writer. Preliminary examination of living material in the Cotswolds showed a marked difference in the ranges of pollen grain diameter between typical specimens of the *sambucifolia* type * (mean 56 μ) and those of the *officinalis-angustifolia* type † (mean 47 μ). This suggested the possibility of predicting the chromosome number from pollen measurements, and this possibility was confirmed by examination of pollen from herbarium specimens and subsequent determination of chromosome numbers of living plants obtained from the same localities.

Prior to Dr. Skalińska's investigations (Skalińska, 1945, 1947), only octoploid forms of *Valeriana officinalis* had been found to occur in Britain (Todd, 1942). Dr. Skalińska proved the existence in Britain of tetraploid forms as well. The two polyploids are intersterile. The tetraploids seem to be confined to south England and parts of the Midlands, whereas the octoploids extend from the south of England to the north of Scotland and westward to west Wales and Cornwall. In England the northern limit of the tetraploid area corresponds roughly to the line connecting the Wash and the Bristol Channel. Although the areas of the two types overlap, the plants occupy different habitats in their common area and are thus separated ecologically.

In Gloucestershire, plants of the *sambucifolia* type are octoploids and those of the *officinalis-angustifolia* type are tetraploids, and in nine cases out of ten, it is possible to predict the chromosome number from the external morphology coupled with the nature of the habitat, but the chromosome number of intermediate plants growing in intermediate types of habitat can be determined only by cytological examination, although, as mentioned above, pollen measurement affords a good method of prediction in nearly all cases, owing to the higher range exhibited by the octoploids. Within the tetraploid area in England, the tetraploids occur in hilly regions, on slopes and escarpments, as well as in dry valleys, whereas the octoploids occur by rivers and canals in swampy soil with a higher degree of acidity. The tetraploids in England occur on Chalk, Oolite, Carbomiferous Limestone, Calcareous Boulder Clay, and possibly on Lias Limestone. Outside the tetraploid area, however, the octoploids not only occur along river banks and ditches and in bogs, as well as along margins of roads, and roadsides, but have been found at higher altitudes, on dry steep slopes, and even

* Subsequently determined as octoploids.

† Subsequently determined as tetraploids.

in cracks of limestone rocks. Outside the tetraploid area, octoploids of the *angustifolia* type have been found which are indistinguishable from tetraploids by external characters.

Many different forms, both of the octoploids and of the tetraploids, occur in the Cotswolds. As the result of Dr. Skalińska's transplant experiments, it appears that some of the morphological differences exhibited by these forms are phenotypic, whereas others have a genic basis. On the same tetraploid individual, collected in the autumn before the year of flowering, there was a transition from the oldest ground leaf, with 9 pairs of narrow leaflets, entire or only slightly toothed on the basisopic margin, to the youngest with 6—7 broad leaflets, coarsely toothed on both margins.

A giant octoploid about 6ft. high, growing in marshy ground beside the river Frome at Sapperton, represented an extreme development of the *sambucifolia* type. It had cauline leaves up to 15 inches long, and leaflets up to 5 inches long, very coarsely toothed on both margins; the lower bracts were *foliaceous* and unifoliolate, with a very coarsely-toothed margin; the leaves on the lateral branches resembled those on the main stem of a plant of the ordinary *sambucifolia* type. Another striking octoploid, found only near the hamlet of Perrott's Brook, on the River Churn, has exceptionally broad leaflets, with the successive pairs *overlapping* downwards. A third octoploid, found only in an alder-ash copse at the south-west corner of Hilcot Wood, Colesbourne, in very spongy black soil close to a permanent spring, has lanceolate lateral leaflets, *hardly toothed on the acroscopic margin*.

Tetraploids with *long- and finely-toothed leaflets* were found in more than one locality. An outstanding tetraploid with a *very short leaf-rhachis* and numerous *crowded* linear-lanceolate acuminate sparsely toothed leaflets occurred near Rendcomb and near Lower Hilcot.

Reproduction of *Valeriana officinalis* in Gloucestershire is mainly vegetative, by means of slender rhizomes arising from the base of the stem: these have relatively long internodes and root at one or several nodes, producing young plants. A further but rare mode of vegetative propagation is by means of bulbils (Sprague, 1944). There seems to be little doubt that *V. officinalis* propagates also by means of seed in Gloucestershire, though no young plants which could be proved to be seedlings were found. As Irmisch (1853) pointed out, however, the slender primary root dies during the course of the first summer, and it is then no longer possible to distinguish the seedlings from young plants produced by vegetative propagation, though the absence of the decayed base of a parent plant close by may point to their seedling nature. Series of young plants, borne successively on a more or less slender rhizome, are of two kinds. In ordinary vegetative propagation from a parent plant the series is a *descending* one, the first young plant being the largest and the others successively smaller. *Ascending* series of much

smaller plants are also found : these presumably arise from seedlings, which die after sending out a short slender rhizome and producing a slightly larger plant, which in its turn produces a still larger one, and dies, until after several years the final plant in the chain is large and vigorous enough to flower. The occurrence of an isolated plant of *V. officinalis* in a small area, in which after careful search in previous years no plants of the species had been detected, also points to reproduction by seed in the Cotswolds. Nevertheless the great majority of the plants of *V. officinalis* seem to arise by vegetative reproduction. Sexual reproduction is by means of cross-pollination, self-pollination yielding negative results.

Two isolated tetraploid colonies were found, one near Little Colesbourne, the other near Pinswell Plantation. Each colony consisted of 20-40 plants all as like as two peas, and it can hardly be doubted that each had arisen from a single seedling.

In *Valeriana officinalis* it seems probable that 90—95% of the plants in a given population have arisen by vegetative propagation, and that individual clones may be represented in small areas by hundreds of plants. Further, owing to the potential great longevity, if not immortality, of these clones, we may get representatives of ancestors of many degrees of remoteness growing side by side with a small proportion of forms which have just been produced by cross-pollination between any two of these ancestors. The natural result will be a kaleidoscopic range of different forms such as is actually found in the Cotswolds. It seems probable that a low proportion of sexual as compared with vegetative reproduction in a particular species acts as a brake on further evolution. Suppose, for the sake of argument, that only one plant of *V. officinalis* in every twenty has grown from seed, and that one out of every hundred surviving seedlings has a combination of characters of increased survival value, it will be one progressive in a population of two thousand non-progressives. Only if the new form has some exceptional vegetative advantage over the old ones, will it be likely to replace them, since plants of *V. officinalis* are self-sterile. The dispersal of *V. officinalis* by vegetative reproduction seems to be very slow, and this may explain why particular forms have a very local distribution, as has been pointed out above, so far as the Cotswolds are concerned.

It seems to be generally agreed that the octoploids have arisen from tetraploid ancestors, and it is suggested that this change may have taken place in many different lines of descent. Speaking generally, the tetraploids in Gloucestershire occur in dry grassy places near woods and at the edges of woods or in clearings, whereas the octoploids are found in much wetter situations by streams and rivers, and in boggy ground. The question arises whether moisture and soil acidity may have played some part in promoting the change from the tetraploid to the octoploid condition. This suggestion might be tested by transplanting known tetraploids to extreme

octoploid habitats, after careful removal of all octoploids from the test area. If such soil conditions can induce chromosome doubling, it would explain the occurrence of a small octoploid population in the woodland hill-top bog (850 ft. alt.) at the south-west corner of Hilcot Wood, in the middle of a large purely tetraploid area. It seems less likely that an octoploid achene could have reached there from the nearest octoploid station in a river-valley at least $1\frac{1}{4}$ mile distant, and 250-300ft. lower, than that the bog had been colonized from the surrounding tetraploid population.

In conclusion it should be mentioned that Dr. Skalińska discovered a case of chromosome doubling in the somatic tissues of a tetraploid plant from Lower Hilcot in the Cotswold Hills. This somatic doubling was detected in a *sector* of the growing point of a young rhizome, comprising about one-eighth of the periphery of a transverse section. A further development of such a sector could give rise to a chimaera with a few octoploid shoots formed on a tetraploid plant.

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The paper was discussed by Mr. A. J. Wilmott and Dr. D. H. Valentine.

Mr. WILMOTT referred to two neighbouring patches of densely crowded seedlings seen in the Manifold Valley, Staffs., in 1947.

TAXONOMIC PROBLEMS IN GALIUM AND JUNCUS

By A. R. CLAPHAM

Galium palustre L. consists near Oxford of two distinct forms, both abundant :

(a) A big robust plant, 50-100 cm. high, but rather weak-stemmed. Stem variable in roughness but never *completely* smooth. Leaves 4-6 in a whorl, large, very variable in shape from lanceolate to elliptic or almost ovate, often broadly oblanceolate, usually blunt. Panicle branches at first erect, then spreading, but even in fruit not strongly reflexed. Flowers 4.5 mm. diam. Mericarps 1.6 mm. in diam., strongly shagreened. Guard-cells of stomata average 35-39 μ in length. Chromosome number : $2n = 96$.

(b) A much smaller plant, 15-30 cm. high, standing erect, variable in roughness of stem but with a higher proportion of very rough plants. Leaves small, 4 in a whorl, oblanceolate, usually blunt but sometimes acute or even slightly mucronate, often very rough on the margins. Panicle branches at first erect but soon spreading and becoming strongly reflexed in fruit. Flowering 2-3 weeks earlier than (a). Flowers 3 mm. in diam. Mericarp 1.2 mm. in diam., less strongly shagreened. Guard-cells of stomata average 25-30 μ in length. Chromosome number : $2n = 24$.

The two forms are more or less differentiated ecologically, the larger plant growing in permanently wet habitats, often at the landward edge of the reed-swamp zones of streams and ponds ; while the smaller tends to occur in localities which are damp, or even with standing water in winter only, but drying out in summer.

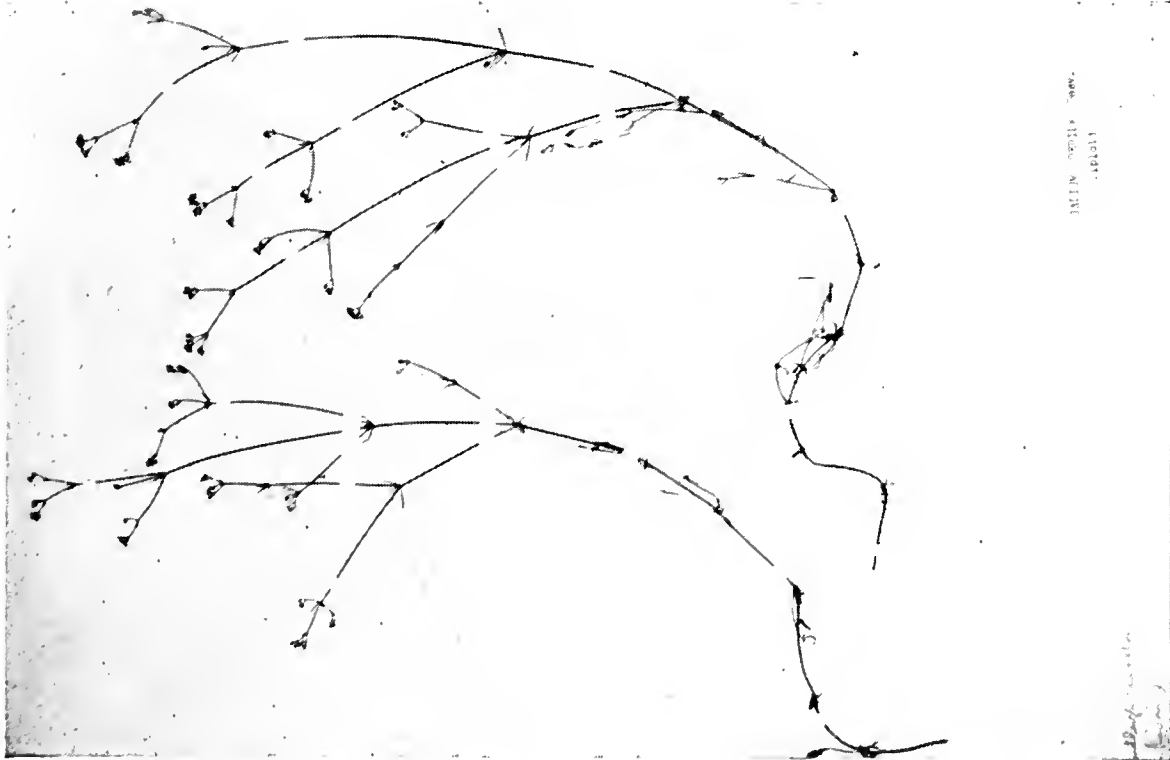
The larger plant appears to correspond with *G. palustre* var. *elongatum* Syme, *G. palustre* var. *lanceolatum* Uechtritz, *G. maximum* Moris. and *G. elongatum* Gren. and Godr. *G. elongatum* Presl is a quite smooth-stemmed plant, but specimens labelled thus in the Druce Herbarium are none of them completely smooth and do not differ in any describable way from some labelled *G. palustre* var. *lanceolatum* Uechtritz. There seems little doubt that all these names refer to octoploids, and that this shows a considerable but more or less continuous variation in leaf shape and stem roughness.

