SPECIES STUDIES
IN THE
BRITISH FLORA

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IN THE

BRITISH FLORA

BEING THE REPORT OF THE

CONFERENCE

UNDER THE TITLE OF

THE SPECIES CONCEPT IN ITS RELATION TO THE BRITISH FLORA

HELD IN 1954 BY

THE BOTANICAL SOCIETY OF THE BRITISH ISLES

EDITED BY

J. E. LOUSLEY

1955

CONTENTS

EDITORIAL NOTE

The theme chosen for the fourth Conference arranged by the Botanical Society of the British Isles is one of considerable importance to everyone interested in contemporary work on the British flora. The "Species Concept" as it concerns individual workers is usually viewed from a more or less narrow angle, and the purpose of the Conference was to bring together problems and evidence from as wide a field of current research as possible.

The papers read proved of outstanding interest and importance. They include relevant studies of fossil botany, fungi, algae, bryophytes, ferns and flowering plants and of cytology, biometrics, experimental taxonomy and ecology. They cover recent and new work, some of which has not been previously published, and collectively they provide a broad approach to the subject not available elsewhere. The papers printed in this report have been arranged so that those covering general subjects appear first, followed by accounts dealing with groups of cryptogams and phanerogams, and concluding with contributions which cover suggestions for future developments. The sequence in which they were given at the Conference is set out in the Programme printed overleaf. Scientific names used in the papers are those selected by the speakers and it has not been thought advisable to attempt to standardise them.

The arrangements for the Conference were in the hands of the Meetings Committee of the Society. Much of the work fell on Dr. J. G. Dony, Honorary Meetings Secretary, and to his energy and enthusiasm, together with that of the other officers and members who assisted, the success of the Conference was due.

I am grateful to J. P. M. Brenan, J. E. Dandy, D. H. Kent, N. Y. Sandwith, H. K. Airy Shaw, and E. F. Warburg, members of the Society's Publications Committee, for reading the proof and making many valuable suggestions, and to J. G. Dony for preparing the index.

<div align="right">J. E. LOUSLEY.</div>

CONFERENCE PROGRAMME
1954

THE SPECIES CONCEPT
in its relation to the British Flora

FRIDAY, April 9th

First Session

10.00 a.m.   Registration

10.15   A welcome to the Conference
  The President: The Rev. Canon C. E. RAVEN

10.30   The Experimental Approach to the Species Problem
  Prof. S. C. HARLAND

11.15   The Importance of Ferns for the understanding of the
  British Flora
  Prof. IRENE MANTON

12.00   Interval for Lunch

Second Session

1.45 p.m.   The *Dryopteris spinulosa* complex in Europe
  Dr. S. WALKER

2.00   The stability of some specific characters as shown by
  the fossil records
  Dr. H. HAMSHAW THOMAS

2.45   The problem of *Asplenium trichomanes*
  Mr. J. D. LOVIS

3.00   The Species Concept among Bryologists
  Dr. E. W. JONES

3.45   The analysis of variation within the genus *Fucus*
  Dr. E. BURROWS and Dr. S. M. LODGE

4.00   Interval for Tea

Third Session

4.45   Problems associated with the Species Concept in
  Mycology
  Prof. A. BURGES

5.30   Problems of speciation in the British species of *Arum*
  Dr. C. T. PRIME

5.45   The conflict of categories
  Dr. J. HESLOP-HARRISON

6.30   The Relationship of the two subspecies of *Asplenium
  adiantum-nigrum* in Britain
  Miss M. G. SHIVAS

6.45   Interval for Dinner

The Hall will be open from 7 p.m. when the exhibits illustrating papers read on both days can be inspected

8.15   OPEN MEETING TO WHICH MEMBERS AND GUESTS NOT ATTENDING THE CONFERENCE ARE ALSO INVITED

The Distribution Maps Scheme
Prof. A. R. CLAPHAM

The part Field Botanists may play in the Maps Scheme
Dr. S. M. WALTERS

There will also be an exhibit of the equipment for recording and mapping to be used in the Scheme

SATURDAY, April 10th

First Session

10.15 a.m.   The Species Concept and Experimental Taxonomy
Mr. J. S. L. GILMOUR

11.0   Species Problems in plants with reduced floral structures
Prof. T. G. TUTIN

11.40   Species Problems in recent Scandinavian works on Grasses
Dr. A. MELDERIS

12.00   Variation in *Salicornia* and its significance
Mr. D. H. DALBY

12.15 p.m   Morphological characters in the discrimination of species and hybrids
Dr. R. MELVILLE

1.00   Interval for Lunch

Second Session

2.30   Problems of hybridization and species limits in some *Erica* species
Mr. P. A. GAY

2.45   The Species Concept in *Euphrasia*
Mr. P. F. YEO

3.00   Variability within species
Dr. J. H. BURNETT

3.45   *Caltha* in the British Flora
Mr. G. PANIGRAHI

4.00   Variation in *Centaurium*
Miss W. T. M. O'CONNOR

4.15   The future of Synthetic Taxonomy
Dr. W. B. TURRILL

5.00   Closing Remarks by the President

SUNDAY, April 11th

FIELD MEETING TO BOX HILL
jointly with British Bryological Society
Leader: MR. E. C. WALLACE

The programme printed above is as circulated before the Conference. It was carried out as stated except that the President was unable to be present and Professor T. G. Tutin and Dr. R. W. Butcher, Vice-Presidents, opened and closed the proceedings in his place. Four additional exhibits were included as follows:—

Stellaria nemorum L. and the Species Concept
Dr. CH. H. ANDREAS

Ecotypical Variation in *Adoxa moschatellina* L.
Dr. H. G. BAKER

Clinal Variation in Flower Size in *Lotus corniculatus* L.
Miss B. A. POULTER

The Section *Eu-Callitriche* in the Netherlands
Miss H. D. SCHOTSMAN

LIST OF MEMBERS AND GUESTS WHO ATTENDED THE CONFERENCE, April 9 and 10, 1954

(The following list does not include those who only attended the open meeting on the evening of the first day.)

F. W. Adams
G A. D. G. Agnew
G Mrs. Alderson
D. E. Allen
K. L. Alvin
G Dr. Ch. H. Andreas
Miss J. Andrews
G. M. Ash
Miss D. E. Ashhurst
A. G. Bailey
G Miss A. M. Baird
Dr. H. G. Baker
G P. W. Ball
E. B. Bangerter
Miss F. M. Barton
G Miss A. A. Baylis
Miss D. Baylis
Miss K. Benson-Evans
Miss D. Bexon
Dr. K. B. Blackburn
Miss N. M. Blaikley
G R. A. Blakelock
M. Borrill
B. N. Bowden
Dr. H. J. M. Bowen
Miss M. E. Bradshaw
Dr. O. E. Brett
D. W. Brett
G. M. Brown
G J. R. Lang Brown
O. Buckle
Miss W. F. Buckle
G Miss N. T. Burbidge
Prof. A. Burges
D. H. Burnett
Dr. J. H. Burnett
Dr. E. Burrows
Dr. R. W. Butcher
Miss D. A. Cadbury
Mrs. C. M. A. Cadell
J. F. M. Cannon
Mrs. J. F. M. Cannon
B. V. Cave
Miss Y. Chamberlain
G S. K. Chaudhuvi

G M. J. Christmas
Prof. A. R. Clapham
G T. H. Clifford
M. J. Cole
T. G. Collett
Miss A. Conolly
J. A. Crabbe
A. C. Crundwell
D. H. Dalby
G Miss G. W. Dalby
G Miss I. Daniels
G Miss E. Davenport
D. Davidson
Dr. E. W. Davies
Dr. P. H. Davis
G Miss M. de Vos
Miss O. R. Dewey
G Miss C. I. Dickinson
G Miss J. Dilnot
Dr. J. G. Dony
T. R. Eagles
Rev. E. A. Elliot
G J. Farrand
G S. Feinsilber
R. S. R. Fitter
H. J. Fletcher
G L. L. Forman
Miss H. Franks
G E. J. Friend
P. A. Gay
Mrs. P. A. Gay
Mrs. A. N. Gibby
J. S. L. Gilmour
Mrs. S. Gilmour
D. R. Glendinning
Miss C. M. Goodman
G Miss B. J. Golding
K. M. Goodway
Miss V. Gordon
R. A. Graham
G S. W. Greene
G Dr. J. W. Gregor
G Miss M. Gregory
Miss M. E. Griffiths
P. C. Hall

Mrs. P. C. Hall
D. J. Hambler
G Miss M. F. Hancock
F. D. Hanson
D. J. Harberd
G Mrs. S. C. Harland
R. Harley
Dr. J. G. Hawkes
G Miss A. R. Haygarth-Jackson
J. H. Hemsley
F. N. Hepper
Dr. J. Heslop-Harrison
G Mrs. J. Heslop-Harrison
G Miss M. M. Hindmarsh
Miss O. Holbek
Dr. M. G. Hughes
G Dr. A. T. Hunziker
G A. A. Idle
Miss E. M. C. Isherwood
G P. W. James
G Miss F. M. Jarrett
A. C. Jermy
Dr. E. W. Jones
G Miss M. Kefallino
D. H. Kent
G C. C. King
G Miss E. E. King
G R. Knowles
Miss R. G. B. Laidlaw
Dr. J. M. Lambert
G Miss J. Laptain
W. N. Lawfield
G Mrs. W. N. Lawfield
Miss S. M. Littleboy
Miss C. E. Longfield
J. E. Lousley
G J. Lovell
J. D. Lovis
G Mrs. J. D. Lovis
Dr. A. G. Lyon
Prof. I. Manton
G A. R. H. Martin
D. McClintock
G Miss C. Macdonald
G Miss C. M. Medd
R. D. Meikle
Dr. A. Melderis
Dr. R. Melville
G Miss D. Meyer
H. Meyer

Miss M. E. Milward
R. Minor
G D. M. Moore
Miss B. M. C. Morgan
E. Nelmes
G P. J. Newbould
P. M. Newey
P. R. Norman
G G. N. Oakeshott
Miss W. M. T. O'Connor
J. Ounsted
J. R. G. Packer
Miss P. A. Padmore
G G. Panigrahi
G K. Parry
G. J. Paxman
R. M. Payne
F. Perring
C. D. Pigott
Miss B. A. Poulter
Dr. C. T. Prime
N. M. Pritchard
Miss J. P. Pugh
R. C. Readett
G D. A. Recaldin
D. A. Reid
B. W. Ribbons
Miss C. M. Rob
N. K. B. Robson
J. Grant Roger
I. H. Rorison
Dr. F. Rose
Dr. E. M. Rosser
Mrs. B. H. S. Russell
J. S. Ryland
R. E. Sandell
N. Y. Sandwith
G Mrs. V. O. Sankey
G J. Sansome
J. A. Sargent
Mrs. N. Saunders
G Miss H. D. Schotsman
G R. C. Seeley
G R. O. Sharples
G J. D. Shepherd
G Miss M. G. Shivas
Miss P. M. Smith
G Miss S. G. Smith
Dr. E. Smithson
J. E. S. Souster

Miss C. J. Spurgin
G W. T. Stearn
E. L. Swann
G Miss A. M. Swinney
G Miss J. Taylor
G R. Teasdale
G Dr. H. Hamshaw Thomas
G R. G. Thomas
G Mrs. Thornton
G Miss K. Tousny
G Miss J. Turnham
Dr. W. B. Turrill
Prof. T. G. Tutin
Prof. D. H. Valentine
Dr. J. G. Vaughan
N. M. Wace
G Miss J. Wakefield
G Dr. S. Walker
E. C. Wallace
Dr. S. M. Walters
P. J. Wanstall
Dr. E. F. Warburg

G P. S. Ward
G Dr. P. J. Watson
Mrs. W. Boyd Watt
Miss M. McCallum Webster
Mrs. B. Welch
G R. P. Weston
A. W. Westrup
Miss D. M. Wethered
G F. White
Miss M. M. Whiting
B. A. Whitton
G D. A. Wilkins
Miss M. A. Williams
M. H. Williamson
Miss R. Witton
Miss A. F. Wood
P. J. Wood
G S. R. J. Woodell
J. E. Woodhead
P. F. Yeo
Dr. D. P. Young

INTRODUCTORY REMARKS

The President of the Society, The Rev. Canon C. E. Raven, was unable to attend the Conference owing to bereavement, and at very short notice, Professor T. G. Tutin, a Vice-President, opened the proceedings with the following remarks:—

I am sure we all greatly regret the absence of our President, and that it would be your wish to offer him our sincere sympathy in his recent loss. We shall miss not only his opening remarks but also the experience and skill which made his chairmanship of the last Conference so memorable.

It is now my pleasant duty to welcome on your behalf our guests and our speakers for today. I feel sure that, with the happy combination of youth and enthusiasm, and experience and enthusiasm, that we see in this hall, our Conference is bound to be a great success.

We are, I take it, here to widen our knowledge of the nature of species, and not necessarily to attempt an improved definition of these important but somewhat nebulous taxa. In fact it seems doubtful whether the time-honoured definition "a species is what a competent taxonomist thinks is a species" can be bettered, except by defining a competent taxonomist. We shall certainly learn more of the kind of criteria used for the recognition of species in different groups of plants and go away, when the time comes, with a clearer idea of the importance of variation.

Though as a Society we are primarily interested in what we are pleased to call the higher plants, we are fortunate in having an opportunity today of hearing about the species problems of those who might be termed lower botanists. I use the word in no derogatory sense: their problems are, I think, of the same basic kind as ours and their difficulties often greater. It will be a matter of great interest to us to see how the idea of the species among bryologists and mycologists compares with our own.

In addition to hearing about the variation which occurs within a species at any given time we shall also learn something of the permanence of certain characters in geological time. This may save us from the taxonomic nightmares we might have if we went away thinking that species are perpetually in a state of flux. It has become increasingly apparent during this century that for an understanding of the nature of species we must turn to the cytogeneticists and the users of experimental grounds. It is equally clear that classical taxonomy will never lose its value and that it will continue, at the very least, to provide a universal filing system for all kinds of botanical knowledge. We are getting off on the right foot this morning with contributions from two of our most eminent cytogeneticists* and I am sure you are looking forward as eagerly as I am to hearing what they have to say.

*See Conference Programme on page 8.

THE EXPERIMENTAL APPROACH TO THE SPECIES PROBLEM

S. C. HARLAND (University of Manchester)

(Professor Harland was unable to attend to read his paper owing to illness. It was read in his absence by Miss Angela R. Haygarth-Jackson.)

When this subject was first suggested to me for presentation I looked at it something like this: Hasn't this subject been discussed over and over again? Hasn't everything that can be said about it already been said? But on further consideration I thought that it might be possible to illustrate by a few examples what I conceive to be some of the most fruitful lines of thought which have been opened up by the use of the experimental method as applied to the species problem.

There are about a quarter of a million species of angiosperms in existence. They have to be classified and described in such a way that any plant brought in from the wild, or grown from a packet of seed obtained from a Botanic garden, can be identified. It can be pigeon-holed, so to speak. This task has been one of great difficulty and great magnitude. On the whole it has been accomplished with considerable skill and precision. Errors have of course been made. Sometimes, as in the genus *Gossypium,* species have been allocated to it which, by the use of the experimental method, clearly belong elsewhere; and sometimes species which have been assigned to other genera have had to be incorporated in the genus.

Two examples may be given. The species formerly known as *Thurberia thespesioides* is now known as *Gossypium thurberi* and the species formerly known as *Gossypium kirkii* is now known as *Gossypioides kirkii*. I have mentioned these two examples because they illustrate how the experimental method works in practice and what are its tools.

First let me reiterate a statement which I have frequently made to my students: that the most important thing about a plant is its chemistry, and the most important biological tools at our disposal are those which reveal in the plant kingdom fundamental biochemical differences and relationships. Orthodox taxonomy does not aim to do this. Its contribution to biochemistry is—to use a phase commonly used elsewhere—purely coincidental.

The experimental method has four main weapons in its armoury. These are, first grafting, second crossing, third cytology and fourth genetics. There are other considerations, such as those arising from ecology, and there is the general information provided by biotic relationships, which are outside the scope of

this paper but are nevertheless important. Let me take up these methods one by one and discuss them in the light of the species problem.

GRAFTING

If two species can be grafted, it means that they possess in common some factors of a biochemical nature—they are biochemically related. Information on grafting relationships can be of quite extraordinary value, but for the most part is lacking. Our information, scanty as it is, has been derived principally from the horticulturist. We know, for example, that the pear, quince, apple and hawthorn are all capable of being intergrafted. At least, the quince can be used as a stock for both apple and pear, and hawthorn for apple. Similarly lilac can be grafted on privet; and tobacco, tomato and petunia on the potato.

Plants in the same genus can probably almost always be grafted. Plants of the same family can often be grafted, though there are many exceptions. Plants belonging to different families can probably never be grafted. I am aware that cases have been recorded in the literature of alleged successful grafts of members of different families. But these require confirmation.

To return to the *Gossypium* case previously mentioned. Here we had a species, *Gossypium kirkii*, which could not be grafted on any other known member of the genus. Morphologically the main difference from other cottons was in the possession of a ribbed or winged stem, a character not regarded as important by the taxonomist. On its grafting relationships it was clearly not a *Gossypium*, that is, it was biochemically different. Now if two species will not graft, they will also not hybridize, and I am not aware of any exception to this rule. *Gossypium kirkii* followed this rule. Later it was found by Skovsted that it possessed 12 pairs of chromosomes instead of 13 pairs and consequently it was put in a new genus, along with an endemic Madagascar species—*Gossypioides brevilanatum*.

This case admirably demonstrates what the experimental method can do. A geologist who encounters a territory for the first time makes a rapid survey of the principal features. He can map the main formations and say a good deal about their geological relationships. But even in this country the detailed and precise study of small areas still goes on. And so it is with taxonomy.

CROSSING AND GENETICAL RELATIONSHIPS

What I have said about grafting applies also to plant relationships as revealed by the results of inter-specific, or even intergeneric, hybridization. If two species will graft, they are in some way biochemically related. If they will both graft and cross, the relationship is presumably closer. Let me refer again to *Gossypium*. The plant known as Arizona Wild Cotton was

formerly called *Thurberia thespesioides*. We found first that it would graft on all the species of cotton in our very large collection. It would also hybridize with several species, and cytological examination showed that it possessed 13 pairs of chromosomes. One cross with the wild Peruvian cotton, *Gossypium raimondii*, which also had 13 pairs of chromosomes, proved to be highly fertile both in the first and second generations, and on these grounds it became necessary to change the taxonomic status of this species and it is now known as *Gossypium thurberi*. Similarly and on the same criteria *Erioxylum aridum* became *Gossypium aridum*.

Another case may be mentioned. In our studies of the cytogenetics of the genus *Senecio*, we have made observations on the status of two species, *Senecio gallicus* and *Senecio squalidus*. The former was obtained from the Jardin des Plantes in Paris, and the latter is, of course, now widely distributed in this country. Both these species proved to be self-incompatible, a condition by no means infrequent in Compositae, but they hybridized with ease, and both possess 10 pairs of chromosomes. Obviously the nomenclature should be revised and one of these names eliminated.

Further preliminary results concerning our experiments with the genus *Senecio* may be mentioned. At first we were concerned only with the possibility of using groundsel (*Senecio vulgaris*) as a sort of plant *Drosophila*. But for this purpose it proved unsuitable. First it is mainly self-fertilised and the progenies of single plants taken from the wild rarely segregate. Second, the great variation exhibited seems to depend on genes leading to minute and unanalysable differences in morphology and physiology. Third, the life history was not so short as we had been led to expect from casual observation.

The discovery of a male sterile form known as "strap", from its narrow strap-like leaves, led to other lines of work in which the possibilities of interspecific hybridization are being explored. It is stated in the literature that hybrids between *S. vulgaris*, with 20 pairs of chromosomes, and *S. squalidus*, with 10 pairs of chromosomes, occur in nature. Using the male sterile *S. vulgaris* as a female we ultimately got a hybrid, which has been carried on by cuttings. It is, as a rule, completely sterile though a few seeds were obtained by open pollination. Treatment of the hybrid with colchicine induced a certain amount of fertility, and we have raised a few seedlings which may be fertile hexaploids and constitute what is virtually a new species. The artificial production of a new species by making sterile hybrids fertile is now a recognised procedure, not only in experimental taxonomy, but also in plant breeding.

Another hybrid has been made between *Senecio vulgaris* and *Senecio inaequidens*. Both these species have 20 pairs of chromosomes but present wide differences in morphology and physiology.

S. vulgaris is annual and self-fertilising: *S. inaequidens* is perennial and self-incompatible. Analysis of the crosses using genetical and cytological methods should tell us a great deal about their relationships.

Perhaps the best example of the kind of result which may be expected when a whole genus is studied using the techniques of cytology and experimental taxonomy, is provided by the monumental and admirable work of Babcock on the genus *Crepis*. We are working on species inter-relationships in the genus *Fragaria*. Without going into details it may be mentioned that a polyploid series exists in this genus. The European wild strawberry, *Fragaria vesca,* has 7 pairs of chromosomes, while the the two species *Fragaria chiloensis* and *Fragaria virginiana* have 28 pairs and are octoploids. The cultivated garden strawberry has resulted from crosses between these two octoploid species, and may be called an octoploid cultigen. Even casual inspection of the diploid and the octoploid must lead to the conclusion that they are members of the same genus and closely related. It is, however, very difficult to get hybrids between diploid and octoploid and when they occur they are pentaploids and almost sterile. However, by first doubling the chromosome number of the diploid and making it a tetraploid, crossing with the octoploid becomes easy and large numbers of relatively fertile hexaploids have been obtained. It now becomes possible to conduct a genetical examination of these synthetic types.

I mention the *Fragaria* case because ease of crossability between species of undisputed taxonomic status varies greatly. At one extreme is the ease with which maize, *Zea mays,* will cross with the Teosinte—a member of another genus, and at the other is the recent hybrid between tomato and a wild *Solanum* made by Rick. Here it was only possible to make the hybrid by employing a whole series of the most refined techniques. The crossed fruits had to be prevented from abscission by the use of hormones. The tiny embryo had to be extracted at an early stage and grown in an artificial medium. The resulting plant proved to be sterile, but when colchicine treatment was used it was converted into what may be called a completely new species.

It is convenient at this point to summarize briefly what are the real aims of the experimental method. First, the direct aim is not that of taxonomic revision. Intensive study of a genus and other closely related genera by means of tools of greater precision—the microscope and the breeding plot, must, however, inevitably lead to taxonomic revision. As I have mentioned, species will often have their taxonomic status changed, though as I emphasized on a previous occasion, what is really surprising is the fact that so few changes are found to be necessary. The aim of the experimental method goes further than that of the relatively naïve one of telling the taxonomist where he went wrong. It seeks to formulate in a very precise way the relationships between species

in terms of genes, chromosomes, and cytoplasm, and ultimately in terms of evolutionary processes.

The taxonomist is interested in orderly and logical classification. The experimentalist is necessarily also interested in classification, but he would like his own criteria brought in to make taxonomy more precise. He is also concerned with species building and species evolution. He wants to know what happens to genes when species are isolated for a few million years. It is suspected that genes do not remain constant throughout long periods of time—that they evolve into new multiple allelomorphic systems with different combinatory properties. But only by intensive studies of the genetical architecture of carefully chosen single genera, can light be thrown on these profoundly interesting questions.

———

Prof. T. G. Tutin congratulated Miss Haygarth-Jackson on the very lucid way in which she had read Prof. Harland's paper, and expressed the gratitude of the meeting to her.

Mr. J. Ounsted asked what methods were used in colchicine treatment.

Miss Haygarth-Jackson replied that many methods have been used. One which was used at Manchester was to grow seedlings and to add a drop of colchicine to their cotyledons. Another was to take seedlings which had just germinated and to soak the radicles in colchicine. Different strengths were used and the period of immersion varied—for example, the radicles might be soaked in a 1% colchicine solution for 12 hours.

Dr. H. G. Baker enquired whether any work had been done on *Senecio squalidus* collected from the areas where the species is believed to be native.

Miss Haygarth-Jackson replied that all the material they had used at Manchester was collected in this country where the species is, of course, an alien. It was quite likely that the aggressive colonising *Senecio squalidus* in Britain had changed its nature, and they were anxious to obtain plants from the Mediterranean for study and comparison.

SPECIES PROBLEMS IN PLANTS WITH REDUCED FLORAL STRUCTURE

T. G. TUTIN (University College Leicester).

It is well known that the great majority of flowering plants can be recognised by their vegetative characters at least as easily as by their reproductive ones. Any experienced field botanist identifies the majority of species he meets by their general 'look', that is by a combination of vegetative and floral characters, and he is not usually greatly disturbed if the plant has no flower or fruit.

In spite of this the characters given in books for the identification of plants and, consequently, those usually recommended to the attention of students, are based mainly on features such as the shape, size and colour of the floral parts, including the fruits and seeds. This is, of course, contrary to the normal practice of botanists in the day to day identification of plants, and has rather the same effect on the speed with which the beginner recognises a species as working to rule has on the operation of a railway.

There seem to be two main reasons for this devotion to floral characters and the relegation of vegetative ones to a very secondary position in botanical writing. The first is the perfectly valid one that reproductive features provide the most convenient and most satisfactory means of making a classification and, further, their validity has been tested and their respectability established by at least two centuries of use.

The second seems to be very largely a matter of convenience reinforced by the limitations of the written word as a means of communication. The vegetative parts of a plant show far more phenotypic variation than the floral parts, and it is obviously both more troublesome to describe a range of variation and less easy to compare patterns of variation than to compare features in which the variation is sufficiently slight to be neglected. Further, to the casual observer the leaves of, for example, sycamore and plane may appear sufficiently alike to be confused with one another. To the practised eye the colour, texture and exact shape of the lobes are, taken together, sufficiently different to make confusion impossible. There are probably several other features as well which go to make up the general 'look' of the leaves but, even neglecting these, how are we to write down in clear terms the difference between the leaves of these two species so that the reader cannot possibly mistake one for the other?

The ecologist, who cannot afford to wait for a plant to flower or to neglect one that is sterile, makes regular use of non-floral characters with, it is to be hoped, great success and reliability.

The taxonomist has been forced to do the same in distinguishing species in which the flowers are devoid of perianth or inconveniently small and apparently lacking in diagnostic characters. *Salix* and *Ulmus* may be instanced as genera in which leaf characters are freely used for the delimitation of species and the recognition of hybrids. In *Alchemilla* (Walters, 1949) also, leaf shape and the distribution of hairs are the main characters used for the separation of the different apomicts. In this case the fact that it is apomicts that are being identified makes the problem easier since the range of variation is small compared with that found in sexual species.

In the *Gramineae* the floral structures are so reduced and condensed that the spikelet, a whole branch of the inflorescence, has to be used for descriptive purposes, in place of the individual flower. The taxonomist's problems are further increased by the apparently very uniform type of leaf and the great number of species. Non-floral characters have been used in this family for at least 50 years, together with floral characters, for the definition of major groups such as tribes and genera and, to some extent, e.g., by Armstrong (1917), for the recognition of species.

The degree of difficulty in discriminating species appears to vary considerably between different genera in this family, as in most others. In some, e.g., *Melica* and *Deschampsia,* characters of the spikelet and inflorescence seem adequate, but in *Agropyron* section *Elytrigia* and in *Puccinellia,* among others, floral features are of more limited application.

In *Agropyron* leaf characters have for long been used. For instance Babington pointed out that *A. repens* has ". . . . ribs on upperside not much raised nor nearly hiding the intermediate surface of the leaf", while *A. pungens* has "Ribs on upperside of leaf so broad and so elevated as nearly to hide the intermediate part of the leaf". Characters such as these seem to provide the easiest and safest means of distinguishing the species in flower and the only means when sterile. It is interesting to note, however, that Babington supplies most of his information about the leaf structure in the notes after the diagnosis proper, as though it were not quite respectable to pay attention to such trivialities. In contrast to this is the recent treatment of the genus in *Flora Neerlandica,* where not only species but also hybrids between them are clearly distinguished by drawings of transverse sections of the leaves. Plants which appear from their leaf structure to be hybrids are found to have a high percentage of abortive pollen, a fact which confirms the value and reliability of these vegetative features.

It will be noticed that, largely on the strength of the leaf structure, Jansen and Wachter have raised *Agropyron repens* var. *maritimum* to specific rank. This plant occurs on the east coast of England and possibly elsewhere and is to be found in herbaria sometimes under *A. repens* and sometimes under *A.*

Plate I.
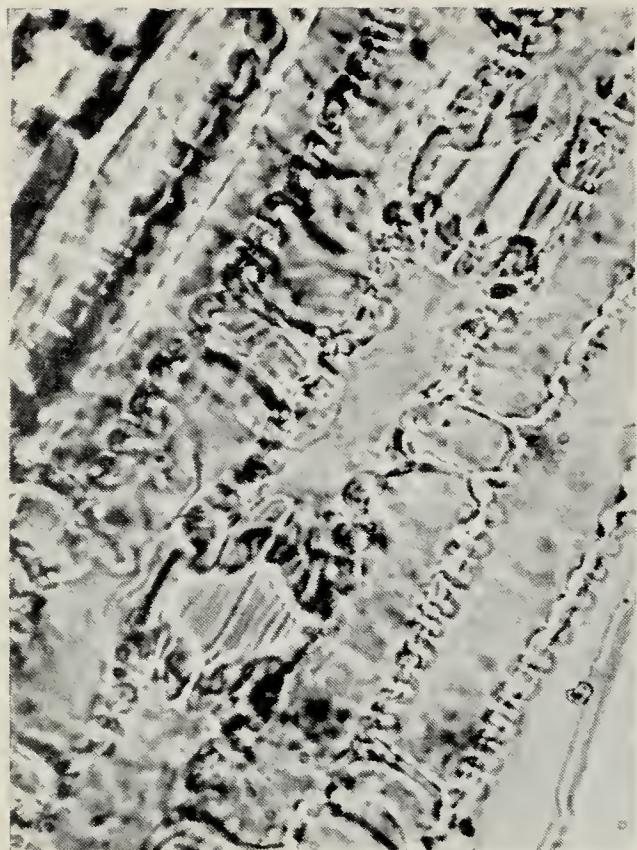

Fig. 1.

Fig. 2.
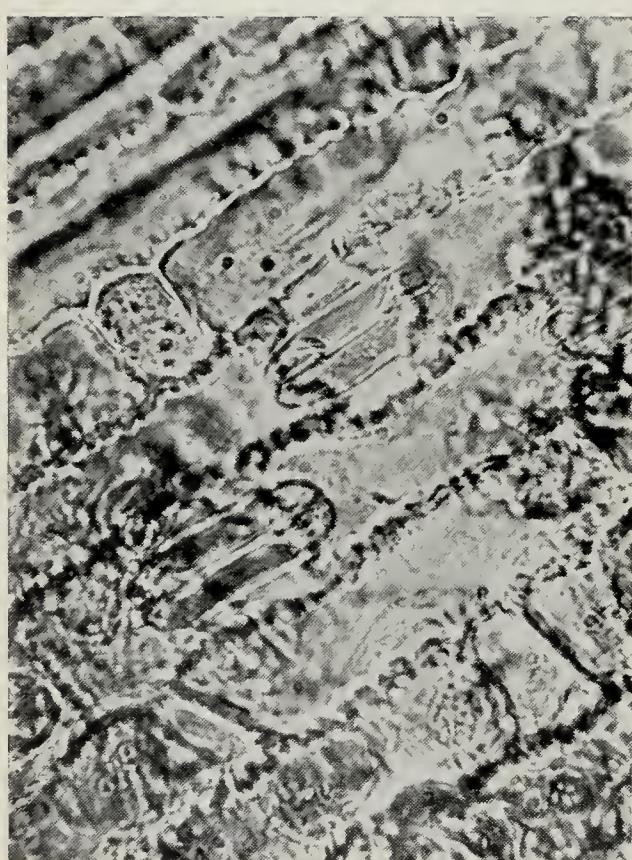
Fig. 3.

Fig. 4.

Lower epidermis of uppermost culm leaves of *Puccinellia* spp. Fig. 1. *P. maritima* from Blakeney; Fig. 2. '*P. maritima* var. *hibernica*' from Strangford Lough; Fig. 3. *P. distans* from Heacham; Fig. 4. *P. pseudodistans* from Bowers Marsh, S. Essex. All × c. 500.

pungens × *repens*. It can be distinguished from the former by the thick ribs and completely smooth upper epidermis, and from the latter by the absence of abortive pollen grains, the completely smooth epidermis and the laxer spike with smaller spikelets.

In *Puccinellia* non-floral characters of a rather different kind have been extensively used by Sørensen in his recent revision of the numerous Greenland species of the genus. He points out that "the rather featureless appearance of the spikelets of *Puccinellia* may render difficult an immediate recognition of the individual species" and goes on to say: "The shape of the panicle is of little value because the branches in certain species may be ascending or reflexed, according to the vigour and the developmental stage." He has, however, used the structure and size of the epidermal cells and stomata, apparently with great success. The range of variation to be taken into consideration is reduced by comparing the epidermis of the uppermost culm leaves at maturity, and seems to be little, if at all, greater than that encountered in floral parts.

In *P. maritima,* for example, some of the cells of the upper epidermis bear conspicuous blunt projections while the lower epidermis is smooth or nearly so. In *P. distans* on the other hand the lower epidermis has rows of pointed conical projections.

In the light of this work it seemed of interest to look at the leaf epidermis of some British *Puccinellia* species. There are known to be in this country two entities in this genus about which there has been a good deal of uncertainty: *P. pseudodistans,* and the Irish plant which has been variously called *P. festuciformis* Praeger (non Hayne) and *P. maritima* var. *hibernica* Druce. The latter has a distinct appearance which attracted the attention of skilled field botanists such as Praeger and Druce, but is rather lacking in floral characters to distinguish it clearly from *P. maritima*. If, however, preparations of leaf epidermis of the two are compared abundant differences are evident. Plate I, fig. 1, represents the lower epidermis of *P. maritima*. The guard cells here are 34-38μ long and the stomata deeply sunk. The surrounding cells overlap the guard cells leaving a roughly cruciform opening which is about 17μ long and 24μ wide. Plate I, fig. 2, shows a corresponding piece of the lower epidermis of what we can call, for the time being, *P. maritima* var. *hibernica*. The guard cells here are 54-56μ long, about 1½ times the length of those in *P. maritima*. The stomata themselves are only slightly below the surrounding epidermal cells, which leave an oval to sometimes almost circular pore giving access to the stoma. This pore is commonly 25-30μ long by 17-20μ wide. There are, of course, other differences in the shape and size of epidermal cells, the sinuosity of their walls, their differentiation into long and short cells, and the proportion of stomata to other cells. This, combined with the difference in general appearance which has struck competent observers who have seen the two plants in the field,

seems to me to justify the recognition of two distinct species. Whether the Irish plant is the same as the southern European plant with which it has been identified or whether it will prove to be an endemic remains to be seen. It is interesting to note in this connection that a variety of different chromosome numbers have been recorded for *P. maritima*. From Sweden the number $2n = 56$ is recorded, *c.* 60 from Portugal, 63 from England and 70 from Germany. Unless there are several errors among these counts there is a strong suggestion that apomixis occurs, at least in some strains, and this would help to explain the occurrence of 'small' and perhaps rather local species. These might well differ in general, but indefinable, appearance and in characters such as epidermal structure, without showing any major differences in reproductive parts.

In comparing the epidermis of *P. distans* and *P. pseudodistans* we find differences at least as great. Plate I, fig. 3, shows the lower epidermis from the uppermost culm leaf of *P. distans*. The guard cells here are 30-35μ long, just as they are in *P. pseudodistans,* but the pore is somewhat cruciform and considerably broader than long. The relatively short and broad epidermal cells are a striking feature of this species.

In *P. pseudodistans* (Plate I, fig 4) the epidermal cells are long and narrow and interspersed with short cells each of which bears a blunt forward-directed protuberance. The epidermal cell immediately below the stoma, though a normal long cell, bears a similar protuberance which makes a flap overlapping the guard cells. The pore is oval and about twice as long as broad.

The upper epidermis of these two species also shows interesting differences. The stomata of *P. distans* have a flap formed by a short narrow protuberance which overlaps the base of the guard cells obliquely; the corresponding structure in *P. pseudodistans* is longer and lies symmetrically over the guard cells.

Once again a variety of chromosome numbers is recorded for *P. distans,* but this time they form a polyploid series: $2n = 14$, 28, 42. It is of course possible that one of these numbers does in fact refer to *P. pseudodistans,* and, though on the face of it there is no evidence of apomixis, it is quite possible that the hexaploid, or even the tetraploid, may prove partially or completely agamospermous.

There are a number of other problems among British grasses where epidermal and other non-floral characters may be of great use. For example the discrimination of *Koeleria* species always seems to be a difficult task, though we are fortunate in having only one common one. The question of the identity of the plant known as *K. albescens* might perhaps be solved by the use of these criteria, which may also prove helpful to anyone interested in the intricacies of the varied and puzzling forms to be met with on continental holidays.

The genus *Salicornia* is once more attracting the attention of a number of workers in this country. It presents problems to the taxonomist resembling in some ways those met with in the *Gramineae* though, owing to the great reduction of the leaves, species seem to be more difficult to delimit than in any grass genus. Most, if not all, experienced field botanists who have studied *Salicornia* at all, have been able to recognise subjectively far more species than they could define on paper.

Obvious vegetative characters such as colour, branching, habit and the length, shape and number of internodes in the fertile branches seem often to provide the only means of recognising the entities in this genus. It is to be presumed that all these features show a considerable amount of variation, but the extent of it needs to be studied in cultivation.

Fortunately it is possible to grow *Salicornia* successfully in pots of ordinary garden soil. The plants develop satisfactorily if the soil is watered with a 3% salt solution at the time the seed is sown. There is some evidence that germination is better without salt, but the seedlings do not seem to grow properly without it.

It might well be profitable to examine carefully the epidermal and other anatomical characters of *Salicornia* species in the hope of getting help from them. Miss de Fraine published in 1913 the results of an investigation of the distribution of spirally thickened cells, but doubt has been cast on the value of this as a specific character and the whole question of anatomical features is in need of re-investigation on a wider basis.

Finally, I should like to stray for a moment beyond the strict limits set by the title of this contribution and say a word or two about groups in which the floral structure is not reduced so much as remarkably simple and uniform.

The genus *Allium* will illustrate the point. Here the flowers consist esssentially of 2 whorls of petaloid perianth segments, 2 whorls of stamens and a trilocular ovary with nearly always 2 ovules in each cell. Fortunately, the leaves are fairly varied and so are the underground parts and certain floral characters such as colour, so the recognition of species is usually not too difficult. It seems likely, however, that this large genus is not in fact a natural group but includes several divergent groups placed together because of their smell, their umbellate inflorescence and their flowers which are, after all, of the basic monocotyledonous pattern and not necessarily a guide to affinities. Non-floral structures suggest that this is so. For instance, different species show epigeal or hypogeal germination, some have rhizomes and no bulbs and among the others there is a great diversity of bulb structure. These are surely features which should be taken into account at the generic level as well as at the species level.

REFERENCES.

ARMSTRONG, S. F., 1917, *British grasses and their employment in agriculture.* Cambridge.

BABINGTON, C. C., 1922, *Manual of British Botany*, 10th edition. London.

DE FRAINE, E., 1913, The anatomy of the genus Salicornia, *J. Linn. Soc.*, **41**, 317-348.

JANSEN, P., 1951, *Flora Neerlandica*, **1**, 2. Amsterdam.

SØRENSEN, THORVALD, 1953, A revision of the Greenland species of Puccinellia Parl., *Meddelelser om Grønland* **136**, 1-180.

WALTERS, S. M., 1949, Alchemilla vulgaris L. agg. in Britain. *Watsonia*, **1**, 6-18.

Dr. J. HESLOP-HARRISON suggested that in using vegetative characters difficulties arose mainly when we had to rely on size. In such cases characters could only be found by statistical methods. Whenever it proved possible to find "either or" characters we should be able to distinguish units.

Mr. J. D. LOVIS said, concerning Professor Tutin's examination of epidermal structure in *Puccinellia pseudodistans*, he would be most interested to know from where his material came; from Britain, Holland or the Mediterranean. Mr. Lovis went on to say that he had found that plants resulting from seeds of *P. pseudodistans* from Pitsea, Essex, given to him by Mr. Lousley, had a chromosome number of $2n = 28$, the same number as *P. fasciculata*. Regarding the three levels of polyploidy reported for *P. distans*, so far he had only been able to recover the hexaploid $(2n = 42)$ from Britain. Experimental garden trials of *P. pseudodistans* and related species had been started at Leeds but he was not prepared to make any comment on these at the present time.

Prof. TUTIN replied that his material of *P. pseudodistans* also came from Mr. Lousley.

THE STABILITY OF SOME SPECIFIC CHARACTERS AS SHOWN BY FOSSIL RECORDS

H. Hamshaw Thomas (Botany School, Cambridge)

The concept of a species as a group of individual plants, distinguishable from other groups in their genetical composition and usually recognisable by morphological characters, involves a time factor. According to our ideas of evolution the ancestors of forms, now recognisable as a distinct species, were part of an assemblage of plants which in the course of time also gave rise to types now regarded as forming other species, and probably to other forms which have since become extinct. Relatively small changes in genetic constitution seem to have resulted in differentiation on the species level, while greater or more frequent changes have given forms which we recognise as distinct genera.

It would be of great interest to know something of the time taken in the differentiation of both species and genera. But although the quantity of plant material that has come down to us from the past is not inconsiderable, it is mainly in the form of fragments, usually isolated from each other. We can seldom reconstruct the original appearance of the whole plant of any extinct vascular type. From the study of the remains of pieces of stems, of leaves, seeds or fruits and pollen grains, we are, however, often able to obtain reliable information about the main morphological features of many types related to plants living today. This enables us to identify genera, or to recognise generic differences, but we are seldom able to state the more important *specific* characters of any extinct form taken as a whole. The conditions necessary for the preservation of plants as fossils are of rare occurrence, and consequently we have little chance of seeing the way in which populations of organisms change during the passage of time. Palaeontologists are much more favourably placed when they study the evolutionary changes in vertebrate animals.

But though the study of fossilised plants does not give much help in reconstructing the history of species, it does provide a very useful background to our studies of living forms. The last fifty years have seen very great additions to our knowledge of the past history of the vascular plants, especially of the gymnosperms and the ferns. The remains of ancient flowering plants have been studied in several parts of the world with results of considerable importance; this work is not very widely known though it carries considerable implications for those interested in angiosperm taxonomy.

Most of the botanists of my generation were taught to think that the evolutionary development of the angiosperms has been a very rapid process. This belief, which is still widely held, had a noticeable influence on the study of the group. It was based on two ideas, both without factual support, but resting on negative evidence:—(a) The flowering plants are thought to have originated in the Cretaceous period. If this were true the widely different types now living must all have evolved in the course of about 100 million years. (b) That the flowering plants sprang from gymnospermous ancestors with groups of fertile leaves arranged in strobili; the diverse forms of flowers seen today were thought to have evolved from these stroboli.

The fact that very few remains of plants looking like angiosperms have yet been found in rocks older than those of the Cretaceous period does not prove that angiosperms did not exist at an earlier period. On the other hand, when we first find dicotyledonous remains in the Lower Cretaceous strata in England (Stopes, M., *Phil. Trans. Roy. Soc. London,* **B203**, 75, 1912) they are so diverse in anatomy that they can scarcely be regarded as having recently sprung from a common ancestor. It seems to me more probable that the early flowering plants were in existence for some fifty million years, or more, before they spread into the vegetation and areas in which they had some chance of being preserved. The second idea is quite without support from historical evidence. If it were true, it would follow that very extensive evolutionary changes have taken place in the floral parts of all modern types. But this theory originated in the idealistic concepts of floral structure current in the early days of the 19th century, and there is no justification for applying these concepts to the problems of plant evolution. The difference between an idealistic morphology and an evolutionary morphology, to which the writer drew attention many years ago, has recently been ably demonstrated by Dr. Agnes Arber in her book on the *Natural Philosophy of Plant Form.*

When one comes to examine all the fossil evidence which has been rapidly accumulating in recent years a very different picture is presented. Angiosperm evolution seems to have been as slow as in other groups of land plants; many types appear to have persisted over very long periods of time with comparatively little change in their morphological characters.

The material available for study is very extensive. From rocks dating back some 90 millions of years we have the remains of the leaves of dicotyledonous plants, often found in abundance, whose shape and venation can be clearly seen. In some examples the cuticles of the leaves are also preserved, and after suitable chemical treatment the details of the stomata and epidermal cells can be studied under the microscope. Many of these forms were collected and studied during the 19th century and it was realised that they could be closely matched with living forms. Early in

the present century there was a strong feeling that the identifications made by the earlier workers in this field could not be substantiated, but more recent investigations have shown that they were probably correct in many instances. This has come through the systematic study of the fruits and seeds of Tertiary plants. Clement Reid and his wife, who recently died, became interested in the many remains of fruits and seeds which could be found as fossils in the Tertiary and Quaternary beds of Britain. They got together a large herbarium of the seeds and fruits of living plants and found that it was possible to identify a considerable number of the fossil forms by matching them with the seeds and fruits of recent species. This work has been ably continued by Miss Chandler and other workers in England and on the Continent. It has led to the identification of a large number of the genera in the successive floras of the Tertiary period from the period of the London Clay onwards.

In addition to the evidence from the leaves, the seeds and the fruits, we now have a considerable body of evidence derived from the study of the pollen which is preserved in layers of peat or fresh water clays. This helps to complete the picture of the earlier flowering plants.

Well preserved remains of flowers are seldom found, but some remarkably perfect flowers, easily recognisable as derived from species of *Quercus* and *Cinnamomum,* were discovered some time ago preserved in amber, the fossilised resin of a tree, of Oligocene age. The remains of inflorescences and flowers have also been found at different places in the United States of America, but the details of their floral structure can seldom be made out.

In many parts of the world pieces of petrified dicotyledonous wood can be found. Their structural features are often beautifully preserved, but in the past their identification has been a matter of great difficulty owing to the absence of collections of woods from living trees and shrubs with which they could be compared. Now that properly arranged and tabulated collections of the wood of almost all of the known trees of the world have been formed in England and America, we can look forward to the discovery of many new facts about the affinities of the trees of Cretaceous and Tertiary times.

Taking the evidence as a whole, it would seem that the majority of the genera known to have existed in Lower Tertiary times are still living somewhere in the world today. In as far as comparison is possible the modern forms do not differ widely from their early representatives.

From an examination of the species included in a genus of living plants, there seems some justification for the view that the leaves of a dicotyledon are the organs most likely to show variation with the passage of time. If, then, the flowering plants have been evolving rapidly during the past one hundred million years, we should find great differences between the form and structure of modern leaves and that of the earlier forms of the same genus.

But in fact the changes in form and venation since the commencement of the Tertiary period are usually small, and many of the types whose cuticles have been studied show that in the Eocene period their stomata and epidermal cells very closely resembled those of the living species. The beautiful British material from Hampshire and the Isle of Wight has not recently received the critical study it deserves, but some years ago the late Miss Bandulska (*Journ. Linn. Soc., Botany,* 1924-28) showed that a number of leaves found in the Eocene beds at Bournemouth closely resembled living species of several genera of the *Lauraceae* in form, venation and cuticular structure. In recent years the critical examination of Tertiary leaves from different horizons has been actively pursued in Western North America by Prof. Chaney and his associates. They have collected considerable numbers of forms from different localities, and have mainly worked with the remains of leaves. The majority of these could be identified with modern genera, and some with species, now living in Mexico, Central America, China and the basin of the Mississippi. So much information of this kind has now been published, often accompanied by photographs of fossil and modern leaves side by side, that it is not possible to hold any longer the view that the leaves of dicotyledonous trees have varied rapidly with the passage of the years.

It must be noticed, however, that the greater part of the evidence for the stability of characters comes from the study of trees or shrubs. Unfortunately we have little evidence from the remains of herbaceous plants, since these are seldom preserved as fossils. It may well be that evolutionary changes in herbs take place more quickly since their life cycle is completed so much more rapidly. We have one valuable piece of evidence which seems to support this view. The seeds of *Stratiotes aloides* have been collected from various localities in beds laid down in the Quaternary period, and comparable seeds have been found at a number of other horizons as far back as the Upper Eocene. All these forms were carefully studied and compared by Miss Chandler (*Quart. Journ. Geol. Soc.,* **79**, 117, 1923) who found that they showed a series of changes in form and structure. The changes suggested a main line of evolution resulting in the present-day form, together with one or two subsidiary lines. Unfortunately we have little or no evidence of the vegetative parts of the plants from which these seeds were derived.

The fossil records of the ferns and the gymnosperms are similar to that of the angiosperms. Many forms seem to persist through very long periods of time with little change, while new forms appear at intervals. When examined without morphological preconceptions the new characters which appear are seen to be gradual modifications of ancestral characters rather than radical changes in structure. Through changes in climate and geographical conditions old types have died out and further

changes have been favoured, but in general the evidence shows that plants of all groups possess great morphological stability.

All this suggests to me that the flowering plants, as a group, must be very much older than has been usually thought, and that the reason why they scarcely appear in the geological record before Cretaceous times is that they originated, grew and developed on dry ground in areas where they could not be preserved as fossils, or in places from which the deposits in which they were buried have been removed by denudation.

Prof. D. H. VALENTINE enquired whether pollen grains referable to Angiosperms had been found in deposits of Jurassic age. Dr. THOMAS said that such pollen grains had been found in Jurassic deposits but there were only three or four records, and much more work was required.

Dr. R. MELVILLE asked how far back the records of *Stratiotes* extended and whether the lecturer could tell us of any sequences of leaf-form in Dicotyledons which went back any length of time. Dr. THOMAS replied that the earliest records of *Stratiotes* were from the top of the Eocene. Nothing of value had been done on leaf sequence. The Americans have material suitable for work of this kind but have been interested in other aspects.

Miss C. LONGFIELD said that a dragonfly, an *Aeschna*, was entirely dependent on *Stratiotes* and a fossil dragonfly wing from the Eocene was almost identical. It was known that the *Odonata* date back to the Permian and an interesting link between plants and dragonflies was suggested.

VARIABILITY WITHIN SPECIES

J. H. Burnett (The University of Liverpool).

Variation is an ubiquitous phenomenon in all organisms. It has been the especial concern of taxonomists to assess the relative importance given to variants in relation to classification. At present this is a particularly difficult activity to undertake for a number of reasons. The study of variation involves two inter-dependent and simultaneous investigations. On the one hand, it is necessary to determine which properties of an organism vary and in what ways; on the other, to determine what are the causes of variation. An ancillary process, important for taxonomy, is the development of adequate techniques to describe the kinds and causes of variation.

The application of the results of these investigations to taxonomy is difficult for three reasons. Variants differ in many ways. They are of different kinds, magnitudes, and stabilities. They may occur with different frequencies, or possess different distributions in assemblages of related individuals. The introduction of new techniques has increased enormously the range of features which may be studied, and each new feature, so introduced, may vary in one or several of the ways described. Initially there is, therefore, the difficulty of appreciating and containing the great amount of information available. A second difficulty arises from progress in the study of the causes of variation. There has been a tendency for the description of unique, restricted patterns of variation to be replaced by the description of universal processes. This tendency can be demonstrated by a selection of statements on the relationship of variation to taxonomic practice over the last three hundred years.

For instance, in 1674 John Ray wrote: —
"Having observed that most herbarists, mistaking many accidents for notes of specific distinction, which indeed are not, have un-necessarily multiplied beings, contrary to that well known philosophic precept: I think it may not be unuseful, in order to the determining of the number of species more certainly and agreeably to nature, to enumerate such accidents and then give my reasons why I judge them not sufficient to infer a specific difference."

After this passage followed an enumeration of different kinds of variants which were regarded as unworthy of specific rank, e.g., floral abnormalities, changes consequent upon transplantation of mountain forms to lowlands, and other conditions induced artificially. Canon Raven has remarked: "It is one of the out-

standing qualities of Ray's achievement that he has refused to base specific differences on other than structural qualities." This is true, but Ray also considered it necessary that forms should breed true within these limits: *"Distincta propagatio ex semine."* Ray recognized that variation arose both from inherent, internal causes and from the influence of the external environment. The study of variation embraced both types but only that due to the former cause was of taxonomic significance.

Two hundred years later Darwin was concerned with the same problem as Ray. He attempted to assess the significance of inherent variation in his theory of natural selection, thus: "I have called this principle, by which each slightest variation, if useful, is preserved, by the term of natural selection." (*Origin,* p. 32). He described the application of this principle to taxonomic method in the last chapter of the *Origin of Species*: —

"When the views advanced by me in this volume or by Mr. Wallace in the Linnean Journal or when analogous views on the origin of species are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present, but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This, I feel sure, and I speak after experience, will be no slight relief. The endless disputes whether or not some fifty species of British Brambles are true species will cease. Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition and, if definable, whether the differences be sufficiently important to deserve a specific name . . . . It is quite possible that forms now generally acknowledged to be merely varieties may hereafter be thought worthy of specific names, as with the primrose and cowslip; and in this case scientific and popular language will come into accordance. In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but at least we shall be freed from the vain search for the undiscovered and undiscoverable essence of the term species."

Read to-day, parts of this extract reveal a streak of the wildest optimism in Darwin, and most biologists will welcome the golden age of taxonomy, which he predicts, with no slight relief! Both Darwin and Ray were concerned with the delineation of species. Because Darwin attempted to account for the processes involved in the origin and maintenance of species he was led to regard species as relative rather than absolute units.

The study of genetics in the twentieth century has resulted in an even greater emphasis on the nature of the processes involved in the development and maintenance of species.. For example, fifteen years ago it was possible to read in *The New Systematics* that—

"The only valid principles are those that we can derive, not from fixed classes but from changing processes. To do this we must go beyond the species to find out what it is made of. We must proceed (by collaboration) to examine its chromosome structure and system of reproduction in relation to its range of variation and ecological character. From them we can determine what is the genetic species of Ray, the unit of reproduction, a unit which cannot be used for summary diagnosis, but which can be used for discovering and relating the processes of variation and the principles of evolution." (Darlington, 1940).

Studies of the kind described in this extract evidently lead to different activities from those commonly engaged in by taxonomists! Divergent procedures with identical materials are likely to lead to confusion and controversy. It is not inevitable that they will lead to different conclusions.

The third difficulty stems from the inadequate development of suitable techniques for describing variation, especially its frequency and distribution. This difficulty is a component of the first distinguished here, that derived from the great increase in the data on variation. No doubt this will be overcome, in time, by application and ingenuity.
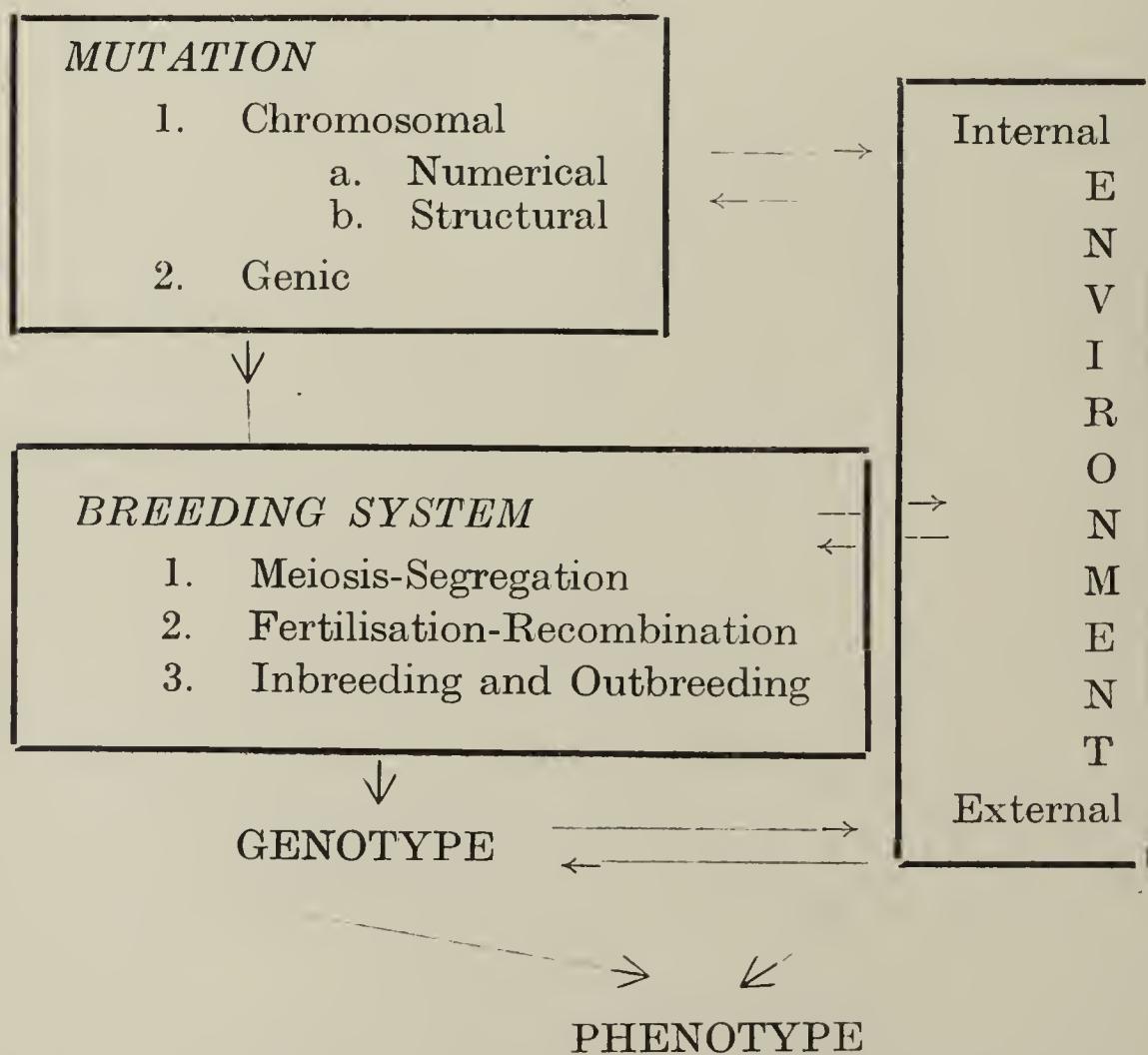

Fig. 1. The relationship of Genotype, Phenotype, the Environment and the processes which cause genetic diversity.

It is not certain that the second source of difficulty can be so readily resolved, for it arises from the application of different methodologies. As Ray realized, the appearance and properties of organisms are developed through the interplay of their inheritance and the environment. From fertilization, when the inherited potentialities come together, there is a constant interplay between them and with the environment outside them, until death. The nett result of this "fruitful struggle" is the phenotype. The origin and manifestation of variation of the phenotype are shown diagrammatically (Fig 1).

Now, in the first instance, taxonomists are concerned to study phenotypes. Their final assessment of the taxonomic status of an entity will be conditioned by the range of information they obtain concerning its phenotypic variation, not excluding any information available on the causes of this variation, genetic or otherwise. But those workers who adopt the principles, "derived from changing processes", will be concerned, primarily, to classify the kinds of genetic diversity involved in the development of the entity.

It is relevant, therefore, to consider the manifestations of phenotypes in relation both to genetic diversity and permanence. Such a consideration makes it possible to judge the kinds of result to be obtained by the study either of "fixed classes" or "changing processes". Accordingly, a number of examples are set out to illustrate the ways in which different kinds of genetic diversity are manifested phenotypically. Save for hybridization, diversity which arises from different kinds of breeding systems has been omitted, since it has been reviewed recently (Baker, 1953;

Gustafsson, 1946-47; Stebbins, 1950). The examples given in the tables are selected to illustrate:—

1. *The magnitude of the phenotypic expression of the variation of the genotype.* Variants detectable without the use of special techniques are classified as "Distinct". Those whose detection requires special techniques, or those where the variation tends to be continuous, are distinguished as "Semi-cryptic" and those not readily distinguishable are classified as "Cryptic".

2. *The frequency or distribution of the variants,* in space and/or time, whenever known.

3. *The taxonomic status,* if any, given to each variant.

TABLE 1

(a) NUMERICAL—POLYPLOIDY

PHENOTYPIC EXPRESSION	PLANT	CHROMOSOME NOS.	DISTRIBUTION	TAXONOMIC STATUS
DISTINCT	*Ranunculus ficaria*	$2n$: 16 and 32	Geographical and (?) ecological	Subspp.
	Eleocharis palustris	$2n$: 16 and 38	Geographical and ecological	Subspp.
	Monotropa hypophegea	$2n$: 16	?	Sp
	M. hypopithys	$2n$: 48	?	Sp.
SEMI-CRYPTIC	*Galium palustre*	$2n$: 24, 48 and 96	Ecological	Vars. or subspp.
	Valeriana officinalis	$2n$: (14), 28 and 56	Geographical and ecological	Spp., subspp. and vars.
CRYPTIC	*Salix caprea*	$2n$: 38, 76	?	—

CHROMOSOMAL VARIATION

COMMENTS

Distinguishable by several morphological characters which seem to be correlated with the cytological condition (Marsden-Jones and Turrill, 1952). They may possibly occupy different ecological niches (Turrill, 1948) and the tetraploid appears to be the predominant form in Sweden and (?) Denmark (Perje, 1952).

Characters by which these forms may be distinguished have been given but the distinction is not always easy or possible to make. The two forms differ both in their ecological tolerances and in their geographical ranges (Walters, 1949).

These plants are readily distinguished morphologically and have been found, recently, to differ cytologically (Hagerup, 1944: Löve & Löve, 1944). It is assumed that the correlation between morphology and cytology is constant and presumably it is on this assumption that they are given specific rank in Clapham, Tutin & Warburg (1952). They are not known to show ecological or regional differences in distribution.

The cytology of this species was described by Hancock (1942), who also described different ecological preferences for each cytotype. Earlier, the diploid and the octoploid had been recognized on morphological grounds as var. *lanceolatum* and var. *witheringii* or var. *angustifolium*, respectively. In its range of morphological expression the tetraploid overlaps both the others. Therefore, precise discrimination is not always possible.

The cytological work on British and Polish material (Skalińska, 1947, 1950, 1951) and the taxonomic work on British and European plants (Walther, 1949; Sprague, 1952) demonstrate that in some parts of the range of this aggregate there is a correlation between morphological and cytological features. This does not always obtain in the British Isles and Western Europe.

Wilkinson (1944) was unable to distinguish cytologically distinct material by morphological characters. The distribution of the two forms is unknown.

TABLE 1

(b) NUMERICAL—DYSPLOIDY

DISTINCT	Viola riviniana	2n : 40, 46 and 47	Sporadic	Forma
SEMI-CRYPTIC	Erophila duplex	2n : 30-40	(?) Regional	Forma or Spp.
CRYPTIC	Iris pseudacorus	2n : 24, 32-34	?	—

(c) STRUCTURAL

PHENOTYPIC EXPRESSION	PLANT	DISTRIBUTION	TAXONOMIC STATUS
	Trillium kamtschaticum	Regional	—
CRYPTIC	Datura stramonium	Geographical	—
	Paris quadrifolia	?	—

CHROMOSOMAL VARIATION (*Continued*)

Certain forms are distinguished by the possession of adventitious shoots. They are sporadic in occurrence and, so far, this morphological feature has always been found to be correlated with a dysploid number of chromosomes (Valentine, 1949).

This aggregate group of cytologically heterogeneous plants shows considerable similarity although distinct forms occur which may have characteristic distributions. In general, there is not a high correlation between morphology, cytology and/or distribution (Winge, 1940).

These chromosome numbers have been recorded but there is no evidence that morphological or distributional features are associated with the dysploidic condition (Ehrenberg, 1945).

COMMENTS

By studying the chromosomes of plants chilled before examination segments which showed differential staining were detected. The frequency of these differential chromosome types was not the same in different populations (Haga & Kurabayshi, 1948).

"Prime-types" occur with different pairs of chromosomes which have reciprocal translocations. These are only detectable by breeding and cytological experiments. The prime-types show different geographical distributions. In eastern U.S.A. several types occur whereas P.Ts 2 and 3 occur almost exclusively in Peru (Blakeslee, Bergner & Avery, 1937).

Populations from the Austrian Tirol possessed inversions in every chromosome arm. Morphologically these plants, and the species throughout its range, were very constant. How widespread this cytological condition is in *P. quadrifolia* is unknown (Geitler, 1937 and 1938).

TABLE 2

(a) AFFECTING SEVERAL CHARACTERS

PHENOTYPIC EXPRESSION	PLANT	DISTRIBUTION	TAXONOMIC STATUS
DISTINCT	*Rumex obtusifolius*	Geographical	Subspp.
	Alnus glutinosa	Ecological	Vars.
SEMI-CRYPTIC	*Veronica anagallis-aquatica*	Sporadic	Vars.
	Lamium purpureum	Geographical & seasonal	—
CRYPTIC	*Deschampsia cespitosa*	Regional & ecological	—
	Fomes pinicola	Geographical & (?) ecological	—

GENIC VARIATION

This species is wide ranging and four well marked subspecies, which differ both in their morphology and geographical ranges, have been described. Three of these have been recorded for the British Isles (Lousley, 1938).

The habit, size and shape of leaf and catkin size are variable in this species. Certain combinations of these features show some degree of correlation and have been described as distinct varieties (Moss, 1914). But this variability can be described more precisely as clinal and can be correlated with a S.E.-N.W. climatic gradient in Britain (McVean, 1953).

Small forms of this species with thicker leaves than are usual and densely glandular-hairy inflorescences have been described as distinct varieties under a multitude of different names. In Britain the majority of these forms are adaptive responses to environmental conditions but occasionally some forms are found which are genetically fixed in this habit.

Müntzing (1932) described winter-annual and summer-annual forms of this species which are virtually genetically isolated and morphologically indistinguishable. The frequency of winter/summer annuals has been shown to vary in a more or less clinal manner from Scandinavia southwards to Asia Minor (Bernström, 1953).

This species is cytologically and morphologically uniform in N. America but physiologically (e.g. in vigour of growth, height, number of flowering stems, fruiting and survival after frost injury) very diverse. There is some correlation between certain of these physiological features and on this basis five groups can be experimentally distinguished (Lawrence, 1945).

This fungus is widely distributed in N. America and Europe. It is rare in this country. There is some morphological variation in the fruit body on certain host trees. From their breeding behaviour isolates can be divided into three partly interfertile groups which are quite independent of the morphologically variant groups. Two of the breeding groups in N. America show very little interfertility although individuals from each may grow side by side. One of the N. American groups is almost completely unable to cross with European forms, the other is quite interfertile (Mounce & Macrae, 1938).

TABLE 2

(b) AFFECTING SINGLE CHARACTERS

PHENOTYPIC EXPRESSION	PLANT	DISTRIBUTION	TAXONOMIC STATUS
DISTINCT	*Panus stipticus*	Geographical	—
	Plantago maritima	Regional	Var.
SEMI-CRYPTIC	*Digitalis purpurea*	Sporadic or (?) regional	—
	Ricinus communis	Ecological	—
CRYPTIC	*Trifolium repens*	Ecological & geographical	—

GENIC VARIATION *(Continued)*

COMMENTS

This fungus is probably distributed throughout the world. All the N. American forms examined possess a phosphorescent mycelium; forms in Europe, including those in Britain, do not. The difference is due to a single pair of allelomorphic genes which apparently have different geographical distributions (Macrae, 1942).

A single dominant gene determines the presence of small, deep wine-red spots on the leaves of this species. The frequency of occurrence of plants with spotted leaves varies in different populations and does not appear to be correlated with any other feature in this country. However, when populations from areas between E. America and Europe are compared, the average percentage frequency of plants with spotted leaves in the various sub-regions tends to follow a geographical sequence or topocline (Gregor, 1939).

Two forms of this species occur in Britain. In one, the plant is uniformly pubescent, in the other, the leaves are less hairy and the stem is glabrous at the base but becomes hairy in the region of the inflorescence. These conditions are due to a pair of allelomorphs, the latter condition being dominant to the former. Its distribution appears to be sporadic although the recessive condition is apparently more frequent (Saunders, 1918).

Leaves with or without a waxy bloom are determined by a pair of allelomorphs $B:b$. In Peru, coastal populations contained 0.15% plants with bloom and this percentage increased in populations at successively higher altitudes, viz. 585 ft.—22.2% ; 1950 ft.—30.1% ; 2762 ft.—50.0% ; 7764 ft.—100.0%. There is evidently a correlation between ecological and climatic features and the presence or absence of a waxy bloom on the leaves i.e. variation is distributed clinally (Harland, 1947).

The presence or absence of cyanogenetic glucosides in this species is determined by the allelomorphs $Ac:ac$. The frequency distribution of this gene pair has been studied in wild populations in the British Isles and in Europe as far as E. Russia and the Near East. There was a general tendency for the frequency of Ac to decrease in the direction Mediterranean Basin to N.E. Europe, and the distribution of the gene was apparently correlated with the January isotherms (Daday, 1954).

TABLE 3

PHENOTYPIC EXPRESSION	HYBRID COMBINATION.
	Veronica anagallis-aquatica × *V. catenata*
DISTINCT	*Senecio aquaticus* × *S. jacobaea*
SEMI-CRYPTIC	*Saxifraga hirsuta* × *S. spathularis*
CRYPTIC	*Symphytum officinale*

VARIATION ARISING FROM HYBRIDISATION

COMMENTS

Hybrids between these species are quite sterile and are readily distinguished by morphological features such as greater size, an increased number of flowers and irregular development of floral bracts.

Hybrids between these species occur frequently in Ireland but are less common in this country. They are not fertile with either parent and a characteristic sight is a hybrid swarm in the area between a population of *S. aquaticus* on wet peat and one of *S. jacobaea* on the well drained part (Praeger, 1951).

Hybrid swarms are developed between these species in Ireland. In S.W. Ireland both parental and hybrid forms occur but in County Mayo only *S. spathularis* and hybrids now occur (Webb, 1950).

A number of variants are known with different flower colours. It has been suggested that this is due to a history of past hybridization (Turrill, 1948).

These examples provide evidence that a particular kind of genetic process may show different kinds of phenotypic expression in different species. Thus, for instance, the phenotypes of polyploids and their diploid progenitors may be distinguished in some cases by their morphology, ecology and distribution or, in the extreme condition, they may only be distinguished on cytological examination. In general then, the possible array of phenotypes associated with a particular kind of genetic situation form a complete series in respect of their readily observable characters, a spectrum of manifestations.

Most situations are more complex than those represented in the tables, which were selected, in part, for their simplicity. Increased complexity may arise from several causes. There may be more than one kind of genetic mechanism giving rise to different kinds of variant. These processes may affect different characters in different or correlated ways. In addition, the kinds and causes of variability may be different in different parts of a species range. Some of the examples given illustrate these points. *Erophila duplex,* cited as an example of dysploidy, is a complex amongst a group of forms comprising a polyploid series (Winge, 1940). Superimposed upon the morphological variation correlated with dysploidy in *Viola riviniana* there is a wide range of morphological expression associated with different ecological tolerances. These reach their extremes in subspecies *nemorosa* and subspecies *minor* (Valentine, 1941). The physiological variation of *Fomes pinicola* is independent of a particular kind of morphological development of the fungus found amongst some of the individuals when they occur on coniferous trees. These morphological variants may belong to either of the physiologically dissimilar and partially inter-fertile races A and B. An even more complex situation in another thallophyte, *Fucus,* is described by Burrows & Lodge (see p. 83). The form of these plants is apparently readily modified by different environmental conditions but some of this variation is probably due also to hybridization. Moreover, different ecological behaviour is shown by some species in different parts of their geographical range, e.g. *F. inflatus* and *F. vesiculosus.* In the former species there is also a continuous gradation in the Faeroes between two forms which are separable both in morphology and ecological tolerance in the British Isles and Scandinavia. Variation also occurs in N. American species of *Fucus* but at present it cannot be correlated with that found in N.W. Europe because critical comparisons have not been made. Different patterns of behaviour are shown in different regions by flowering plants. *Valeriana officinalis* is an excellent example. In the British Isles there is a range of morphologically intergrading forms superimposed upon a genetic background of two polyploid variants. This condition also occurs on the western mainland of Europe but in Poland there are three morphologically and cytologically distinct forms. These forms overlap both phenotypically and cytologically with some of the forms which

occur in N.W. Europe (Skalinska, 1951). A more subtle form of regional differentiation is that which occurs in *Lamium purpureum*. This species is known to occur as both a summer-annual and a winter-annual form (Müntzing, 1932). More recently it has been shown that the proportion of summer-annuals increases in the more north-westerly populations while in Portugal, France, Switzerland, Italy, Syria and Central Europe, winter-annual forms predominate. There is also an increase in the degree of development of the winter-annual habit from N.W. to S.E., i.e. the most southerly summer-annuals approach the winter-annuals in habit and behaviour more than those from more northerly latitudes (Bernström, 1953).