The smaller plant has often been called *G. palustre* var. *Witheringii* Sm. (*G. montanum* With., non L.), described as much smaller than the preceding, with very rough stems and ascending panicle-branches. The emphasis on the roughness of the stems has led many botanists to assign any extremely rough specimens to this variety.

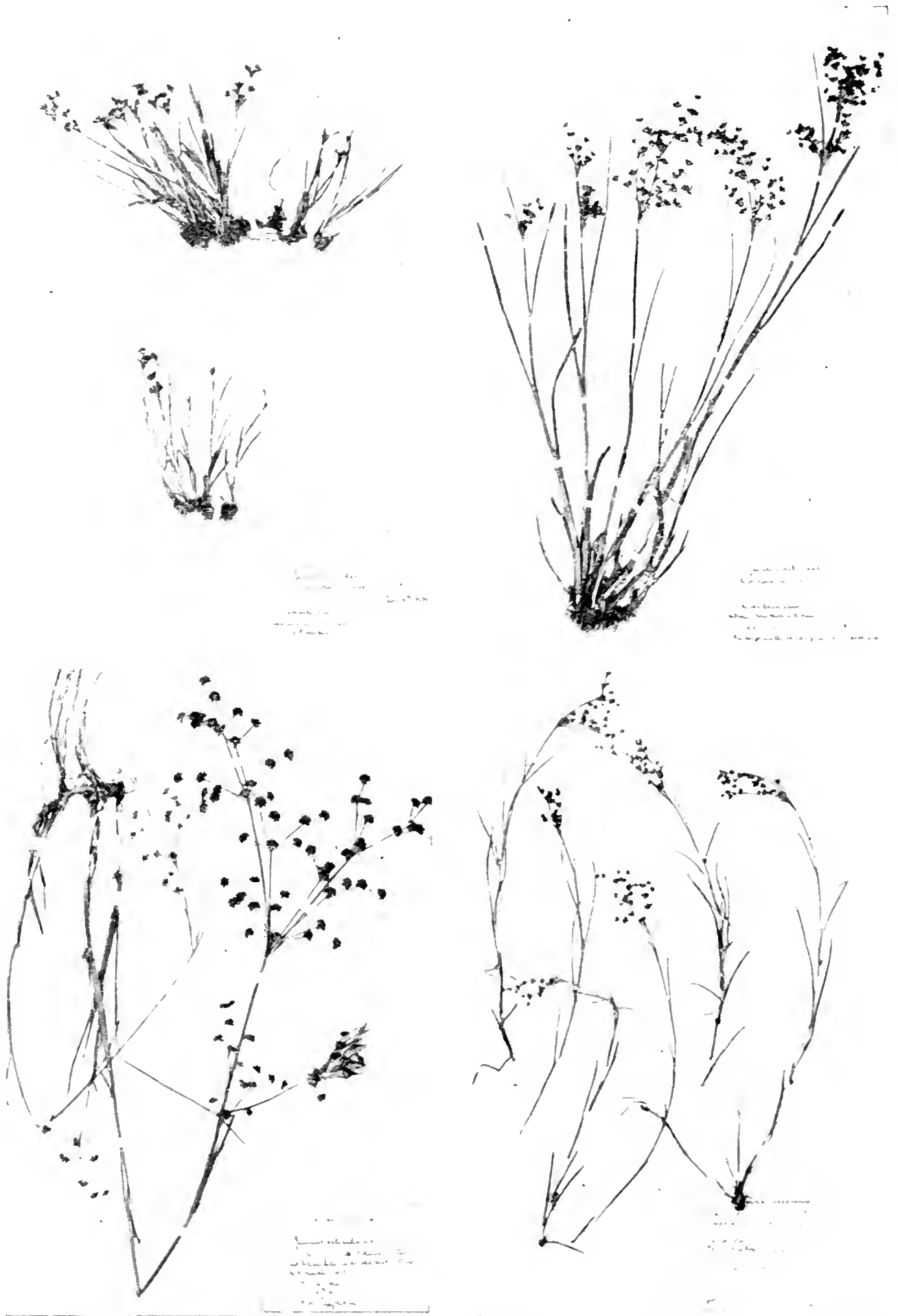
It is interesting that Jordan described what appear certainly to have been the octoploid and diploid forms of *G. palustre* in 1846, from his observations round Lyons.



Diploid, tetraploid and octoploid *Gallium palustre* L. ($2n = 24, 48, 96$). Diploid and octoploid plants from Hagley Pool, Berks, near Oxford; tetraploid from Chudleigh Knighton, Devon.



Gallium debile Desv. ($2n = 24$) from Chudleigh Knighton, Devon.



Ecovarieties of *Juncus articulatus* L.

- Top left : short rigid superect plant from gravelly shore of Loch-an-Eilean, Inverness.
- Top right : portion of large decumbent plant from bank of Thames near Godstow, Berks.
- Bottom left : tall robust suberect plant from Meare Heath, Somerset.
- Bottom right : prostrate plants from closely grazed damp turf, Port Meadow, Oxford.

If this were the whole of the story I think there would be no hesitation in giving specific rank to the octoploid and diploid *G. palustre*. - They can ordinarily be separated in the field, and when some of the individuals in a mixed population cannot, in the absence of flowers or ripe fruits, be assigned with certainty to one or other, examination of the stomata will usually give the answer : no evidence of hybridization has been found.

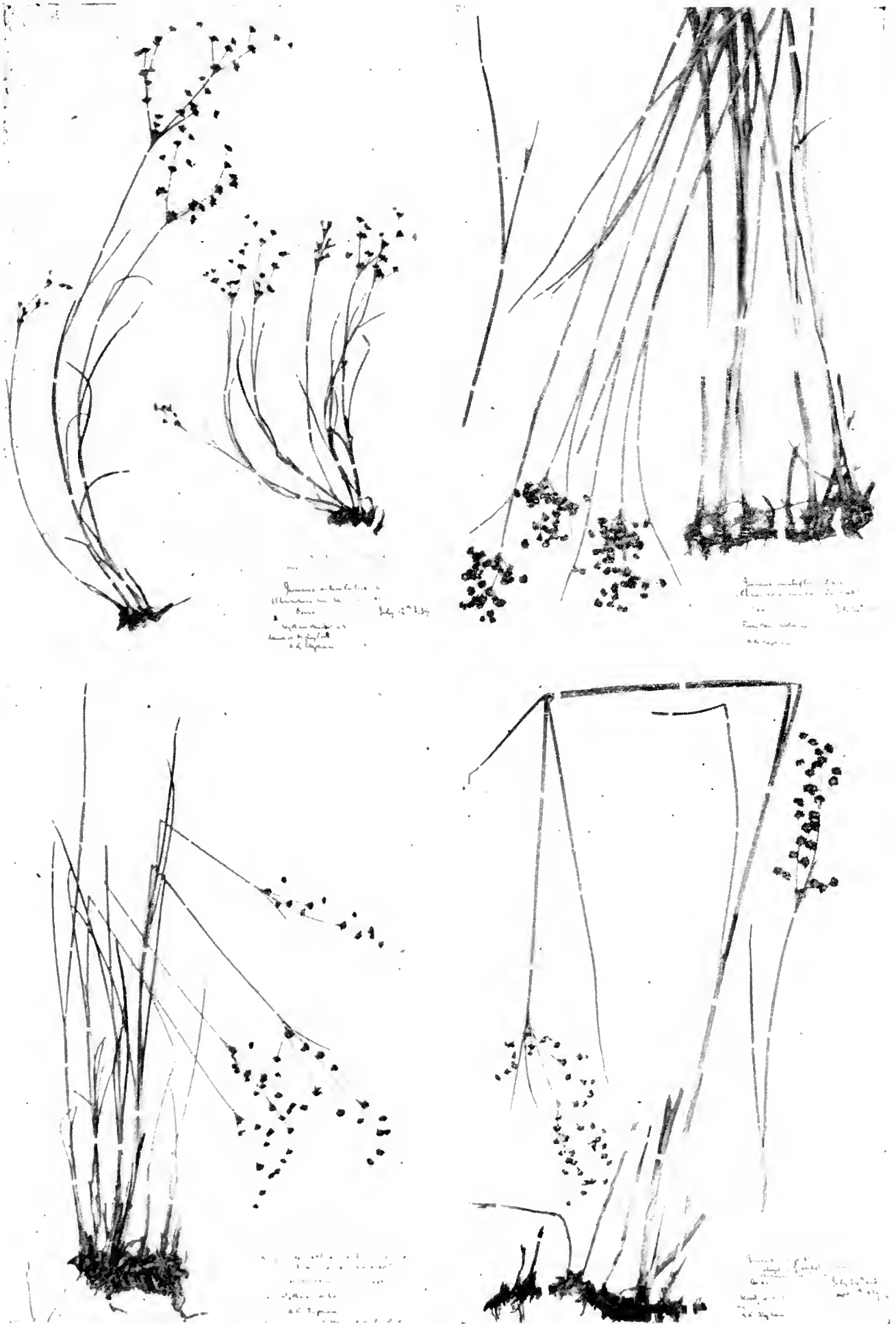
But this is not the whole story. Mr. B. Hancock found at Chudleigh Knighton, Devon, in the pond where *G. debile* grows, a *G. palustre* which puzzled him and which he found to be a tetraploid with 48 chromosomes. It was intermediate, in dimensions of stem, leaves, flowers, fruits and guard-cells, between the octoploid and the diploid. There is reason to believe that this tetraploid occurs in other parts of the country, and it complicates the situation because in the field it cannot be distinguished with certainty from the two other forms. Here then is our first taxonomic problem. How shall we deal with these three cytologically different marsh bedstraws which do not seem to hybridize but which cannot be distinguished with certainty except by microscopic examination? The suggested solution is that they should be treated as cytological subspecies of *G. palustre*, rather than as separate species.

Turning to *Juncus* we find in the *Juncus articulatus-acutiflorus* complex some further problems for the taxonomist. *J. articulatus* and *J. acutiflorus* are species with different but overlapping ecological ranges. They are distinguishable morphologically without much difficulty, the slender, ascending stems and short much flattened dull ribbed leaves of *J. articulatus* contrasting with the stouter erect stems and long slightly flattened shining smooth leaves of *J. acutiflorus*. Their inflorescence-architecture and ripe fruits are also very different. *J. articulatus* has 80 somatic chromosomes, while *J. acutiflorus* has only 40, and the hybrid between them, a locally very abundant plant, is, in my experience, quite sterile. While investigating these two species in the Oxford neighbourhood Mr. Timm and I discovered a small patch of a plant which we supposed at first, from its stout creeping rhizome, stiffly erect stem and few long leaves, to be *J. acutiflorus*. To our surprise it turned out to have 80 chromosomes. This is the plant we called "large 80", and which we found later to show a curious mixture of *acutiflorus* and *articulatus* characters. Vegetatively and in the form of its inflorescence it resembled *J. acutiflorus* but in the size of the inflorescence and the clusters of flowers and in the shape and glossiness of its bright chestnut-coloured fruits it agreed more closely with *J. articulatus*. How are we to treat this plant taxonomically. As a variety of *J. articulatus* with which it agrees in chromosome number ; or of *J. acutiflorus* which it resembles more closely in general appearance ; or as a new species?

Finally *J. articulatus* itself presents a further taxonomic problem. It is, as you know, a widespread and abundant plant all

through the British Isles, from sea-level to nearly 3000 ft. above it. And it is extremely variable in all its obvious morphological characters. A conspicuous feature of this variability is that populations of plants uniform in habit recur in widely separated localities which are ecologically similar. Thus plants with creeping rhizomes and short stout erect shoots are found on the unstable shingle round lakes or by fast-running streams ; slender erect plants simulating *J. alpinus* occur on mountains in Scotland ; prostrate and very leafy plants are found in wet pastures, and so on. Now when different populations from the same kind of habitat are examined closely, two characteristics become obvious. Firstly, these populations often grade into those of neighbouring but ecologically different habitats ; and secondly, though similar in habit the plants from different but ecologically comparable localities may differ greatly in any of the other variable characters of the species. Two littoral populations may be quite different in size and shape of the inflorescence, in shape and relative lengths of outer and inner perianth segments, in shape and size of the capsule, etc. There has clearly been a strong ecological selection for mode of growth but not for these other features. Now what are we to do with intra-specific groups such as these ? Ought we to ignore them taxonomically ? A case might be made for doing so, but I incline to the view that they deserve a place in the taxonomic hierarchy. They can hardly be given sub-specific rank. They are neither sufficiently distinct nor based on a sufficiently large number of differentiae for that to be justified. I think the best suggestion is that made by Mr. A. J. Wilmott, that they be called *varietates ecotypicae*, or ecovars.