There is little doubt that the study of the variability of British species outside the United Kingdom has not been prosecuted as vigorously as it might have been. A less parochial attitude in this matter is desirable. This is especially so in respect of the status, frequency and distribution of "minor" variants which are often dismissed as "not worthy of distinction by name" (Wilmott, 1949). A recent study of *Trifolium repens* illustrates the value of such an investigation. Twenty years ago, in a discussion on the taxonomic treatment of biological races, Turrill (1931) mentioned that some individuals of *T. repens* possess a cyanogenetic glucoside, others do not. The condition is due to a pair of allelomorphic genes. The study of the distribution of these two forms in wild populations was begun by the late R. D. Williams and has been completed and published by Daday (1954). The frequency of the occurrence of the glucoside-determining gene in populations is correlated with the January isotherms. In general, its frequency decreases from Asia Minor and W. Central Russia to N.W. Europe. There is evidence that similar trends occur in morphological characters e.g. length of the corolla tube, but this requires further study. It may be noted that this kind of pattern of variation can only be adequately represented as a gene-frequency map. The striking relationship between this "cryptic" character and an environmental factor could never have been detected by a study of British material alone. In quite a different way the data presented by Manton (see pp. 90-97) on the causes of variation in British, European and N. American ferns has contributed valuable information. Not only has it provided data on geographical distribution and possible migrations but it has provided direct evidence for the immediate phylogeny of certain species. Such an unequivocal demonstration of natural relationships is obviously of value to taxonomists.

It is convenient at this point to consider briefly phenotypic variation against a constant genetic background. Such variability is shown by most plants and has been studied for a longer period than other forms of variation. Some species and races vary in this way more than others. Dr. F. H. Whitehead, of Oxford, has studied a particularly interesting case, *Cerastium*

tetrandrum, and has generously permitted me to quote some of his unpublished results. He has shown that, in response to different light intensities, different individuals from cloned material have shown variation which transcends that found in nature as a result of either genetic or environmental causes. The features studied included general habit, and relative xeromorphy of the leaves as measured by their hairiness and stomatal frequency per unit area. Thus *Cerastium tetrandrum* evidently possesses an extraordinary range of phenotypic plasticity which appears to be adaptive in relation to the environment. How widespread such behaviour may be is unknown. It is still true that "our knowledge of the plasticity of even common plants is very meagre and even facts already known are sometimes ignored" (Turrill, 1938).

There is some evidence that most of the modifications which are apparently adaptive to environmental conditions are due to variation and selection of the genotype. This adaptive response may be manifested in at least two ways. Either, distinct genotypes may be found in different environments, e.g., in *Achillea borealis* and *A. lanulosa* (Clausen, Keck and Hiesey, 1948: Hiesey, 1953), or, the same genotypes may occur with different frequencies in different environments, e.g., *Plantago maritima* (Gregor, 1946). Doubtless intermediate conditions between these extremes will be found.

Another very frequent condition of some interest is the occurrence of phenotypically similar individuals whose appearance is determined in different ways. In some the growth form is inherent and invariable, in others it is an adaptive response to the environmental conditions. An example of this situation is known in *Veronica anagallis-aquatica.* Individuals in exposed, well-drained situations often have short, stout stems, a small leaf area and highly glandular-pubescent inflorescences. Usually such individuals become taller, develop larger leaves and show a reduction of pubescence when transplanted to a medium loam soil in protected pot cultures. However, a plant found on the Kenfig dunes and sent to me by Mr. B. L. Burtt has now maintained its original characters for two generations of pot culture. Its reduced, pubescent habit is genotypically conditioned. It may be suggested that careful observation of such cases might provide evidence for, or against, the "Baldwin effect" recently described by Simpson (1953). This is a condition simulating the inheritance of acquired characters. Whether or not this will be the case, it is certain that more precise studies of the nature and extent of phenotypic plasticity are necessary. Preliminary investigations using the transplant technique will give useful results, and can be carried out by amateur and professional alike, but more precise experimentation is also desirable.

This rapid survey of the causes and manifestations of variation in plants reveals one feature with great clarity. This is, that variation is rarely manifested in a discontinuous manner. Even

when a particular genetic process gives rise to discrete classes of individuals, e.g., diploid *v.* tetraploid, allelomorph *A v.* allelomorph *B*, their phenotypic expression may or may not reflect this distinction. Moreover, in many cases where the alternative genetic determinants and their phenotypes are distinguishable, e.g., presence *v.* absence of glucoside in *Trifolium repens,* the frequency distribution of the characters varies continuously over the range of the species. This feature, the continuous manifestation of variation, is one of the main reasons why variability, especially at the infra-specific level, is difficult to describe with precision.

It is now desirable to assess the taxonomic use of knowledge of the causes of variation and the kinds and patterns of its phenotypic manifestations.

The great attraction of an approach which classifies variation by processes rather than by their products is that the former are relatively few in number and distinct from each other. The genetical behaviour consequent upon them is now quite well known and the results of any process can be predicted with some certainty. In this way the indescribable phenotypic chaos can be avoided and the material reduced to comparative orderliness. For example, most of the British species of *Taraxacum* are probably triploid or tetraploid and apomictic. Some non-British forms are regularly amphimictic, some occasionally amphimictic and many more apomictic. Different degrees of polyploidy also occur. This information effectively summarises the genetic situation. It does not assist the identification or the ordering of the many hundreds of distinct morphological forms that exist. Turrill (1937) has written: "From the standpoint of genetic isolation the biotypes are species; from the standpoint of character-combinations, morphological differences and similarities, and ecology, the biotypes, within any one section and within any one distributional area at least, are varieties of one or a few species". The genetic information demonstrates how the baby has been delivered but it leaves the taxonomist still holding the baby! This is not always the case. The work on polyploidy in ferns, described by Manton, has provided evidence of species relationship and so has assisted classification directly. More striking instances are the grouping of the numerous forms within *Viola* section *Melanium* into polyploid groups (Clausen, 1931) or the separation of *Veronica* and *Hebe* on cytological as well as morphological grounds (Frankel, 1941). In a similar manner observations on the correlation between gene frequencies and particular environmental factors, e.g., in *Ricinus communis* (vide Table 2), demonstrate the importance of such factors for both the past and the future of the species. But they do not greatly affect the taxonomic treatment of the species. This does not mean that such studies are irrelevant for taxonomy. One of the most desirable and difficult accomplishments which a taxonomist can acquire is to so develop his judgment or intuition that he can determine the "taxonomic value" of any particular character. In this matter the study of the causes

of variation may be of inestimable, objective value. If it is necessary to select some character for taxonomic weighting, it is desirable that it should either be important for the structure and future of the species, or that it should be correlated with such a character. This kind of information is available from studies on the processes involved in speciation.

The apparent conflict, or rather, lack of common objective, between these two methods of studying variation is to be resolved by a consideration of their respective aims. This is a matter to which attention has been drawn by Gilmour (see pp. 173-176). Here it is sufficient to compare two statements on the aims of taxonomy. The first is due to Huxley (1940). "Fundamentally, the problem of systematics, regarded as a branch of general biology, is that of detecting evolution at work". The second is adopted from Mayr (1942). "The field of activity of the systematist can perhaps be subdivided under three headings: identification (analytical stage) . . . : classification (synthetic stage) . . . : study of species formation and the factors of evolution". For Mayr the "basic task of the systematist" is identification. To which Huxley might be expected to retort: "But identification of what?"

So far as variability within species is concerned, it seems that little can be gained by accepting either attitude to the exclusion of the other. At the infra-specific level, variation is to be observed in its most protean guise. For the constant flux and reflux of genotype and environment either has not yet resulted in the stabilisation of new specific patterns or else they are maintained in a dynamic equilibrium. The more stabilisation sets in, the more readily the situation becomes amenable to description in terms of fixed classes, *i.e.* to taxonomic treatment. All other situation must be described, as precisely as possible, in terms both of the processes involved and their consequences and manifestations. The interest of these situations is more evolutionary than taxonomic. It would be a matter of surprise if a foetus could be described by the same terminology and judged by the same yardstick as would be employed to describe it when it had developed into a man in the prime of life. So it is within the species. Just as there is some connection and correlation between adult and foetus, so there is between species and infra-specific entities. The first of each of these are assessed according to their achievements and status, the second are of interest for their development and potentialities.

It is some encouragement, perhaps, to realize that the problem of describing natural phenomena with accuracy is of long standing. Mrs. Arber has discussed Plato's views on scientific method and has remarked: "few would dispute that . . . Plato had seized the essential fact that any scientific *system* of explanation has a certain static finality, and hence must be imperfectly compatible with the unceasing flux of Nature". (Arber, 1954).

It is our privilege and our pleasure to improve taxonomy so that it will become as nearly compatible with nature as ever human ingenuity can devise.

SUMMARY

The study of variation by taxonomists is difficult at present for three reasons: —

1. The numbers and kinds of characters which vary are large and increase with every application of new observational techniques.

2. There is an apparent conflict between those who seek to describe and define classes of variants and those who wish to classify variation in terms of the processes which cause it.

3. Techniques of description are not yet sufficiently comprehensive or precise to summarize the different manifestations of variation adequately.

Examples are given, in tabular form, of variations due to different genetic processes. The phenotypic manifestation, frequency or distribution and taxonomic status of each variant is given.

It is evident that particular genetic processes may be manifested in different ways in different species. In widespread species the kinds of genetic diversity as well as the phenotypes may be different in different regions. Attention is drawn to the desirability of studying variation in British species outside the United Kingdom as well as within it. Variation due to phenotypic plasticity is briefly discussed. Adaptive variation may be due either to phenotypic plasticity or genetic diversity.

It is observed that variation is rarely discontinuous in its expression. This is one of the reasons which make it difficult to classify.

The relative value of the study of the kinds, causes and descriptions of variation for taxonomy are discussed.

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REFERENCES

ARBER, A., 1954, *The mind and the eye.* Cambridge.

BAKER, H. G., 1953, Race formation and reproductive methods in flowering plants, *S.E.B. Symposia*, **7**, 114-145.

BERNSTRÖM, P., 1953, Cytogenetic intraspecific studies in Lamium II, *Hereditas*, **39**, 381-437.

BLAKESLEE, A. F., BERGNER, A. D. & AVERY, A. G., 1937, Geographical distribution of chromosomal prime types in Datura stramonium, *Cytologia*, *Fujii Jubilee Vol.*, 1070-1093.

CLAPHAM, A. R., TUTIN, T. G. & WARBURG, E. F., 1952, *Flora of the British Isles.* Cambridge.

CLAUSEN, J., 1931, Cytogenetic and taxonomic investigations on Melanium Violets, *Hereditas*, **15**, 219-308.

CLAUSEN, J., KECK, D. D. & HIESEY, W. M., 1948, Experimental studies on the nature of species III—Environmental responses of climatic races of Achillea, *Carnegie Inst. Washington, Publ. No. 581*.

DADAY, H., 1954, Gene frequencies in wild populations of Trifolium repens I—Distribution by geography, *Heredity*, **8**, 61-78.

DARLINGTON, C. D., 1940, Taxonomic species and genetic systems, in *The New Systematics*, ed. J. S. Huxley. London.

DARWIN, C., 1859, *The Origin of Species*, ed. 1. London.

EHRENBERG, L., 1945, Kromosomtalen hos några kärlväxter, *Bot. Notiser*, **1945**, 430-437.

FRANKEL, O., 1941, Cytology and taxonomy of Veronica, Hebe and Pygmaea, *Nature*, **147**, 117.

GEITLER, L., 1937, Cytogenetische Untersuchungen an natürlichen Populationen von Paris quadrifolia, *Zeitschr. Indukt. Abstamm. & Vererbungsl.*, **73**, 182-197.

——, 1938, Weitere cytogenetische Untersuchungen an natürlichen Populationen von Paris quadrifolia, *op. cit.*, **75**, 161-190.

GREGOR, J. W., 1939, Experimental taxonomy IV—Population differentiation in North American and European sea plantains allied to Plantago maritima L., *New Phyt.*, **38**, 293-322.

——, 1946, Ecotypic differentiation, *New Phyt.*, **45**, 254-270.

GUSTAFSSON, A., 1946-47, Apomixis in Higher Plants 1-3, *Lunds Univ. Årsskr.*, (N.f.), **42/3**; **43/2**; **43/12**.

HAGA, T. & KURABAYSHI, M., 1948, Chromosomal variation in Trillium kamtschaticum, *Jap. J. Genet.*, **23**, 12-13. Summarized in, Kihara, H., 1950, Japanese papers on genetics, 1942-1948. English abstracts—*Heredity*, **4**, 391-408.

HAGERUP, O., 1944, Notes on some Boreal polyploids, *Hereditas*, **30**, 152-160.

HANCOCK, B. L., 1942, Cytological and ecological notes on some species of Galium L. emend. Scop., *New Phyt.*, **41**, 70-78.

HARLAND, S. C., 1947, An alteration of gene frequency in Ricinus communis L. due to climatic conditions, *Heredity*, **1**, 121-125.

HIESEY, W. M., 1953, Comparative growth between and within climatic races of Achillea under controlled conditions, *Evolution*, **7**, 297-316.

HUXLEY, J. S., 1940, Introductory: Towards the New Systematics, in *The New Systematics*, ed. J. Huxley, London.

LAWRENCE, W. E., 1945, Some ecotypic relations of Deschampsia caespitosa, *Amer. J. Bot.*, **32**, 298-314.

LOUSLEY, J. E. 1938, Notes on British Rumices, I., *Rep. Bot. Soc. & E.C.*, **12**, 118-157.

LÖVE, A. & LÖVE, D., 1944, Cytotaxonomical studies on Boreal plants III—Some new chromosome numbers of Scandinavian plants, *Arkiv f. Bot.*, **31A**, 12.

MACRAE, R., 1942, Interfertility studies and inheritance of luminosity in Panus stipticus, *Canad. J. Research*, **20**, C, 411-434.

McVEAN, D. N., 1953, Regional variation of Alnus glutinosa (L.) Gaertn. in Britain, *Watsonia*, **3**, 6-32.

MARSDEN-JONES, E. M. & TURRILL, W. B., 1952, Studies on Ranunculus ficaria, *J. Genetics*, **50**, 522-534.

MAYR, E., 1942, *Systematics and the origin of species.* New York.

MOSS, C. E., 1914, *Cambridge British Flora*, **2**, 83-88. Cambridge.

MOUNCE, I. & MACRAE, R., 1938, Interfertility phenomena in Fomes pinicola, *Can. J. Research.*, **16**, C, 354-376.

MÜNTZING, A., 1932, Untersuchungen über Periodizität und Saison-Dimorphismus bei einigen annuellen Lamium-Arten, *Bot. Notiser*, **1932**.

PERJE, A.-M., 1952, Some causes of variation in Ranunculus ficaria L., *Arkiv f. Bot.*, (N.f.) **2**, 251-264.

PRAEGER, R. L., 1951, Hybrids in the Irish Flora, *Proc. Roy. Irish Acad.*, **54B**, 1-14.

RAY, J., 1674, The specific differences of plants. Cited from: C. E. Raven, *John Ray, Naturalist, his Life and Works.* Cambridge.

SAUNDERS, E. R., 1918, On the occurrence, behaviour and origin of a smooth stemmed form of the Common Foxglove (Digitalis purpurea), *J. Genetics*, **7**, 215-228.

SIMPSON, G. G., 1953, The "Baldwin" effect, *Evolution*, **7**, 110-117.

SKALINSKA, M., 1947, Polyploidy in Valeriana officinalis L. in relation to its ecology and distribution, *J. Linn. Soc., Bot.*, London, **53**, 159-186.

——, 1950, Studies in the Chromosome numbers of Polish angiosperms, *Acta Soc. Bot. Polonica*, **20**, 45-68.

——, 1951, Studies in cytoecology, geographic distribution and evolution of Valeriana L., *Bull. Acad. Polon. Sci. Lett. B.*, **1**, 149-175.

SPRAGUE, T. A., 1952, The British forms of Valeriana officinalis, *Watsonia*, **2**, 145-147.

STEBBINS, G. L., 1950, *Variation and Evolution in plants.* London.

TURRILL, W. B., 1931, Biological races in seed bearing plants and their significance in evolution, *Ann. Appl. Biol.*, **18**, 442-450.

——, 1937, Material for a study of taxonomic problems in Taraxacum, *Rep. Bot. Soc. & E.C.*, **11**, 570-589.

——, 1938, Taxonomy and genetics, *J. Bot.*, London, **76**, 33-39.

——, 1948, *British Plant Life.* London.

VALENTINE, D. H., 1941, Variation in Viola riviniana Rchb., *New Phyt.*, **40**, 189-209.

——, 1949, Vegetative and cytological variation in Viola riviniana Rchb., in, *British Flowering Plants and Modern Systematic Methods*, ed. A. J. Wilmott. London.

WALTERS, S. M., 1949, Eleocharis, in: *Biological Flora of the British Isles.* Cambridge.

WALTHER, E., 1949, Zur Morphologie und Systematik des Arzneibaldrians in Mitteleuropa, *Mitt. Thüring. Bot. Ges.*, **1**, 7-105.

WEBB, D. A., 1950, Hybridization and variation in the Robertsonian Saxifrages, *Proc. Roy. Irish Acad.*, **51B**, 233.

WILKINSON, J., 1949, The cytology of Salix in relation to its taxonomy, *Ann. Bot.*, N.S., **8**, 269-284.

WILMOTT, A. J., 1949, Intraspecific categories of variation, in, *British Flowering Plants and Modern Systematic Methods*, ed. A. J. Wilmott. London.

WINGE, Ö., 1940, Taxonomical and evolutionary studies in Erophila based on cytogenetical investigations, *Comptes-rendus Lab. Carlsberg, Sér. physiol.*, **23**, 41-78.

MORPHOLOGICAL CHARACTERS IN THE DISCRIMINATION OF SPECIES AND HYBRIDS

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In most angiosperms the flowers and fruits provide the most critical and most widely used criteria for delimiting species. Species in some groups with small flowers and simple fruit shapes are difficult to separate on their reproductive structures alone, and it is then necessary to give more consideration to vegetative characters. The oaks, elms and ashes fall into this category, though, so far as the British flora is concerned, only the elms cause much trouble. In woody genera especially, habit, stem, bark, leaf and bud characters are often of critical value.

The habit of a species is frequently a reliable character if hybrids are not present. As with other characters, the habit of hybrids is often intermediate, though one species may be dominant in a number of crosses. *Ulmus glabra* is an example, its rounded head and spreading branches constantly appearing in its hybrids. Bark characters concern us little in the British flora. In Australia, features of the bark have been used as the basis of taxonomic groupings in *Eucalyptus* as gums, stringybarks, iron-barks, boxes and bloodwoods. Recent anatomical studies by Dr. Chattaway in Melbourne have provided independent confirmation of these groupings. The winter buds of *Fraxinus* can be used for the recognition of the species. This, again, is not one of our problems. A bud character, the presence of reddish brown hairs on the mature bud scales in *Ulmus glabra* Huds., is a dominant character constantly appearing in its hybrids. Hairs of a similar colour appear on the leaves of *Salix atrocinerea* Brot. and they too are dominant in its hybrids.

Apart from the reproductive structures, leaves provide more features of taxonomic value than any other organ. Their great variability has in the past led some to decry their value, an un-critical attitude that depends on a failure to understand the regularities that underlie the variability. One source of confusion is found in the varying size of teeth or lobes, the eye being readily led astray by irregularities in the leaf margin. A basic leaf shape can be obtained by drawing around the tips of the serrature or of the lobes of a deeply incised leaf. If one does this with the leaves of our native oaks, the shapes are obovate for *Quercus robur* L. and elliptical for *Q. petraea* (Matt.) Liebl. A secondary shape is obtained by connecting the bases of the sinuses between the teeth or lobes. This secondary shape often tends to impress the eye, since it outlines the solid body of the lamina and one has to train the eye to observe the primary shape.

A second source of confusion is the progressive change in the shape of successive leaves as the plant develops. In herbs, there is an annual sequence of leaf shapes, repeated year after year in annuals or herbaceous perennials. The position in woody plants is more complex. The annual sequence of the seedling changes year by year through adolescence to adulthood, when the fully characteristic leaf shapes of the species are at last developed. Any happening such as the felling of a tree with the development of coppice shoots or the lopping of branches, which may stimulate epicormic branches to grow from the trunk, puts back the annual leaf shape sequence on the renewed growth to an earlier phase of the ontogenetic cycle, the more juvenile the more drastic the damage. It is convenient to call these annual leaf shape sequences a leaf spectrum.

In my studies of elms I have found the fully adult leaf spectrum to be of most value for the discrimination of species. There is a tendency for the juvenile leaf shapes of different species to resemble one another rather closely. In fact, they tend towards a generic mean from which species diverge to an increasing degree as they progress towards adulthood. It is very necessary in the face of such leaf diversity to consider carefully the material to be chosen for interspecific comparisons. Choice falls upon the short shoots that form the lateral spurs on the branches of the adult phase of the tree. These are shoots of determinate growth, since the terminal bud falls after a limited number of leaves have been produced—generally 4 or 5. If one subscribes to the foliar theory of the flower, a direct comparison may be made with the flower, which is also a shoot of determinate growth. For the discrimination of species comparisons are made between corresponding parts—petals with petals, not with sepals, stamens or carpels. But what matters most is the flower as a whole; the correlation between all its parts. Similarly, if the leaf spectrum is to be used as a taxonomic tool, it is the correlation of shapes of the whole leaf spectrum that has the greatest significance, and comparisons of species must be made only between leaves from corresponding positions in the leaf spectrum, or of entire leaf spectra. Failure to make critical comparisons has led to much confusion in the past.

Let us now examine a few representative leaf spectra. In all of these, the leaf sequence of a single normal adult short shoot is represented as faithfully as possible by direct copying, basal leaves to the left, distal to the right. Fig. 2 shows the characteristic leaf spectrum of *Ulmus procera* Salisb. This is the typical form of the species, like that growing near Goodyer's old home at Maple Durham on the border of Sussex and Hampshire, the classical locality of the species. Notice the almost semicircular outline of the short side of the leaf and the very uniform spacing of the lateral nerves along the midrib.
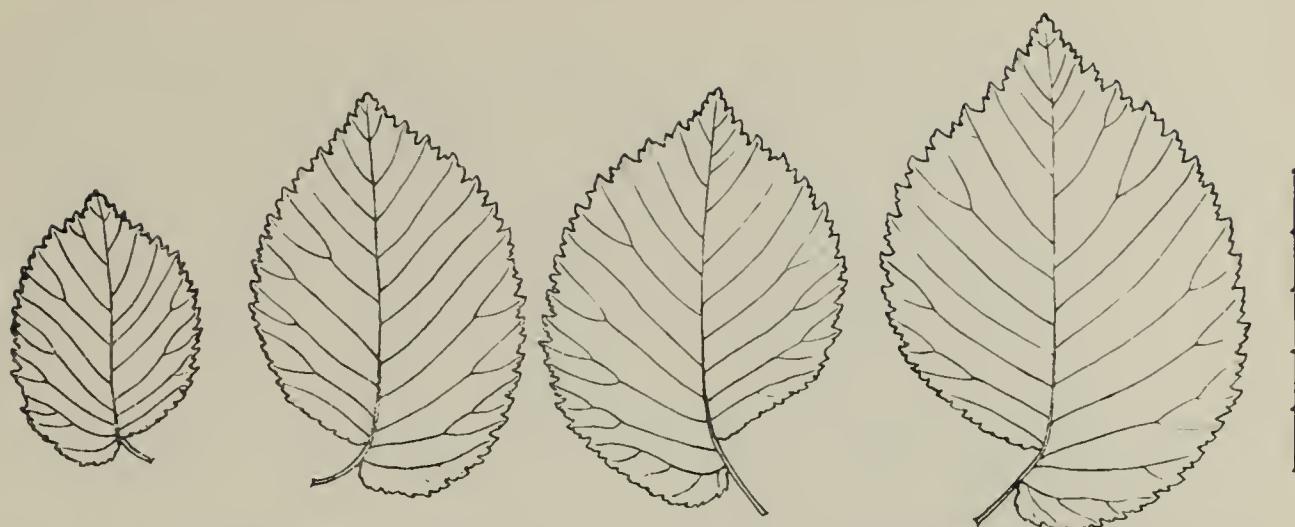
Fig. 2. *Ulmus procera* Salisb. Leaf spectrum of a short shoot of a tree (Melville no. 37.104) growing near Tidenham, Gloucestershire.

The scale in this, and the nine figures which follow, is 5 centimetres.
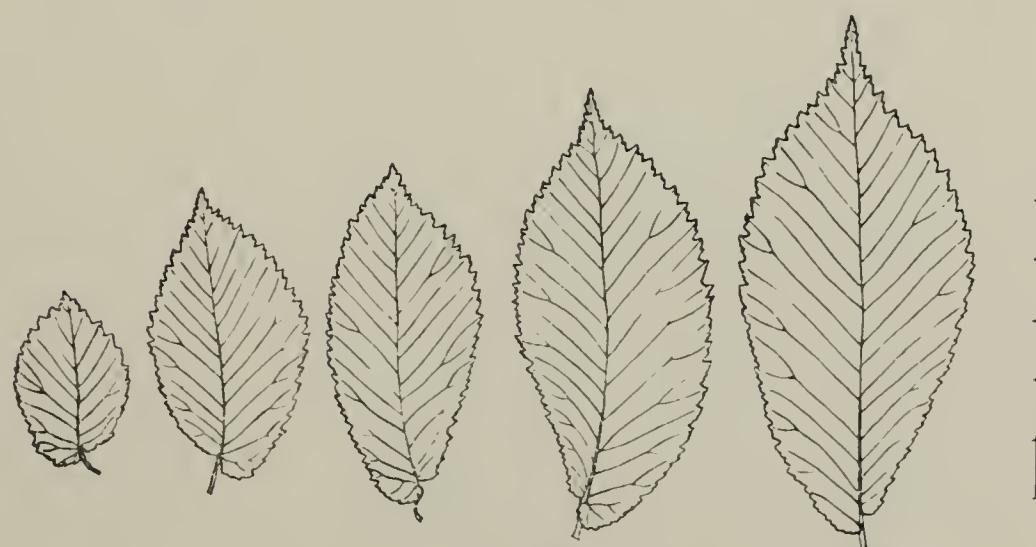
Fig. 3. *Ulmus glabra* Huds. var. *montana* Lindq. Leaf spectrum of a short shoot from a tree (Melville no. 39.109) growing near Corbridge, Northumberland.

The more highly differentiated leaf spectrum of *U. glabra* Huds. var. *montana* Lindq. is shown in Fig. 3. The leaves are often larger than in this individual. Note here the well developed apical cusp of the distal and subdistal leaves, the basal lobe of the long side which overlaps the short petiole, and the numerous lateral nerves—about 16 pairs. The basal leaf approaches rather closely to the shape of the corresponding leaf of *U. procera*.

Another very distinctive leaf spectrum is that of *U. plotii* Druce (Fig. 4). Notice the subequal leaf bases of the distal and subdistal leaves, their rather coarse blunt serrature and the uneven spacing and small number of the lateral nerves—about 9 pairs. The leaves become more asymmetrical and the nerves more evenly spaced towards the base of the shoot. The basal leaf is nearer in shape to the corresponding leaf of *U. procera* than any other leaf of the spectrum. This leaf spectrum, of itself, is sufficiently characteristic, but *U. plotii* is distinguished by a feature shared by few other elms. The apical bud of the
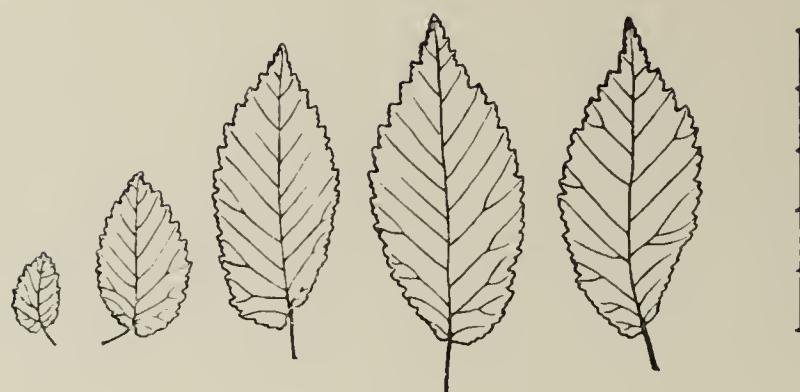
Fig. 4. *Ulmus plotii* Druce. Leaf spectrum of a normal short shoot from the type tree at Banbury, Oxfordshire (Melville no. 37.63).
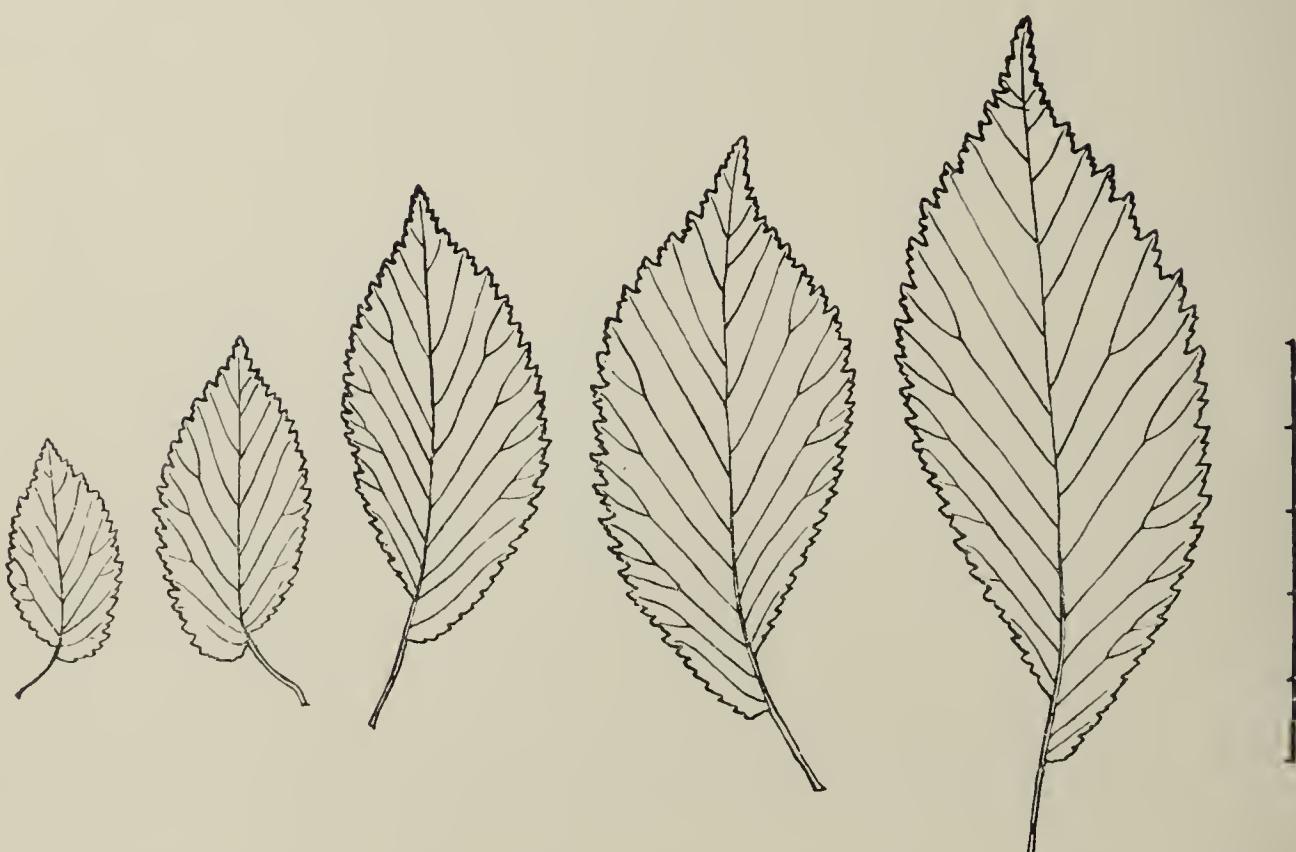
Fig. 5. *Ulmus carpinifolia* Gleditsch var. *glandulosa* (Lindl.) Melville. Leaf spectrum of a short shoot of a tree from the type locality, Ludlow, Shropshire (Melville no. 39.62).

short shoot does not always fall off at the usual stage, so that growth continues for a while and one or several additional leaves develop. The additional leaves are successively smaller, rounder and more coarsely toothed than those of the normal sequence. Such shoots I have called proliferating short shoots. The factors controlling their inheritance appear to be dominants, since this feature commonly appears in hybrids of *U. plotii*.

The leaf spectrum of *U. carpinifolia* Gleditsch var. *glandulosa* (Lindl.) Melville is shown in Fig. 5. Notice the very sharp serrature, the rectangular shape of the basal lobe of the long side, and the increasing intervals between the lateral nerves in the mid and upper part of the distal and subdistal leaves. Once again, the basal leaf is nearest in shape of any in the spectrum to the corresponding leaf of *U. procera*. This is a general

tendency in the genus. Comparison with the leaf shapes of the juvenile phases of these trees indicates that the basal leaves are relatively juvenile in form. There is, in fact, an ontogenetic sequence of leaf shapes along which the leaf spectrum progresses with each successive growth phase until the adult condition is reached. Furthermore, within the species, individuals can be picked out that in their distal leaves reach only to the successively earlier leaf shapes of the one here illustrated. There is, accordingly, evidence of an ontogenetic sequence within the species, which makes it possible to decide which are the more primitive and which the advanced in the evolutionary sense. It follows that from a given leaf spectrum, it would be possible to calculate the trends of leaf shape backwards or forwards in this evolutionary progression. In addition to the main line of development in *U. carpinifolia,* as here outlined, there are lateral branches such as that leading to broad leaf bases discussed in an earlier paper (*Journ. Linn. Soc., Bot.,* **53**, 88, 1946). Such lateral branches may lead in the course of time to the development of new species.

It is evident that the ontogenetic sequence of leaf spectra in a species must be governed by a corresponding series of changes in the concentration, timing and balance between the enzyme systems controlling growth. The regularity of the transitions in leaf shape suggest that the controlling factors are so interlocked that the possible lines of development, and hence of evolution in the species, are strictly circumscribed. This would lead to orthogenetic evolution of the kind indicated by fossil lineages in Echinoderms, in Ammonites, Lamellibranchs and other Mollusca and in other animal groups that are much better provided with fossils than are plants. Leaf fossils do not appear to have been examined from this point of view, but in his contribution to this conference Dr. Hamshaw Thomas mentioned a comparable series among fossil fruits of *Stratiotes.* In discussing the time necessary for these changes to take place under natural conditions, Zeuner concluded that the fastest rate of evolution of species, per species step, is about half a million years. A slow rate of species evolution is also in accordance with the great similarity observed between leaves of many Cretaceous plants and those of to-day. There is no time to explore this theme further and I will turn to a consideration of leaf spectra in the discrimination of hybrids.