This was discussed by Dr. D. H. Valentine.



Top left : *Juncus articulatus* L. from Wytham, Berks. ($2n = 80$).

Top right : *Juncus acutiflorus* Ehrh. from Pixey Mead, Wolvercote, Berks. ($2n = 80$).

Bottom left : *J. articulatus* X *J. acutiflorus* from Wytham, Berks. ($2n = 60$).

Bottom right : *Juncus* "Large 80" from Wytham, Bucks. ($2n = 80$).



EXHIBITS

VARIATION AND ECOLOGY IN THE BRITISH WATERCRESSES

By H. K. AIRY SHAW

NASTURTIUM OFFICINALE R.Br.

An attempt was made to correlate British material of *Nasturtium officinale* R.Br. (*sensu stricto*) with the "varieties" distinguished by Rouy and Foucaud, *Flore de France*, i, 204-5 (1893), whose account probably represents the most analytical treatment of the group so far published. This included: var. *genuinum* Gren. et Godr. (1848), var. *asarifolium* Kralik ex Rouy et Fouc. (1893), var. *intermedium* Gren. (1865), var. *siifolium* (Rchb. 1831) Steud. (1841), var. *grandifolium* Rouy et Fouc. (1893), and var. *parvifolium* Peterm. (1838).

Probably none of these "varieties" possesses any genetic stability. They all appear to merge insensibly into one another, without showing any tendency to cluster around particular "nuclei." As Rouy and Foucaud remark (trans.)— "One sometimes finds, *on the same stem*, leaves of var. *asarifolium* and *genuinum*, *siifolium* and *genuinum* etc."

NASTURTIUM MICROPHYLLUM Boenningh. ex. Rchb.

(*N. uniseriatum* Howard et Manton)

The original form described and figured by Reichenbach was illustrated by means of a specimen from Lower Morden, Surrey (*C.E. Britton* 30). Reichenbach's plate (*Icones Fl. Germ. et Helv.* 1. tab. 50, fig. 4360 : 1837-8) was exhibited for comparison.

Such forms of the allotetraploid are often closely paralleled by specimens of *N. officinale* falling within the range of Grenier's "var. *intermedium*".

A few other forms were exhibited, but none of these appear to have received names. *N. microphyllum* is on the whole a less variable species than *N. officinale*.

A few specimens of the triploid hybrid were also shown. No extremes of variation in leaf-shape in this have so far been noted.

ECOLOGY

Insufficient data are as yet available for any definite statement on the ecology of the Watercresses. The information given on herbarium labels rarely includes particulars as to the soil or geology of the locality.

In Gloucestershire (where the watercresses have perhaps been examined more attentively than elsewhere) there appears to be a tendency for *N. officinale* to be restricted to calcareous soils—the oölite of the Cotswolds and the limestone of the Wye Valley—with *N. microphyllum* preferring the non-calcareous areas, particularly the Vale of Severn. This results in the majority of the occurrences of *N. officinale* falling in the Thames drainage area, and v.-c. 33, with those of *N. microphyllum* mainly in the Severn drainage area, and v.-c. 34.

It seems however certain that this division can in no way be expected to hold good over the whole country. There are at least two definite records of *N. microphyllum* from chalk (Totternhoe, Beds. and Congham, W. Norfolk), and one of *N. officinale* from a somewhat acid habitat (Penderyn, Breconshire).

Collections of watercresses (*with fruits!*) are much needed from all over Great Britain, accompanied as far as possible by notes on the soil or geology. Gatherings from either *extreme* of the pH range (strongly acid or strongly calcareous) are especially desired. The exhibitor will at all times be grateful for the opportunity of examining material, which should be sent to him at the Royal Botanic Gardens, Kew, Surrey.



Nasturtium officinale R. Br.
E. Gloucestershire (North Cerney).



FIG. 1. V. H. B. I. S. 1851.

HERB. HORT. BOT. REG. KEW.

Nasturtium microphyllum (Boenn.) Rchb.
Bedfordshire (Souldrop).

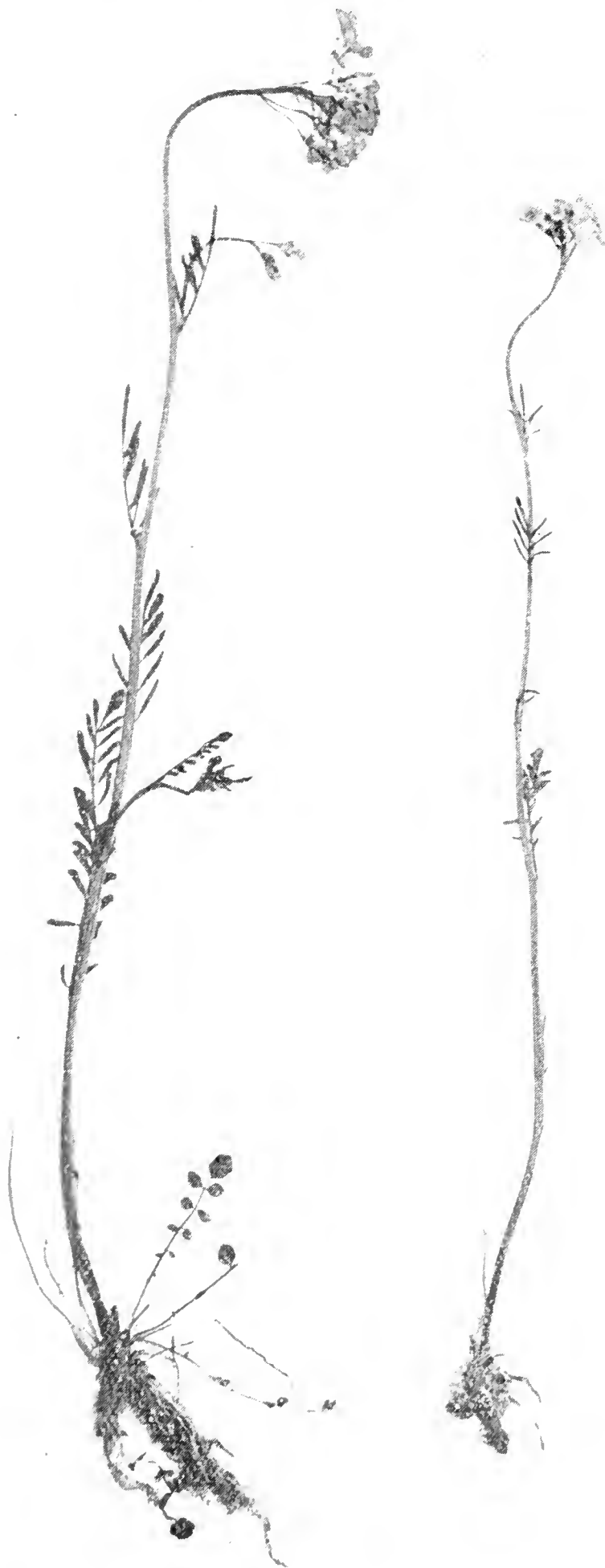


Nasturtium microphyllum × *officinale*
Anglesey (Llanddona).



Cardamine pratensis
Single flowers
South Surrey

Cardamine pratensis L., with normal "single" flowers and chromosomes $2n = 30$. (Surrey).



Cardamine pratensis L., with normal "single" flowers and chromosomes
 $2n = 56$ (Northumberland, Gosforth).



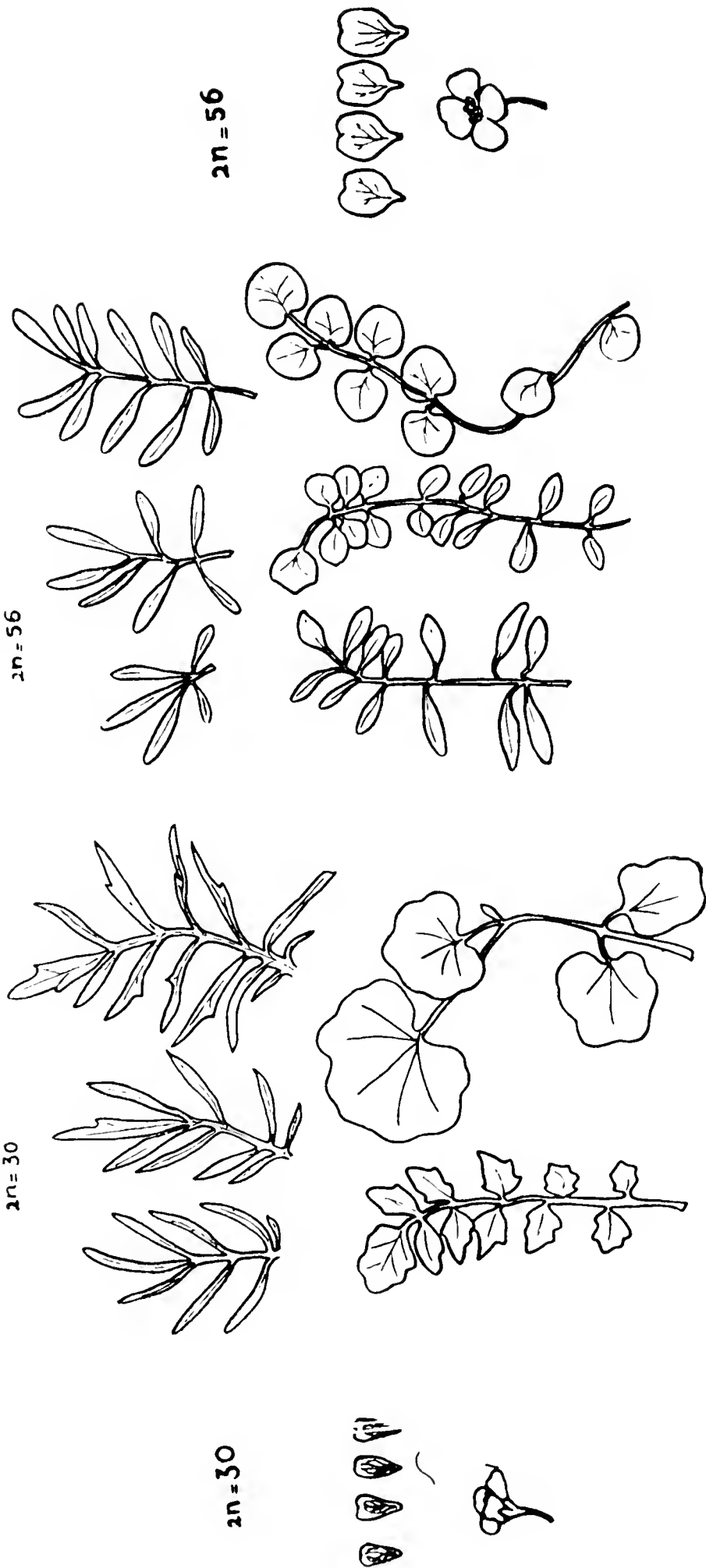
ABNORMAL

Cardamine pratensis

Petals in place of some arils.
'muggerock'