In the Midlands, hybrids of *U. plotii* are very numerous and cover a wide range of variation. They will serve to illustrate the application of leaf spectra to the identification of hybrids. Fig. 6 depicts the leaf spectrum of a typical short shoot of an individual *U. glabra* × *plotii* growing near Halstead, in Leicestershire. The tree was of a rather erect habit but with somewhat pendulous branches. The habit was therefore intermediate between that of the parents and the leaf shapes also are intermediate. The general aspect of the leaves is closer to *U. glabra* than *U. plotii,*
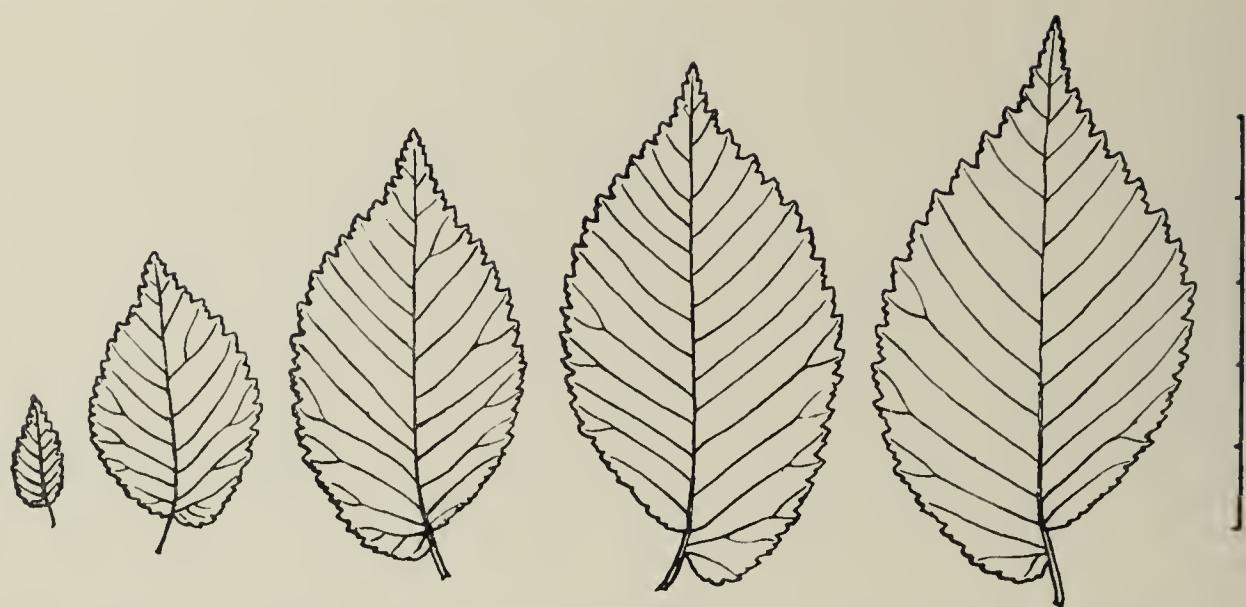
Fig. 6. *Ulmus glabra* × *plotii*. Leaf spectrum of a representative short shoot of a nothomorph growing near Halstead, Leicestershire (Melville no. 37.83).
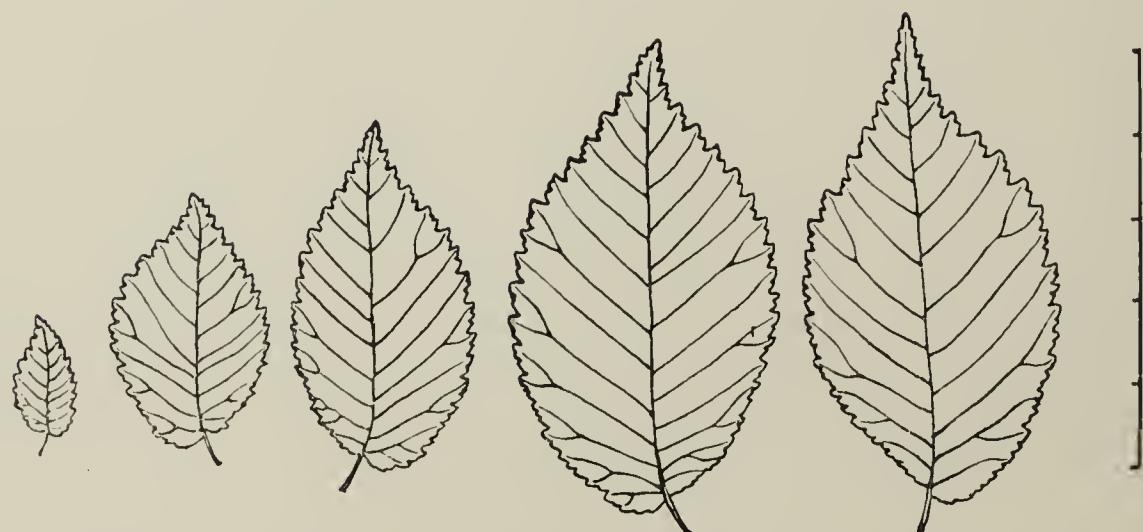

Fig. 7. *Ulmus glabra* × *plotii*. Leaf spectrum of a short shoot with leaf shapes tending towards *U. plotii*, from the same tree as Fig. 5 (Melville 37.83)
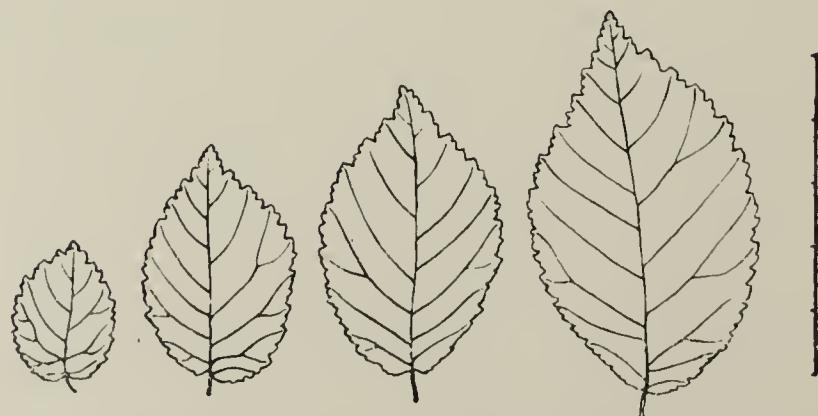

Fig. 8. *Ulmus* × *elegantissima* Horwood (*U. glabra* × *plotii*). Leaf spectrum of a short shoot with shapes closely resembling those of *U. plotii*. Tree from the type area near Launde, Leicestershire (Melville no. 36.261).

but the apical cusp is not so well developed and the basal lobe does not overlap the petiole. There are other more subtle differences also. Notice the relatively wide spacing of the lateral nerves of the distal leaf. The variation between short shoots is greater than in the species. The leaves of a second short shoot from the same tree are shown in Fig. 7. Here the distal and subdistal leaves resemble more closely those of *U. plotii,* though the apical cusp is more strongly developed and the spacing of the lateral nerves is intermediate. The leaves towards the base of the shoot resemble the corresponding leaves of *U. glabra* more closely so that in this shoot there is a change in the balance of growth factors from one parent to another—from *U. glabra* to *U. plotii.* On looking back at the first shoot (Fig. 6) it can be seen that a change in the balance between the parents has taken place there also. It is in the same direction, but has not gone so far. There is a fluctuating balance between the two parents in the hybrid which changes from shoot to shoot in the adult and also changes during the ontogenetic sequence.

The phenomenon of fluctuating balance between alternative parental characters is widespread in hybrids. In segregates and back crosses the mean balance point may verge toward one or other of the parents. For example, another segregate from *U. glabra* × *plotii* (Fig. 8), closely matching Horwood's type of *U. × elegantissima,* approaches to *U. plotii* in its leaf shape. The spectrum of the short shoot illustrated suggests, even, some of the leaves of the proliferating shoots of *U. plotii* and the nervature is very like that species. Nevertheless, the habit, branching and bud characters were closest to *U. glabra.* Some other shoots had leaf spectra close to that shown in Fig. 7, but with the sequence finishing at the subdistal leaf. Such was the maximum expression of *U. glabra* in the leaves of this individual.

As another example of a hybrid segregate closely resembling in foliage one of its parents, I illustrate a roadside tree (Fig. 9) growing near Hitchin in Hertfordshire. Any novice gathering this could be pardoned for identifying it as a form of *U. carpinifolia.* The habit was erect and moderately spreading, but with rather long slender pendulous branchlets. The latter and the dark green pigmentation of the leaves were probably inherited from *U. plotii.* That *U. plotii* contributed to its inheritance was shown by the occurrence on the epicormic shoots of leaves almost identical in shape and nervation with those of *U. plotii.* One is shown at the left of the figure; insect damage prevented my obtaining a complete leaf spectrum of the epicormic shoots. The number of lateral nerves in the distal and subdistal leaves of the normal short shoots is larger than was to be expected. Other studies of hybrid leaves indicate that the number is usually intermediate between those of the parents. In this tree, there are generally one or two extra pairs above that usual for *U. carpinifolia* and four or five more than in *U. plotii.* For this reason, I

Fig. 9. *Ulmus carpinifolia* × *plotii* (×*glabra*). Leaf spectrum of a representative short shoot from a tree growing near Hitchin, Hertfordshire, with, at left, a leaf from an epicormic shoot having leaf shape and nervation similar to *U. plotii* (Melville no. 51.5).
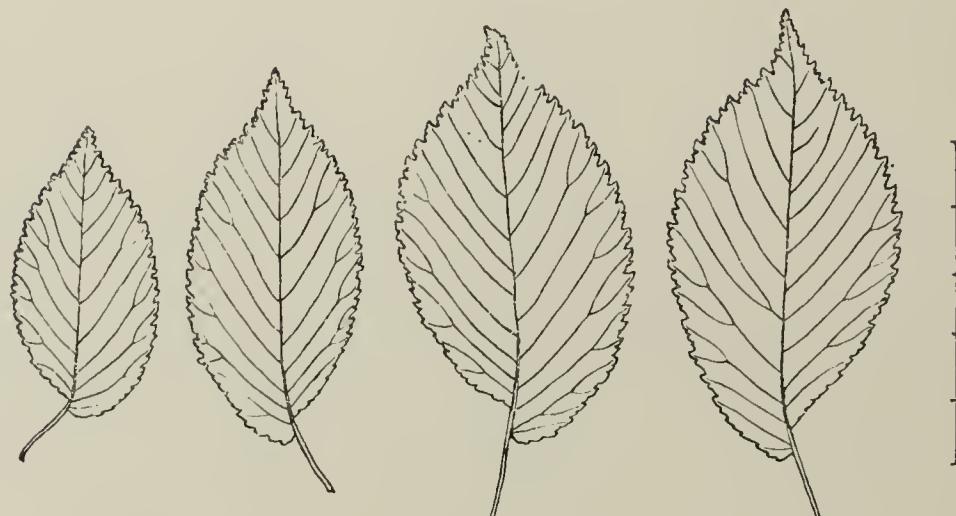
Fig. 10. *Ulmus carpinifolia* × *plotii*. Leaf spectrum of a representative short shoot from a tree (Melville no. 39.79) growing at Norton Bridge, Staffordshire.
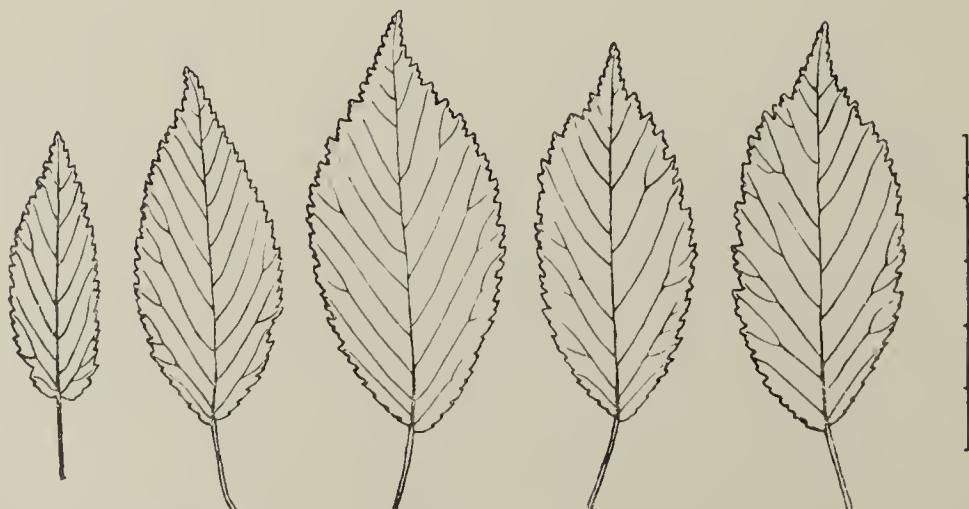
Fig. 11. *Ulmus carpinifolia* × *plotii*. Leaf spectrum from a short shoot with symmetrical leaves, same tree as Fig. 9 (Melville no. 39-79).

suspect that *U. glabra* contributed to its inheritance. Two neighbouring trees showed definite evidence of this triple parentage. Apart from its parentage, the tree is interesting as an example of the change of balance with the developmental phase. Early in the ontogenetic sequence *U. plotii* is subdominant, but *U. carpinifolia* is virtually dominant in the adult.

As a final example I will take another individual *U. carpinifolia × plotii,* a tree approaching *U. carpinifolia* in habit, growing near Norton Bridge in Staffordshire. The leaf spectrum of a characteristic short shoot is depicted in Fig. 10. These leaves approach nearest to *U. carpinifolia* in shape, but the lateral nerves are rather too widely spaced, and the third leaf from the right in its upper half closely resembles the comparable portion of the corresponding leaf in *U. plotii.* In addition to the asymmetrical-leaved short shoots, smaller numbers of others occur with symmetrical leaves. Both kinds are found in the adult phase, intermingled on the normal branches. Comparison of the leaves of the parent species suggests that the four upper leaves of this shoot (Fig. 11) consist of two short sides of an asymmetrical leaf juxtaposed. Notice that the petioles are longer than in ordinary leaves, as would be expected if a basal lobe had been suppressed. A greater petiole length in such leaves has been confirmed by numerous measurements. The distal and subdistal leaves are built on the plan of *U. plotii* short sides. At the third leaf, the balance swings over to *U. carpinifolia* and the basal leaf is best explained as consisting of two long sides of the corresponding leaf of *U. carpinifolia.* There is evidently a complex interaction here between the parent species, a fuller explanation of which must await another occasion.

Perhaps sufficient has been said to indicate both the complexity and diversity of leaf form that occurs in elm hybrids. The variation is greater than is found in individuals of species. Moreover it contains discordant elements. The variation in species is more circumscribed and harmonious. The two kinds of variation can be called concordant and discordant. Critical study of the discordant variation in the leaf spectra of the hybrids makes it possible to determine the parentage.

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Dr. H. G. BAKER said that it was evident that there had been extensive hybridisation in *Ulmus* and it seemed that the hybrids were extremely fertile. He asked whether Dr. Melville recognised subspecific or ecotypic variation in the group.

Dr. MELVILLE replied that eight species were recognised in the new *Flora*, and there was evidence of another in East Anglia which had been almost hybridised out of existence. *Ulmus glabra* and *U. procera* have distinct varieties, but he did not recognise any subspecies. There was a tremendous number of hybrid individuals and there were indications that they are usually fertile.

Prof. D. H. Valentine asked whether all or some of the hybrids were of the F₁ generation, as one would expect the F₁ plants to show concordant rather than discordant variation. Dr. Melville said that studies of garden hybrids had revealed interesting examples of discordant variation as, for example, in *Ribes odoratum* × *R. sanguineum*, and it did not necessarily follow that concordant variation would be found in F₁ plants.

Mr. S. Walker enquired whether any cytological or genetical work had been done on *Ulmus*.

Dr. Melville, in reply, pointed out that breeding experiments were hardly practical with *Ulmus* as it would take more than a lifetime to obtain useful results. It was therefore necessary to rely mainly on morphological characters.

PROBLEMS ASSOCIATED WITH THE SPECIES CONCEPT IN MYCOLOGY

ALAN BURGES (University of Liverpool).

Systematic and Taxonomic Botany has developed during the last two to three hundred years a fairly satisfactory system of delimiting species, despite all the controversies concerning the Species Concept and the value of the Type Method. However, it cannot be emphasised too strongly that this success has been primarily in the study of higher plants. It has been a great loss to systematic botany that, particularly in academic circles, it was for so long regarded as synonymous with the classification of the angiosperms. "To know one's plants" was to be able to identify the seed plants and ferns. To look at Bryophytes, Lichens or Fungi was indecent. It was something that the mycologists, or such people, did, but it wasn't systematic Botany! It is not surprising therefore that the problems confronting the mycologists and workers in comparable groups were seldom included in discussions on systematics. When attempts are made to apply the general concepts and methods current in angiosperm systematics to the fungi, many difficulties arise. From classical times onwards fungi have been regarded generally as "a treacherous and mutable tribe". Their capacity to vary is notorious and is largely responsible for the difficulties associated with their classification. Some of the variability is associated with the growth form of fungi and the shortness of their generation time, but a large part comes from their possession of evolutionary and nuclear mechanisms not found in other groups. The difficulty of preparing good herbarium specimens, especially in the Agarics, is a further hindrance.

We may represent the gradual evolution of species diagrammatically, as in Fig. 12. This is, of course, open to many objections, but even if we complicate and refine the picture by considering convergent evolution and reticulate systems or intermittent periods of speciation, this would not affect the present argument.

The line A may be regarded as an instantaneous observation.* Of the various species observed, A_1, A_2, A_3, A_4, etc. are all good species, distinct from each other, although A_2 might be regarded as very "plastic". A_5 and A_6 on the other hand would be difficult, the so-called "critical" species. If we were to observe A_1, there would probably be a considerable change between X and Y, but this would be a gradual change.

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*I believe Professor A. R. Clapham of Sheffield has used a similar idea to this in his "time slice".
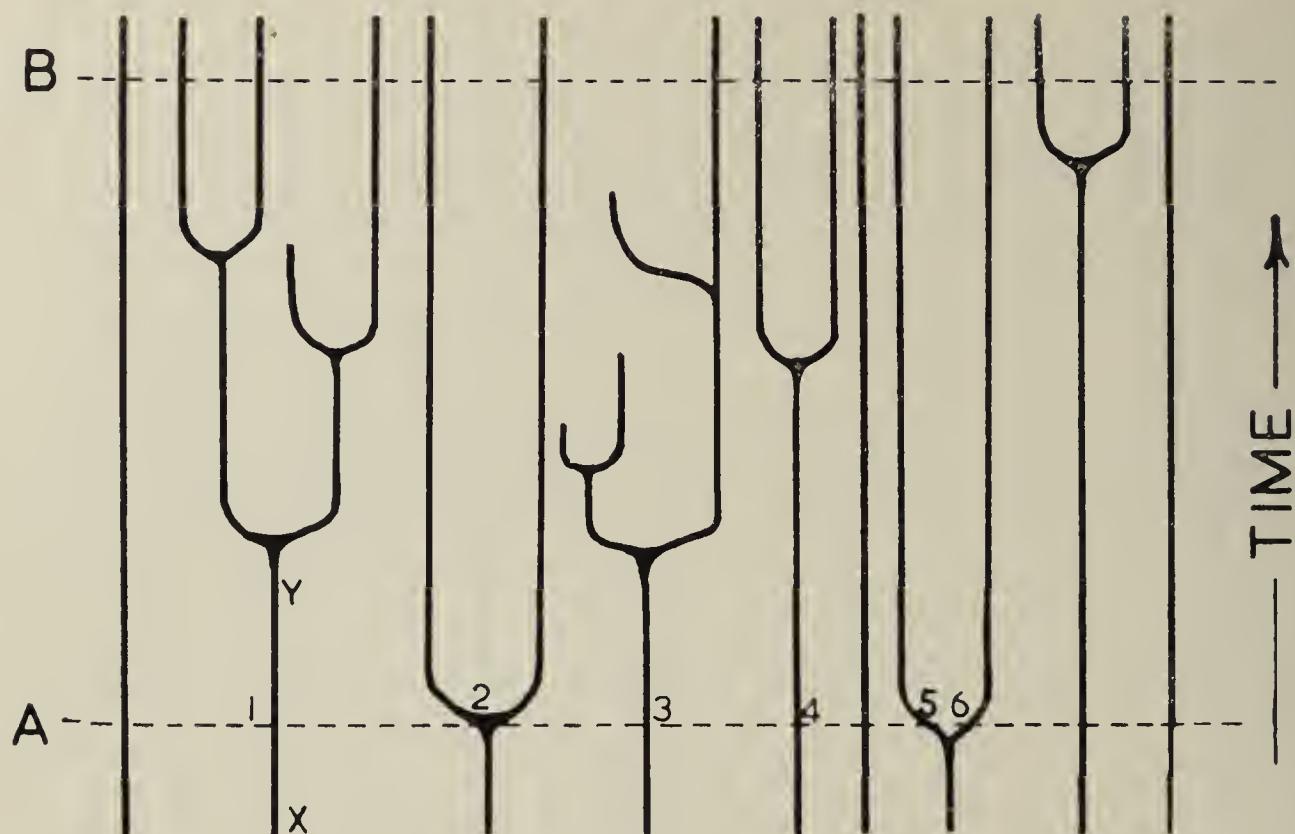
Fig. 12.

Diagram showing the relation between the constancy of species and the rate of evolution. (For full explanation, see text.)

The situation given by our observation A probably represents fairly well the situation in any angiosperm systematics. The slow change from X to Y is not detectable in the short period (300 years) of systematic botany. In comparison with the life of an angiosperm species the life of the systematist is brief. If now we observe not just at instant A but continuously from A to B, the position becomes vastly more complicated. Many species show continued and irreversible variation and the proportion of "difficult" to "good" species rises alarmingly. The important thing about the time-scale is not the time itself but the rate of change of the species. If this is high, then the period A to B may well fall within the lifetime of an observer.

The rate of the change is governed by many factors, but it would seem that the generation time of the individuals in the species, and the nature of the evolutionary mechanisms, are two of the more important. It is only when progeny are tested in the environment that selection can act. Thus, although a bacterium with a generation time of 20 minutes and a tree with a generation time of 20 years may both have the same mutation rate per generation, the rates of evolutionary change are potentially vastly different.

Most fungi have a short generation time, particularly if vegetative reproduction is considered, and the unfortunate mycologist is often faced with a situation resembling the interval from A to B.

Most of our knowledge of rapid change in fungi comes from laboratory studies of organisms in culture. Rapid change is,

however, known also in the field. Waterhouse (1952) has shown that in the rusts new physiological races can appear and rapidly displace the older races, particularly where the new race is able to attack a previously immune host. Race *34* of *Puccinia graminis tritici* first appeared in West Australia in 1926, it spread rapidly through the wheat growing areas of Australia and New Zealand and by 1929 had completely supplanted the six previously occurring races. A similar situation arose in 1941, when a new race, *r. 126,* a close relative of *r. 34,* in turn replaced *r. 34,* its possible parent. A third major change occurred in 1948. A single specimen from Queensland of a wheat variety "Yalta" previously resistant, was found to be heavily infected by a new race, *r. 222.* In 1949 it was identified in 5 out of the 122 field collections, 4 from Queensland and 1 from New South Wales. In 1950 the new race formed 512 out of the 704 isolations and was widespread in Queensland, New South Wales, Victoria and Tasmania. The new races apparently arise as mutants which are rapidly propagated by uredospores, successive generations following each other at 10-14 day intervals. The old races are at a disadvantage owing to host resistance and the new races, free from serious competition, increase rapidly and soon become epidemic.

It is difficult to compare such changes directly with those in flowering plants. A comparison between a generation of time of 20 mins. and 20 years gives a factor of approximately 500,000, but it is highly improbable that a bacterium or a yeast would maintain such a high rate of division for long, and it might be necessary to take a figure. of something like 10,000. Thus, on these grounds alone, one might anticipate seeing changes in a yeast or a bacterium during an experimental study, comparable to those occurring in a tree species during the course of some 10,000 years. In addition, in the fungi, the selective pressure can be very high, particularly where a new mutant attacks a previously resistant host. Such high selective pressures lead to rapid changes in the populations and are probably rare in flowering plants. One might perhaps regard the rapid success of *Spartina townsendii* in colonising a previously "resistant" habitat as a comparable example.

When the general evolution of fungal species is considered, it is difficult to assess the importance of rapid selection due to a short generation time. It may well be that it has played only a small part in the general picture but under certain circumstances, as in the case of the wheat rusts, or in organisms like yeasts or bacteria, it provides a means by which changes in the population may occur with surprising speed.

Sources of Variation in Fungi.

Fungi have long been noted for their variability. This variation may take many forms. There is first the variation found in any particular character, such as spore size, and graphs of the distribution of size about a mean are familiar to most workers in

systematic mycology.   The degree of dispersion about the mean
for different characters may differ considerably as in Fig. 13a,
character A being less variable than B.   Then there is the varia-
tion brought about by the change in position of the mean for a
character or group of characters as in Fig. 13b.   This change may
be a temporary one due to a change in environment, or a
permanent one due to some form of mutation.   This is, of course,
the situation in all organisms.
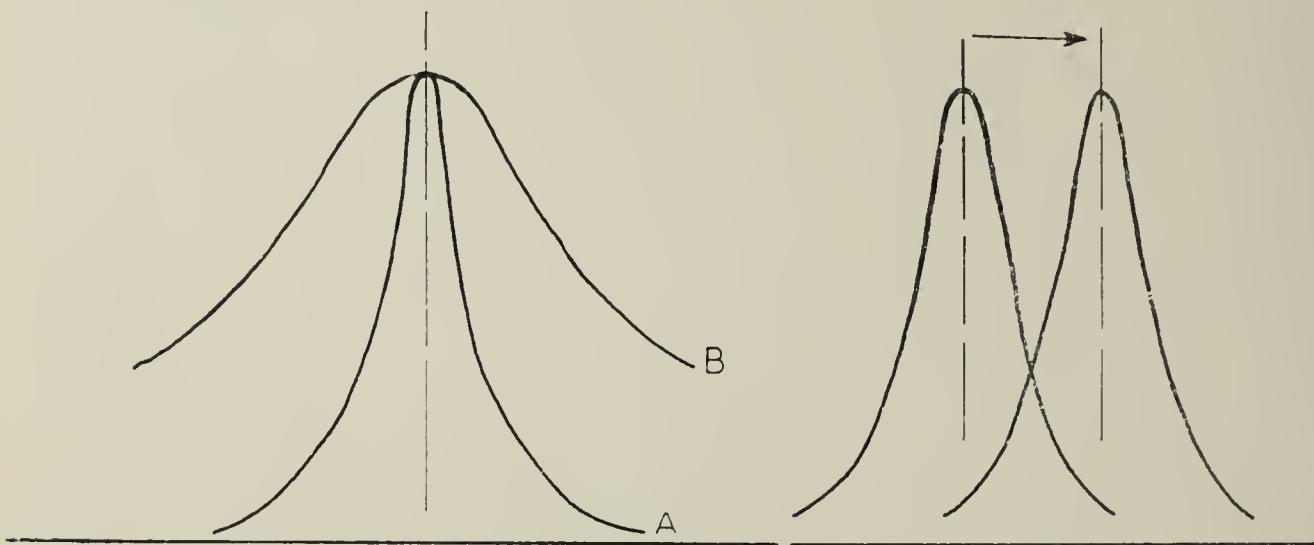

Fig. 13a.   Fig. 13b.

Fig. 13a. A comparison between the frequency diagram of a character—(A) which
          is fairly constant, and (B) which is more variable.
Fig. 13b. The shift of frequency curve for a given character or species. This may
          be temporary due to transplanting to a new environment or permanent
          due to mutation.

In delimiting a species we would naturally prefer to base a
diagnosis on characters which vary least.   The work of Vuillemin
(1910) and of Mason (1933) has shown that different types of
spores have different origins.   Measurements show that conidia
which are associated with a nuclear division (*Conidia vera*), or
spores such as ascospores, vary far less in their measurements than
do spores such as phragmospores which are essentially detached
fragments of hyphae.   The ease of specific or generic discrimina-
tion is often closely associated with the spore type available. This
is particularly true in the Fungi Imperfecti.

Phenotypic Plasticity.

The organism as we see it (phenotype) is the outcome of the
interaction between the genetic make-up of the organism and its
environment.   Fungi are as a whole extremely tolerant of big
changes in their environment and phenotypic plasticity is often
very marked.   Many fungi will thrive over a pH range from 3-9
and survive a multitude of changes in carbon and nitrogen
sources.   Under such conditions, colour, growth-form, and even
spore size are very susceptible to change.   The change may even
be of the order which has frequently been given generic status.
The genera *Gloeosporium* and *Colletotrichum* are closely allied.

The latter has a zone of setae surrounding the acervulus but there are no setae in *Gloeosporium*. Pure culture experiments have shown that one fungus, usually known as *Colletotrichum gloeosporioides,* which is widespread in the tropics, is capable of infecting 40 different host species. The resulting infections had been attributed to 25 different species in two genera. On mango, if the fruit were infected, no setae were formed and the fungus was a typical *Gloeosporium*; on stems and leaves setae occurred and the fungus was regarded as a *Colletotrichum* (Bessey, 1950, p. 552).

Usually the variations produced by transferring the fungi to different media are edaphic only, and correspond to variations seen in transplant experiments. Return to the original substrate restores the organism to its original form.

Mutations.

Mutational changes in fungi are well known. The intensive studies of *Neurospora* include many dealing with gene mutations and the subsequent morphological changes which may occur. Striking changes due to modification of the cytoplasm are also known, from the work of Ephrussi (1952) and his colleagues. When large numbers of colonies of yeast were grown, it was found that some of them had a very much reduced growth rate and an altered physiology. On normal media the proportion of new types produced was small, but the addition of acriflavine to the medium gave almost 100% conversion to the new form. It was suggested that during the normal process of budding, occasional cells were formed in which the cytoplasm going into the bud lacked some of the cytoplasmic components and the deficient cells thus formed gave rise to the new type colonies. Addition of acriflavine inhibited the reproduction of the cytoplasmic component without preventing cell division, thus almost all the new cells produced lacked the component.

Genic or cytoplasmic mutations are represented by a permanent shift of the mean in figure 13b.

The rapidity with which a fungus may undergo a permanent change is at least partly dependent on the ease with which a mutant can be perpetuated. A higher plant has many millions of nuclei so that we can reasonably expect that in any particular individual there are a large number of mutated genes but, unless these mutants occur in a germ cell or in tissue which will give rise to germ cells, the mutants will be lost. Since the proportion of germ to vegetative cells is very low, only a minute fraction of the mutants has any hope of survival. Occasionally a vegetative mutant may arise, but its chance of propagation under natural conditions is small. In a fungus the situation is very different. A culture in a petri dish will, like the higher plant, have many nuclei and numerous mutated genes but, unlike the higher plant, these mutations, unless they are deleterious, have a good chance of being perpetuated and the hyphal tip containing the mutant gene may rapidly develop a "sector" different from the parent.

Heterokaryosis.

In the higher organisms 'there is a fixed relation between nucleus and cell and a fixed alternation between haploid and diploid. In many fungi this is not so. In the Phycomycetes and Ascomycetes, cell-wall formation is not usually associated with nuclear division. The compartments into which the hyphae are divided do not correspond to cells in higher organisms. On the whole, the number of nuclei in a compartment is usually about the same. For instance, one often finds five or six nuclei per "cell" but elsewhere in the same hypha one may find as few as one or as many as ten. In most organisms, the plant is derived from a single nucleus, either haploid or diploid, so that any single gene is present in only one form or at the most two, as in a heterozygous diploid. In fungi, fusions between hyphae from several different spores are common and interchange of nuclei occurs. This can lead to the formation of a mycelium with hyphae containing nuclei of several different genetic constitutions (heterokaryosis) and the resulting mycelium is the outcome of the interaction between the nuclei with different gene complements. During growth of the organisms, hyphae may be formed which have a different grouping of the nuclear types, a difference either in kind or in proportion, and a new variant is born.

There appear to be at least two types of heterokaryosis. The best known is common in the Ascomycetes and Fungi Imperfecti, which have multinucleate compartments in their hyphae. The nuclei may be of several genetic kinds and come together as the result of fusion between hyphae derived from different spores. In nature, selection pressure probably keeps the heterokaryons fairly stable, but, in the laboratory, removal of competition and stringent selection leads to a burst of variation and presents the mycologist with a multitude of different strains. A less familiar form occurs in fungi like *Fusarium* where Buxton (1954) has shown that although the tip of the hypha is multinucleate and presumably heterokaryotic, cross-wall formation produces uninucleate compartments. Thus cells are produced containing single nuclei, but adjacent cells may have nuclei with different gene complements. Lateral outgrowths from these cells will give initially hyphae of a single genetic type. Local areas may, therefore, be wholly or predominantly of one genetic origin, probably corresponding to the patch mutants of Miller (1946). Secondary anastomoses restore the heterokaryotic condition at the growing tips.

Raper and Antonio (1954) have described a form of heterokaryosis in Basidiomycetes where a mycelium which is haploid as regards mating type still carries two types of nuclei physiologically distinct. Whether such a condition will be found in nature remains to be seen.

Recently Pontecorvo *et al.* (1953) have emphasized the importance of another source of variation in fungi. In forms such as *Aspergillus niger,* where no sexual reproductive mechanism is known, it has been found that among the normal haploid nuclei

there is a small proportion of diploids. If the original mycelium was heterokaryotic, some of these diploids can be shown to be heterozygous for characters derived from the different genetic types forming the heterokaryons. In an artificially produced heterokaryon, Pontecorvo found that 3 in 10^7 conidia contained heterozygous diploid nuclei. Subsequent growth of conidia gave colonies which showed mitotic segregation and recombination of the characters and a small proportion of the nuclei in these, 1 in 10^4, that is 3 in 10^{11} of the original nuclei, became haploid (Pontecorvo, 1953b).

The rate of occurrence of the heterozygous diploids is of the order which would be expected for a normal gene mutation. The additional factor of the slow rate of haploidization means that the nett effect of the whole process may be small. The ability to achieve new combinations of groups of genes by mitotic segregation confers on the organism some of the benefits of sexual reproduction. The variability and the adaptive capacity of such a mechanism would presumably be intermediate between gene mutation and normal sexual reproduction.

GROWTH IN CULTURE.

A great many of our difficulties in specific discrimination in the fungi are of our own making. By the isolation and continued growth of organisms on media which are often very different from their natural substrates, we induce a multitude of variants and impose entirely new selective conditions. The dangers associated with the culture technique were well appreciated by some of the older mycologists, and it was indeed a source of continual friction between the older and younger mycologists at one time. The epilogue to volume 2 of Grove's *British Stem- and Leaf-Fungi* (1937) is a relic of what was once a widespread dissension. He describes the plight of systematic mycologists. "Some have plunged into the thorny thickets of synonymy, floundering amid the multitudinous meticulosities of Nomenclatorialism, from which they rarely emerge unscathed; others wandered disconsolate over arid deserts of Petripatellism, plodding dully along a path, meandering and redeless, which could of necessity lead nowhither; still others filled up their space with frills, such as a boring discussion of the dietetical predilections of the patient for concocted foods." He describes 'Nomenclatorialism' as "an intricate esoteric art which strives to affix to every living creature (plant or animal) a definite unchangeable Latin label in strict accordance with the very latest views about Scientific Nomenclature. The object of the art was to reach finality; but it has not attained that end, nor can it, so long as the multiplicity of nature is rivalled by the variety of men's minds. A naturalist should take heed lest he become too nomenclatorialistically minded". He describes 'Petripatellism' "as the state of mind of a mycologist who studies his fungus in a laboratory, on agar-slants or *Petri-dishes* without paying equal regard to what the fungus

can do out of doors in the wide and untrammelled field". Unfortunately, few people seem to have read or at least paid much attention to this epilogue. It is true, of course, that Grove was equally at fault when he dismissed so readily and unsympathetically the results obtained from pure culture work.

The breeding programmes associated with modern genetical studies have brought home very clearly to geneticists the way in which intensive breeding and culture of an organism, such as *Drosophila* or *Neurospora,* has produced a host of laboratory strains differing in their morphology and physiology from each other and from the original form from which they came, and for which it was necessary to find a special designation—the "wild type". As yet, in mycology, there has been little recognition of the need to define a "wild type" as distinct from the tamed and modified laboratory organisms, and the work of Miller in the *Fusaria* is a most valuable contribution to this aspect of the study of systematics. In the maintenance and identification of culture collections it is of importance that the "wild type" be cultivated and not the laboratory mutant.

APPLICABILITY OF ANGIOSPERM TAXONOMIC CONCEPTS TO MYCOLOGY.

With the development of experimental taxonomy of Angiosperms the concepts of taxa at specific and subspecific levels underwent numerous changes. Although there are still many matters in dispute a number of terms and ideas have met with general acceptance. It is of interest to see how some of these concepts can be applied to systematic mycology.

Linneons and Jordanons.

Close on a century ago Jordan showed that *Draba* (*Erophila*) *verna* of Linnaeus could be analysed into a large number of distinct strains. Since then it has been found that a large proportion of the species studied are similarly complex. In some cases, experimental work has shown that the smaller units are all interfertile but ecological or other factors tend to give some degree of isolation to groups of characters.

In mycology, it has also been found that many "Linneons" can be split into smaller and distinctive units, for example *Corticium coronilla* H & L., which Biggs (1937) has shown contains a large number of strains differing in cultural characteristics, spore and basidium size, etc. For normal purposes, there is little to be gained by giving such strains special status and to rank them as species would merely produce confusion.

Aggregates and Coenospecies.

Where a species seems to be particularly plastic, or where there is a group of very closely allied species differing from each other by relatively few characters, it is convenient to use some term to indicate that a broad view of the species is being taken.

The term coenospecies, proposed by Turesson (1922), was designed for some groups of closely allied species and would at times be applicable to fungi. Subsequent attempts to redefine the term have not been happy and its use has tended to decrease. Recently the more vague term *aggregate species* has gained popularity, perhaps because of its fewer implications. In the new British *Flora* there are a number of examples of the convenient use of the aggregate species. One may cite *Alchemilla vulgaris* agg. under which eleven critical species are described. For many purposes the aggregate species is adequate, but for critical work identification to the finer level is necessary.

In the difficult genera *Aspergillus* and *Penicillium,* the idea of an aggregate species has proved extremely useful as Thom (1952) has pointed out. The early monographs by Thom and Church on the *Aspergilli* in 1926 and the *Penicillia* in 1930 were landmarks in systematic mycology, and emphasised very clearly the special problems associated with such difficult groups of fungi. In recent years, both these monographs have been replaced by new ones from the same authors, the *Aspergilli* in 1945 and the *Penicillia* in 1949. The contrast between the old and the new treatments makes a most interesting study. In the work on *Aspergillus,* the difficulties of identifying the innumerable strains, often differing from one another by minute morphological characters, or by a single chemical property, has meant the abandonment of the narrower specific limit found in the earlier works. The various strains are now placed into groups, and each group contains a number of series. Within the series specific rank is still accorded to certain well marked forms, but it is clear that there is no difficulty in finding a complete range of forms linking a number of the so-called species which had previously been regarded as distinct. For most purposes identification of an organism to its series is adequate.