Collected by Mr J. Hume
1943

Partials - seeds germinate readily

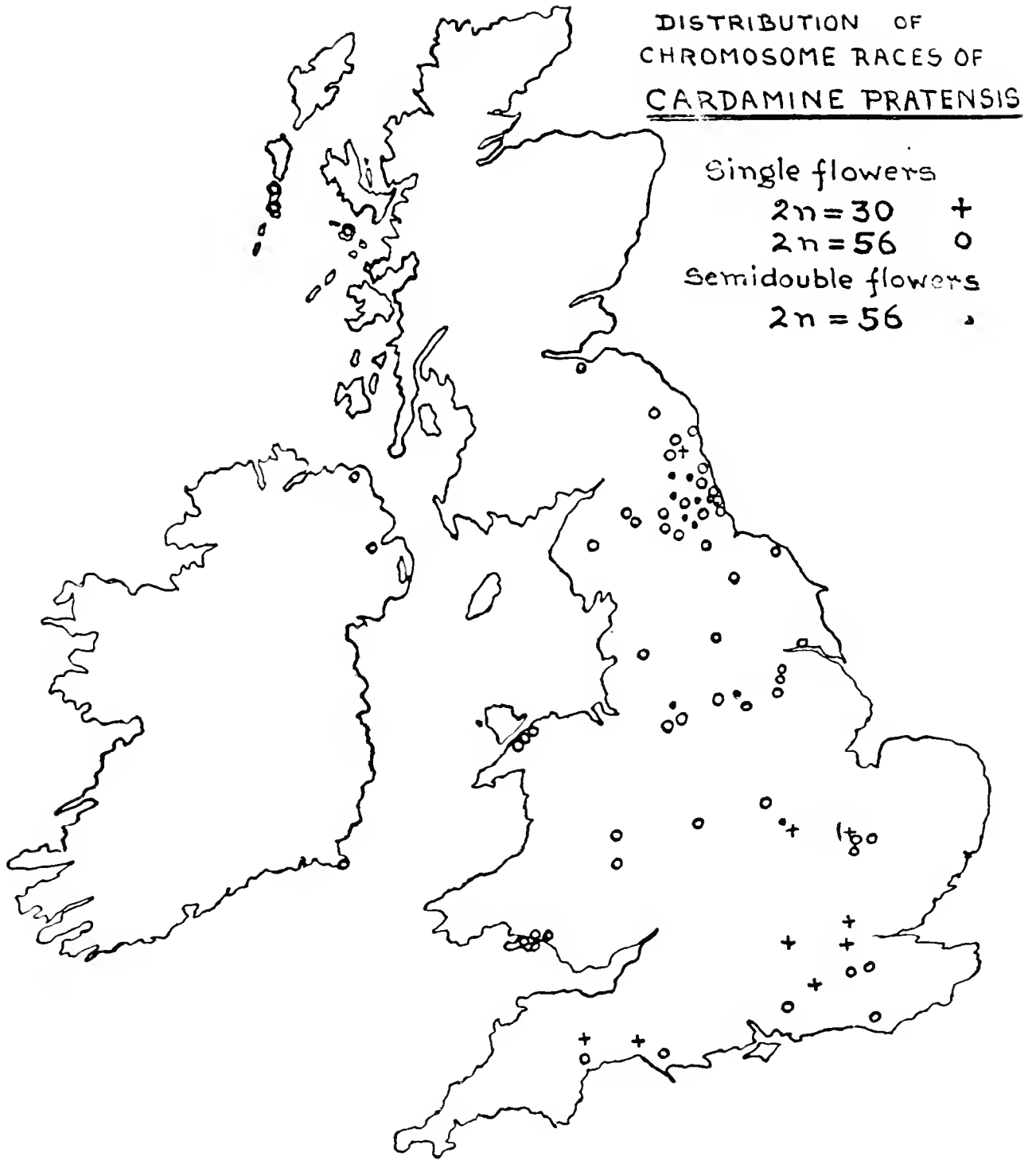


Cardamine pratensis L. (reduced)

A, B. Chromosomes $2n = 30$. C, D. Chromosomes $2n = 56$.

A, D. Flower and petals.

B, C. Leaves ; radical below cauline above.



CHROMOSOME RACES OF *CARDAMINE PRATENSIS* IN THE BRITISH ISLES

By F. HUSSIEN.

Two chromosome races have been found :

(1) ($2n = 30$), characterised mainly by lighter green colour, bigger dimensions, and fewer organs : the flower is either single (plate 11) or sterile double.

(2) ($2n = 56$), with darker green colour, smaller dimensions, and luxuriant growth : the flower is either single (plate 12), or semi-double, (plate 13).

The distribution map (plate 15), shows the restriction of race (1) to the south and the prevalence of race (2) all over the country. Attention was also drawn to the presence of the semi-double form in the Tyne area. More living material from other parts of the country was requested for investigation.

See preceding Plates 11-15.

AGRIMONIA

By H. BRITTAN.

The exhibit consisted of dried specimens of *A. Eupatoria* L. and *A. odorata* Mill. from northern England, which together with *A. Eupatoria* var. *sepium* Bréb. are being investigated cytologically.

The more common *A. Eupatoria*, which is distinguished morphologically by the possession of an obconic fruiting calyx distinctly furrowed and surmounted by a ring of spines none of which are reflexed, has a chromosome number $2n = 28$. Further systematic characters which, are not so reliable, are that the leaves are usually devoid of large, stalked, glands and that the plant as a whole has little or no smell.

A. odorata differs from *A. Eupatoria* in the possession of a campanulate calyx tube usually without furrows in the ripe state and bearing spines of which the lower series are reflexed. The leaves usually possess large, stalked, yellowish glands on the underside, and the whole plant is aromatic with what has been described as a "somewhat turpintinish odour." It is more usual to obtain "false fruits" of *A. odorata* with 2 achenes, whereas *A. Eupatoria* usually has only one. *A. odorata* has a chromosome number $2n = 56$.

In addition to normal plants of *A. odorata* a plant was shown which possesses leaves with serrate-dentate leaflets instead of the more normal crenate-dentate type. It has the same chromosome number as the normal form.

ALCHEMILLA VULGARIS L. (agg.)

By S. M. WALTERS.

The exhibit contained sheets of British and Scandinavian material of the eleven microspecies at present recognised as occurring in Britain (except that *A. obtusa* Bus., only recently discovered in Britain, was represented by a Swiss sheet), and also of photographs of plants in cultivation belonging to seven of these species, showing their differences of habit. In addition, the species "key" prepared for an account to be published in *Watsonia*, part 1, was also shown. The British species, with their synonyms, are as follows:—

Pubescentes Buser: *A. minor* Huds. (*A. pubescens* Lam.)

Eu-Vulgares E.-G. Camus

Hirsutae Lindb. fil. *A. vestita* (Bus.) Raunk. (*A. minor* auct., olim); *A. filicaulis* Bus.; *A. minima* Walters; *A. monticola* Opiz (*A. pastoralis* Bus.); *A. acutiloba* Opiz (*A. acutangula* Bus.); *A. xanthochlora* Rothm. (*A. pratensis* auct., haud (Schmidt)).

Subglabrae Lindb. fil. *A. glomerulans* Bus.; *A. obtusa* Bus.; *A. Wichurae* (Bus.) Stéf. (*A. acutidens* auct. angl.); *A. glabra* Neyg. (*A. alpestris* auct., haud (Schmidt)).

In the introductory remarks, reference was made to the paper by Turesson (1943: *Bot. Not.*), in which an account of cultivation experiments on Scandinavian material is given, showing that within certain microspecies there is ecotypic differentiation (in habit, disease resistance, etc.). It is clear from this work, however, that this intraspecific variation is in no way sufficient to confuse the specific distinctions—a conclusion confirmed by my own so far very limited cultivation experiments. The genetic dwarf new species *A. minima* was mentioned, and it was suggested that further investigation of upland limestone populations may reveal other similar distinct species. Finally, the taxonomically difficult "*acutidens* complex" was mentioned; in Britain we have *A. Wichurae* and almost certainly a second species not yet described.

RUBUS

By W. C. R. WATSON

Specimens were shown illustrating the various Sections of *Rubus* represented in Great Britain ; and also a few of the species known on the Continent and found in Britain by the exhibitor. The latter were as follows :—

- | | |
|---|---|
| <i>R. Arrhenii</i> J. Lange (<i>Sprengeliani</i>) | 22, Berks.
near Crowthorne. |
| <i>R. nemorensis</i> Lef. and Muell (<i>Nemorenses</i>) | 16, W. Kent,
Tunbridge Wells. |
| <i>R. pubescens</i> Weihe (<i>Discolores</i>) | 30, Beds, Claphill. |
| <i>R. melanoxylon</i> M. and W. (<i>Apiculati</i>) | 16, W. Kent,
Tunbridge Wells. |
| <i>R. Reichenbachii</i> Koehl (<i>Apiculati</i>) | 14, E. Sussex,
near Tunbridge Wells. |
| <i>R. saxicolus</i> P. J. Muell (<i>Hystriees</i>) | 17, Surrey,
Wimbledon Common. |
| <i>R. horridicaulis</i> P. J. Muell (<i>Hystriees</i>) | 16, W. Kent,
near Westerham. |
| <i>R. purpuratus</i> Sudre (<i>Glandulosi</i>) | 16, W. Kent,
Shooters Hill. |

RUBUS SPECIMENS FROM NORTHUMBERLAND AND DURHAM

By YOLANDE MASSEY

A selection of brambles collected in Northumberland and Durham was chosen to illustrate the characteristics shown by the *Rubi* in different sections of the Subgenus *Eubatus*. All sections but the *Sprengeliani* were represented. A description of the characters typical of each section (see W. Watson's Appendix I to the Check-list of the British Flora; *J. Ecol.* 33, No. 2) was given, together with herbarium specimens of species from each of the sections.

Some of the species were included in the demonstration because the finding of them in Northumberland or Durham marks an extension in their distribution in England, according to Mr. W. C. R. Watson. These species included the following:—
R. durescens Lint., *R. atrocaulis* P. J. M., *R. villicaulis* Koehl., *R. cryptadenes* Sudre, *R. Schmidelyanus* Sudre, *R. Wolley-Dodii* Sudre, *R. Griffithianus* Rog., *R. mutabilis* Genev., *R. Hystrix* Weihe and *R. rubriflorus* Purch. Some of these species were collected by the exhibitor and others were taken, in one locality, under the direction of Prof. J. W. Heslop Harrison.

A DEMONSTRATION OF THE CYTOLOGY OF RUBUS SPECIES.

Drawings of somatic plates of typical diploid, triploid, tetraploid, pentaploid and hexaploid *Eubati* were exhibited.

R. ulmifolius Schott was shown as the only diploid *Rubus* species in this subgenus; drawings of *R. idaeus* L. (Subgenus *Idaeobatus*) chromosomes were also shown.

Plates of *R. vulgaris* var. *mollis* W. and N., *R. angustifolius* Rog. and *R. Braeuckeri* G. Braun were shown to illustrate species which have been found to be triploid. These are the first triploid *Rubus* species to be recorded for Britain. Naturally occurring triploid hybrids have also been noted.

Tetraploid species, which are in the majority in the Subgenus *Eubatus*, were represented by drawings from *R. cuspidifer* Muell. & Lef., *R. Bakeranus* Bart. and Ridd., *R. macrothyrsus* Lange, *R. aspericaulis* Lef. & Muell, *R. Warrenii* Sudre and *R. Sprengelli* Weihe.

Pentaploid species were represented by drawings of somatic plates of *R. sublustris* E. Lees, *R. conjungens* (Bab.) W. Wats., and *R. tuberculatus* Bab.; and hexaploid species by *R. magnificus* P. J. Muell (ex. Sudre). An octoploid species shown was *R. Chamaemorus* L. (Subgenus *Chamaemorus*).

Drawings of meiosis in the tetraploid *R. scissus* W. Wats. var. *acicularis* (Areschoug) and in the pentaploid *R. sublustris* Lees were shown to illustrate the meiotic irregularities characteristic of many of the species in the Subgenus *Eubatus*.

All the identifications in this work were made by Mr. W. C. R. Watson, who also kindly supplied much of the material for the cytological investigations.

EPILOBIUM

By G. M. ASH

Sheets of most of the British species and hybrids were on view together with separately mounted flowers and leaves etc., to facilitate the examination of the pubescence. A series of twelve sheets of *Epilobium obscurum* from widely different localities showed the great variability of this species.

LIMOSELLA

By K. B. BLACKBURN

This exhibit illustrated the experimental production of a fertile hybrid *Limosella* by means of colchicine. Two species, *L. aquatica* and *L. subulata*, growing together at Morfa Pools, Glamorgan, produced a sterile hybrid, shown to be such on morphological and cytological grounds. The sterile hybrid was treated with colchicine and, by means of the doubling of the chromosome complement, a perfectly fertile and somewhat more robust plant was produced. This was illustrated by means of photographs, specimens and drawings.

MENTHA

By R. GRAHAM

(1) *M. longifolia* (L.) Huds. var. *horridula* Briq. This well-known mint, for which there has hitherto been no satisfactory name in this country—Fraser erroneously called it “ $\times M. Nouletiana$ Timb.-Lagr. ? ” (*B.E.C. 1926 Rep.*, 222)—is chiefly characterised by its extremely salient leaf serratures. When I examined Briquet's specimens at Geneva last summer I found that he had named it as a variety of *M. longifolia*; British material agrees well with the Continental except that whereas the stamens are either exserted or included in the latter they are apparently always included in the British.

(2) $\times M. rubra$ Miller and $\times M. Smithiana$ R. Graham $\times M. rubra$ Sm., non Mill.). The new name is required because $\times M. rubra$ Sm. is greatly antedated by $\times M. rubra$ Miller, which belongs to the *M. rotundifolia* \times *viridis* group, more recently named $\times M. cordifolia$ (Opiz) Fraser, for which Miller's name must stand. The two specimens exhibited are the nearest I possess to the types of $\times M. rubra$ Miller and $\times M. Smithiana$ in Smith's herbarium at the Linnean Society.

THE IMPORTANCE OF CYTOLOGY IN THE STUDY OF RUMEX

By J. EDWARD LOUSLEY

Although a considerable amount of cytogenetical work has been done on *Rumex* abroad, and especially in Japan and Scandinavia, there has been no attempt to study British material. The purpose of this exhibit is to draw attention to the necessity for such work to enable taxonomic studies to proceed.