It is difficult to make a direct comparison between the units in *Aspergilli* and species in higher plants, but it is probably justifiable to regard the series of Thom and Raper as approaching very closely to the aggregate species as used by Clapham, Tutin and Warburg in the new *Flora of the British Isles,* and the species of Thom and Raper as corresponding to the critical species.

The intensive study of *Penicillia* and *Aspergilli,* stimulated by biochemistry and industrial chemistry, has been paralleled in the genus *Fusarium* because of its interest to agriculture and plant pathology. The widespread occurrence of forms of *Fusarium* attacking the underground parts of economic plants, and the occurrences of apparently saprophytic forms in the soil, has made it desirable to have some methods of species discrimination within the group. For many years, the works of Reinking, Sherbakoff, and Wollenweber have formed the basis for identification. The most detailed treatment of Wollenweber and Reinking (1935) listed some 65 species, with 78 varieties, grouped into 16 sections. Despite this careful monograph, the identification of a particular

isolate was the task for a specialist and involved a great deal of cultural work and examination. The most recent discussions of the problem by Hansen and Snyder (1940) and by Miller (1946), have both proposed drastic simplification of the older works. As a broad generalisation, it may be said that the recent workers regard the sections of Wollenweber as equivalent to species, and the majority of the older species as varieties of a few well marked pleomorphic species. Again, one is tempted to equate the new concept of the fungal species with the aggregate species of the angiosperm systematist. Any detailed consideration of the problem though must await the results of genetical evidence regarding the infertility of the various units.

Infra-specific Units.

In mycology, as in all other branches of botany, there is a great variation in the use of infra-specific units. The most detailed studies have come from workers in the rusts where the economic importance of being able to recognise individual strains has led to intensive investigation of minor taxonomic units.

In *Puccinia graminis* it has long been realised that there are groups of strains which attack predominantly wheat or barley or oats, etc. These strains have been grouped as sub-species and the trinomial nomenclature favoured by zoologists adopted. Thus the strains on wheat and on oats are grouped as *P. graminis tritici* or *P. graminis avenae* respectively. Genetical work has shown that these groups are somewhat interfertile but have each become adapted to their own ecological niches. They are in effect eco-species.

The subspecies are themselves capable of being further subdivided into physiological races. These differ by very minor morphological characters and are distinguished on their ability to attack different members of a range of test varieties of the host. The individual races are given a number. Genetical analysis has shown that the differences between many of the races are very small and may be due to a small number of gene differences. Some of the races, e.g., *r.34*, are known to be heterozygous, the common segregates from *r.34* being *r.11* and *r.56*. (Waterhouse, 1952).

Natural hybrids.

References to the natural occurrence of hybrids between different species of fungi are usually vague. Perhaps the best example is that of *Allomyces javanicus* which Emerson and Wilson (1954) have shown is a natural hybrid with a complex and unstable chromosome complement.

Reports of hybrids in the higher fungi are often based on little evidence, difficult forms being attributed to hybridisation solely on the grounds that the specimen is intermediate between the concepts a mycologist has of the two presumptive parents. The tendency to class certain forms of *Mycena* or *Hygrophorus* as

hybrids may simply be an expression of the difficulty of placing the large numbers of apomictic races in these genera.

Careful analyses of presumed hybrid populations in the Basidiomycetes are rare. Parker-Rhodes (1950), as the result of the application of his method of tetrasporic analysis, considers that natural hybridisation occurs between *Psilocybe bullacea* and *P. coprophila* on Skokholm Island giving rise to a population of intermediates which he has described as *P. scocholmica*. Accounts of the artificial production of hybrids are not uncommon particularly in the Phycomycetes, for example, that of Raper (1950) who cross-mated a number of species of *Achlya*. In some, e.g. *A. ambisexualis* and *A. americana,* he obtained complete compatibility. In others, the incompatibility was either partial or complete. In the higher groups artificial hybrids are rare. Romagnesi (1948) has reported the experimental production of a hybrid between *Agrocybe* (*Pholiota*) *praecox* and *A. sphalenomorpha*.

There seems little doubt that under laboratory conditions there is no difficulty in obtaining hybrids in some genera. The apparent scarcity of natural hybrids might well be due to the difficulty of recognising a hybrid as such when it is found.

Apomixis.

Development of a gamete or a gametangium without sexual fusion is common and widespread in the fungi, and mycology courses are full of examples of "progressive loss of sex". Many species possess no distinct morphological differentiation of sex organs yet still retain the essentials of sex, the fusion of nuclei followed by meiosis. True apomixis, however, occurs in all the groups. In the Phycomycetes, Cutler (1942) has shown that *Sporodinia grandis,* although forming apparently good gametangia which fuse, does not follow this with nuclear fusion but develops a zygote which subsequently germinates to give a sporangium containing the original haploid nuclei.

There are numerous examples of the development of a fruit body in the Ascomycetes without nuclear fusion. In many of these well developed sex organs still occur, as, for example, in *Ascobolus equinus.*

In the Basidiomycetes it has been shown by Kühner (1938) that in the genus *Mycena* apomixis is common. It is interesting that the species of this genus are generally regarded as not difficult provided care is taken to observe the fine details of the shape of the basidia and cystidia and the spore size.

Work with angiosperms has shown that apomixis is often associated with the occurrence of a large number of forms, each reasonably distinct and constant, but separated from other forms by very small differences in morphological characters. This would seem to be the situation in the agarics such as *Mycena* and *Hygrophorus*. In the Ascomycetes it is possible that the apparent absence of the fine splits usually associated with apomixis may be due to the occurrence of heterokaryosis, which, with its intro-

duction of different gene complements, confers a plasticity unknown in the gene isolation of the angiosperm apomict.

CYTOTAXONOMY.

Few detailed cytotaxonomical studies of fungi are available. It is clear, however, that both allopolyploidy and aneuploidy have played a part in the evolution of fungal species and genera. Figure 14 summarises most of the available chromosome numbers
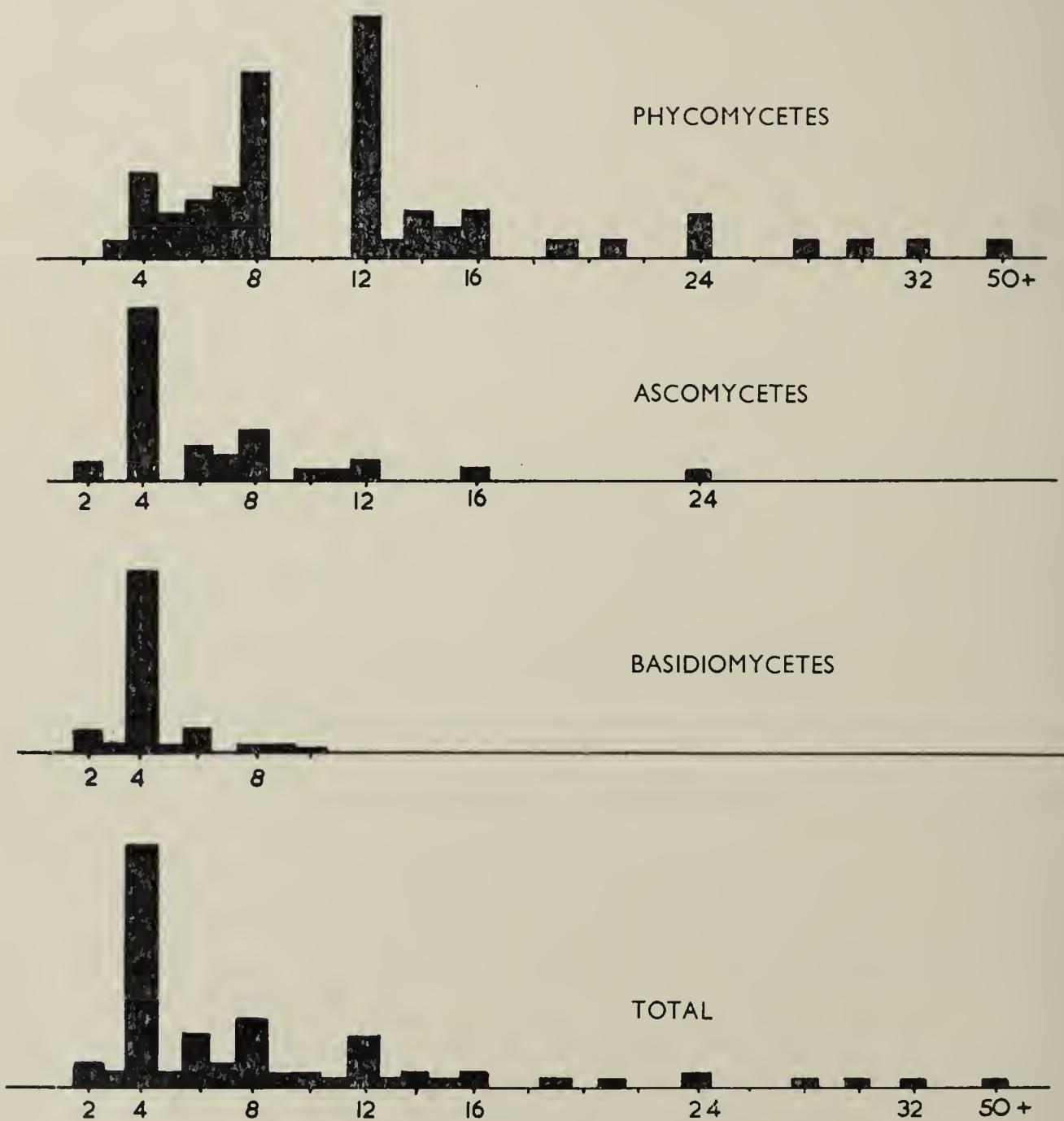

Fig. 14.

The distribution of chromosome numbers in the different groups of fungi.

for fungi.   No attempt has been made to assess the relative reliability of the counts and all records seen have been included except for the yeasts and the smuts.   In both of these groups two chromosomes are frequently reported.   The text figures, however, are so unconvincing that it seems best to disregard them for the present.

Figure 14 suggests very strongly that the basic chromosome number in the fungi is $n=4$. In the Phycomycetes, 2 and 3-ploid series are common and higher polyploids occur. Most of the high counts are in the genus *Allomyces* but high numbers also occur in the few available counts for Myxomycetes. In contrast, the Basidiomycetes show little evidence of polyploidy.

The best and only detailed cytotaxonomic study at present available is that of Emerson and Wilson (1954) in the genus *Allomyces*. The chromosome numbers of the different species and strains are given in Table 1. This shows clearly that polyploidy occurs both within a genus and within what is normally regarded as a single morphological species.

TABLE 1.

Chromosome numbers in *Allomyces* from Emerson and Wilson (1954).

Species.	Chromosomes.	
A. arbuscula.	8	Brazil, Portugal, India, Fiji, Philippines, U.S.A., Australia.
	16	Trinidad.
	24?	Belgian Congo.
	22-26	Queensland.
	32	Illinois.
A. macrogynus.	14	India.
	28	Burma.
	50 +	Philippines.
A. javanicus.	13, 14, 14 or 15, 16 or 17, 19, 21.	This species is regarded as a natural hybrid.
A. arbuscula × A. macrogynus.	20, 22, 27, 36, 42, 42 +, 44.	An artificial hybrid.

Recent investigations of McGinnis (1953 and 1954) suggest that in the rusts the basic chromosome number is 3, as, for instance, in *Puccinia coronata*. *P. graminis*, with $n= 6$, is regarded as a polyploid and the clear evidence of secondary association of the chromosomes suggests that it is of hybrid origin.

DIFFICULTIES PECULIAR TO CERTAIN GROUPS.

In the Phycomycetes, systematic discrimination does not seem to have presented any outstanding difficulties. Certain groups, e.g. the Mucorales by Zycha (1935), have been well monographed and most workers find it possible to place with reasonable confidence the majority of the strains they isolate. This is also true of the aquatic Phycomycetes which have been monographed by Sparrow (1943).

The Ascomycetes, again, as a group, do not seem to present any major difficulties except for a few orders. Some of these, how-

ever, are particularly troublesome, like the yeasts. It is inevitable that in unicellular organisms the number of available morphological characters is small and it is necessary to fall back on physiology and biochemical reactions. This is notoriously unsatisfactory owing to the rate at which characters are lost or "adaptations" occur.

Romagnesi (1948) has given an excellent summary of the problems and methods of systematics in the Basidiomycetes. Many of the problems in this group arise from the difficulty of preparing good herbarium specimens. This has meant that tradition has played a very large part in the concept of the different species. Much of the accumulated knowledge of Agarics has been passed on by word of mouth and traditions have been built up in the different countries regarding the local concept of what constitutes a particular species. Probably in no other group is it necessary so often to qualify a specific name by a comment such as "*sensu* Lange, *non* Bresadola" etc. In recent years there has been an attempt to correlate the traditional concepts from different countries and to encourage the collection of herbarium material. This is particularly important in association with species-lists of plants occurring in any district, as there is hardly an example of a check-list supported by reference specimens.

In most genera of the Agarics the species appear to be reasonably well separated, and the number of presumed naturally occurring hybrids is very small. In certain groups, as e.g. *Tricholoma*, it seems that the older concept was too narrow, and that it is necessary to lump some of the earlier species, as, for example, in the *T. terreum* Fr.—*T. scalpturatum* Fr. group, where forms such as *T. argyraceum* (Bull.) Fr. and *T. chrysites* (Jungh.) Gill., mark distinct points in a wide range of colour and scaliness of the pileus or again to place the different colour forms and variations such as *T. brevipes* (Bull.) Fr., *T. excissum* Fr., *T. humile* (Pers.) Fr., *T. oreinum* Fr., *T. paedidum* Fr., *T. patulum* Fr., *T. phaeopodium* (Bull.) Quél., *T. subpulverulentum* (Pers.) Fr. etc., all under *T. melaleucum* (Pers.) Fr. Colour has, of course, played a great part in the recognition of species in the Agarics, and while on the whole it is an extremely valuable character, it does at times appear to depend on very small genetic differences.

From time to time, attempts have been made to apply chemical tests to the identification of fungi and of lichens. This has often aroused most violent partisanship, and the sensible view that the chemical tests simply add one or two more characters to the already recognised morphological characters is surprisingly seldom taken. In a group which is already difficult and in which characters are few or very variable, one would imagine that any additional evidence would be welcome. The opposition therefore to the introduction by Schaeffer and Möller (1938) of chemical tests to aid specific discrimination in the notoriously difficult genus *Psalliota* seems inexplicable. There is no essential difference between recognising a chemical in the pileus because it

is brightly coloured and can be seen by the eye, and perceiving its presence by means of a chemical test.

The problems associated with the classification of the Fungi Imperfecti are largely due to the absence of the perfect stage. Many higher plants have vegetative forms of reproduction but most of the species still retain their normal sexual mechanisms as well. In the fungi it seems that large groups of organisms spread primarily by vegetative spores and seldom, if at all, reproduce sexually. Since the systems of classification are based primarily on sexual reproductive mechanisms and spores, the mycologist is left with a host of organisms producing no apparent sexual stage. These he has dumped in a group called the Fungi Imperfecti. It was at one time assumed, tacitly at least, that each fungus would eventually reveal a sexual stage and could then be rehabilitated and placed into its proper systematic position. It seems, certainly at the moment, that this is a vain hope and since taxonomy is mainly a matter of convenience and expediency, names have been given to these imperfects. The systematic arrangement has been frankly artificial on the form and grouping of the vegetative reproductive units.

Suppose we were forced to exclude flowers from the classification of the angiosperms and use vegetative reproduction only. We might form a genus containing all the species with *bulbs*— this would not be a bad group, in fact surprisingly close to the *Liliaceae*: a genus based on *corms,* however, would be poor— while one based on *tubers* would bring together *Dahlia, Solanum, Orchis,* etc. The difficulties of classification in the Fungi Imperfecti are of this order. It is true, though, that they are usually difficulties of generic rather than specific level.

The Fungi Imperfecti present a further taxonomic problem since several fungi which are distinct in their perfect stage may have very similar imperfect forms, e.g. *Neurospora* spp. and *Monilia sitophila.* If we had only the *Monilia* stages, we would almost certainly consider that we had only a single species—and a fairly constant one at that. It is not at all improbable that some of our variable species of the Imperfecti are aggregates of the imperfect stages of several different fungi.

The treatments accorded the different genera have varied greatly with the author concerned. In some, as in *Fusarium,* the modern tendency is to "lump". In others, like *Alternaria,* a large number of species is still accepted.

General Discussion.

It is clear that it is possible to define a group or groups of organisms either in terms of their morphological pattern, or in terms of their genetic behaviour elucidated by breeding experiments or cytological investigations. Often the two definitions coincide and the new systematics confirms the old, but where differences occur some compromise is usually sought. In the higher plants most of the lack of agreement is due to polyploidy

unaccompanied by marked morphological changes, or by apomixis. The former seldom causes practical difficulties in systematics. Apomixis, on the other hand, is only too well known in the genus *Rubus*, with its some 4000 morphological units in North Western Europe alone, or in *Hieracium*, which probably has twice as many. Some special convention will have to be devised to handle such situations.

In the fungi the impact of apomixis on systematics has been slight. It is clear that in the genus *Mycena* a mixture of mictic and apomictic forms is common, so that one might expect a chaos comparable to that found in *Rubus*. Perhaps because of the difficulty of getting good herbarium specimens for comparison of collections from many localities the careful studies of slight differences of morphology have not been made, and a Pandora's box of microspecies awaits opening. On the other hand, the efficiency of the spore dispersal mechanisms may mean that individual apomicts can potentially spread over very wide areas and competition has eliminated all but the most successful forms.

The phenomenon of heterokaryosis confers a potential plasticity far in excess of that seen in a normal haploid or diploid organism. It would seem reasonable, therefore, to have much wider species concepts in genera where heterokaryosis occurs. The use of aggregate species in *Penicillium* and *Aspergillus* and the recent lumping in *Fusarium*, although based on older systematic methods, can be strongly supported on the genetical grounds that heterokaryosis occurs in these genera.

When dealing with pathogenic forms, the assumption that a species is distinct because it is on a different host, even though there may be accompanying morphological differences, is far from justified. It is essential that transplant experiments to a more familiar host be attempted to eliminate the possibility that the so-called different species is not just an ecad.

It seems reasonable to conclude that the problems of species discrimination in the fungi are essentially the same as in other organisms, although they may be accentuated by the rate of speciation or by great plasticity. One cannot dismiss the fungi from the general schemes nor can one ignore the lessons learnt from fungi in considering the species concept in higher organisms.

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LITERATURE CITED.

BESSEY, E. A., 1950, *Morphology and Taxonomy of Fungi.* Blakiston Co., Philadelphia.

BIGGS, R., 1937, The species concept in Corticium coronilla, *Mycologia,* **29**, 686-705.

BUXTON, E. W., 1954, Heterokaryosis and variability in Fusarium oxysporium f. gladioli (Snyder and Hansen), *J. Gen. Microbiol.*, **10**, 71-84.

CUTLER, V. M., 1942, Nuclear behaviour in the Mucorales. II. The Rhizopus, Phycomyces and Sporodinia patterns, *Bull. Torr. Bot. Club*, **69**, 592-616.

EMERSON, R. & WILSON, C., 1954, Interspecific hybrids and the cytogenetics and cytotaxonomy of Euallomyces, *Mycologia*, **46**, (in press).

EPHRUSSI, B., 1952, *Nucleo-cytoplasmic relations in micro-organisms*, 1-127. Oxf. Univ. Press.

GROVE, W. B., 1937, *British Stem and Leaf Fungi*, **2**. Cambridge Univ. Press.

KÜHNER, R., 1938, Le genre Mycena, *Encyclopédie Mycologique*, **10**, Paris.

McGINNIS, R. C., 1953, Cytological studies of chromosomes of Rust Fungi. I. The mitotic chromosomes of Puccinia graminis, *Canad. J. Bot.*, **31**, 522-526.

——, 1954, II. The mitotic chromosomes of Puccinia coronata, *Canad. J. Bot.*, **32**, 213-214.

MASON, E. W., 1933, *Annotated account of fungi received at the Imperial Mycological Institute*, List II, Fascicle 3.

MILLER, J. J., 1946, Cultural and Taxonomic studies on certain Fusaria, I and II, *Canad. J. Res.*, C., **24**, 188-223.

PARKER-RHODES, A. F., 1950, The basidiomycetes of Skokholm Island. IV. A case of hybridization in Psilocybe (Deconica), *New Phyt.*, **49**, 335-343.

PONTECORVO, G., 1953, Diploids and mitotic recombinations, p. 18, in *Adaptation in Micro-organisms—3rd Symposium of the Society for General Microbiology*.

PONTECORVO, G., ROPER, J. A. & FORBES, E., 1953, Genetic Recombination without sexual reproduction in Aspergillus niger, *J. Gen. Microbiol.*, **8**, 198-210.

RAPER, J. R., 1950, Sexual hormones in Achlya. VII. The hormonal mechanism in homothallic species, *Bot. Gaz.*, **112**, 1-24.

RAPER, J. R. & SAN ANTONIO, J. P., 1954, Heterokaryotic mutagenesis in hymenomycetes. I. Heterokaryosis in Schizophyllum commune, *Amer. J. Bot.*, **41**, 69-86.

ROMAGNESI, H., 1948, Les problèmes et les méthodes de la systématique des champignons supérieurs, *Bull. Soc. Mycol. France*, **64**, 53-100.

SCHÄFFER, J., 1938, Beitrag zur Psalliota-Forschung, *Ann. Myc.*, **36**, 64-85.

SPARROW, F. K., 1943, *Aquatic Phycomycetes*. Univ. Mich. Press.

SNYDER, W. C. & HANSEN, 1940, The species concept in Fusarium, *Amer. J. Bot.*, **27**, 64-67.

THOM, C., 1952, Molds, Mutants and Monographers, *Mycologia*, **44**, 61-85.

TURESSON, G., 1922, The genotypical response of the plant species to the habitat, *Hereditas*, **3**, 211-350.

VUILLEMIN, P., 1910, Matériaux pour une classification rationelle des Fungi Imperfecti, *Compt. rend.*, **150**, 882-884.

WATERHOUSE, W. L., 1952, Australian rust studies. IX. Physiologic Race Determinations and Surveys of cereal rusts, *Proc. Linn. Soc. N.S.W.*, **77**, 209-258.

WOLLENWEBER, H. W. & REINKING, O. A., 1935, *Die Fusarien, ihre Beschreibung, Schadwirkung and Bekämpfung.* Berlin.

ZYCHA, H., 1935, *Mucorineae, Kryptogamenflora der Mark Branden-burg,* **6**a. Leipzig.

THE ANALYSIS OF VARIATION WITHIN THE GENUS FUCUS

E. Burrows and S. M. Lodge (University of Liverpool).

The exhibit under this title illustrated for the Algae a species problem of a type frequently found among flowering plants. Within the British Isles there are to be found five taxonomic species of *Fucus*. Of these *F. spiralis* L., *F. vesiculosus* L. and *F. serratus* L. are common on rocky places all round the coast. *F. ceranoides* L. is also widely distributed in its habitat in the mouths of fresh-water streams. The fifth species, *F. inflatus* L. has its centre of distribution much further north and has only a very limited distribution in the British Isles. The status of these species and their ecological relationships are still far from clear.

Of *F. ceranoides* little can be said at present but it presents an interesting problem. It is readily distinguished by its dark colour, delicate papery texture, fine thread-like stipe and very pointed receptacles. These are, however, all characters influenced by habitat conditions. At different tide levels *F. ceranoides* may show, in addition, characters of any of the other three species, *F. spiralis*, *F. vesiculosus* and *F. serratus*, and it is possible that it includes estuarine forms of all three.

F. spiralis, *F. vesiculosus* and *F. serratus* are distributed in relation to tide levels in such a way that, when all three are present on the shore in abundance, they are limited to fairly well defined zones with *F. spiralis* in the upper part, *F. vesiculosus* in the mid-tide region and *F. serratus* in the lower part and extending well below L.W.S.T. Under such conditions the species appear to be separated by clear cut characters. In situations where the shore is more sparsely covered by vegetation or where clearance experiments have been carried out, the zones become less distinct, the species extending their ranges up and down the shore, and individuals are then often more difficult to refer to one or other taxonomic species. *F. serratus* is usually distinct, but *F. spiralis* and *F. vesiculosus* have often little to separate them except the hermaphrodite condition of the former and the dioecious condition of the latter. It is to be emphasised that, for intertidal species, a difference of only two or three vertical feet in tidal position may mean a considerable difference in ecological conditions in terms of exposure to a drying atmosphere, changing light intensity and temperature.

These three species are interfertile and hybrid sporelings have been raised in culture. There is a good deal of evidence to show that hybrid sporelings are also formed in nature, but that competition with the parent species, under the conditions prevailing

in a well developed shore zonation, prevents their establishment. Suspected hybrid swarm populations have been found in a number of places under either naturally or experimentally disturbed conditions. The results of an analysis of a suspected hybrid swarm population between *F. spiralis* and *F. vesiculosus* was shown in the exhibit. Anderson's hybrid index method was used for the analysis and the characters included were those normally employed by taxonomists in separating the species. The analysis showed about 20% of *F. spiralis,* a little less of *F. vesiculosus* and a large range of intermediates between them. It is possible, however, that this range of intermediates is merely giving an indication of the degree of plasticity of the species and does not, in fact, represent a hybrid swarm. On the information available at present it is difficult to decide between these two interpretations.

The exhibit was particularly concerned with the variation shown by *F. vesiculosus* and *F. inflatus.* All the species of *Fucus* are variable but these two are particularly so. In both cases the form of the plant varies with the degree of exposure to the effects of open sea breakers. The effect of rough water is to reduce the growth rate by rendering photosynthesis difficult so that narrow dwarfed plants are produced and, in the case of *F. vesiculosus* these lack the typical air vesicles. For *F. vesiculosus,* an attempt has been made to analyse this variation on a population basis and, for this purpose, an adaptation of Wilmott's grid method for recording variation within a critical group has been used. Several populations growing under different degrees of exposure to open sea breakers have been analysed and defined by this method, and the results show variation on an ecocline from sheltered to exposed conditions. The extremes of this range have long ago been defined as varieties of *F. vesiculosus.* The sheltered water form was distinguished as *F. vesiculosus* var. *vadorum* Aresch. and that from rough water as *F. vesiculosus* var. *evesiculosus* Cotton. How far this variation is accounted for by plasticity of phenotype or what degree of isolation the extremes have is not known, but the problem is now being tackled by culture methods. The plants can be grown under standard culture conditions to a length of 5 or 6 cms. and attempts are being made to plant them out on selected shores to finish their growth.

F. inflatus, which differs from *F. vesiculosus* in a number of characters and especially in being hermaphrodite instead of dioecious, varies in form very strikingly with degree of exposure. Here again the extremes of the range have been distinguished, for sheltered water as *F. inflatus* f. *edentatus* (de la Pyl.) Rosenv. and for rough water as *F. inflatus* L. f. *distichus* (L.) Børgesen.

This species is common further north in the Faeröes, Iceland and Norway and there the extremes are linked by intermediate forms. In Britain only the extreme forms are found and these are restricted both ecologically and geographically: *F. inflatus*

f. *edentatus* is found only in Lerwick and Scalloway harbours in Shetland and in North Haven in Fair Isle; all of these are functioning harbours. *F. inflatus* f. *distichus* is confined to exposed coasts on the Atlantic facing shores of the British Isles. It occurs as far south as Kilkee in the west of Ireland but its extreme southern limit is not known.

One feature which is very striking is the similarity in appearance between *F. vesiculosus* var. *evesiculosus* and *F. inflatus* f. *distichus*. The two species are very different and easy to distinguish at one end of their variation range, but almost identical in appearance under rough water conditions. The two can be separated on the sexual characters in that the former is dioecious and the latter hermaphrodite.

The exhibit did little more really than illustrate the species problem for *Fucus*. A start has been made on its solution by the development of suitable culture techniques and an attempt to sort out the variants of the taxonomic species on a population basis. Experimental work in the field has begun to give information on the ecological relationships of the components of the genus, but of the real status of the components still very little is known.

REFERENCE.

WILMOTT, A. J., 1950, A new method for the identification and study of critical groups, *Proc. Linn. Soc.*, **162**, 83-98.

THE SPECIES CONCEPT AMONGST BRYOLOGISTS

E. W. JONES (Imperial Forestry Institute, Oxford).

Bryologists have tended to apply to bryophytes the concepts of species formed in the study of flowering plants; they have not been great innovators of new concepts. The amateur status of a high proportion of our leading bryologists is doubtless one important reason for this situation; the late H. N. Dixon, for example, was a school-master with a classical education, Richard Spruce a mathematical school-master, and Max Fleischer, whose work on the mosses of Java forms the basis of our modern classification of mosses, was an artist by profession. Men such as these had neither the training nor the resources to allow them to develop new methods, even if such were needed. Moreover, most bryologists have served their apprenticeship in the study of flowering plants and they are at a disadvantage compared with the student of flowering plants because mosses and liverworts are relatively difficult to cultivate, particularly from spores. Consequently the criteria used for defining species have changed and multiplied but the fundamental concepts have altered but little.

The earlier bryologists attached great importance to the gross morphological features of the vegetative and (from analogy with flowering plants) more especially the reproductive organs. When, at the close of the 18th century, Hedwig introduced the use of finer details, he was criticised, e.g. by Menzies (1797) who wrote 'No generic or specific characters ought ever to be adopted that cannot easily and distinctly be seen by the assistance of a single-lens magnifier such as botanists commonly carry in their pockets' (quoted by Steere, 1947). Bruch and Schimper figured many anatomical details in their great *Bryologia Europaea* (1836-55), and Limpricht described in detail the anatomical structure of all species in his volumes on European mosses in Rabenhorst's *Kryptogamenflora* (1890-1904). The size and character of the cells of the leaf are now universally recognised as giving specific characters of great value, and the structure of the stem, midrib etc. as seen in cross section is often characteristic, especially in mosses. The search for additional characters of systematic importance continues, and increasing attention is being paid to the nature of the cell-contents. Thus the oil-bodies, which are present in most hepatics, often present valuable specific characters, but unfortunately in many species they disappear soon after death in specimens preserved by the usual methods. In some groups also chromosomes have been studied. Lorbeer found that European female plants otherwise indistinguishable from the

American *Sphaerocarpus texanus* Austin differed from the American plants of this species in some details of the X-chromosome, and he therefore separated the European plant as a different species under the name of *S. europaeus*—a course which has not met with the approval of so excellent a hepaticologist as K. Müller (1951); this affords an excellent illustration of the difficulty of knowing how far to proceed in splitting up into specific units and of the necessity for taking into account what is practicable when doing so.

Many bryophytes are extremely plastic, and one of the greatest practical difficulties of the bryologist lies in distinguishing between true genotypes and modifications which are the direct result of the influence of environment. Many of these latter have been described in the past as species or varieties, and indeed some bryologists, even in relatively recent years, have not always excluded the environmentally-produced modification from their concept of the species; thus in 1916 when Douin (a mathematician) had by cultivation produced a *Cephaloziella* completely different in appearance from the plant which he originally gathered, he described it as a new species because, as he said with a mathematician's logic, he would have described it as a new species had he found it growing wild (quoted by K. Müller, 1947, p. 15); similarly Ingham in 1908 could speak of *Drepanocladus wilsoni* (Schp.) as being a derivative of *D. lycopodioides* (Brid.), and of *D. sendtneri* (Schp.) as originating from various species. Thus critical work has, in the course of time, generally reduced the number of forms admitted as species. During the past twenty-five years, however, some critical studies combined with experimental work have revealed hitherto unsuspected genotypical variants, and there has been a tendency to describe all such genotypes as 'species'. This practice, which may be compared with that followed by the students of *Salices* or *Rubi,* leaves no place for 'varieties', and in my opinion it goes too far.

There is perhaps no reason why the concept of the species as applied to bryophytes should be any different from that applied to flowering plants unless it lies in the different relationship between sporophytes and gametophyte. In most ferns both gametophyte and sporophyte are independent, though the former, in the form of the prothallus, is reduced and plays a brief part in the life cycle. In flowering plants the gametophyte is no longer independent and is represented only by a short phase in the development of the egg-cell and the pollen-grain. In bryophytes, on the contrary, it is the gametophyte which is the independent plant, and the sporophyte, though sometimes complex in structure, remains attached to and dependent upon the gametophyte and has become the biological equivalent of a seed-vessel. The principal effect of this difference on the practice of systematy is to reduce greatly the part which is ascribed to

hybridisation as a source of variation. When an archegonium is fertilised by an antherozoid of another species, a hybrid capsule is produced, which of course remains attached to the unaltered parent plant. Such hybrid capsules have been frequently produced experimentally; they are generally sterile. They have also been recorded as occurring naturally, when they have been recognised by the occurrence together of both parents and the presence of abnormal capsules, variable and intermediate in character, or sterile, and usually mixed with normal capsules. A few such plants with hybrid capsules have been described as species. Hybrid capsules may well be much more frequent than we imagine, for they would obviously be very easily overlooked. When they produce fertile spores it is probable that in reduction division the genes of either parent will tend to segregate, but they might well produce some offspring of intermediate character. There would be no clear evidence in the field, however, to distinguish between these intermediate gametophytes of hybrid origin and genotypic variants of other kinds; it may well be therefore that hybridisation contributes far more than we suspect to variability in some groups of species. Experimentally it is possible to induce portions of a hybrid capsule to produce a protonema aposporically, and from this protonema a hybrid gametophyte can arise; it is not known whether any process akin to this ever occurs in nature.

While processes homologous with apomictic reproduction of flowering plants are not known among bryophytes, the same perpetuation of every genotypic variation is brought about by profuse vegetative reproduction, which may be effected not only by specialised gemmae but also by broken leaves, fragments of rhizoid, protonema etc.

Polyploidy seems to be relatively uncommon among bryophytes; haploid and diploid gametophytes are the most usual, though a few triploid and tetraploid species are known.

References.

INGHAM, W., 1908, Notes on Harpidia, *Revue Bryologique*, **35**, 8.

MÜLLER, K., 1947, Morphologische Untersuchungen zur Aufklärung einiger europäischer Lebermoose, *Beitr. zur Kryptogamenflora der Schweiz*, **10**, Heft 2.

——, 1951, Die Lebermoose Europas, in Rabenhorst's *Kryptogamenflora von Deutschland, Oesterreich und der Schweiz*, **6**, Ed. 3, Leipzig.

STEERE, W. C., 1947, A consideration of the concept of genus in Musci, *The Bryologist*, **50**, 247-258.

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In reply to Mr. J. D. LOVIS, Dr. JONES said that he did not wish to give an impression that spore characters should not be used in Bryophytes—on the contrary, he was quite willing to make use of them if they proved to be of value.

Dr. H. G. BAKER remarked on the infrequency of polyploids amongst Bryophytes. He said he had been impressed by the high chromosome numbers given in Vaarama's papers on Finnish material, and these numbers do not appear to be arrangeable on a basic number. Dr JONES replied to the effect that cytology provides only one set of characters out of many, and should not be over emphasised.

Dr. R. W. BUTCHER enquired whether the protonema offered characters of value. Dr. JONES said that there were small differences but generally speaking the characters of the protonema are common to those of the family rather than of species. Nevertheless it was possible with sufficient experience to recognise the protonema of some common species in the field.

THE IMPORTANCE OF FERNS TO AN UNDERSTANDING OF THE BRITISH FLORA

I. Manton (University of Leeds).

My subject has been chosen under pressure from my Department in Leeds who have begged me to give a general picture of the scheme of work into which the separate problems being developed by students and colleagues can be fitted in proper perspective. I was at first reluctant to do this owing to the extent of unpublished data, mostly compiled by other people, which it would be necessary to quote. It is, however, undoubtedly a subject relevant to the topic of this meeting and, on reflection, it became clear to me that by an audience of this kind the discussion of unpublished work would be unlikely to be abused.

I shall not, however, discuss the species concept as such, since whatever concept one uses it is an inescapable fact that behind the morphologically recognisable taxon there is always heterogeneity of some kind, except perhaps in the special case of obligate apomicts with no mutation rate, for which the species is, in fact, a clone. Elsewhere, as has been shown with dazzling clarity by the papers of Clausen, Keck and Hiesey in the *Experimental Studies in the Nature of Species* (1940-48), one must recognise the existence at least of physiological heterogeneity on which the main pressure of natural selection of biotypes operates, regardless of whether there is or is not a correlation between physiology and visible structural variation. Similarly, at the cytological level, one must recognise the existence of populations of more or less similar plants with different chromosome numbers or attributes, irrespective of the names by which one chooses to designate them. I do not therefore propose to discuss names, but rather to show the types of conclusions which can be drawn if the analysis of populations by cytological means is carried out on a large enough scale. The question of scale is, however, all-important and an alternative title for my talk might have been to the effect that you cannot understand either individual British species or the British flora as a whole if you confine your attention to this country. The next few minutes will explain this statement.

At the outset I must reluctantly remind my audience of the book I published in 1950 under the title of *Problems of Cytology and Evolution in the Pteridophyta*. It will be necessary to quote some essential facts from it although I will not recapitulate more than is indispensable to the understanding of the work which has been carried out since. Table 1 contains a list of the complexes which cytology had revealed among previously recognised British fern species.

TABLE 1.   SEXUAL 'SPECIES' WITH SEVERAL FORMS—EUROPE.

Dryopteris filix-mas agg.	$2n$	$4n$	
D. dilatata	$2n$	$4n$	
D. villarsii	$2n$	$4n$	
Asplenium trichomanes	$2n$	$4n$	
A. adiantum-nigrum	$2n$	$4n$	
Polypodium vulgare	$2n$	$4n$	$6n$
Cystopteris fragilis		$4n$	$6n$

Enumerating the facts for each more precisely, we have:—

1.   The *D. filix-mas* complex with two forms.   The diploid, subsequently named *Dryopteris abbreviata,* is characteristically a plant of screes and rocks in mountains.   The tetraploid *D. filix-mas* proper is a lowland plant, probably more abundant in individuals than the diploid in the country as a whole.

2.   The *D. dilatata* complex, likewise with two forms.   The tetraploid is abundant and widespread but the diploid has so far only been traced to one plant brought from Ben Lawers by Mr. A. H. G. Alston, though it will probably turn up elsewhere.   This subject is being studied by Mr. Stanley Walker.

3.   *D. borreri* (*D. paleacea*) is an obligate apomict (therefore not in the list) existing in two forms, diploid and triploid, which when hybridized with *D. filix-mas* (tetraploid) give the occasional single plants of tetraploid and pentaploid which have been found in Britain.

4.   *D. villarsii* is a tetraploid virtually confined to the limestone of the northern Pennines.   It is the sole type in Britain but it is listed here because all the plants reputed to be *D. villarsii* so far examined from Switzerland and the French Alps have been diploid.   There is therefore a problem as to its nature which takes one at once outside the British Flora.   This problem is being studied by Mr. G. Panigrahi.

5.   *Asplenium adiantum-nigrum* exists in two forms of which the common one is tetraploid.   A diploid has, however, been collected in Ireland by Miss M. G. Shivas, who went there to look for it and she is exploring the situation further.

6.   *A. trichomanes.*   The diploid of this turned up originally at Kew in a plant sent in from Wales.   Diploid populations have since been located not only in Wales but also in the Lake District by Mr. J. D. Lovis, who is studying the problem in detail and who hopes to extend the investigation to Scotland and Ireland. Diploid populations are not very extensive, and over most of the country only the tetraploid occurs.

7.   *Cystopteris fragilis* contains three spore forms and two chromosome numbers.   The commonest type is hexaploid with large spiny spores.   A tetraploid with smaller spiny spores has been found locally in Scotland and the Lake District and a tetraploid without spines on the spores (the var. or species *dickieana* of floras) was originally known wild near Aberdeen but has perhaps now been exterminated by collectors though,

fortunately for science, stocks have been kept alive in the gardens of amateur fern enthusiasts.

8. *Polypodium vulgare* also exists in three forms which can hybridize with each other. The commonest is tetraploid. The next commonest, especially in the western parts of the country, is the hexaploid. The diploid is local, being known only from special calcareous localities such as South Devon, Galway Bay and the Cheddar Gorge.

The existence of this kind of cytological variation has, of course, been known for a long time and in many countries other than Britain. Various comments have been made upon it from time to time in the literature and one in particular is perhaps important to recall, namely the correlation between percentage of polyploids and latitude, which was first suggested by Tischler. Hagerup and others, and elaborated in greater detail by Löve and Löve, whose table was quoted on p. 282 of Manton, 1950. These last authors worked with Monocotyledons and Dicotyledons on statistics drawn from a range of latitudes in Northern Europe (Spitzbergen and Iceland to Denmark and Schleswig Holstein). Rather similar figures were obtained in ferns by us when comparing Britain with Madeira, a flora which is, however, perhaps too small to be wholly significant. The interpretation of these statistics is the doubtful question and though some correlation with recent geological history involving glaciation is a possibility to be borne in mind, the correlation, even if it exists, is not a simple one.

This was clearly shown by our first considerable excursion away from the British flora when we examined the tropical flora of Ceylon. Some of the results of this were discussed at the Oxford Symposium of the Society for Experimental Biology in 1952 and others will be mentioned here. Table 2 shows a list of the heterogeneous "species" which we found in a mere five weeks of random collecting in Ceylon.

TABLE 2.   SEXUAL 'SPECIES' WITH SEVERAL FORMS—CEYLON.

Gleichenia linearis	$2n$	$4n$		
Thelypteris brunnea	–	$4n$	$6n$	
T. flaccida	$2n$	$4n$		
Cheilanthes farinosa	$2n$	$4n$		
Leptochilus lanceolatus	$2n$	$4n$		
Hypolepis punctata	$2n$	$4n$		
Asplenium lunulatum	$2n$	$4n$		
Pteris ensiformis	$2n$	$4n$		
Cyclosorus parasiticus	$2n$	$4n$		
Antrophyum plantagineum	–	$4n$	$6n$	
Athyrium macrocarpum	–	$4n$	$6n$	
A. solenopteris	–	$4n$	$6n$	
Asplenium affine	–	–	–	$8n$	$12n$

This list can only contain a small proportion of the variants actually present on the island because multiple cytotypes cannot be detected unless a species has been examined from at least two places and many of our species were only successfully examined once. In actual fact, as one knows from European experience, multiple types may escape detection in spite of very numerous random samples if one type is much more abundant than another, so that it is obvious that cytological heterogeneity must be extremely well represented in the Ceylon flora.

For polyploidy as a whole figures quoted in 1952 showed that not less than 60 per cent. of the Ceylon fern flora examined was polyploid, as opposed to 53 per cent. in Britain and 42 per cent. in Madeira. Moreover the grade of polyploidy often encountered was very much higher than in Europe, a fact which was discussed in 1952 in a way which need not be repeated here, except to the extent necessary to point the moral that polyploidy as such cannot possibly be either a simple climatic response to latitude or a direct adaptation to the Ice Age as has sometimes been suggested in all seriousness by students of European floras.

What then can we infer? And what further action can we take? There are two lines of enquiry which can be applied to our British (or any other) cytotypes which can give important further insight if they are applied on a sufficient scale. These are, firstly, the study of geographical distribution over as large a part of the earth's surface as possible and, secondly, the study of genetical affinity as revealed by chromosome pairing in hybrids.

The first, geographical distribution, is the more difficult to work out with any completeness since the facts must necessarily be based in the first instance on new collecting. They can never be ascertained accurately from the literature owing to widespread confusion of the cytotypes both with each other and with other taxa. Thus on two occasions when floristic lists citing *Dryopteris filix-mas* in Madeira and Ceylon respectively were followed up, we encountered apogamous cytotypes, diploid in Madeira and triploid in Ceylon, having a general resemblance to *D. borreri* and not to *D. filix-mas* at all. On the other hand, herbarium studies can yield reliable results if it has been possible at the outset to correlate morphological criteria with the cytology. An example of a favourable case in which a herbarium has been so used is in Mr. Panigrahi's work on the tropical *Cyclosorus parasiticus* complex quoted in Table 2. *C. parasiticus sensu lato* is a well known taxonomic tangle of numerous and common species spread all over the oriental tropics and extending as far west as Madeira. Many collections from Malaya, Ceylon, Africa and Madeira had proved to be tetraploid, but one diploid specimen was detected in Ceylon. This proved to correspond, on herbarium characters, to a much less common species, *C. repandulus,* previously only known from six gatherings scattered in New Guinea, Malaya, and Madagascar but not previously known from Ceylon itself. The facts at once sug-

gest an analogy with diploid *D. dilatata* in Britain, and the genetical behaviour has indeed proved to be similar.

The weakness of herbarium studies is that, especially in remote regions, insufficient opportunity may be afforded of checking the determinations by direct cytological analysis. For this reason we have preferred, in dealing with our own flora, to compile our geographical information directly from the cytological records, even though this, at the moment, precludes the possibility of drawing maps in which the distributional areas detected are delimited by accurate lines. In view of this limitation we may list the available data for the non-British ranges of the various cytotypes previously enumerated as follows:—

1. *D. filix-mas.* The tetraploid is widespread in Europe. We have no records for America and most of the extra-European records which we have followed up (e.g., Madeira and Ceylon) have been attributable to other species. The diploid (*D. abbreviata*) has been found in the Auvergne, but personal communication from Dr. A. Löve reports that this is the only type known to him in Iceland, a fact which may be highly significant.

2. *D. dilatata.* The tetraploid is abundant in Britain and extends to the edge of Scandinavia where we found it on Björkö in the outer archipelago near Stockholm. Over most of the Scandinavian peninsula, however, only the diploid is recorded and we have also a diploid from Greenland. In Switzerland diploids occur at a high altitude (cf. Manton, 1950) and they are widespread in North America (cf. Manton and Walker, 1953).

3 *D. borreri.* The diploid in Madeira and the triploid of the same or a related species in Ceylon mentioned above are the only non-European records known to us. Otherwise the facts, as in Manton (1950), indicate that triploids are the commonest type in Europe, though they may not be uniform genetically owing to the possibility of frequent re-synthesis from the diploid by crosses with the sexual species.

4. *D. villarsii.* Nothing to add to the statement on p. 91.

5. *Asplenium adiantum-nigrum* as studied by Miss Shivas is diploid in Portugal, in the Mediterranean basin, in Madeira and in parts of Ireland. It is tetraploid in its one American locality and also tetraploid in Kenya.

6. *Asplenium trichomanes* has been studied in detail both by Mr. Lovis and by Dr. D. Meyer in Germany. Diploids are abundant in north-eastern Germany and in Norway. They are reported from Canada by Britton (1954) and have been detected by Mr. Lovis in recent collections from the Himalayas and Australia. Tetraploids are present both in Europe and America and perhaps elsewhere.

7. *Cystopteris fragilis.* The tetraploid with smooth spores has been found in Northern Europe and in Greenland. The tetraploid with spiny spores is the dominant type in Northern Scandinavia, in east and west Canada, and one plant has been sent

to us from Australia. The hexaploid occurs in southern Scandinavia and across Europe as far as Madeira. It has not yet been found in America.

8. *Polypodium vulgare.* Most parts of Europe are dominated by the tetraploid, though the hexaploid is abundant along the Atlantic seaboard from Portugal to Denmark and probably S. Norway. It also occurs in the Alps. The diploid has a Mediterranean distribution closely resembling that of *Asplenium adiantum-nigrum,* though it penetrates northward in favoured localities such as the Rhone Valley. In America diploids occur along both the eastern and western seaboards, and there is a tetraploid of probably separate and local origin on each side of the continent (cf. Manton and Shivas, 1953; Manton, 1951).

Focussing attention for the moment on Europe and summing up these various results, there are two important generalisations which arise from them. On the one hand, it is clear that in every case it is the higher numbered cytotype which is the commoner one in the particular latitudes which cross the British Isles. Secondly, in every case the lower numbered cytotype has a restricted, or even discontinuous, distribution within Great Britain, while outside it, at least as regards Europe, they all fall into one of two alternative distribution patterns, *viz.*: two (*Polypodium* and *Asplenium adiantum-nigrum*) show Lusitanian affinities, having a continuous range for their diploids in the Mediterranean region; the remainder, in so far as the facts are known, *i.e.* certainly for *Dryopteris dilatata* and *Cystopteris fragilis* and probably for *D. filix-mas* and *Asplenium trichomanes,* have boreal affinities with a continuous range for the low numbered cytotypes in the latitude of northern Scandinavia.

Before interpreting these facts we need to add the evidence concerning phyletic relationship between the cytotypes which is given by chromosome pairing. For this it is convenient to quote a list (Table 3) reproduced in Manton, 1953, which sums up the facts not only for the cytotypes under discussion but also for a number of well marked pairs of generally accepted species with the $2n : 4n$ cytology.

TABLE 3. CHROMOSOME PAIRING IN TRIPLOID FERNS
(*not apogamous*).

s denotes a synthesized hybrid, the others are wild.
Many trivalents:
s *Osmunda regalis* autotriploid
n pairs + *n* univalents:
    Asplenium trichomanes ($2n$) × *septentrionale*

> $A.$ $adulterinum$ × $viride$
> s $A.$ $adiantum$-$nigrum$ $2n$ × $4n$.
> $Polystichum$ $lonchitis$ × $aculeatum$
> s $P.$ $setiferum$ × $aculeatum$
> $Woodsia$ $ilvensis$ × $alpina$
> s $Dryopteris$ $filix$-mas × $abbreviata$
> s $D.$ $dilatata$ $2n$ × $4n$

$3n$ univalents:

> $Polypodium$ $vulgare$ $2n$ × $4n$

The uniformity of pattern is impressive.   We have only one case ($Polypodium$) in which our local diploid does not show signs of close genetical affinity with the tetraploid hybridising with it.   All the others (and $Polypodium$ also when crossed with some American diploids) are manifestly related to each other in a manner suggesting that the tetraploids are allopolyploid, in each case with the genome of the diploid used as one ancestral type.

This is not a result which would necessarily be repeated in every small area which one cared to examine, for we have already reason to think that, both in Ceylon and in eastern North America (unpublished work of Mr. S. Walker on the $D.$ $spinulosa$ complex), hybrids showing complete failure of chromosome pairing are relatively far commoner than here.   It is therefore one of the local characteristics of the west European flora.

The interpretation, for Britain, would appear to be as follows. Our flora seems fairly recently to have been enriched by a large number of tetraploid forms well adjusted to our present climate and which are still closely akin to diploid components in our flora.   In almost every case, however, we have only been able to trace one diploid ancestral type within our area and moreover these diploids, when closely examined, show distributional characteristics suggesting relict status in some kind of relation to recent glaciation.   The Lusitanian group may perhaps be the oldest, since they are southern biotypes which could have survived the glacial periods, or part of these, in the Mediterranean area, but which cannot now spread very effectively away from this area, since their physiological powers of adjustment are now too limited.   The boreal group, on the other hand, could have entered Britain more directly in relation to the colder climatic periods, since when they seem to have persisted in mountains. All three elements, however (the tetraploids and the boreal and Lusitanian diploids) have quite definitely entered this country from outside; they have not been formed here.   They have presumably come to us via the European mainland, but it is doubtful whether any of them were formed even there, for we have clear evidence in several cases, $e.g.$ $Polypodium,$ $D.$ $dilatata,$ $Cystopteris,$ $Asplenium$ $trichomanes,$ of a circumpolar range

among the ancestral types which, within Britain itself, seem to be relicts.

As a small island on the edge of a large land mass such a history is not unexpected, but the study of the continental mainland immediately adjacent to us will not carry us much further. Continental Europe, like Britain, reflects the marks of recent gross changes of climate, but not many components of our present flora have been originated there (hexaploid *Polypodium* is the best known case where this *has* happened). It is possible that, with further search, a few more parental types will come to light, but, as things stand at present, the rule, that one only has been found of the necessary two parents of almost all the allopolyploid immigrant species detected, applies as much to Europe as to Britain. If it were only a single case, this would be of no consequence and one could postulate extinction of the second parent in explanation. Wholesale extinction of one parent only in species after species is, however, more difficult to accept and a more plausible explanation is that they must be sought for elsewhere.

If we look at the map of the world even Europe is a very small part of the continental land masses of the northern hemisphere. Of far greater geographical extent are North America and Asia, and both these are relevant to us. North America, however, is intrinsically unlikely to solve our whole problem owing to its position at the opposite end to ourselves of the land mass joined by "Beringia" (cf. Hultén, 1937). Asia is intrinsically likely to be far more important, both as the possible cradle for our tetraploid immigrants and also as the place which may still, perhaps, harbour their missing diploid ancestors.

Further progress in our understanding of the British Flora therefore requires rather urgently some botanical penetration of the Iron Curtain. This perhaps exemplifies as well as anything could do the thesis with which my talk began.

REFERENCES.

Hultén, E., 1937, *Outline of the history of the arctic and boreal biota.* Stockholm.

Manton, I., 1950, *Problems of cytology and evolution in the Pteridophyta.* Cambridge.

——, 1951, The cytology of Polypodium in North America, *Nature*, **167**, 37.

——, 1953, The cytological evolution of the fern flora of Ceylon, in *Symposia of the Society for Experimental Biology*, **7** (*Evolution*).

Manton, I. & Shivas, M., 1953, Two cytological forms of Polypodium virginianum in Eastern North America, *Nature*, **172**, 410.

Manton, I. & Walker, S., 1953, Cytology of the Dryopteris spinulosa complex in eastern North America, *Nature*, **171**, 1116.

Meyer, D., 1952, Untersuchungen ueber Bastardierung in der Gattung Asplenium, *Bibliotheca Botanica*, **30**, Heft 123.

Dr. W. B. TURRILL said that it had been assumed that tetraploids have arisen from diploids, but could it not happen that diploids arose from tetraploids and other polyploids?

Prof. MANTON replied that this was a theoretical possibility but the available evidence points in the other direction.

Prof. T. G. TUTIN said that *Dactylis glomerata* provided a good example of autopolyploidy, and Prof. MANTON said that *Biscutella* was another good example.

Dr. E. F. WARBURG enquired whether the lecturer had found both parents in any of these polyploid ferns. Prof. MANTON replied that she had—in *Polystichum aculeatum*.

THE PROBLEM OF ASPLENIUM TRICHOMANES
(Exhibit)

J. D. Lovis (University of Leeds).

Asplenium trichomanes L., a common and familiar fern in Britain, is very widely distributed over the surface of the world, occurring in upland districts in temperate regions of every continent.
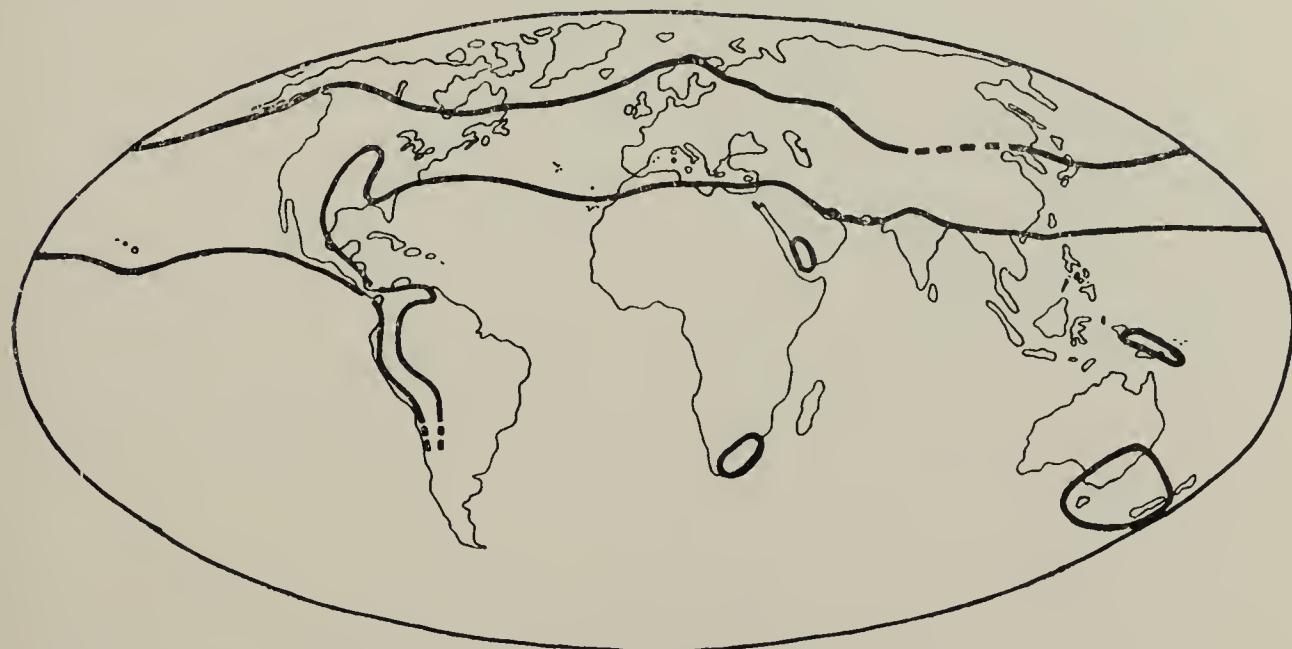
Fig. 15.

Distribution of *Asplenium trichomanes* agg., compiled from floras and the herbaria at Kew and the British Museum.

Professor I. Manton (1950) discovered that two cytological forms of *A. trichomanes* occur in Britain. Of these two forms, the diploid (with $2n = 72$), was detected only from North Wales, and the Auvergne of France. The tetraploid ($2n = 144$), was found to be common in Britain.

Recently, these two forms have been studied in some detail by myself under the guidance of Professor Manton. Both diploid and tetraploid *A. trichomanes* have been found to be widespread within the range of the aggregate species. The diploid has been identified from other localities in Europe, i.e., from Germany (Meyer, 1952), Switzerland and Norway. It has also been found in Canada (Britton, 1953), from several localities about the Himalayas, and also from Australasia. The tetraploid is known certainly from Canada (Britton, *op. cit.*) and Europe, and probably ranges more widely through the Northern Hemisphere.

In Britain the diploid is much the rarer form; as yet it has been found only in North Wales and the Lake District, although

it is most probable that it occurs in Scotland and the Border Country. It does not seem to have any close edaphic preference. This was found to be particularly clear in Norway, where it displays rather catholic tastes, occurring both on base-poor rocks and on mica-schist and "olivinstein", the last a rock of the serpentine group. It will probably transpire that the restriction of the diploid in Britain to submontane levels in mountainous districts is determined by the limits of its climatic tolerance.

In contrast, the tetraploid is characteristically, though not exclusively, a limestone fern, and has been able to extend its range eastwards across England into the lowlands, following the construction of mortared walls.

Both diploid and tetraploid are highly fertile. Meiosis is regular in both, 36 bivalents being formed in the diploid, and 72 bivalents in the tetraploid. No sign of multivalents has so far been found in the tetraploid. The diploid and tetraploid are genetically isolated by sterility in the triploid F_1 hybrid, and therefore represent distinct coenospecies according to the definition of Clausen, Keck, and Hiesey (1945). A wild triploid hybrid collected near Dolgelly in September 1952 shows highly irregular meiosis, and complete abortion of its spores. A preliminary analysis of chromosome pairing in this plant showed a rather complex situation. Two of the three genomes present pair, but not quite completely. 34 or 35 associations are formed, of which 1-4 are trivalents. Between 34 and 37 chromosomes remain unpaired, and consequently appear as univalents.

It is clear from this result that diploid and tetraploid are closely related, though precisely how remains open to question. Breeding work now in progress may help us to determine whether perhaps the tetraploid is an ancient autotetraploid which has so evolved as to have lost the power of multivalent formation, or else is an allotetraploid with our known diploid as one of its parents.

Before considering morphological differences between diploid and tetraploid *A. trichomanes,* it must be emphasised that a basic difficulty in fern taxonomy is that their reproductive structures present very few characters for use by the taxonomist, in comparison with the details of floral structure available in the majority of flowering plants. Many vegetative characters are considerably affected in expression by environmental influences, but fern taxonomists are frequently forced to use them to distinguish species.

It is not easy to distinguish diploid and tetraploid *A. trichomanes* on the basis of gross morphology alone. There are no obvious *qualitative* differences, such as sorus position or pinnashape, which serve to distinguish other species within the *A. trichomanes* group.

The fronds of *A. trichomanes* are even more susceptible than those of most ferns to modifications by environmental conditions. Scatter diagrams which illustrated this plasticity in frond form

Plate II.
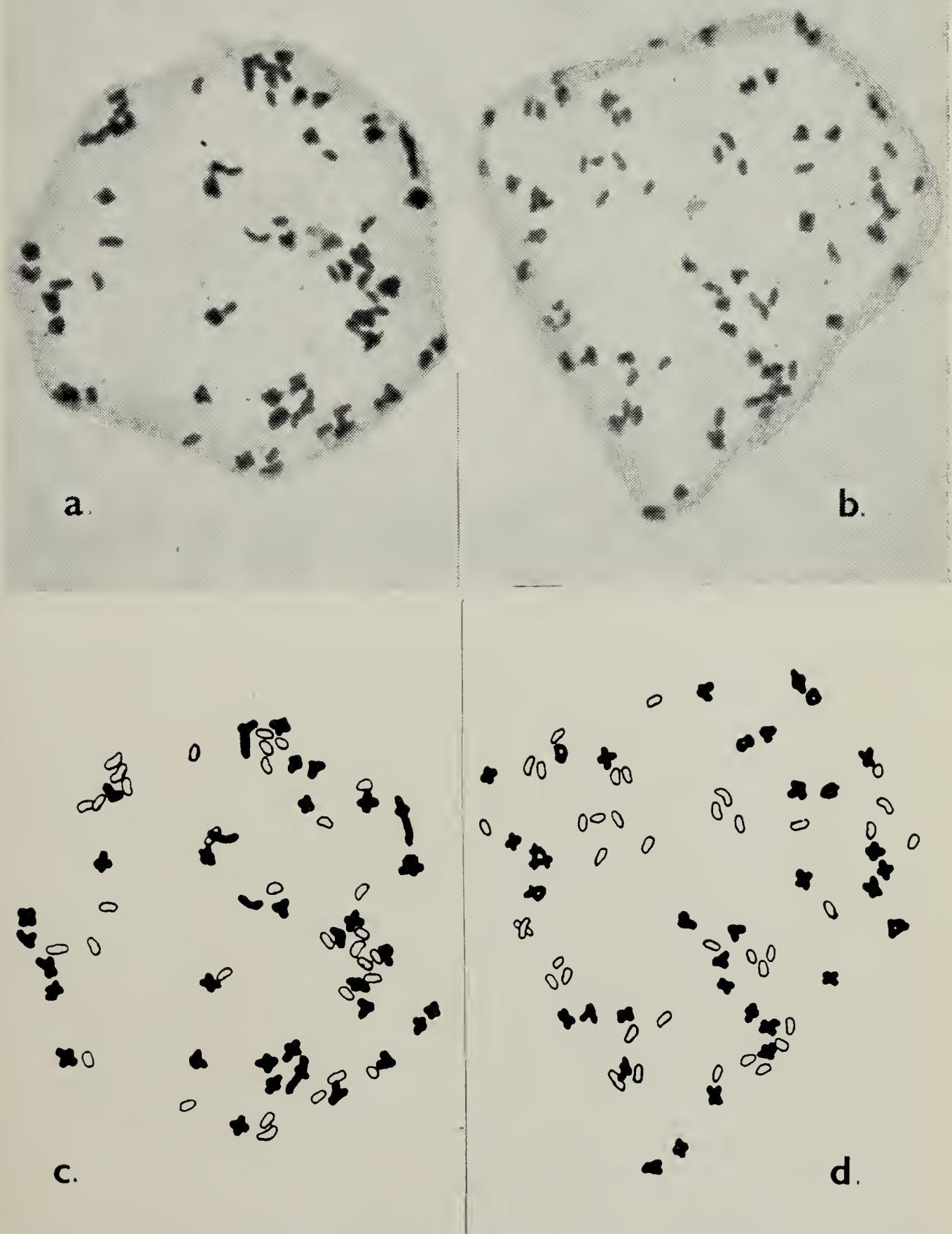
Asplenium trichomanes agg. Figs. *a* and *b*, permanent acetocarmine prepara-
tions of spore mother cells in meiosis from a wild triploid hybrid found near
Dolgelly, Merioneth. Magnification ×1000. Figs. *c* and *d*, explanatory diagrams
of the preceding showing univalents in outline and pairs and trivalents in black
There are four trivalents in fig. *c* but only one in fig. *d*

were exhibited at the Conference, and a sample is included here (fig. 16). These scatter diagrams show that both length and area of pinnae, considered in relation to the distance between pinnae, tend to be greater in the tetraploid than in the diploid, although even when single plants are considered there is an overlap, which makes this character valueless as an absolute criterion.
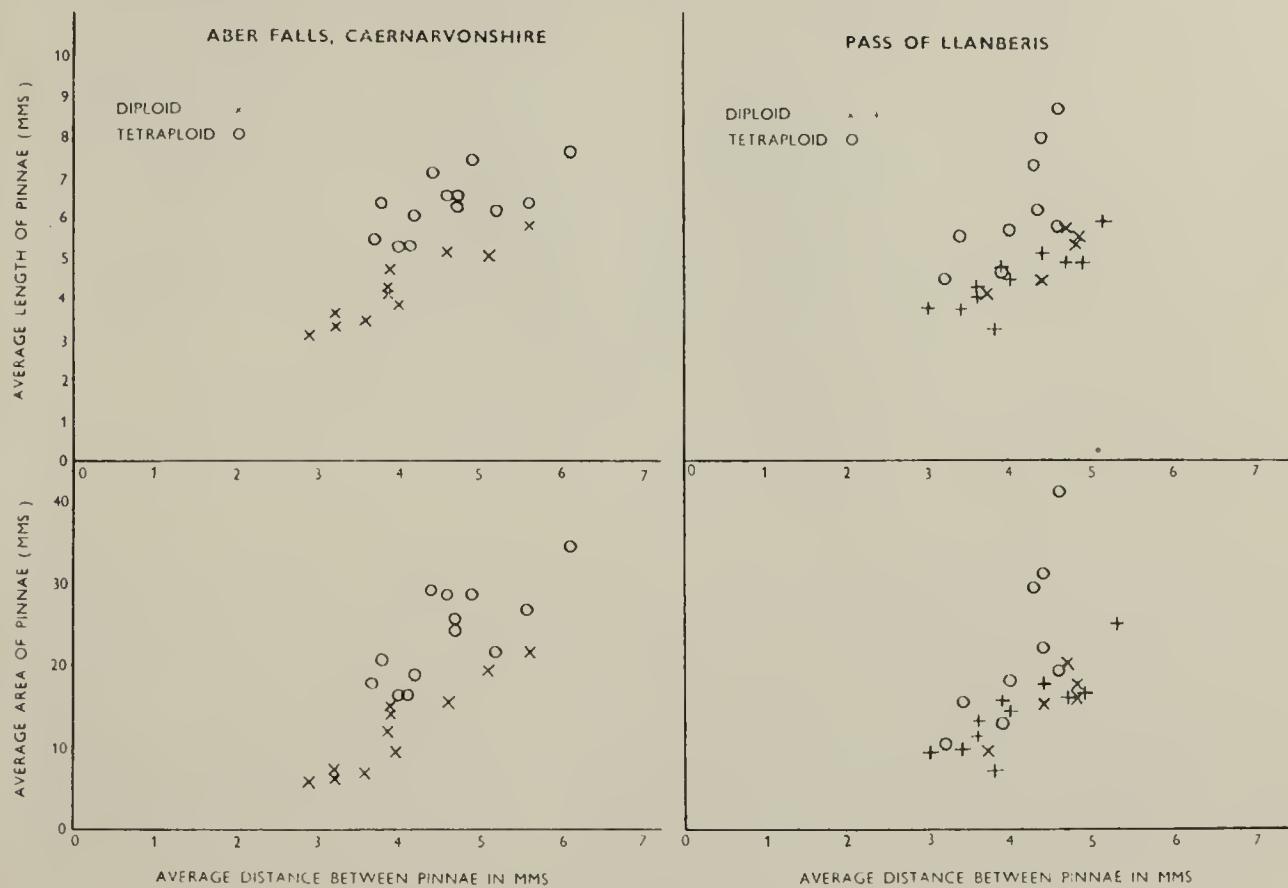
Fig. 16.

Scatter diagrams to show pinna size (length and area) plotted against pinna-spacing in individual plants of diploid and tetraploid from two localities. Each entry represents the average for the middle ten pinnae of one frond, the same fronds being used for both area and length measurements. Only one plant of each type is represented in the diagrams for Aber Falls but those for Llanberis contain entries from two diploid plants and one tetraploid.

It is possible to distinguish diploid and tetraploid satisfactorily on the basis of spore size. The standard used has been at least 50, preferably 100, determinations of exospore length for each plant. Average spore lengths in diploid plants range from 29-33μ; in tetraploid plants from 35-42μ. A typical histogram derived from spore measurement of a diploid and a tetraploid plant from the same locality is illustrated here (fig. 17).

Other characters which are usually affected quantitatively by increase in level of polyploidy, e.g., stomata size and epidermal cell size, would probably also serve as satisfactory criteria for distinction, but the measurement of spore size is more convenient in practice, especially for the determination of herbarium material.

Conclusion.

It is already clear that diploid and tetraploid *Asplenium trichomanes* display the fundamental characteristics of two dis-
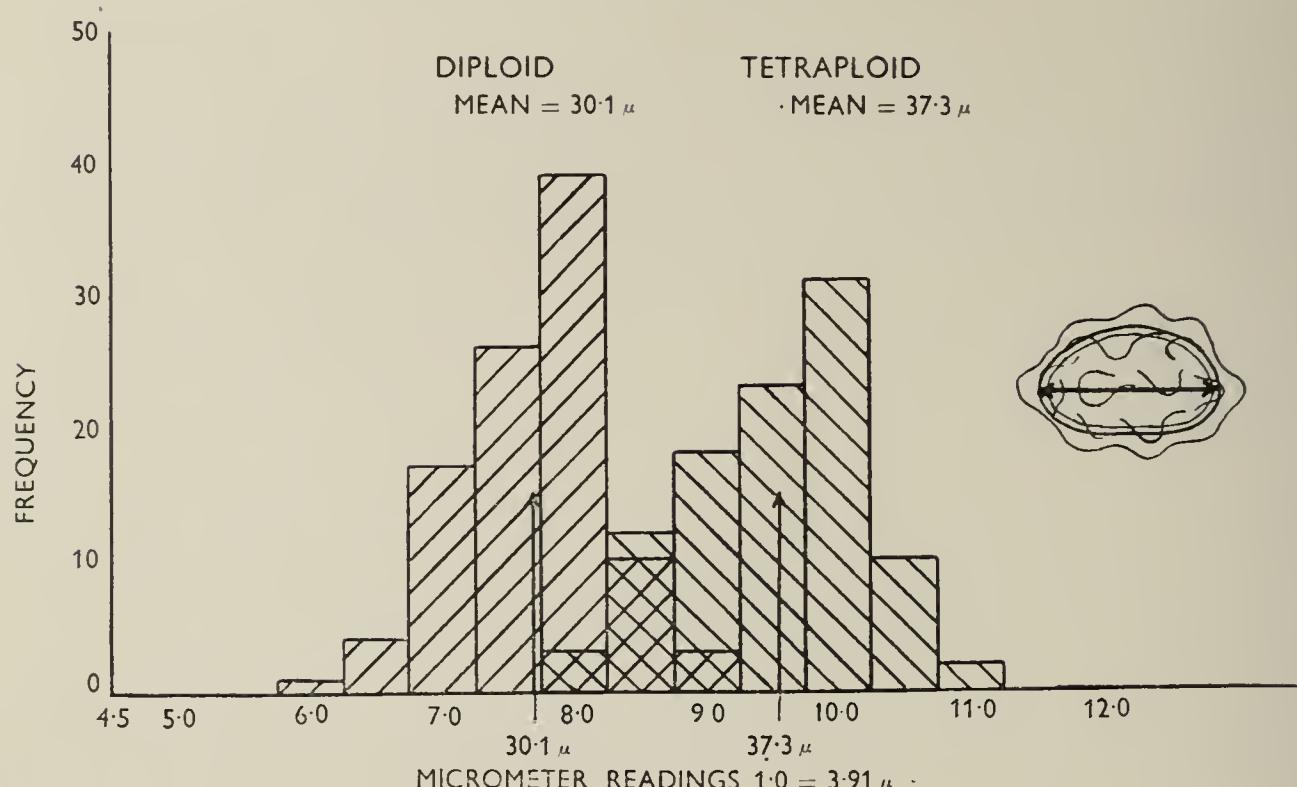
Fig. 17.

Spore length measurements (taken as in inset diagram) of one hundred spores from each of a diploid and a tetraploid plant from the pass of Llanberis.

tinct natural species: 1, *they are reproductively isolated*; 2, *possess distinctive geographical and ecological distributions*; and 3, *can be distinguished morphologically* (although admittedly not with ease).