By the use of morphological characters it has been shown that the British species of *Rumex* fall under three subgenera as follows :—

Subgenus *Acetosella* (Meisn. apud DC.) Rech. fil.—the Sheep's Sorrels ; to include *R. Acetosella* L. and *R. tenuifolius* (Wallr.) Löve.

Subgenus *Acetosa* (Campd. p.p. ; Meisn. apud DC.) Rech. fil.—the Common Sorrels and French Sorrel ; to include the native *R. Acetosa* L., the erroneously recorded *R. arifolius* All., and the alien *R. scutatus* L.

Subgenus *Lapathum* (Campd.) Rech. fil.—the Docks.

These three subgenera differ also in important cytological and genetical characteristics.

In subgenus *Acetosella* the plants are dioecious, the chromosomes are small and the basic number is 7 with no sex chromosome difference. It has been divided by Löve into the four following species which form a polyploid series :—

R. angiocarpus Murb. The diploid with $2n = 14$.

R. tenuifolius (Wallr.) Löve. The tetraploid with $2n = 28$.

R. Acetosella L. The hexaploid with $2n = 42$.

R. graminifolius Lamb. The octoploid with $2n = 56$.

The last is an arctic plant and I am not yet certain that the first occurs in Britain. *R. tenuifolius* can be distinguished from *R. Acetosella* by the very narrow leaves and by the size of the fruits and anthers. It is found chiefly on sandy soils, especially in Breckland though I have seen it as far afield as Wales and Scotland, and I had shown that it remained constant in cultivation before Löve's work was available to me.

In subgenus *Acetosa* the plants are also dioecious but the chromosomes are large. *R. Acetosa sensu lato* has the basic number 7, 8 ; the diploid number being 14 in the female and 15 in the male individuals. In field populations it is noticeable that females are not only more conspicuous, since they continue to grow taller as the fruit forms, but also much more numerous than the shorter male plants. According to Löve the proportion is about 100:40 but my observations tend to suggest that the discrepancy is often greater in Britain. Roth detected agamospermy and later work has tended to confirm this in a fairly small percentage of cases. It

should be noted that seed produced from diploid females without fertilisation must necessarily have 14 chromosomes and will therefore always produce female plants.

Löve has divided the Scandinavian *R. Acetosa* into four subspecies but has not published cytological differences. I cannot agree with all his taxonomic work and in particular with his interpretation of *R. arifolius* (his subsp. *alpestris*).

Of the alien *R. scutatus* a tetraploid form has been described from British material and the appearance of the horticultural plant which has been called *R. ambiguus* Grenier and *R. Acetosa* var. *hortensis* Dierbach (exhibited) suggests that it would be well worth examining for polyploidy.

In subgenus *Lapathum* the plants are monoecious with the basic chromosome number of 10. The diploid numbers of British species as determined on foreign material are as follows:—

2n = 20. *R. alpinus*, *R. conglomeratus*, *R. sanguineus*.

2n = 40. *R. maritimus*, *R. palustris*, *R. obtusifolius*.

2n = 60. *R. longifolius*, *R. crispus*.

2n = c200. *R. Hydrolapathum*, *R. aquaticus*.

Hybrids are formed in nature and under controlled conditions with the greatest facility. Apart from *R. alpinus*, which apparently does not enter into crosses, it seems likely that all the combinations of British species which are geographically possible will eventually be found. The list is already nearly complete.

Dock hybrids are usually characterised by a very large proportion of abortive fruits round which the enveloping tepals fail to enlarge. Hence they may often be recognised at sight as hybrids by the ragged and irregular production of enlarged tepals in the whorls. A few crosses, however, may be found occasionally with well-formed fruits more uniformly developed and the tepals regularly enlarged and this is especially the case with the very common *R. crispus* × *obtusifolius*. Even then the highest percentage germination of fruit sown which I have obtained is 3%—and in this instance one of the seedlings exhibited tricotyledony. So far I have failed to grow any plants to maturity from the seed of hybrids and I am convinced that F₂ hybrids are extremely rare if indeed they occur at all.

Recognition of the widespread occurrence of hybrids in wild populations has greatly simplified the study of Docks as very few of the species are “critical” in the usual sense. Nevertheless a number of problems remain which require cytogenetical investigation. In particular some of the variants which appear to be due to environmental conditions may well have a genetical basis.

As an example of variation certainly due to habitat I have exhibited *Rumex maritimus* from (a) Ringmere, near Thetford, where the plants form a series graduated in size from individuals

only 2-3 cms. tall to quite large specimens—they range down the side of the mere according to the time available for growth after germination as the water level recedes ; and (b) from Wennington where the plants perennate through the winter. Both states produce identical plants when grown from seed under garden conditions.

For an example of a very plastic species I exhibit a few of the forms of *R. crispus* which occupies a very wide range of habitats. Some of the variants come more or less true from seed under cultivation and I suspect the presence of ecotypes.

As a less complicated example which has caused trouble to taxonomists I exhibit the “sun” and “shade” variants of *R. viridis*. These may be ecotypes.

Attention must also be drawn to variation coupled with geographical distribution. In *R. obtusifolius* there are three main subspecies :—*agrestis* (Fries) Danser of Western Europe, *transiens* (Simonkai) Rech. fil. of Central Europe, and *sylvestris* (Wallr.) Rech. of Eastern Europe. Where their areas overlap puzzling intermediates occur, but where each one occurs alone the characters are very distinct. In Britain *agrestis* is the “native” plant and the other two are found as rare aliens. Comparable subspecies with definite geographical distribution occur in *R. pulcher* and it would be interesting to know if any cytological differences can be detected.

If any cytologist can find time to take an interest in *Rumex*, I should be very glad of his collaboration.

CAREX FLAVA L. AND ITS ALLIES

By E. NELMES

Specimens were shown of the four British species of this group of *Carices* : *C. flava* L., *C. lepidocarpa* Tausch, *C. demissa* Hornem., and *C. serotina* Mérat. The first and second of these have long been known to British botanists under these names, and the fourth as *C. Oederi* Retz., a name now recognised to be synonymous with *C. pilulifera* L. The third species, which is the commonest of the group in Britain, has, until recently, been much misunderstood. It was treated by various authors as a form, variety, or subspecies of "*C. Oederi*", by others as a variety of *C. flava*, and by many botanists confused with *C. flava* itself. When it was at last accepted as a distinct species and Andersson's epithet *tumidicarpa* applied to it, it was realized that Hornemann's earlier epithet might be found to be the correct one when the type could be examined. This has now been shown to be the case by the publication of a photograph of Hornemann's type (see K. Wiinstedt, 1947 : *Bot. Tidsskr.* 48., 192-206). Incidentally, Wiinstedt has also a photograph, in the same paper, of the type of *C. serotina* Mérat, which is also unmistakable. It appears to represent a rather tall form of the species, such as is found on peat moors in Somerset. For further information on the British "flavas", see my paper in the *B.E.C. 1945 Report*.

Hybrids are formed between all the possible pairs (6) of the above-mentioned four species. Specimens of these were exhibited. Three are known to occur in Britain, viz., those in which *C. flava* itself is not involved, this species being very rare, so far as is known.

The four hybrids resulting from the "flavas" crossing with *C. Hostiana* DC. (three in Britain) were also exhibited.

Also shown were most of the close allies of *Carex flava* from other parts of the world : an undescribed species from Albania ; *C. pulchella* (Lönnr.) Lindm., N. Europe ; *C. philocrena* Krecz., Turkestan and Kashmir ; *C. viridula* Michx., N. America and Japan, and *C. cataractae* R. Br., N. Zealand.

The Albanian plant, discovered by Mr. N. Y. Sandwith, closely resembles *C. serotina* but has bent utricles. *C. pulchella* is also near *C. serotina*, differing chiefly in its smaller spikes and utricles. *C. philocrena* can be briefly described as intermediate between *C. demissa* and *C. serotina*, the terminal spike tending to be gynæcandrous or androgynæceous instead of its wholly male condition common to the subgenus *Eucarex*. *C. viridula* is not yet fully understood and caricologists differ in interpreting it, but it appears to differ from *C. serotina* in its taller stems, grey-green colour, less crowded spikes, and usually gynæcandrous terminal spike. Finally, *C. cataractae* is distinguished from all its allies by its androgynæceous and less dense-flowered spikes. The spikes are crowded and the utricles large, with straight beaks.

HIEROCHLOË ODORATA (L.) WAHL. FROM NORTHERN IRELAND

By R. D. MEIKLE

A plant cultivated at Isleworth, Middlesex, from the Lough Neagh locality, where it was discovered, in 1946, by Mr. E. N. Carrothers and the exhibitor (see *Irish Naturalists' Journal*, 8,378).

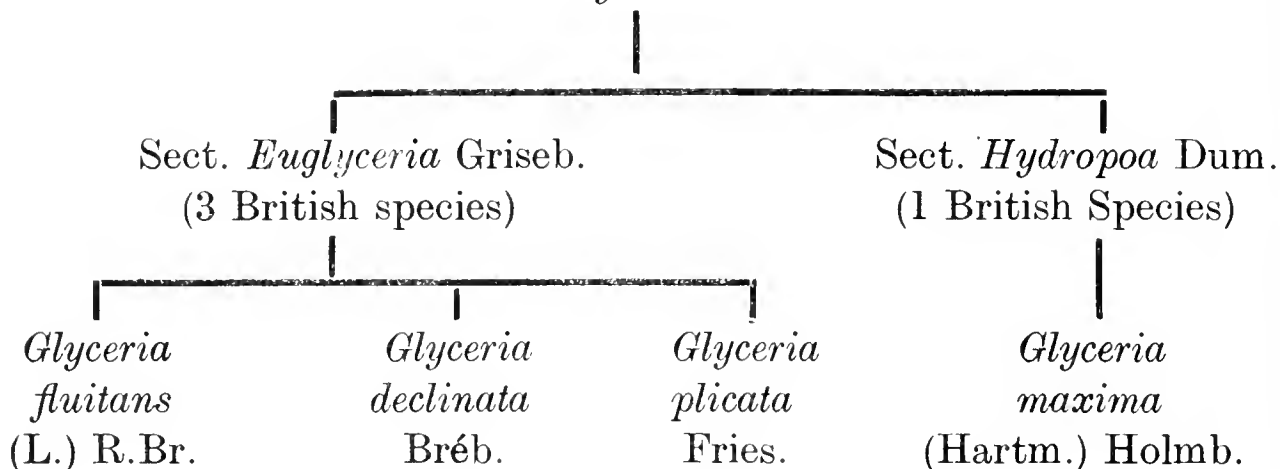
The N. Ireland plant does not appear to differ in any important respect from Scottish specimens.

THE BRITISH SPECIES OF GLYCERIA

By J. M. LAMBERT

The four British species of *Glyceria*, all of which are characteristic of aquatic or paludal habitats, may be grouped as follows:—

Genus *Glyceria* R. Br.



Of these, *Glyceria maxima* is easily distinguished from the others by its open panicle with widely spreading branches and ovate compressed spikelets, whereas the species of the *Euglyceria* section possess a narrower panicle, with typically erect branches and long, linear, nearly terete spikelets. The three British forms of the latter section were originally all included under the Linnean *G. fluitans*, but they have now been recognised for some time in Britain as distinct species. Sterile hybrids between *G. fluitans* and *G. plicata* are frequently found under natural conditions, and, although less common, *G. fluitans* × *declinata* hybrids also occur.

The main points of similarity and contrast between the four British species of the genus were illustrated in the exhibit by herbarium material and drawings, which are reproduced here as Plates 16-18. The major critical differences are summarised in the following

table (partly after Fitzpatrick, 1946) :—

<i>Glyceria fluitans</i>	<i>Glyceria declinata</i>	<i>Glyceria plicata</i>	<i>Glyceria maxima</i>
<i>Habit</i> tufted, with tillers fairly short, erect or somewhat spreading.	<i>Habit</i> tufted, with tillers short and more or less declining.	<i>Habit</i> somewhat tufted, with tillers often long, widely spread and prostrate.	<i>Habit</i> rhizomatous with tillers generally long and erect, but sometimes more or less prostrate.
<i>Leaves</i> bright green; sheaths smooth, blades generally long and narrow.	<i>Leaves</i> greyish-green; sheaths smooth, blades generally stiff, short and narrow.	<i>Leaves</i> dark green; sheaths rough and sulcate, blades long and broad.	<i>Leaves</i> bright green; sheaths smooth, blades long and broad.
<i>Panicle</i> sparingly branched, with lower branches arising singly or in pairs.	<i>Panicle</i> sparingly branched, with lower branches arising 2 or 3 per node.	<i>Panicle</i> much branched, with lower branches arising 4 or 5 per node.	<i>Panicle</i> much branched, with lower branches arising 4 or 5 per node.
Branches of fruiting panicle closely appressed to axis.	Branches of fruiting panicle appressed to axis or slightly divergent.	Branches of fruiting panicle widely spread or even reflexed.	Branches of fruiting panicle widely spread.
<i>Spikelet</i> rather lax, very slightly compressed laterally.	<i>Spikelet</i> compact, very slightly compressed laterally.	<i>Spikelet</i> compact, cylindrical.	<i>Spikelet</i> compact, ovate, much compressed laterally.
<i>Lemma</i> 6-7 mm. long; apex slightly scarious and generally acute.	<i>Lemma</i> 4-5 mm. long; apex scarious, distinctly trifid.	<i>Lemma</i> 4-5 mm. long; apex deeply scarious, blunt or rounded, occasionally slightly trifid.	<i>Lemma</i> 3-4 mm. long; apex very slightly scarious, rounded.
<i>Palea</i> acuminate, generally equal to or slightly longer than lemma.	<i>Palea</i> acuminate, generally exceeding lemma.	<i>Palea</i> obtuse, generally shorter than or just equal to lemma.	<i>Palea</i> obtuse, generally equal to or just shorter than lemma.
<i>Anthers</i> 2-3mm. long (4-5 times as long as broad); generally purple, sometimes yellow.	<i>Anthers</i> under 1 mm. long (2 times as long as broad); generally purple, sometimes yellow.	<i>Anthers</i> 1-1.5mm. long (3 times as long as broad); generally yellow, sometimes purple.	<i>Anthers</i> 1.5-2 mm. long (3-4 times as long as broad); yellow or purple.
<i>Caryopsis</i> 2.5-3 mm. long, oblong-elliptical, mid-brown.	<i>Caryopsis</i> 1.5-2 mm. long, oblong or oblong-elliptical, light to mid-brown.	<i>Caryopsis</i> 1-2 mm. long, obovate, dark brown.	<i>Caryopsis</i> 1.5-1.8 mm. long, elliptical dark brown or black.
<i>Chromosome No.</i> 2n = 40	<i>Chromosome No.</i> 2n = 20	<i>Chromosome No.</i> 2n = 40	<i>Chromosome No.</i> 2n = 60(?)
<i>Development</i> : 1st inflorescences produced during 1st season of growth from seed.	<i>Development</i> : 1st inflorescences produced during 1st season of growth from seed.	<i>Development</i> : 1st inflorescences not produced until 2nd season of growth from seed.	<i>Development</i> : 1st inflorescences not produced until 2nd season of growth from seed.

This table and the accompanying illustrations indicate several points of interest. In the first place, there appears to be a much closer relationship between *Glyceria fluitans* and *G. declinata* than between either of these species and *G. plicata*. This is of especial interest in that a number of the older synonyms of *Glyceria declinata* (e.g. *G. plicata* var. *depauperata* Crépin 1863; *G. plicata* var. *nana* Towns. 1864) suggest affinities with *G. plicata* rather than with *G. fluitans*, and that moreover Jansen and Wachter (1920) have stated that *Glyceria declinata* Bréb. should be classified among the forms of *G. plicata*.

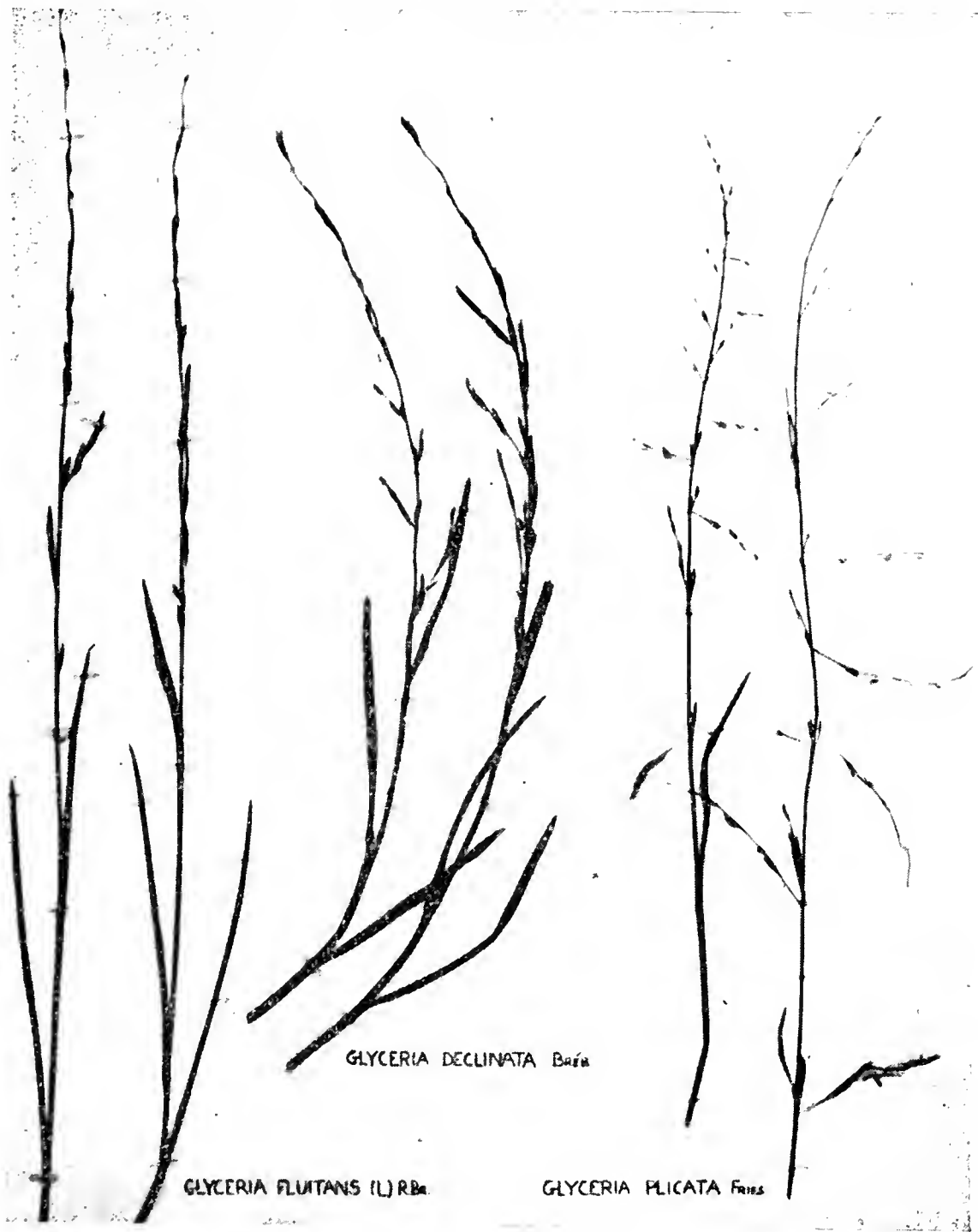
A second point of interest lies in the rather numerous characters of *G. plicata* which approximate to those of *G. maxima*. Although the former is assigned to the *Euglyceria* section of the genus by virtue of its terete cylindrical spikelet and rather narrow panicle, other features such as the broad leaf blades, the more numerous

branches of the panicle and their divergence throughout the time they are in fruit, the blunt lemma and obtuse palea, and the delay of flowering until the second season of growth, are all characters in which *G. plicata* and *G. maxima* resemble each other and differ from the other two species. In some ways, therefore, it seems that *G. plicata* might possibly be regarded as representing an intermediate type between the *Euglyceria* and *Hydropoa* sections.

This possible affinity between *G. plicata* and *G. maxima* is further strengthened by a comparison of their general habit and vegetative morphology. Although *G. maxima* is typically described as erect in habit, diagrams and photographs (cf. Lambert, 1947a) were exhibited to show that under certain habitat conditions the long aerial tillers may become prostrate and floating over the surface of the water, in which event they generally root extensively and produce abundant lateral shoots at the nodes. Herbarium material exhibited showed a similar production of long floating tillers with numerous roots and lateral shoots by plants of *G. plicata* raised in pots from seed collected from different natural habitats, while corresponding plants of *G. fluitans* and *G. declinata* showed a much more compact and tufted habit, with shorter ascending tillers. These differences in general habit between the various species of *Glyceria* are being investigated further by means of pot cultures, and the results will be given elsewhere.

Despite such differences as have been mentioned, there exists a general similarity between all the British species of *Glyceria* which indicates a close relationship between them. This similarity is extended to the structure of the young seedlings, which were illustrated in the drawings exhibited. In the seedlings of all the species the epiblast and coleorhiza are both well developed, with the primary root emerging laterally through the latter. *G. maxima* seedlings differ in possessing an acutely-tipped epiblast in contrast to the blunt dentate apex of the epiblast in the others, while those of *G. fluitans* vary in that the fully-developed coleorhiza is here short and blunt in contrast to the longer and more pointed coleorhiza of the other three. Moreover, whereas all four species develop abundant hairs on the coleorhiza, in *G. declinata* such hairs are absent altogether from the epiblast, in *G. fluitans* and *G. plicata* they are developed at its apex only, while in *G. maxima* they are abundant over its whole surface.

Finally, drawings and specimens were exhibited illustrating the occurrence of "vivipary" in species of *Glyceria*. Masters (1869), referring to vivipary in grasses, includes *G. aquatica* (= *maxima*) and *G. fluitans* (sens. lat.) amongst species 'most commonly affected in this manner'. In *G. maxima* (the only species where the phenomenon has been examined in any detail by the present writer (cf. Lambert, 1947b), the viviparous appearance is given by elongation of the ovary, accompanied in more advanced cases by proliferation of the floret axis to produce a small leafy shoot emerg-



Photograph of herbarium specimens of typical fruiting panicles of British species of the *Euglyceria* group

Glyceria fluitans

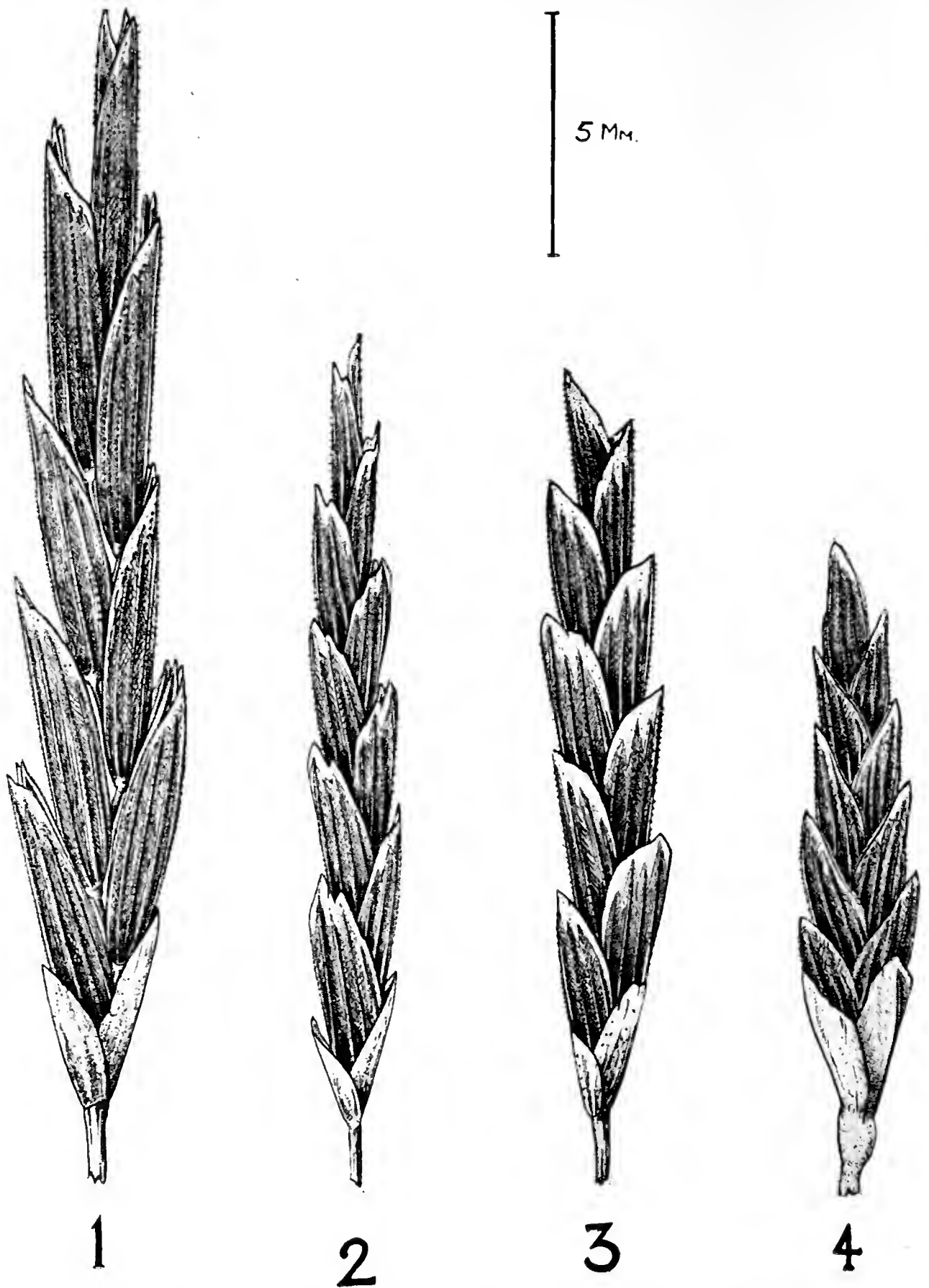
Note straight infructescence axis with practically all panicle branches adpressed.