It is nowadays generally agreed that the genetic criterion is of primary importance in the delimitation of specific limits within a group. Nevertheless, there is still a tendency to disregard, on considerations of practical convenience, natural species which cannot be distinguished with certainty without recourse to the microscope, and which therefore cannot be determined with complete confidence in the field.

But the lack of easy and convenient morphological distinctions should not be an inducement to ignore evidence that what has previously been regarded as one clearly defined species in Floras and herbaria is in fact composed of two separate natural species. Numerous examples of polyploid series within familiar Linnean species are now known, sufficient for the question of the status of the units within these complexes to represent a taxonomic problem which urgently requires clarification.

REFERENCES.

Britton, D. M., 1953, Chromosome studies on ferns, *Am. J. Bot.*, **40**, 575-583.

Clausen, J., Keck, D. D. & Hiesey, W. M., 1945, Experimental Studies in the nature of species, *Publ. Carneg. Instn.*, no. 564.

Manton, I., 1950, *Problems of Cytology and Evolution in the Pteridophyta.* Cambridge U.P.

MEYER, D. E., 1952, Untersuchungen ueber Bastardierung in der Gattung Asplenium, *Bibliotheca Botanica*, **30**, Heft 123.

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Prof. D. H. VALENTINE enquired whether *A. trichomanes* as found in Australia differed from the European plants. Dr. R. MELVILLE remarked that the distribution of the aggregate species extended to Tasmania and New Zealand.

(Since this paper was read to the Conference, Brownlie (1954, *Trans. Roy. Soc. N.Z.*, **82**, 665-666), has recorded that in New Zealand *Asplenium trichomanes* has $2n=108$, i.e., is hexaploid. Further comparative studies are now being made which include this most interesting plant. J. D. LOVIS. June 1955.)

THE TWO SUB-SPECIES OF ASPLENIUM ADIANTUM-NIGRUM L. IN BRITAIN
(Exhibit)

Miss M. G. SHIVAS (University of Leeds).

A plant of *Asplenium adiantum-nigrum* ssp. *onopteris* (L.) Heufl. was collected in July 1951 at Glencar, Co. Kerry. On investigating this plant cytologically, it proved to be a diploid.

Fig. 18 shows a silhouetted frond of this plant with one of a tetraploid plant of *A. adiantum-nigrum* L. ssp. *adiantum-nigrum* for comparison. The tetraploid also came from an Irish locality, Graiguenamaugh, Co. Carlow.

Fig. 18. *Asplenium adiantum-nigrum* L.
(a) ssp. *adiantum-nigrum*. Graiguenamaugh, Co. Carlow. Tetraploid.
(b) ssp. *onopteris* (L.) Heufl. Glencar, Co. Kerry. July 1951. Diploid.

THE DRYOPTERIS SPINULOSA COMPLEX IN EUROPE

(Exhibit)

S. WALKER (University of Liverpool).

In modern floras the *D. spinulosa* complex is represented by three recognised species and the hybrids between them. These may be listed (Christensen, 1905-6, 1906-12):

(i) *Dryopteris cristata* (L.) A. Gray.

(ii) *Dryopteris spinulosa* (Müll.) Watt.

(iii) *Dryopteris dilatata* (Hoffm.) A. Gray.

(iv) × *Dryopteris uliginosa* (Newm.) Druce (=*D. cristata* × *D. spinulosa*).

(v) *D. dilatata* × *D. spinulosa*.

D. cristata, *D. spinulosa* and *D. dilatata* were first given separate recognition during the latter half of the 18th century, but many times since they have been considered merely as sub-species or as varieties of a single species (Newman, 1844 and 1865; Druery, 1912). The three species differ morphologically (viz. pinnation, shape of frond, rhizome habit and colour of ramenta) and in habitat, but are cytologically uniform; each is tetraploid with $2n = 164$ (Manton, 1950).

Cytogenetical investigation has confirmed *D. cristata*, *D. spinulosa* and *D. dilatata* as distinct species, each being an allo-tetraploid, but interrelated by common ancestral diploids. One of these ancestors is at present represented in Europe by a diploid form of "*D. dilatata*" and found in Norway, Sweden, Switzerland and Scotland.

It is suggested that the diploid "*D. dilatata*" should be recognised as a distinct species, though morphological differences from tetraploid *D. dilatata* are not always evident since the tetraploid itself is very polymorphic. The degree of pinnation and shape of the basal pinnae are a good guide but probably the final distinction will rest with spore characters.

This work will be published in detail elsewhere. (See *Watsonia*, **3**, 193-209.)

LITERATURE CITED.

CHRISTENSEN, C., 1905-6, *Index Filicum*. Copenhagen.

——, 1906-12, *Index Filicum, Supplementum I*.

DRUERY, C. T., 1912, *British Ferns and their varieties*. London.

MANTON, I., 1950, *Problems of Cytology and Evolution in the Pterido-phyta*. Cambridge.

NEWMAN, E., 1844, *History of British Ferns*, Ed. 2. London.

——, 1865, *History of British Ferns*, Ed. 4. London.

Mr. J. OUNSTED asked whether a hybrid was known between *D. cristata* and *D. dilatata*. Dr. WALKER replied that this hybrid was not known to occur in nature.

Dr. R. MELVILLE enquired whether Dr. Walker had any evidence of a cline in diploid *Dryopteris*. For comparison he instanced *Ulmus coritana*, where the two ends of the cline might be taken for different species. Dr. WALKER replied that he did not know of a cline but had in mind the possibility that two diploids, which were very different morphologically, might have a common ancestor.

The Rev. E. A. ELLIOT asked what was the relationship of *D. aemula* to the complex which had been discussed. Prof. MANTON said that it was diploid. She had asked Dr. R. Lloyd Praeger whether in his wide experience of this species in Ireland he had seen anything likely to be a hybrid of *aemula*, but he replied that he had not.

CALTHA IN THE BRITISH FLORA

(Exhibit)

G. PANIGRAHI (University of Leeds).

Caltha palustris L. has posed a serious problem to taxonomists over the last two hundred years and, more recently, the genus has proved to be very complex cytologically. Our present knowledge of the somatic numbers of chromosomes of non-British materials of *Caltha* reveals that there is an aneuploid series including polyploid types with a basic number of 8 (*cf.* Leoncini, 1951).

After Linnaeus founded the species *Caltha palustris* in 1753 (Linnaeus, 1753), Miller (1768) in this country, was the first to propose *Caltha minor* for plants having round, crenate, heart-shaped leaves and a smaller flower as a separate species from *C. palustris* also possessing round, crenate leaves but with a larger flower. All subsequent authors, however, have treated *C. minor* Mill. as a mere variety or subspecies of *C. palustris* L. Forster (1807) considered a plant sent to him by Mr. J. Dickson from Scotland to be distinct from *C. palustris* and described a new species, *C. radicans,* having triangular, crenate leaves and rooting at the nodes of the aerial, procumbent stems as its chief distinguishing characters. Beeby (1887) proposed a variety *zetlandica,* for plants of *C. palustris* from the Shetland Islands which had radical leaves like those of *Caltha palustris* but rooted at the nodes like *C. radicans.* Later authors have considered Beeby's *zetlandica* to be a form or variety of *radicans* on the basis of the rooting nodes.

Thus British taxonomists have recognised the existence of at least three taxa, *viz.* lowland *palustris,* montane *minor* and Scottish *radicans.* They differ as to whether *radicans* is a separate species or a variety of *palustris* L. and whether *minor* is to be treated as a variety of the lowland *palustris* or as a subspecies including *radicans.* In this last treatment, Beeby's *zetlandica* is submerged in the variety *radicans* (cf. Clapham 1952).

The morphological features believed to separate these taxa refer mostly to vegetative characters. They appear to be quantitative rather than qualitative in nature and are subject to considerable variation.

It appears that, whether *radicans* is treated as a distinct species or simply as a variety of *Caltha palustris,* there is general agreement that material exactly matching Forster's description and drawing is rare in the British flora. There is greater inclination amongst those who have studied the species to use rooting at the nodes of the aerial procumbent stems as the chief distinguishing feature of *radicans* rather than leaf shape. Praeger (1934-35,

1951), who considers both these features important, has proposed additional characters to distinguish *C. radicans* from *C. palustris* in Ireland. There, according to him, *C. radicans* of Forster represents a mass of hybrids between the typical *C. palustris* and an extreme form, which he refers to as *C. radicans* sensu Babington. He not only considered that the true *radicans* "was being hybridised out of existence" in Ireland, but believed that the "varieties" of *C. palustris* which appear in the British and continental floras also owe their origin to this kind of hybridisation.

Counts of the chromosomes in the root tips of some British collections have now been made. Although based on a single plant in each case, they are of considerable cytological interest in recording the highest number of chromosomes for *Caltha* so far reported, and are tabulated below.

Cytology of *Caltha* in the British Flora.

Names of taxa	Locality	2n
1. *C. palustris* subsp. *palustris*	Golden Acre (near Leeds, West Yorks.)	56
	Dungeon Ghyll (Westmorland)	56
	Kettlewell (West Yorks.)	c. 80
2. *C. palustris* subsp. *minor* var. *minor*	Bow Fell (Westmorland)	64
3. *C. palustris* subsp. *minor* var. *radicans*	Whiteness Parish Mainland, Shetland Isles	72

The present investigation showed that plants representing the three taxa are self-incompatible and that agamospermy does not appear to occur as a reproductive method in *Caltha*. With only two exceptions, every attempted crossing within subsp. *palustris* and also those between *palustris* and each of the varieties, *radicans* and *minor,* resulted in the development of mature follicles with abundant seeds in them. In spite of the good seed-setting, however, the percentage germination of these seeds is rather low and shows a wide range of variation. Study of the relatively few hybrids obtained will be extremely interesting.

In the material which we have examined, more often than not the cauline leaves of *Caltha palustris* are deltoid or deltoid-reniform, whereas the radical leaves of the same plant are cordate with

basal lobes which may be overlapping or parallel to the petiole. Nevertheless the variability of the angular divergence between the basal lobes of radical leaves, their size and crenations of their margins, may be striking even in one small population of the lowland form of *C. palustris*. Occasionally individual plants having deltoid radical leaves are met with in populations of subsp. *palustris* where there is no likelihood of *radicans* having occurred, at least in recent times.

Again, rooting at the nodes of aerial stems is not restricted to *Caltha radicans*. Some of the lowland *palustris* from Leeds and Scotland have rooting nodes although possessing cordate radical leaves.

Lastly, three of the other characters listed by Praeger (1934-35) (*viz.* unbranched rootstock, short lowermost internode and small flowers) also appear to go together in the montane var. *minor,* which, however, usually possesses heart-shaped radical leaves and shows rootless nodes, both in its natural habitats and in garden culture.

It must, therefore, be concluded that each particular morphological character is unreliable on its own for the separation of species on British material of *Caltha*. Only future studies can show whether there are significant statistical differences between populations in respect of a number of these characters taken together.

Does, then, cytology provide any solution to this species problem? Frankly, it does not. *Caltha* is characterised by the possession of an extensive aneuploid series. None of the taxonomic units has a constant chromosome number of its own. It also appears that there is no correlation of the karyotypes with latitude or with the geographical distribution of the species in general.

This lack of correlation between cytology and geography coupled with the great morphological variability of the group, all suggest that for the present *Caltha palustris* L. may best be treated as a polymorphic species with a complex network of interrelated forms in a polyploid and aneuploid series.

Despite the difficulty of reconciling morphology, cytology and geography, however, ecogeographical races within this complex do seem to exist. Hultén (1950) and some American and Canadian authors generally consider that *radicans* is a more northern race and is arctic-circumpolar in distribution. On the other hand *palustris* is more southern and is boreal-circumpolar in distribution. In subalpine situations in England one finds genetically dwarfed forms, which are contained in subsp. *minor*. Those who would investigate *Caltha* in the British Isles do so in a region of overlap between the northern *radicans* and the more southern *palustris*. This position, which is so difficult for the morphologically minded taxonomists, is stimulating to the student of populations and evolution.

On this ecogeographical basis, then, must rest the justification
for continuing to pursue a quest for the means of separating at
least three taxa (races) in the British flora despite possible blend-
ing between them.   There is slight evidence that genetical dis-
harmony occurs between these forms.   Even if this be true,
however, obligate outbreeding, coupled with the long life of
individual *Caltha* plants (as long as 50 years, according to Syme,
(1863) and the ease of vegetative reproduction, militate against a
sharp separation of taxa.

Grateful thanks are due to Dr. H. G. Baker for his encourag-
ing guidance and supervision.

Literature cited.

Beeby, W. H., 1887, *Scot. Nat.*, *N.S.*, **3**, 21-22.

Clapham, A. R., 1952, in, *Flora of the British Isles.* London.

Forster, T. F., 1807, *Trans. Linn. Soc. Lond.*, **8**, 323-24.

Hultén, E., 1950, *Atlas of the distribution of vascular plants in N.W.
    Europe.* Stockholm.

Leoncini, M. L., 1951, *Caryologia*, **3**, 336-50.

Linnaeus, C., 1753, *Species Plantarum*, **1**, 558. Holmiae.

Miller, P., 1768, *Gard. Dictionary*, ed. 8. Yverdun.

Praeger, R. L., 1934-35, *Irish Nat. J.*, **5**, 98-102.

——, 1951, *Proc. Roy. Irish Acad.*, **54**B (1), 6.

Syme, J. T. B., 1863, *English Botany*, ed. 3, **1**, 49-53. London.

STELLARIA NEMORUM L. AND THE SPECIES CONCEPT

Ch. H. Andreas (University of Groningen).

The Species Concept in its relation to the British Flora being the subject of the lectures at this conference, I shall try to say a few words using *Stellaria nemorum,* a species common to both Great Britain and the Netherlands, as an example. It is necessary to state that in the early part of this paper I am using the name in a wide sense, for a closer study of *Stellaria nemorum* in the Netherlands in recent years has shown that we should divide the species into two taxa. The decision as to the taxonomic rank of the two divisions justifies the title of my paper.

Stellaria nemorum is a plant of rare and local occurrence in the Netherlands. With only few exceptions, known from herbaria of earlier years and which I shall not discuss today, it is restricted to the eastern part of the country, mainly to the very south-east (southern part of the province of Limburg) and the middle north-east (near the village of Norg in the province of Drente). When collecting specimens in Limburg and Drente, I found them to be of different appearance, especially on account of the indumentum and the length of the leaf stalks. Further investigation, however, brought to light many more differences in morphology, biology and probably even in ecology and genetics. Moreover, in the Netherlands a geographical barrier between the two taxa apparently exists. Yet we cannot verify such a barrier when studying the distribution of the two groups in a wider sense, that is in their European area. Both forms occur all over Europe; only in Scandinavia one of the two goes a little further north than the other.

As it is sometimes difficult to decide between geographic and ecological differences, we feel inclined to ask whether the distribution pattern in the Netherlands does not mean an ecological barrier instead of or together with a geographical separation. The two Dutch habitats are very different from an eco-sociological point of view. The southern habitat in Limburg is a Querceto-carpinetum filipenduletosum of the alluvia along little streams. This signifies a very rich, soft, humus-like soil with pH between 6 and 7. The more northern habitat near Norg (Drente) is a transition between Querceto-carpinetum Stachyetosum and Querceto-sessiliflorae-Betuletum molinietosum, signifying vegetation on more acid, rough humus-like soil than that of the normal humid Querceto-carpinetum[1]). Thus, in the light of ecological considerations we might conceive the two taxa as ecotypes or even ecospecies in the sense of Turesson.

[1] My thanks are due to Dr. V. Westhoff for sociological information.

We now turn to a study of biological and genetical barriers. In the Netherlands there is a difference in time of flowering of about three weeks between the two taxa in their natural habitats. This difference might be caused by the distance of nearly 200 miles in a north-south direction between the two localities, as it can be observed in many species in our country. From growing the two types side by side in the ecological garden of the University of Groningen, however, we learned that this explanation does not hold for *Stellaria nemorum,* that the difference in flowering time has a genetical base and that it continues to exist under uniform conditions. The phenomenon is of great importance in nature, as it generally will prevent cross-pollination, even where distributional areas of the two taxa might meet, and this is probably not impossible in certain European localities.

The next step is to study cross-pollination and to determine whether or not cross-fertilization will result. Experiments have been made thus far on a very small scale only. The first results, however, point to incompatibility between the taxa or even impossibility of hybridization. If, after further investigation, the questions on ecological and genetic barriers could be answered in the affirmative, as we expect, we should not hesitate to give those taxa species rank on the strength of morphological, biological and probably also ecological and genetic considerations. In many cases we might wish species limits to be as obvious.

Nomenclature is still confused and discussion is not essential here. The current naming in the rank of subspecies is *Stellaria nemorum* subsp. *montana* (Pierrat) Murbeck for our southern and *S. nemorum* subsp. *glochidosperma* Murbeck for our northern type. But it is not quite clear from Pierrat's description which form he actually meant when describing *Stellaria montana* as a species and I have not yet seen any material named by him.

When comparing the species of this genus, we might feel inclined to unite the two subspecies treated above. Many workers would consider them closely related, very often on the strength of external morphological likeness, that is, of their phenotypes—which certainly is not always a good basis for estimating relationships—and so might come to the conclusion that the two subspecies have arisen from one parent-species, or the one subspecies from the other. This seems to be a common way of thinking. In taxonomic, geographical and cytogenetical publications, we find one species described as easily derived from another, still living species, notwithstanding the fact that in many cases the data for such a conclusion apparently are quite insufficient. We cannot do without good hypotheses as stimulating factors in the development of science, but before they have been turned from theories into facts we should be aware that they are only hypotheses, not more.

Gradual divergence is often seen as a principal process in species formation, but it is not the only one. We have good evidence of the origin of species after interspecific hybridization

and chromosome doubling. Modern species concepts centre about intercompatibility, the degree of which, however, need not always be correlated with that of morphological equalness. We cannot always predict results concerning phenotype and hybrid sterility, even in an experiment where we know both parents well. One example is the extravagant hybrids known within the genus *Salix*.

While considering the two taxa of *Stellaria nemorum s.l.* as different species, we should not give the concept a phylogenetic interpretation. In more modern terminology we should call the two taxa not species, but probably "ecospecies" (Turesson) or "commiscua" (Danser). The two terms have the same meaning and are more or less of the same age (25-30 years). Most workers in the field of plant taxonomy are likely to prefer the term eco-species over Danser's commiscuum. Yet it is worth comparing the two terminologies.

Though Danser was aware of ecological influences in taxon formation, he laid stress upon the biological aspects of interfertility and intersterility even in the terms "comparium", "commiscuum" and "convivium" which denoted his taxa. Turesson did the reverse; his terms "coenospecies", "ecospecies" and "ecotype", though running more or less parallel with Danser's, lay stress upon ecological influences. The coenospecies, however, also has a phylogenetic meaning, while in the lower categories of the con-vivium on one side and the ecotype on the other, Danser's term has a wider meaning than the purely ecological indication of Turesson. When preferring, therefore, two of Danser's terms over those of Turesson, we might also choose the third and use the term commiscuum, which, as an indication of the taxonomic unit he had in mind, is not less valuable than the word ecospecies. We expect the two subdivisions of the present *Stellaria nemorum* to represent two commiscua, every commiscuum being a group of forms which hybridize freely and yield fertile progeny. Preliminary results on intercommiscual hybridization were negative in the sense that they did not even yield sterile hybrids. To conclude from this that each of the two commiscua, though morphologically much alike, is a comparium of its own, would be highly premature. Fieldwork has to be continued on a larger scale. Though Danser recognized the processes of evolution, it is essential that he kept his species concept free of phylogenetical interpretation, which he often thought too speculative. Instead, he denoted his taxa com-parium, commiscuum, convivium in a way which primarily points to biological processes, so closely related to the gaps between the species as we generally know them.

Whatever terminology we may choose, we can say that many taxonomists of to-day delimit their species in such a way that they are commiscua or ecospecies. As a consequence, taxonomy is no longer merely theoretical; experimental work can make its con-tributions as an objective tool in the hands of taxonomists. We must, however, keep in mind that nature's ways are always com-plex in the field of multiformity in plants. I might point to

an article by Camp and Gilly in *Brittonia*, 1943, which, I think, is very interesting, distinguishing not less than 12 types of species.

Experimental work has shown that hybrids are not always fully fertile nor completely sterile. The difficulty of interpreting experimental results lies in their complexity and in the fact that the delimitation of species on the strength of hybridization as well as on other criteria, is not only a matter of quality, but also of quantity. However, we may say that the species concept has gained a sound and biological basis, although the species themselves may change in the course of evolution in a changing world, so that the species of the future may not be the same as those of to-day, or of the past.

REFERENCES.

CAMP, W. H. & GILLY, C. L., 1943, The Structure and Origin of Species, *Brittonia*, **4**, 323-385.

DANSER, B. H., 1929, Ueber die Begriffe Komparium, Kommiskuum und Konvivium, und über die Entstehungsweise der Konvivien, *Genetica*, **11**, 399-450.

——, 1950, *A Theory of Systematics.*—Leiden.

HEGI, G., 1911, Zwei Unterarten von Stellaria nemorum L., *Mitt. d. Bayer. Bot. Ges.* **2**, 340-341.

——, 1911, *Ill. Flora v. Mittel-Europa*, **3**, 350-352.

MURBECK, S., 1890-91, Beiträge zur Kenntniss der Flora von Südbosnien und der Hercegowina, *Acta Univ. Lund*, **27**.

——, 1899, Die nordeuropäischen Formen der Gattung Stellaria, *Bot. Notiser*, **1899**, 193-218.

PIERRAT, D., 1880, Note sur le Stellaria montana Pierrat sp. nov., *Comptes-rendus de la Soc. Bot. Rochelaise*, **2** (1879), 58 (La Rochelle, 1880).

TURESSON, G., 1929, Zur Natur und Begrenzung der Arteinheiten, *Hereditas*, **12**, 323-334.

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Mr. J. E. LOUSLEY enquired whether Dr. Andreas had seen any material of subsp. *glochidosperma* from Britain. Dr. ANDREAS replied that she did not know whether this occurred or not*. Mr. R. D. MEIKLE said that Mr. D. N. McVean had told him that *glochidosperma* did occur, but was confined to Wales.

*See *Watsonia*, **3**, 122-6, t. II (1954)—EDITOR.

CLINAL VARIATION IN FLOWER SIZE IN LOTUS CORNICULATUS L.

(Exhibit)

B. A. POULTER (Royal Botanic Garden, Edinburgh).

A series of graphs and diagrams was shown to demonstrate the possible occurrence of a cline in flower size in *Lotus corniculatus* L. within the British Isles.

The measurement used as an indication of flower size was the length from the base of the calyx to the tip of the wing, the range being from 8·25 mm. to 20 mm. The axis of the cline was from S.E. to N.W., the smaller-flowered forms being most numerous in S.E. England, and being replaced by larger-flowered forms towards the north and west.

Before this cline can be fully substantiated, much more evidence is required. In particular, it will be necessary to determine as far as possible to what extent the variation is on a geographical basis, and how much is a response to variation in ecological conditions. Examination of populations growing under varying ecological conditions within small geographical areas may help to elucidate this point.

THE SECTION EU-CALLITRICHE IN THE NETHERLANDS
(Exhibit)

HENRIETTE D. SCHOTSMAN (University of Groningen).

This exhibit included photographs of plants in various modifications, drawings of fruits and flowers, distribution maps and cytological peculiarities of the five *Callitriche* species of the section Eu-Callitriche in the Netherlands, viz. *C. hamulata, C. obtusangula, C. stagnalis, C. platycarpa* and *C. palustris*.

Most of these species are very polymorphic, sometimes resembling each other very closely in the vegetative parts. This makes it often rather difficult to distinguish them with certainty in the field without cultivating them and without cytological investigations. On account of the polymorphy many difficulties have arisen in nomenclature. Moreover, varieties of each species have been described. From culture experiments under various conditions it appeared, however, that most of these varieties are modifications only.

Based on cytological, morphological, geographical and ecological characteristics the section Eu-Callitriche in the Netherlands can be divided into the five species mentioned above.

C. hamulata Ktzg. As a water form, this species is a winter annual. The plants grow quickly in autumn, producing linear leaves only. When the water is not too deep, in spring floating rosettes with spathulate leaves are formed. The flowers are totally submerged and consequently pollination also takes place below the water surface. The anther turns towards one of the stigmata and after dehiscence the pollen-grains—without exine—germinate quickly, the pollen tubes forcing their way through the stigmatic tissue. *C. hamulata* occurs in dune sandy soils and pleistocene sandy soils. The water is slightly acid to neutral. In its chromosomes *C. hamulata* is different from the other species. The number of chromosomes is $2n = 38$; it is the only species having chromosomes with median centromeres.

C. obtusangula Le Gall. This species is a perennial and generally occurs in slightly brackish water in the coastal region. The rhomboid leaves, the fruit with very blunt edges, the unwinged seeds and the ellipsoidal pollen are characteristic for this species, as shown in the exhibit. The number of chromosomes is $2n = 10$. In the province of Zeeland we found plants with a different leaf shape, possessing 2 *SAT*-chromosomes. These plants proved to tolerate a higher salt concentration.

C. stagnalis Scop. *C. stagnalis* is not very common in the Netherlands. It generally occurs in valley regions and in estuaries and is rather salt-tolerant, like *C. obtusangula*. The

number of chromosomes is $2n = 10$; the chromosomes are smaller than those of *C. obtusangula*. Plants were found with 0, 1 and 2 *SAT*-chromosomes. *C. stagnalis* is the most constant species under varying conditions; linear leaves are never formed.

C. platycarpa Ktzg. *C. platycarpa* is a very polymorphic species. Especially as a land form or in shady localities it may resemble *C. stagnalis*. In winter (*C. platycarpa* is perennial) linear leaves are formed and in this period it resembles *C. hamulata* and *C. obtusangula*. It is common in the Netherlands, occurring in slightly acid to slightly alkaline water on different soils. Only in brackish water is the species absent. The number of chromosomes is $2n = 20$.

C. palustris L. This arctic-alpine species is rare in the Netherlands. It is a summer annual and occurs in "cowpuddles" in brook-valleys. As a water form, it possesses more or less normal flowers, though the act of dehiscence is often lacking. In well developed forms normal air pollination may occur, but as a land form the species is apogamous. The male flowers are abortive or totally absent, and the stigmata have been nearly wholly reduced. The small, obovate, blackish fruits are characteristic of this species. The number of chromosomes is $2n = 20$; these chromosomes are the smallest in this section.

ECOTYPICAL VARIATION IN ADOXA MOSCHATELLINA L.
(Exhibit)

H. G. Baker (University of Leeds).

Adoxa moschatellina is the only species of the only genus in the isolated family Adoxaceae. Although circumboreal in its distribution it lacks discrete morphological variation and only a single, unsatisfactory variety (var. *inodora* Clarke from Kashmir) has been described apart from the type. *Adoxa* has the appearance of a species which has "run out of morphological variation". It is interesting, therefore, to see if it retains the potentiality of "physiological" variation which may be adaptive.

Plants collected from deep, damp crevices in the Yoredale limestone cliffs near the summit of Ingleborough (at c. 2,150 feet) regularly come into leaf and flower later than lowland (woodland) material from several parts of the British Isles when kept in an unheated greenhouse at Leeds.

Although, in general, subalpine races of plants come into flower earlier than lowland races when these are grown together in a garden, the reversal in this case may be related to the woodland habitat of the lowland race. There the emphasis is upon early development before the trees come into leaf.

Material from about 1,000 feet elevation on Ingleborough (growing amongst Carboniferous limestone rocks amidst scrubby trees) is intermediate in behaviour. There is a complete disjunction between the plants at this elevation and those near the summit. All races shown have the same chromosome number ($2n = 36$) and have been proved to be self-incompatible. Vigorous vegetative reproduction accompanied by self-incompatibility is probably responsible for the "shy seeding" of this species.

VARIATION IN CENTAURIUM IN WEST LANCASHIRE

(Exhibit)

WINEFRIDE M. T. O'CONNOR (University of Liverpool).

An investigation of the species of *Centaurium* on the dunes at Freshfield, Lancashire (v.c. 59), is in progress. The commonest species which occur are *Centaurium minus* Moench and *Centaurium littorale* (Turner) Gilmour. *Centaurium pulchellum* (Sw.) E. H. L. Krause has been recorded but not recently (Green, 1933), while the only known stations for *Centaurium latifolium* (Sm.) Druce were in this area. The latter was last recorded in 1871 (Green, 1902; Stansfield, 1936) and is now believed to be extinct. This investigation has, therefore, been concentrated on the two former species.

Both species are very variable and a list of the described varieties (Gilmour, 1937) together with their discriminatory characters is given in Table 1. The varieties concerned in the populations studied at Freshfield are *Centaurium minus* var. *fasciculare* and *Centaurium littorale* var. *occidentale*.

Centaurium minus is a plant of dry grassland, dunes and clearings in woods. It is widely distributed in England and Wales but is less frequent in Scotland. *Centaurium littorale* is much more restricted. It occurs in coastal districts of northern England, North Wales and Scotland. The distribution of both species in Ireland is inadequately known from available herbarium material. Distribution maps are given in figs. 19 and 20. Further details and records *with voucher specimens* for examination would be welcome.

Mixed populations of the two species occur in certain areas of the coast of northern England and Wales, and the populations studied lie within this area. At Freshfield there are distinct populations of each species, and other populations which contain both species, together with plants which cannot be referred to either. Similar plants were found by Salmon and Thompson (1902) at Ansdell, near Lytham, v.c. 60, and described by Wheldon (1902) as *Erythraea littoralis* var. *intermedia* (*Centaurium* × *intermedium* (Wheld.) Druce).* Wheldon's specimens from Hightown, v.c. 59, near to Freshfield, are in Herb. Mus. Brit.

*Since this paper was submitted it has become clear that the plant originally described by Wheldon as *E. littoralis* var. *intermedia* is in fact a polyploid form of *C. littorale*. The status of this form will be discussed more fully elsewhere.

TABLE 1.

	General	var. *minus* (=var. *centaurium* (L.))
		1. Basal leaves obovate-oblong.
Centaurium minus	Leaves 1-5 cm. × (4) 18-20 mm., obovate to elliptical, prominently 3-7 veined. Calyx less than corolla-tube at anthesis. Corolla limb flat.	2. Stem simple or branched. 3. Stem leaves elliptic oblong 4. Flowers sessile or subsessile in fairly compact clusters. 5. Calyx less than corolla-tube at anthesis. 6. Not scabrid.
		var. *littorale* (Turner) Gilmour 1. Stem 2-8 cm. subglabrous.
Centaurium littorale	Leaves 1-2 cm. × 3-5 mm., linear-spathulate to ligulate (normally parallel-sided). Indistinctly 1-3 veined. Calyx equalling corolla-tube at anthesis. Corolla limb concave.	2. Basal lvs. obovate spathulate; cauline lingulate, lanceolate or ovate-lanceolate. 3. Flowers in lax or ± compact few-flowered cymes. 4. Sepals linear not attenuate, nearly or equal to corolla-tube at anthesis.

(after Wheldon and Salmon, 1925)

var. *fasciculare* (Duby)	var. *subcapitatum* (Corb.)	var. *sublitorale* (Wheld. & Salm.)
1. Basal leaves ovate-oblong.	1. Basal leaves broad often suborbicular.	1. Basal leaves oblong or ovate-spathulate.
2. Simple or branches from ½ up stem.	2. Short, stout, 3-10 cm.	2. 10-30 cm.
3. Stem leaves elliptic-oblong, often 5-nerved.	3. Stem leaves elliptic-oblong, often 5-nerved.	3. Linear to ovate-lanceolate.
4. Flrs. numerous, sessile or subsessile in compact clusters.	4. Flrs. sessile or sub-sessile in crowded compact heads.	4. Flrs. in terminal few-flowered cymes.
5. Calyx less than corolla-tube at anthesis.	5. Calyx less than corolla-tube at anthesis.	5. Calyx not quite as long as corolla-tube at anthesis.
6. Not scabrid.	6. Not scabrid.	6. Slightly scabrid.

var. *occidentale* (Wheld. & Salm.)	var. *baileyi* (Wheld. & Salm.) Gilmour	var. *minus* (Hartm.) Gilmour
1. Stem 2-25 cm. Wings usually scabrous-ciliate.	1. Stem 4-10 cm. (branched plant usually as broad as tall) usually scabrous.	1. Stem 2-5 cm. Glabrous.
2. Basal leaves linear to linear-obovate or spathulate, cauline erect ligulate, margins scabrous.	2. Leaves linear to linear-spathulate.	2. Basal leaves spathulate, cauline narrow, linear.
3. Flowers few in fastigiate cymes.	3. Flowers numerous, crowded in compact heads.	3. Flowers in compact cymes.
4. Sepals linear, attenuate, equalling or exceeding corolla-tube at anthesis, densely scabrous.	4. Sepals linear, attenuate, equalling or exceeding corolla-tube at anthesis, densely scabrous.	4. Sepals linear, attenuate, equalling corolla-tube at anthesis, smooth or rarely slightly scabrid.

THE NEW NATURALIST VICE-COUNTY MAP OF THE BRITISH ISLES

Fig. 19. Distribution of *Centaurium minus*.

THE NEW NATURALIST VICE-COUNTY MAP OF THE BRITISH ISLES

Fig. 20. Distribution of *Centaurium littorale*. Material from other localities will be welcomed.

(These maps include only material seen by the writer to date of Conference

With acknowledgment to "The New Naturalist" for use of the base-map.

The most useful characters for discriminating between the two species are:—

(a) Length, breadth and shape of leaves. In *Centaurium littorale* the leaves are narrow and approximately parallel-sided, in *Centaurium minus* they are broader and ovate to ovate-lanceolate.

(b) Length of inflorescence and number of flowering nodes. These characters give a measure of the difference in the amount of contraction of the inflorescence in the varieties of *Centaurium minus* and *Centaurium littorale* at Freshfield. They do not hold for the whole range of variation of the species. *Centaurium minus* var. *fasciculare* is characterised by a contracted inflorescence involving a number of nodes of the main axis. *Centaurium littorale* var. *occidentale* has a loose cymose inflorescence composed of laterals from only one or two of the main axis nodes.

(c) Relative length of calyx and corolla tube. The calyx normally equals or exceeds the corolla tube in *Centaurium littorale*. In *Centaurium minus* it is shorter than the corolla tube.

These characters are scored in populations subjectively determined as pure or mixed and the results plotted as a scatter diagram using the following indices:—

(a) (Leaf length/length from base of leaf to widest point) × breadth of leaf.

(b) Length of inflorescence/number of nodes in inflorescence.
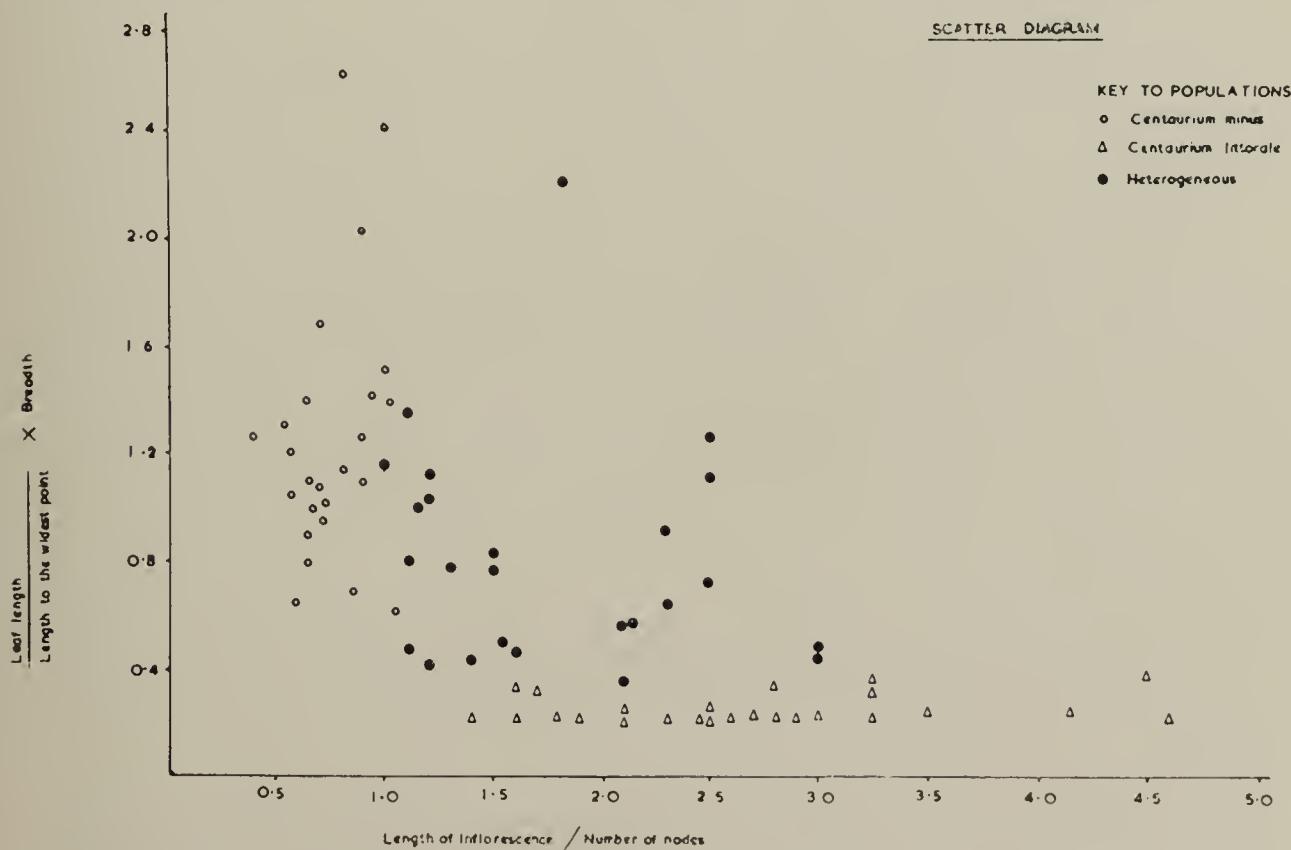
Fig. 21.