Glyceria declinata

Note curved infructescence axis with slightly divergent panicle branches.

Glyceria plicata

Note straight infructescence axis with panicle branches standing out or reflexed.



Characters of the spikelets of the British species of *Glyceria*

1. *Glyceria fluitans*

Note the rather lax, slightly compressed spikelet, with florets standing slightly apart.

2. *Glyceria declinata*

Note the compact, very slightly compressed spikelet, shorter than in *G. fluitans*.

3. *Glyceria plicata*

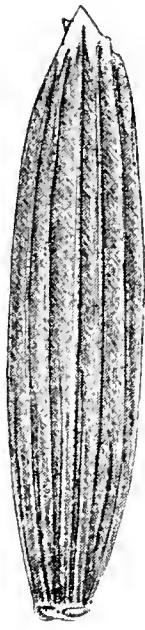
Note the compact terete spikelet, shorter than in *G. fluitans*.

4. *Glyceria maxima*

Note the compact, laterally compressed spikelet, smaller and more ovate than those of the *Euglyceria* group.

In all species, note the spikelets are many-flowered, the glumes short and scarious, and the lemmas prominently nerved.

1



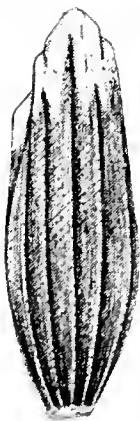
1 MM



2



3



4



Adaxial and abaxial views of the glumed and naked grains of the British species of *Glyceria*

In all the species, note the 7 prominent nerves of the lemma.

1. *Glyceria fluitans* (L.) R.Br.

Note especially :—

- a) The acuminate palea, equal to the lemma.
- b) The acute, slightly scarious, apex of the lemma.
- c) The oblong-elliptical caryopsis.

2. *Glyceria declinata* Bréb.

Note especially :—

- a) The acuminate palea, equal to (generally exceeding) the lemma.
- b) The distinctly trifold scarious apex of the lemma.
- c) The oblong-elliptical caryopsis, lighter in colour and smaller than that of *G. fluitans*.

3. *Glyceria plicata* Fries

Note especially :—

- a) The obtuse palea, shorter than the lemma.
- b) The blunt, deeply scarious apex of the lemma.
- c) The dark, obovate caryopsis.

4. *Glyceria maxima* (Hartm.) Holmb.

Note especially :—

- a) The obtuse palea, equal to lemma.
- b) The rounded, slightly scarious, apex of lemma.
- c) The dark elliptical caryopsis.

ing from the ovary apex. Evidence so far at hand suggests that this false 'vivipary' may be resultant upon late infection by the smut *Ustilago longissima* (a disease affecting all species of *Glyceria*, but especially *G. maxima*.)

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BROMUS

By T. G. TUTIN

The three species *Bromus mollis* L. sec. Holmb., *Bromus Thominii* Hard. (*B. hordeaceus* L. sec. Holmb.) and *Bromus lepidus* Holmb., which are recognised as occurring in Britain, form a closely related group. They all vary considerably in size and to some extent in hairiness and the density of the panicle. They are, perhaps, most readily distinguished by the length of the lemma, which in *B. mollis* is 8-9 mm., in *B. Thominii* 6.5-7.5 mm., and in *B. lepidus* 5.5-6.5 mm. In addition *B. mollis* has the lemma rounded and is nearly always pubescent, *B. Thominii* has it somewhat angled and is nearly always glabrous, while *B. lepidus* has a strongly angled lemma and is also usually glabrous.

These three species all have the somatic chromosome number of 28 and, in *B. mollis* at least, the chromosomes are large. In addition there is a closely allied plant ('*B. velutinus* var. *minor* Hook.') which occurs, apparently very locally, near the Lizard and in Alderney. This has been called *B. molliformis* Lloyd (*B. Lloydianus* Gren. and Godr.), but differs from this species in the shape of the lemmas as well as in other features. It appears to agree most closely with *B. Ferronii* Mabile, a species described from the neighbourhood of Bordeaux, but its identity has not yet been finally settled. Its most striking features are the dense, nearly simple panicle of shortly stalked or sessile spikelets; the rather spreading florets, giving an ovate-oblong outline to the spikelet; and the broadly ovate lemmas (6.5-7.5 mm. long and more than half as wide) with awns 3-4.5 mm. long and curving outwards in fruit. The most striking feature of all is that the somatic chromosome number is 14, while the chromosomes themselves are about half the size of those of *B. mollis*. *B. molliformis* Lloyd appears to occur only as a rare casual. The main characters of each species are:—

Bromus mollis L.

Panicle narrow, rather lax.

Spikelets 5-7(-11)-flowered, usually pubescent, lanceolate in outline.

Upper glume 5-7-nerved.

Lemma 8-9 × 3-4.5 mm., ovate, margins rounded.

Awn 5-8 mm. long, ± straight.

Anthers 0.2-1.2 mm.

2n = 28.

Bromus Thominii Hard.

Panicle narrow, rather lax.

Spikelets 5-7(-9)-flowered, usually glabrous, lanceolate in outline.

Upper glume 5-7-nerved.

Lemma 6.5-7.5 × 2.5-3 mm., ovate, margins bluntly angled.

Awn 5-6.5 mm. long, ± straight.

Anthers 1-1.5 mm., slender.

2n = 28.

Bromus lepidus Holmb.

Panicle linear-lanceolate to broad lanceolate in outline. rather lax.

Spikelets=(5-)7-9(-11)-flowered, usually glabrous, lanceolate in outline.

Upper glume 5-7-nerved.

Lemma 5.5-6.5 × 2-2.5 mm., ovate, margins sharply angled.

Awn 4.5-7 mm. long, ± straight.

Anthers 1-2 mm., slender.

2n = 28.

Bromus cf. *Ferronii* Mabilie

Panicle ovate, dense.

Spikelets 7-11-(13)-flowered, pubescent, ovate-oblong in outline.

Upper glume 7-9-nerved.

Lemma 6.5-7.5 × 3.7-4 mm., bluntly angled.

Awn 3-4 mm. long, curving outwards in fruit.

Anthers 0.5-1 mm., stout.

2n = 14.

Bromus molliformis Lloyd

Panicle ovate-oblong, dense.

Spikelets 7-11-flowered, pubescent or rarely glabrous, oblong-lanceolate in outline.

Upper glume 7-nerved.

Lemma 7-8 × 2-2.7 mm., oblanceolate, margins bluntly angled.

Awn 3.5-6 mm. long, spreading in fruit.

Anthers 0.75-1.2 mm., rather stout.

2n = ?.

SOME INTERESTING BRITISH SPECIMENS

By Miss E. VACHELL

(a) VARIATION OF *SENECIO SQUALIDUS* IN LEAF FORM AROUND CARDIFF.

S. squalidus var. *subinteger* Druce ; waste ground, Cardiff—November 1935 ; December 1935.

S. squalidus var. *incisus* Guss. ; waste ground, Cardiff. November 1935 ; Barry, January 1936.

S. squalidus, more usual form : Penylan, 1935.

(b) VARIATION IN *CARDUUS TENUIFLORUS* CURT. IN GLAMORGAN.

Normal form abundant near coast.

Variable forms, one approaching *C. pycnocephalus* L. in having no prickles on the stems below the rather larger capitula ; Barry.

(c) SPECIMENS OF *CIRSIUM* FROM MONKNASH, GLAMORGAN (collected by E. Vachell and G. Bruce, August, 1935).

C. acaule × *tuberosum* (× *C. Fraserianum* Druce) ; from a fairly large and very distinctive patch noticed by Mr. G. Bruce growing between the two parents.

C. tuberosum (L.) All. ; growing with the hybrid.

C. acaule var. *caulescens* (Pers.) DC. ; growing with the hybrid.

(d) VARIATION IN *RUMEX ACETOSA* L. (Collected by E. Vachell).

Specimens from Lochnagar, S. Aberdeen, named *R. arifolius* All. by Dr. G. C. Druce :

Specimens very similar to the above from Caenlochan, Forfar ; July, 1934.

Specimens not resembling the above (for comparison), which have the basal leaf-lobes incurved ; high ground on The Quiraing, Skye.

COLOUR DRAWINGS OF BRITISH PLANTS

By Rev. W. KEBLE MARTIN

Sixteen plates (15 figures to each plate) from his collection. The plates included illustrations of some species of Batrachian *Ranunculus*, *Rosa*, *Rubus*, etc.

BRAINS TRUST

J. S. L. Gilmour (*President*), Question Master ; Miss M. S. Campbell (*Hon. Gen. Secretary*) ; Mr. J. E. Lousley (*Treasurer*) ; Prof. C. E. Raven ; Prof. T. G. Tutin ; Dr. E. F. Warburg ; Mr. A. J. Wilmott.

[The opportunity given in the final session for the posing of general problems by those attending the Conference was seized with avidity, and the Question Master was provided with a plentiful store of questions, ranging from serious to frivolous. The experiment proved a great success, the lighter mood introduced by the Q-M. affording a welcome relief after the more weighty sessions. Fortunately one of those present wields a pen which does justice to the lighter vein, and it is hoped that his account will be appreciated as an appendix to the more solid results of the Conference. ED.]

RAMBLINGS WITH THE BRAINS TRUST

By "AUDITOR"

Replete with the highly nutritious but, to me, somewhat concentrated fare so far offered in the Society's menu, my digestion struggling with a rich mixture of paramorphs, topodemes, bivalents, soboles, transitios and the like, I awaited the last item of the Conference in a mood of hopeful expectancy. I was not disappointed, for the President's masterly introduction of the final session gave sure promise of lighter refreshment. In his capacity as Question-Master he identified the "Brains"—I append my own observations in parentheses—as follows:—

Maybudia hebridensis, the only female specimen present (but with notable influence on the community).

Moneybaggia perennis (characterised, of course, by a strong degree of the "Trust").

Johannes Raius redivivus (remarkable for light-shedding rays).

Flora preli Cantabrigiensis (auct. angl. = two representatives of polyploid series shortly to be put in the press).

Wilmottia Wilmottia Wilmottia, "the well-known triverbum" (hardy ever-green).

In this well mixed association I was able to identify the Q-M. himself as the dominant *Wisleya hortensis*. The absence of var. *barbatus* of a common and widely-broadcast multiverbum, was commented upon, but not deplored. This taxonomic feat was but the forerunner of other treats in store for us, and erudition went hand in hand with wit, experience hobnobbed with humour to give us a happy hour.

One question, perhaps, had ominous leanings towards matters not yet satisfactorily dealt with by my mental digestion. "The taxonomic status of plants morphologically indistinguishable but

cytologically different" is a subject inviting a whole paper, but, after Prof. Tutin's admirable effort to sidestep the issue by asking if there were any plants absolutely identical in morphology, Dr. Warburg clearly and concisely demonstrated how to deal with them, existent or non-existent. He called forth Mr. Wilmott's biverba and triverba ⁽¹⁾ to put them in their proper place, whether good little polyploids in series, or whether, like Dr. Valentine's pet-dog-violets ⁽²⁾, they allowed their chromosomes far too much numerical latitude; biv. and triv. should be employed according to the opinion of, or as convenient to, those unfortunate botanists who worked upon such awkward plants. One man's opinion, however, is not another's fact; what is convenient to the taxonomist may not be so to the ecologist; so the field was set for a little interchange between Dr. Warburg and Mr. Wilmott, which proved most instructive until stopped by the Q-M.'s ruling that the question was answered, and, indeed, I am sure that he who sought went not empty away. Other questions, which I might term of the "Text-Book" variety, also tested the technical and specialised knowledge of the B.T. For the enquirer who wished to know "What is the Bullace, and how does it differ from the Damson, the Wild Plum and the Skeg?", Dr. Warburg, ably assisted in detail by his colleagues, pulled the plums apart systematically, and put them back again genetically; the Bullace has a round fruit unlike its oblong-fruited allies, but their chromosome numbers are the same and other characters are not correlated with those of the fruit, so that *Prunus insititia* is not specifically separable from *P. domestica*. Among other thorny points, yellow and black-fruited varieties of the Bullace were mentioned, and we were told that the Wild Plum has crept out of cultivation; but the poor Skeg had a thin time—nobody could place it—and I feel that even Mr. Lousley's valiant effort to dig up from his fertile memory an illustration (see *Watson B.E.C. 1930-31 Rep.*, 54: 1931) of a Wild Plum-Bullace hybrid did not quite get to the root of the matter. [I find that Canon Robert Fisher in Part 2 of his "English Names of our Commonest Wildflowers" gives: "Skeg, Skegg = Blackthorn, Bullace, from Anglo-Saxon Scæg, a ragged stump"].

The best definition of a biennial "to differentiate it from an over-wintering annual" should be based, argued Mr. Wilmott, upon the limit of time allowed for each to come to maturity; only a twelve-month period—even if composed of the latter half of one calendar year plus the first half of the next—for the annual; two similar seasons for the biennial.

The "Brains" had plenty of scope for airing themselves on the above, but there were, too, problems of a more diversionary kind. Dr. Dony's query, for instance, deserves to be quoted verbatim:—"As to everyone, except to members of the B.S.B.I., Bullrush is

1. See Mr. Wilmott's paper on Intra-specific Categories.

2. See Dr. Valentine's paper on *Viola Riviniana*.

Typha latifolia and not *Scirpus lacustris*, and as this arises, no doubt, from an impression in childhood that Moses was hidden in *Typha*, do the Brains Trust think:—(a) that we should start a campaign to convert the clergy, Sunday-school teachers, etc., to a view that Moses was after all hidden in *Scirpus lacustris*, or (b) begin to call *Typha* “ Bullrush ”, and find a new English name for *Scirpus lacustris*? This really had the B.T. tangled up in *Typha* and skipping about in *Scirpus*: Mr. Lousley tried to put the blame on Smith’s *English Flora*; Prof. Raven waved the clergy out of it; Prof. Tutin fell back on deploring the confusion caused by popular names; but one and all they could not do for us what Pharoah’s daughter did for the Patriarch, and we and Dr. Dony remain unrescued. I should like to ask that a Papal Bull be rushed from the Vatican on the subject of “ Moses in the Reedmaces ”.

A request for the correct pronunciation of *Danaa* gave Mr. Wilmott, vociferating classical vowels and in rare bucolic vein, the opportunity to shine as a farmyard impersonator, and to exercise his ba-a-a-a-ass notes. His effort was highly appreciated, both by the audience, and by the Q-M, who was thereby enabled to bleat that *Danaa* should be pronounced *Danaa* with a strong ovine accent on the last recurring syllables. In connection with the origin of this name, mention was made of Danaë, a lady who was visited, by Jove!, with a shower of gold. (Hegi in his *Fl. v. Mitt.-Eur.* tells us that the genus was named after J. P. M. Dana).

Then “ Lone-Wolf ” wanted to know the “ relative advantages of botanising alone, with a few friends, or with an organised party ”. The Q-M invited each member in turn to state his preference, to which Mr. Wilmott briefly replied, “ with a few friends ”, an opinion shared by the two others of the “ Professionales ” group. On the other hand, Prof. Raven’s “ Because I’m such a bad botanist—with a lot! ”, was met with Miss Campbell’s “ Because I’m such a bad botanist—alone! ” Mr. Lousley neatly summed up with: “ Alone for concentration, with an organised party for education, but, ideally, with two or three friends ”, which conclusion the Q-M, the B.T. and we heartily endorsed.

The wag and the wiseacre being served, the wayfarer (*Botanicus vulgaris*) came in for his turn. Among a number of questions of general botanical interest, two were concerned with plant names. First, “ Would the B.T. agree that it is essential to have a good English name for a wild flower; if so, would they suggest rules for its determination? ” Perhaps it is not essential, hopefully suggested Prof. Raven. But it is essential for popular audiences, replied Mr. Lousley; for children and agricultural students, added Dr. Warburg; for the British Museum postcards, said Mr. Wilmott. Prof. Tutin pointed out that many common *nomina* are *ambigua*, and that, from his personal experience, Latin names sometimes come more easily to children. We take his word for it, as we picture the proud professorial pater listening to the first lispings of “ *Chrysosp-*

lenium oppositifolium". What then should be the rule? Mr. Lousley recommended the old botanists as a basis for a much-needed catalogue, Mr. Wilmott having already indicated that he started with Ray on behalf of his postcards. Pity it is that the wild flower cannot speak for itself, as I should love to hear the Hon. Gen. Sec. sweetly singing to *Bellis perennis*, "Dai-sy, Dai-sy, give me your answer, do". Whether or no common names are essential—and the Q-M ruled that they cannot be entirely dispensed with—Latin ones certainly are.

The writing of small initial letters for all specific and varietal epithets in the latter was regarded as a "lazy method" by "Diehard", who indignantly sought its justification. Mr. Lousley would find proof-reading easier if the practice were universally adopted: Dr. Warburg regarded attachment to most instances of the use of capitals as mere sentiment; Mr. Wilmott, on the contrary, saw no difficulty in retaining a relatively few easily remembered cases—Miller in his "Gard. Dict." may have gone a bit too far; Prof. Tutin, to support him, accentuated the botanical history inherent in these cases, and, further, demonstrated the ambiguity in such an example as *Schinus Molle*, which has nothing of the softness that a small-lettered epithet would give it. The Q-M had to admit that the matter rested between the devil of laziness and the deep blue sea of sentimentality. Should we write *Pyrus Malus* or *P. malus*, according as the apple is good or bad?

A trio of teasers, perhaps of even more general interest, produced both divergencies and conformities of opinion. The Lizard and Ben Lawers tied for the honour of the richest square mile in the British Isles for rarities—Messrs. Wilmott, Tutin and Raven for England; Messrs. Lousley, Warburg and Miss Campbell for Scotland. For richness in the number of species represented, Mr. Lousley's proposal for an area in Sussex with both Atlantic and Continental elements was roundly acclaimed. From the richest field to "The greatest Field Botanist" is an obvious step. Who has most claim to this title among giants of the past? John Ray needed not his famous champion; the pioneering spirit and scientific stature of the man was so well acknowledged by those who are proud to wear his mantle today that no voice was raised against his pre-eminence. As runner-up Robert Brown ("*facile botanicorum princeps*") was proposed by Mr. Wilmott—although "field botanist" could perhaps be applied to him in a limited sense. H. C. Watson and Thomas Johnson both found protagonists and disclaimers. In this way the B.T. gave us the best places and the best men; they gave us, too, the best pictures. They told us where to look for "the finest published illustrations of British wildflowers." It is in Curtis's *Flora Londinensis*, the merits of which were extolled by Prof. Tutin, Mr. Wilmott and Miss Campbell. *Flora Graeca*, *English Botany*, and Hunnybun's originals came in for honorable mention, but Curtis won the day.

Finally, a question, which must not be treated in frivolous fashion and deserves the serious attention that it drew from the B.T., was posed by "Furious":—"What steps could and should be taken to prevent the uprooting of local and rare plants by Rock Gardeners?" I dare venture to remark, nevertheless, that the gleam in the eye of the Hon. Gen. Sec. spoke volumes. Mr. Lousley made the concrete suggestion that the sympathy of landowners be enlisted, and that an endeavour be made to educate the rock gardeners. This was endorsed by all, with a further appeal by Prof. Raven to the Q-M for the support of the R.H.S., to which appeal Mr. Gilmour promised his earnest consideration. We all, who love our wild flowers whether common or rare, cannot but feel most indignant and perturbed that man's own cupidity or ignorance should be responsible for the possible extinction of plants that have survived the exigencies of countless years of evolutionary change. We are confident that the capable hands of Mr. Gilmour will steer this cause to a safe haven.

Those who plucked of the tree of knowledge ate, thus, of the fruits of wisdom; those who gathered the blossoms of wit were rewarded with a nosegay of laughter. For my part:—

With vasculum and a friend or so
To Lizard or Ben Lawers I'll go,
A gun I'm sure that you will pardon us
To scare predatory rock-gardeners;
In left-hand pocket Ray's *Synopsis*
In t'others *Flora Londinensis*;
These twain will then surely tell me
If my Eyebright is *Campbellae*.
There I or one or other fellow
Will seek the Common Black or Yellow
Globose-fruited Thorny Bullace
(Not the tangled Reedrush-Bulmace);
Then in meadows we will join a
Chorus of Dana, Danaaya.

It would not be fair, however, to sum up the Brains Trust either in flight of fancy or doggerel rhyme, for their success is undeniable and deserved. At the outset the President remarked that it was the first Botanical Brains Trust ever; sincere congratulations are due, then, to the B.S.B.I. on its enterprise and will the organisers please see to it that it is not the last.

[E.B.B.]

REQUESTS FOR LIVING MATERIAL FOR INVESTIGATION

Some short intervals available between items on the programme were used to give opportunities to those taking part of asking for living material needed for investigation. Dr. Butcher suggested that a central bureau should be established to which people could send their desiderata, which would circulate such wants and keep a register of those willing to search for and collect the material wanted. He thought that if definitely explained requests were made to definite people it was much more likely that material would be obtained.

The requests made were :—

Cardamine pratensis L. Any double-flowered variety, especially when it bears some fertile flowers and fruits (semi-double). Miss F. Hussien, Department of Botany, King's College, Newcastle-upon-Tyne, 2.

Viola canina L. and *V. lactea* Sm. Specimens showing adventitious shoots from the root system, especially of *V. canina*. Ripe seeds from such plants would be useful but are not easy to collect and two or three rooting plants would be best. Dr. D. A. Valentine, Department of Botany, University Science Laboratories, South Road, Durham.

Taraxacum. Plants producing pollen. Dr. W. B. Turrill, Royal Botanic Gardens, Kew.

Mentha. Plants of interesting mints for cytological study. R. Graham, 3, Anderson Street, London, S.W.3.

Primula vulgaris Huds., homostyle form. This form, with a long style and anthers in the thrum position, has been investigated in a Somerset locality where it seems to be replacing the ordinary form. Specimens other than from Somerset would be welcomed by Dr. Valentine (address above).

Bromus. (1). Plants or seeds of curious forms of *B. mollis* L., particularly maritime ones.

(2). Plants or seeds of *B. molliformis* Lloyd and the so-called *B. molliformis* found at the Lizard, the latter only wanted from outside the area Gue Graze—Poltesco (Cornwall). Prof. T. G. Tutin, Department of Botany, University College, Leicester.

Polypodium vulgare L. Specimens (British or foreign) to determine the distributions of the diploid, tetraploid, and hexaploid forms. Prof. Irene Manton, Department of Botany, The University, Leeds.

CONCLUDING REMARKS BY THE PRESIDENT

We have had two days packed with interest, two days that I find it very difficult to sum up at all adequately. Before making the attempt, I would like to withdraw unreservedly my earlier definition of a critical group and substitute "Any group that has been studied by a taxonomist, especially if helped by a cytologist"!

The main idea of organizing this Conference was to bring so-called "field and herbarium botanists" together with cytologists, geneticists and ecologists so that each could contribute his quota of experience and knowledge to the study of critical groups of British plants. In other words, it was an attempt to further what Dr. Turrill has called the "synthetic" approach to taxonomy. My impression is that, from this point of view, the Conference has been an outstanding success. Not only the more general papers, like the three opening ones and Mr. Wilmott's, but also the more detailed expositions of particular problems (and even the Brains Trust!) have all contributed towards building up a picture of work accomplished, work in hand, and work to be done, which cannot fail to have an inspiring effect on the future study of the British Flora. The Society will do all in its power to ensure that the note of collaboration and synthesis sounded at this Conference shall not be allowed to die down.

Before closing you will, I know, wish me to thank all those who have contributed to the success of the Conference. These can, perhaps, be grouped under three heads: firstly, the Royal Horticultural Society for permission to use their premises and catering facilities, which have added so much to the comfort of our meeting; secondly, the lecturers and exhibitors, for the trouble and time they have given to preparing material for our instruction and entertainment; and thirdly, but by no means least, the Secretary, Assistant Secretary, and other members of the Society, for the work they have put into the organisation of the Conference.

Before the President declared the Conference closed, Prof. Tutin rose and said:—

We have heard for many years past a lot of talk about the revival of interest in taxonomy and now this Conference has, I think, amply demonstrated that at last interest in taxonomy has been fully revived. Ten years ago a meeting of this kind could not have been the success that this one has been. Twenty years ago, when our Chairman and I were undergraduates, taxonomy was still considered rather disreputable, and we had to pursue it rather in spite of than with the assistance of most of our teachers. A conference to discuss critical groups would then have been completely unthinkable.

A great change has occurred since then which has, I think, been largely due to the increasing activities of this Society.

Finally, I should like, I am sure on behalf of all those present, to give our best thanks to our Secretary and to all those who have done the hard work involved in the organisation of this meeting. We have had two days exceedingly well arranged, and packed full of interest.

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