Scatter diagram of populations of *Centaurium minus* and *C. littorale*.

A representative diagram is given in fig. 21. It can be seen that these measures give a clear discrimination between populations subjectively determined as pure *Centaurium minus* or *Centaurium littorale* but the plants from the mixed population show a much wider scatter.

The presence of this group of intermediate plants is not unreasonable evidence for putative hybridisation. Opportunities must occur, for at Freshfield the populations are in flower at the same time, although *Centaurium littorale* commences flowering about two weeks earlier than *Centaurium minus*. The overlap in flowering time is about twelve weeks. The morphology of the flower and the results of open pollination tests (Gilmour, 1934) suggest that *Centaurium minus* is largely self-fertilised but *Centaurium littorale* is probably more of an outbreeder.

Crosses made reciprocally between the two species both set seed. The amount of seed set was only slightly less than in normal open-pollinated capsules. This seed germinated but the plants are still too young for it to be possible to recognise whether they differ from or resemble either parent. Gilmour (unpublished) and Melderis (1932) have obtained hybrid plants by artificial crosses.

The recorded chromosome numbers are *Centaurium littorale* $2n = 38$ (Wulff, 1937; Warburg in Maude, 1939) and $c. 56$ (Warburg in Maude, 1939) and *Centaurium minus* $2n = 42$ (Rork, 1949). Unambiguous counts of the experimental material have not yet been obtained from somatic plates but there is no evidence for the presence of the 56 chromosome plant in the Freshfield material so far examined. It is hoped that meiotic studies will give better discrimination. Since the difference between the somatic chromosome numbers of the two species is only four this is a matter of some importance in detecting hybrids cytologically.

It has been remarked that *Centaurium littorale* does not occur in southern England. Nevertheless plants possessing characters similar to those classed as intermediates in the northern mixed populations have been found in the south, in Norfolk and in South Wales. The question is, therefore, posed as to whether they represent the relicts of previous populations of the two species where *Centaurium littorale* has either been replaced by introgression or has died out. If this is so then the position cannot always be the same since, both in this country and on the continent, mixed populations of both species retain their identity, or at least hybrids have not been recorded from all such mixed colonies.

My thanks are due to Mr. J. S. L. Gilmour, who has very kindly made available his manuscript notes on the genus *Centaurium*, and also to Dr. E. F. Warburg for the loan of specimens from the Druce Herbarium of the University of Oxford, used in the exhibit.

REFERENCES.

GILMOUR, J. S. L., 1934, Preliminary note on pollination in Centaurium, *Proc. Linn. Soc. Lond.*, **3**, 109.

——, 1937, Notes on the Genus Centaurium, I. The nomenclature of the British Species, *Kew Bull.*, **1937**, 497-502.

GREEN, C. T., 1902, *Flora of Liverpool.* Liverpool, D. Marples & Co.

——, 1933, *Flora of Liverpool.* Arbroath, T. Buncle & Co.

MAUDE, P. F., 1939, The Merton Catalogue: A list of the chromosome numerals of species of British Flowering Plants, *New Phyt.*, **38**, 1.

MELDERIS, A., 1932, Genetical and taxonomical studies in the Genus Erythraea Rich.—1, *Acta Hort. bot. Univ. latv.*, **6**, 123.

RORK, C., 1949, Cytological studies in the Gentianaceae, *Amer. J. Bot.*, **36**, 687.

SALMON, C. E., & THOMPSON, H. S., 1902, West Lancashire Notes, *J. Bot. Lond.*, **40**, 293.

STANSFIELD, H., 1936, The Broadleaved Centaury—Centaurium latifolium Druce (Erythraea latifolia Smith), *N.W. Nat.*, **11**, 245.

WHELDON, J. A., 1902, Short Notes: Erythraea littoralis × Centaurium, *J. Bot. Lond.*, **40**, 326.

WHELDON, J. A. & SALMON, C. E., 1925, Notes on the Genus Erythraea, *J. Bot. Lond.*, **43**, 345.

WULFF, H. D., 1937, Karyologische Untersuchungen an der Halophytenflora Schleswig-Holstein, *Jahrb. wiss. Bot.*, 812.

Dr. H. G. BAKER said that he felt that to say that a "species had been hybridised out of existence" was unfortunate terminology. It is preferable to say that a species has disappeared and left genes behind it, which covers the possibility that it has merely become extinct.

Miss O'CONNOR pointed out that climatic conditions may have changed.

Dr. D. P. YOUNG suggested that the expression to which Dr. Baker took exception might nevertheless be apposite. Under conditions of changing habitats, hybridisation pressure from other species might well lead to one being "hybridised out of existence". *Viola canina* in places appears to have hybridised *V. lactea* out of existence, while on the Freshfield Dunes themselves the *Cardamine* populations are very complex and at least one species is represented only by relics.

PROBLEMS OF HYBRIDIZATION AND SPECIES LIMITS IN SOME ERICA SPECIES

(Exhibit)

Peter A. Gay (University College, London).

In considering problems where hybridization is thought to occur, we should first satisfy ourselves that the system is not merely a case of wide and anomalous variation with the two putative species at opposite ends of a variation range. In the case exhibited, *Erica ciliaris* L. crossing with *E. tetralix* L., the two taxa have long been recognised, but this in itself is not a sufficient argument. However, when the geographic distribution of the two species is studied, their very different ranges, one tending to be northerly and easterly and the other southerly and westerly, with an overlapping range between, it is at least strongly suggestive that they are two "good" species. Their ecological ranges are also somewhat distinct, although in this country at least this seems to be breaking down due to man's action.

Although no strict barriers are demonstrated above, they do exist when considering other aspects of the two species. One barrier to *free* gene flow is the low fertility of the hybrids. Slides were exhibited to demonstrate this. Differences in flowering time of the two species will render the gametes less readily available for fusion with those of the other species. Thus we are dealing with two distinct entities.

The putative hybrids usually show in most of their characters a complete gradation between the two parent species, for example, in anther characters (which were demonstrated), leaf shape, corolla shape, branching type. Occasionally unpredictable forms turn up because of the totally new gene combinations. The odd corolla shapes demonstrated illustrate this. Both these states of affairs are characteristic of hybrids.

A useful method of studying hybrids is Anderson's technique involving a Hybrid Index. Nine characters were employed in the scheme here. However, for comparisons of whole populations especially in relation to habitat studies and evolution, a more complex scheme has been devised involving taking the means of both the Hybrid Index and of a new term, the Hybrid Number, for the whole population. This system has proved a very useful method of population analysis where the hybrids are involved.

The old problem of the exact status of *E. mackaiana* Bab. was considered. Morphologically it appears to be a hybrid between *E. ciliaris* and *tetralix* but it differs greatly from those which we know to be hybrids. Its distribution is not what would be expected from a distinct taxon except by polytopic origin. Its

pollen fertility is low and of an odd type. It certainly does not seem to be of the same taxonomic category as the other species and a tentative suggestion put forward is that it is something between an autotetraploid and an allotetraploid arising somewhere from the *E. ciliaris/tetralix* hybridization complex. Such a hypothesis will explain the above anomalies and also the fact that *E. ciliaris* was formerly recorded from the vicinity of the Connemara locality of *E. mackaiana*. However, at the moment it should not be considered as more than a tentative working hypothesis.

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Prof. D. H. VALENTINE asked how the chromosome number of *Erica mackaiana* was related to these of *E. ciliaris* and *E. tetralix*.

Mr GAY replied that the chromosome number of *E. mackaiana* was not known.

Mr. N. Y. SANDWITH enquired about the Dorset hybrid between *E. ciliaris* and *E. tetralix*, *E.* × *watsoni*.

Mr. GAY said that in *watsoni* pollen fertility was very low, usually less than 1%. He said he did not agree with giving a name to this hybrid which was only one biotype of many.

Mr. J. OUNSTED pointed out that *E.* × *praegeri* was usually regarded as a hybrid between *E. mackaiana* and *E. tetralix*, which was interesting if *E. mackaiana* was itself of hybrid origin and had low pollen fertility.

THE SPECIES CONCEPT IN EUPHRASIA
(Exhibit)

P. F. YEO (University Botanic Garden, Cambridge).

This talk deals with the taxonomic problems in *Euphrasia,* as well as the species concept.

Twenty-five species of *Euphrasia* were recognised by Pugsley in the British Isles. The characters which are used to distinguish them are internode length relative to leaf length, the node at which flowering starts coupled with number of the branches, the date at which flowering starts, indumentum of leaves and calyx, shape of leaves and leaf teeth, size of flower, and shape of calyx and capsule. Each species has its own set of characters, and differs in several characters from its nearest relatives.

The forms distinguished on the basis of these characters have, as a rule, distinct habitats, and more or less extensive distributions. These distributions usually show discontinuities, due to discontinuity of suitable habitats, and the discontinuities may be quite considerable; for example, those which separate *Euphrasia montana* in Yorkshire and Belgium, or *E. frigida* in Scandinavia, Scotland, and Ireland.

Sympatric species, of which there are often several in an area, generally show differences in habitat which keep the populations of different species apart. Sometimes, however, two species grow together, and in the same habitat. It is then most often the case that one is a diploid and the other a tetraploid. In some cases, though their chromosome numbers are the same, one or both may be minute-flowered forms, and these are habitually self-pollinated. They thus remain distinct, though growing intermixed.

Ecology and distribution support the distinctions made on morphological grounds, and this is the justification for regarding these morphologically defined groups as species. This is not to say that *Euphrasia* taxonomy is easy, or that the group is not a critical one. There are three sources of taxonomic difficulty, which I shall now describe.

The first lies in the fact that a large proportion of the features used to distinguish the species are quantitative, and are thus significantly affected by environmental and genetic variation. Regarding environmental effects, it can be said that all the differences used taxonomically are ones which have a genetic basis. But environment may accentuate them. For example, cultivation in pots suggests that *E. pseudokerneri* has smaller leaves than *E. nemorosa,* but this difference may be increased in nature owing to the extreme dryness of the chalk soil in which

pseudokerneri usually grows. Probably the character least affected by environment is indumentum. Next comes flower size, which varies much less than the luxuriance of individuals. Another fairly stable character is average date of commencement of flowering. But this is probably controlled partly by temperature, and an early warm spell may bring a species into flower prematurely.

There are two principal influences on all other characters, that is, characters of the vegetative parts. They are shade and nourishment, including water supply.

The influence of shading and nourishment is shown by comparison of plants grown in the garden, with those grown in pots in the greenhouse. Greenhouse plants of *E. nemorosa* resembled wild ones fairly closely, as is usually the case with Euphrasias grown in the greenhouse. Garden plants, however, were very much more luxuriant, having larger, darker, shinier leaves, and being much more branched. These plants also had shorter internodes than wild or greenhouse ones, and their branching started at a lower node. It seems that the supply of nutrients in the pot was approximately what is available in nature, while in the garden it was greater, and that the effect of the greenhouse roof in reducing light intensity was similar to that of the vegetation that surrounds the plants in the wild. The host provided for the garden plants, *Plantago lanceolata,* was cut back from time to time and produced little or no lateral shading.

A fairly wide variation in the appearance of plants can be caused by variation in luxuriance. In luxuriant plants, leaf size and flower size are at their largest, and favourable nutritional conditions seem to bring out the greatest number of differences between forms. When nourishment is really poor the species begin to lose the characters by which they are distinguished and to resemble one another more closely. There are evidently a number of nutritional factors affecting luxuriance. Thus leaf size is not always correlated with the vigour of growth and branching of the plant. Some, which, judging by stature and number of branches, are vigorous plants, have leaves of about normal size, while others of the same stature, or even smaller plants, have relatively large leaves, dark shining green, like those of garden-cultivated plants. Small plants with large healthy leaves are ones that got established late, but when they did so, it was on a particularly favourable host plant. Two nutritional factors are, therefore, the type of host plant, and the time of establishment on the host.

Euphrasias exhibit a great deal of variation of this kind because they are annuals and parasites. This means that population studies have to be carried out on cultivated plants.

The genetic variation which is normally present in a species will affect its taxonomic characters, for the same reason that environmental variation does, namely that most of the taxonomic characters are quantitative ones. An example of genetic varia-

tion is probably to be seen in the differences between West Country *E. confusa,* and that in Derbyshire and Staffordshire. The latter tends to be more compact, and robust, not quite so freely branched, and to have larger capsules and flowers.

In addition to genotypic variation within a species, there occur forms which diverge too much from recognised taxa to be included in any of them. This is the second source of taxonomic difficulty. The exhibit shows examples of this. It is not clear whether the plants from the north of Scotland exhibited ought to be included in *E. confusa,* though they have some characters in common with the south-western plant. The form shown from North Wales, however, though it has sometimes been referred to *E. confusa,* lacks some of the most important characters of that species.

It seems probable that all the easily recognisable British species have been described, and though some of the problematical forms may possibly have to be described as species this cannot be undertaken without careful study in the field. For example, the form from N. Wales needs to be seen at all ages, its habitat observed, and its range investigated, and attention paid to the possibility of its varying towards *E. confusa* in any part of its range.

In addition to variation within species, and the occurrence of forms falling outside recognised species, hybridisation causes difficulties. Species with minute flowers are habitually self-fertilised, the anthers dehiscing and shedding pollen just before the flower opens. But even these can give rise to hybrids by the transference of their pollen to the flowers of larger-flowered species. The species that can most easily hybridise are usually kept apart by their ecological differences, but this obstacle to hybridisation is frequently overcome. Hybrids occur in spite of ecological differentiation, either as a result of two different habitats being adjacent, and perhaps intergrading, or because tolerances overlap. An example of the latter is provided by *E. occidentalis,* which is a plant characteristic of short turf on cliff tops round the coast. In S.W. England, however, it occurs inland on limestone. As a result, it meets *E. confusa* on Carboniferous Limestone in the Mendips, and *E. pseudokerneri* on chalk in Dorset, and in both cases hybrids are produced.

Hybrids between species with the same chromosome number are fertile; they can therefore segregate and backcross, so that a great range of forms is possible among the descendants of a cross. Consequently, groups of individuals descended in this way may show a close resemblance to one of the parent species and yet be untypical of it. And it may be that while the taxonomist can recognise this, he could not say with certainty, on the evidence of such individuals alone, what was the other parent, or even whether or not they were hybrids. Another possibility is that a hybrid between species "A" and "B" may resemble "C".

An instance of this was observed at Bettyhill, Sutherland, where there occur *E. brevipila* var. *reayensis,* and the north Scottish form of *E. nemorosa.* The first, which is a very marked variety, perhaps deserving specific rank, has long glandular hairs, and the second is eglandular. Along the roadsides these hybridise and plants with short glands occur. A gathering of these might pass for *E. brevipila,* which has short glands.

These facts show that certain recommendations to botanists interested in *Euphrasia* are needed. Firstly, in view of the existence of local forms or hybrids, the attempt should not be made to force every population into some recognised species. Such forms may run down in a key to a particular species. These present a particular difficulty to the beginner. As far as possible one should take one's conception of a species from specimens from an authentic locality in the species' main area of distribution. Unfortunately, in the case of *E. confusa,* some gatherings determined by Pugsley are widely different from the south-western form on which the species is based. Whatever one's original conception of the species, one should collect and take note of divergent forms. We must be resigned to not being able to give a name to every plant, but the unnameable or untypical populations should not be ignored. Improved knowledge of variation may make possible improvements in taxonomy. The second recommendation is that anyone who collects Euphrasias in a particular area is advised to make a gathering of every form he finds in the district, if possible, whether or not it belongs to a species known to him. If he then submits them to a specialist it will make it easier for the specialist to recognise hybrids and to come to conclusions. The specialist will then find the material more instructive, and will be able to be more informative to the collector. Advice on how to select individuals of *Euphrasia* is given in Clapham, Tutin, and Warburg's *Flora of the British Isles.*

I have now described the differences which distinguish species, and the sources of the taxonomic difficulty which makes *Euphrasia* a critical group, and now wish to sum up the situation regarding the species concept in the group.

The facts of close morphological similarity, and ease of hybridisation, apart from creating difficulties for the taxonomist, indicate close relationship between the species. Species boundaries are comparatively close together in *Euphrasia,* but they have been placed in the most convenient places, coinciding with the most marked morphological and ecological discontinuities.

In addition to the peculiarity of *Euphrasia* that its species are rather "small", there are two others, namely great variability and a high rate of endemism. This last is a general phenomenon, though particularly marked in Britain. The existence of many endemics in Britain suggests their recent and rapid evolution.

and the variability of the forms is consistent with this. The species tend to be unstable, and the group is probably in a phase of rapid evolution.

I have at times tried to envisage the result of lumping Euphrasias, to see whether any more satisfactory groupings would result. One could either reduce the British forms to three species, the absolute minimum, or carry the lumping to some intermediate level. I cannot see that any lumping can reasonably be done. The first course would leave one species, at least, that was extremely heterogeneous, while there is no satisfactory basis for lumping to an intermediate degree.

I consider that the present taxonomic situation is broadly satisfactory, though it involves a rather special concept of the species. This narrow view of the species involves less distortion of the concept, as it is generally understood, than would be caused by reducing the number of species to three, with a large array of subspecies.

In connection with this talk an exhibit of herbarium sheets was shown, intended to illustrate the following points about *Euphrasia confusa* : —

1. The species occurs in the Peninsula counties, the Derbyshire and Staffordshire Dales, and in Yorkshire.
2. Forms occur in Scotland showing affinities with the English plant, but which are not identical with it.
3. In N. Wales there occurs a plant which has apparently been referred to *E. confusa* but which appears to have little in common with it.
4. The differences that separate *E. confusa* from *E. nemorosa* and *E. occidentalis*, which are allied to it.
5. These two species hybridise with *E. confusa*.
6. The kind of differences that occur between individuals in the same population, due mainly to environment.
7. The difference in the appearance of the same form at different ages.

Prof. D. H. VALENTINE asked how the pattern of variation in Britain compared with that in other parts of Europe and whether this country is especially rich in *Euphrasia* species.

Mr. YEO replied that it seemed that there are quite a lot of endemic species of restricted range in Europe and these seemed to occur especially in mountain areas.

Dr. J. G. HAWKES said that in south-east Australia nearly every mountain range had its own series of Euphrasias.

Mr. YEO in reply suggested that this was particularly interesting since the Australian species belonged to a different Section of the genus from the European plants.

Dr. E. F. WARBURG said that he felt far from sure that all the recognisable species to be found in Britain had been described. As an example he mentioned three distinct plants found in Buckinghamshire which hybridise and have all been referred to *E. nemorosa*. He felt doubtful whether it was right to treat so many taxa as species and it might be better to lump the British plants under only three species with a large number of subspecies. This seemed desirable in view of the numerous intermediates and had the merit that it would be possible to put some sort of a name to every gathering.

Mr. YEO replied that from his experience he would have said that all *easily* recognisable species had now been described and he thought the treatment of existing taxa as species or subspecies was a matter of opinion.

SOME VARIATION IN SALICORNIA AND ITS SIGNIFICANCE
(Exhibit)

D. H. DALBY (University College, London)

The number and nature of the taxa recognised within the annual section of the genus *Salicornia* in Britain have varied considerably according to the differing conceptions as to what constitutes a species in this difficult genus. The earliest workers considered there were but one or two species; subsequently the outlook has become more and more critical and the number of supposed species has risen sharply. This variable treatment of the group is a result of the fact that the various characters used in species discrimination show very few correlated discontinuities; in general variation is continuous between extremes. The main reason for this continuous variation appears to be the extreme plasticity of the plants in response to environmental factors.

Some of the effects of environment have so far been deduced from comparative field studies and from plants grown in standardised conditions. Small and more or less simple plants, usually markedly red when in fruit, and with few fertile segments, may be referred to as the *gracillima*-type (although it is not to be assumed that they are necessarily identical with Woods' *S. gracillima*). Such plants may grow in the densely colonised upper saltmarsh pans, whilst plants that are morphologically similar are often to be found along the upper margin of colonies bordering creeks, especially when the soil is rather sandy or stony. These plants probably represent the ultimately reduced condition in *Salicornia* induced by intense physical competition in the one instance, and by water shortage during the growing season in the other.

There is evidence also of environment having an important effect in determining whether a plant be erect or prostrate in its growth habit. When grown in saline mud in shallow tins, the progeny of about 15 plants showed little variation in growth habit when mature, even though two of the parent plants were prostrate. All the progeny were completely erect, or with a slightly bent or shortly decumbent portion below the bottom node. This bending is due to the seedling falling over at the cotyledonary stage. However, a third prostrate parent plant did produce progeny which were mostly prostrate, indicating that the procumbent habit may sometimes have a genetic basis.

Small colony differences can be detected in the field when the observer is familiar with the plants, although these differences may well be difficult or impossible to measure as they often concern such attributes as branching posture, shininess of the seg-

ment surface and subtle colour variations. The colonies so far examined in this study can be distinguished one from another by the biometrical treatment of certain characters, and it is likely that most colonies can be separated statistically if a variety of characters be used. Of necessity, the characters that can be treated biometrically are gross and rather crude, but they are none the less real. The colonies themselves, or the component parts of heterogeneous colonies, show varying degrees of separation for different reasons. Thus the separation may be due to the differences in chromosome number between diploid and tetraploid plants. It is often found that whilst the plants belonging most nearly to the *ramosissima*-type (occurring at the upper edge of a colony) prove to be diploid, those belonging to the *dolichostachya*-type (at the lower edge) are tetraploid. Another cause may be differences in flowering time, as sometimes occurs between the *stricta*-type and *ramosissima*-type plants, the former flowering perhaps a fortnight earlier than the latter. Allied to this is the marked variation in the relative times of expansion of the stigmatic lobes and the stamens. Many plants (as at Blakeney) are definitely protogynous, every flower having receptive stigmas but no externally visible anthers. Other plants (as on Hayling Island) have their anthers and stigmas maturing simultaneously and in mutual contact. In plants such as the latter, self pollination is very likely to occur and experimental evidence suggests that *Salicornia* is frequently autogamous. Seedlings from one parent plant usually resemble each other very closely, but differ from seedlings from other parent plants grown in similar conditions. The principal characters concerned here are time of germination, cotyledon size and shape, presence or absence of anthocyanin in the hypocotyl and number and origin of the primary branches.

Autogamy will lead to the production of pure lines, and must be considered as a cause of local population or colony differentiation. *Salicornia* has rather special requirements as far as its natural habits are concerned, namely a freedom from competition and a soil that is both saline and permanently moist. In Britain these habitats will occur naturally only along the coast, distributed in a discontinuous linear manner. Inter-colony gene exchange would thus be limited even if the plants were amphimictic. It seems very likely that it may be impossible to determine specific limits in this genus, as a result of polymorphism and breeding behaviour. Furthermore, rather than that they exist but are obscure, it is possible that these specific limits do not, in fact, exist at all. The exact interpretation of the species concept in such a group is not at all clear, and must await the results of detailed cytological and ecological investigation.

PROBLEMS OF SPECIATION IN THE BRITISH SPECIES OF ARUM
(Exhibit)
C. T. PRIME.

Two species of *Arum* are undoubtedly native to Britain, one *Arum maculatum* L., too well known to need description, and the other *A. neglectum* (Townsend) Ridley, an aptly named species which has not received the attention it deserves. It was formerly included under *A. italicum* Miller and was described as var. *neglectum* by Townsend, 1883, and later raised to specific rank by Ridley (1938). Whether it is really specifically distinct from *A. italicum,* and whether the *A. italicum* we find occasionally in this country is truly native, are two of the problems to which final solutions have not yet been found.

A. maculatum is a common plant of soils with a high base status, and it shows a wide range of variation. Some of this variation is associated with differences in chromosome number. The earliest chromosome count for the species is that of Schmucker (1925) who gives the number *c.* 32 for the diploid plant from German material. More recently Maude (1940) has given $2n = 56$ and $2n = 84$ for British material. The number $2n = 56$ has been confirmed for plants from all over the country. J. D. Lovis (unpub.) and H. G. Baker (1949) have also confirmed this figure, and it is certain that most of the plants in Great Britain are of this race. The plants with $2n = 84$ were recorded from Oxted and Merton, but despite repeated search have not been refound. To rediscover and study this rare plant is one of the first problems concerned with *A. maculatum* which await solution.
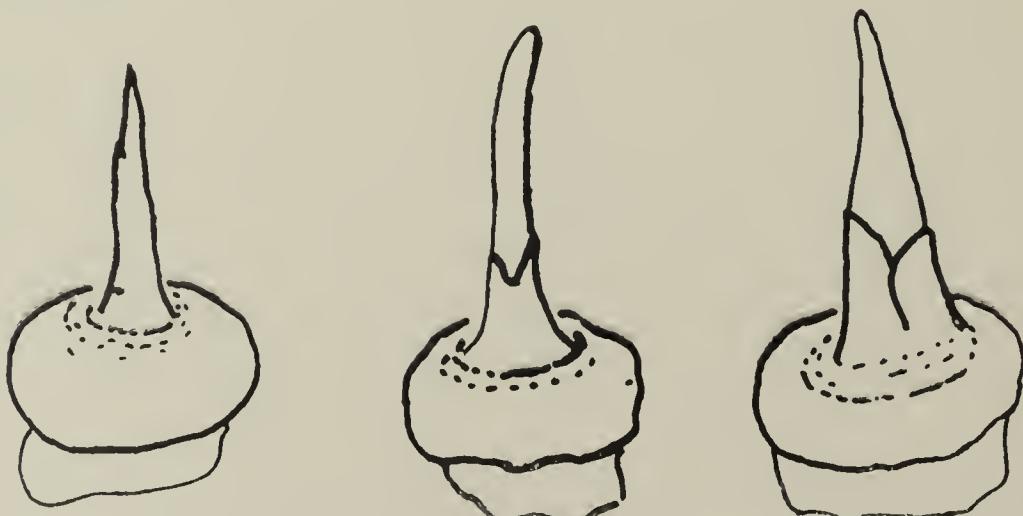
Fig. 22. *A. maculatum* corms ($2n = 28$) from Tubsong Storskov, Laaland.

Hagerup (1944) records plants with $2n = 28$. *A. maculatum* is rare or absent over most of Denmark except in woods in the south of Zeeland. These plants show several differences from

those of this country, differences confirmed by examination of herbarium material from Copenhagen. Firstly, the main shoot of the corm is centrally situated much as in the manner of a crocus corm, and not placed laterally as in most of the British plants (Fig. 22). The leaves of these plants are all unspotted and Dr. Hagerup tells me that plants with spotted leaves are virtually unknown in Denmark. The leaves are darker than the average, smaller, and show less hastate development when compared with leaves of British plants.

TABLE I.   LEAF SIZE IN DANISH AND ENGLISH *A. maculatum*.

	No. of leaves examined.	Av. length.	Width.	Length/width.
Denmark	70	8·8 cm.	6·6 cm.	1·2
England	74	10·2	5·4	1·9

The stomatal index is variable and within the range of British material. A few plants grown in this country have flowered and the ratio of the spathe length to the basal portion (that enclosing the flowers) was less than in *Arum maculatum* ($2n=56$) and the proportion of spadix to spathe length approximates more closely to that of *A. neglectum*.

TABLE II.   THE RELATIVE LENGTH OF SPATHE AND SPADIX IN *A. maculatum* ($2n=28$)

(data from Copenhagen herbarium material)

Length spathe	spadix
18·0 cm.	5·0 cm.
16·5	6·0
10·0	5·3
9·5	4·6
8·2	4·6
11·8	4·8
12·5	5·7
15·0	6·8
18·0	7·6
12·0	5·6
11·0	6·0
13·0	6·5
14·0	6·5
12·0	6·0
15·0	5·6

Average ratio 1 :   2·3
Average ratio in *A. maculatum* 1 :   3·3
Average ratio in *A. neglectum* 1 :   2·6

The spadix is a uniform cylinder unlike those of the "56" race where the base is always slightly wider than the tip (Fig. 23).

Fig. 23.   The shapes of the spadices of *A. maculatum* $2n=28$ (left) and $2n=56$ (right).

The inflorescence axis bears three to four rows of sterile males as in the "56" race, but there are 1-2 rows of sterile females whereas there is usually only one row in the "56" race. This latter difference seems to be confirmed by the herbarium material. The pollen grains are the same size in the two races.

Three plants of the Danish race were pollinated in 1951 with pollen from the "56" race and set viable seed. So far (1954) in time of appearance, size of leaf and other characters the seedlings appear indistinguishable from those of the "56" race sown at the same time.

The Danish habitats seem to be similar to those of this country. In one beechwood there was a shrub layer of *Corylus avellana*, *Acer pseudoplatanus*, and *Sambucus nigra,* while the ground flora at the time of collection of the seed (July 31, 1952) included *Aegopodium podagraria* and *Circaea lutetiana*.   Another locality was in scrub consisting mostly of *Corylus avellana* growing near a pond.

The 28 chromosomes of this plant pair as bivalents only and meiosis is regular, so as a working hypothesis one may assume the basic number to be 14. On this assumption, the plants with $2n=56$ is a tetraploid and it behaves as an autotetraploid at meiosis. The plant with 84 chromosomes would be a hexaploid.

Arum maculatum $2n=28$ on the evidence given above constitutes a geographic subspecies and is to be described accordingly.

Finally, G. Malvesin-Fabre (1944) quotes *A. maculatum* as having 64 chromosomes but I have not as yet been able to trace the source of this reference.

To pass to the second species, *A. neglectum*. Firstly, it should be recognised that both this and *A. italicum* are very distinct plants from *A. maculatum*. *A. italicum* and *A. neglectum* are winter green species, being in full leaf by the end of October, while *A. maculatum* usually appears in the first week of February. There are several other distinct differences fully described elsewhere.   The two species rarely hybridise, but in one instance hybridity has been proved by cytological investigation (J. D. Lovis, unpub.).

A. italicum and *A. neglectum* are closely related species; *italicum* is distinguished by the narrow dark green shining leaves with widely diverging lobes and marked white veining. Further

it is a slightly larger plant and the fruits have 2-4 or 5 seeds, while *A. neglectum* usually has two or three. The chromosome number of the two species is the same ($2n = 84$) and the two plants are interfertile.

Ridley (1938) considered that *A. neglectum* was confined to the coast of N.W. France, the Channel Isles and south and west Britain. All *A. italicum* plants in this country he regarded as cultivated or escaped from cultivation. Recent searches show that the distribution does not conform to so simple a pattern (Prime, 1954 & 1955). *Arum neglectum* occurs on the Continent in districts other than north-west France and it is possible that isolated colonies of *A. italicum* in this country may be native. The most likely answer is that *Arum neglectum* becomes more common as one passes from south to north across the area of distribution of the two species, becoming the dominant and possibly the only native in Britain. On this evidence *Arum neglectum* should be relegated to the status of a geographical subspecies.

REFERENCES.

BAKER, H. G., 1946, see Sowter, F. A.. 1949.

HAGERUP, O., 1944, *Hereditas*, **30**, 152.

MAUDE, P. F., 1940, Chromosome numbers in some British Plants, *New Phyt.*, **39**, 17.

MALVESIN-FABRE, G., 1946, Remarques sur la phytogéographie et la biologie d'Arum italicum Mill. et d'A. maculatum L., *Proc. Soc. Linn. Bordeaux*, **93**, 112.

PRIME, C. T., 1954, Arum neglectum, *J. Ecol.*, **42**, 241.

PRIME, C. T., BUCKLE, O., & LOVIS, J. D., 1955. The distribution and ecology of Arum neglectum in Southern England, *Proc. B.S.B.I.*, **1**. 287.

RIDLEY. H. N., 1938, On Arum neglectum (Towns.) Ridley, *J. Bot.*. **76**, 144.

SCHMUCKER, TH, 1925, Beiträge zur Biologie und Physiologie von Arum maculatum. *Flora*, **18** and **19**, 460.

SOWTER, F. A., 1949, Arum maculatum, *J. Ecol.*, **37**, 207.

TOWNSEND, F., 1883, *Flora of Hampshire*. London.

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Dr. E. F. WARBURG pointed out that the count of $2n = 84$ for *Arum maculatum* might be due to a mistake, particularly as this was the number recorded for both *A. neglectum* and *A. italicum*.

SPECIES PROBLEMS IN RECENT SCANDINAVIAN WORKS ON GRASSES

A. MELDERIS (British Museum (Natural History)).

The species has long been regarded as a fundamental unit in taxonomy. Not only taxonomists, but also other biologists such as phyto- or zoo-geographers, geneticists, cytologists, physiologists and others, are concerned with it. All of them are studying organisms and using the nomenclatural system established by Linnaeus for classification or designation of plants or animals. According to this system, which is based on natural affinities between organisms, individuals are classified into various categories such as species, genera, families, etc., which are designated by names and described to facilitate identification. Botanical nomenclature is regulated by the International Code. Every plant (a member of a natural species) is denoted by a binomial or a biverbal name (taxonomic species) composed of the name of the genus and a specific epithet to which epithets of intraspecific categories (subspecies, varieties or forms) may be added. Classification, however, is a matter of individual opinion, and in many cases there is no agreement in the use of taxa (taxonomic units). The species of one botanist is the subspecies of another, a variety or form of a third. It is due to the fact that different workers studying material by different methods form different concepts of the taxonomic categories. Efforts to give a precise definition of the species have led to much discussion which is still going on.

The concept or definition of the species in Scandinavian literature has been the subject of many arguments and different opinions have been expressed. Thus, according to Du Rietz (1930), the species are "the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes". Size, polymorphy and amount of variation in characters have not been considered by him to be important bases for the delimitation of a species, which includes natural units of widely different kinds (cf. also Müntzing, Tedin & Turesson, 1931, Nannfeldt, 1935).

Turesson (1922a, b, 1929) has proposed a classification of plants based on the relationships between the genetical composition of populations and their environments (genecology). His basic unit is the ecotype, a group of biotypes which is recognizably distinct as a result of the selection of suitable hereditary forms by particular habitats. He introduced the term "ecospecies"—"an amphimict-population the constituents of which in nature produce vital and fertile descendants with each other, giving rise to

less vital or less sterile descendants in nature, however, when crossed with constituents of any other population". As examples of ecospecies, several species of *Phleum*, i.e., *P. pratense* L., *P. nodosum* L., *P. alpinum* L. and *P. commutatum* Gaud., could be mentioned (cf. Nordenskiöld, 1945). These species are morphologically close to one another, but genetically and cytologically are distinctly separated. They form a coenospecies, a group of ecospecies within the genus *Phleum*. Concepts of the categories proposed by Turesson have been further substantiated by Clausen, Keck and Hiesey (1940, 1945), Gregor and his collaborators (cf. Gregor, 1944, 1946), etc.

Nilsson (1930) has regarded the species as a circle of genotypes (a combination sphere), which, as a population, is approximately constant, but in crosses with other species does not intermix due to incompatibility of parental genomes and sterility or non-vitality of crossing products—hybrids (cf. also Turesson, 1931).

Recently Lamprecht (1949, 1953), in his discussion on the relation between the modern conventional species and the natural species, has pointed out that the conventional species has been used for various, quite different taxonomic categories, such as real or primary species, allopolyploids (addospecies), autoploids (superspecies), types with different structure of the chromosomes (mixtospecies), apomicts and ecotypes. The real species, according to him (1953), is "the totality of all biotypes, characterized by the same alleles of the interspecific genes", which causes simultaneously the morphological differences and the barrier of sterility between two real species. According to Lamprecht, it should be designated by a binary name, e.g., *Pisum sativum* L. Of the other five taxonomic categories mentioned above, which in Lamprecht's opinion should all be kept apart from the real species, only addospecies should be designated by a binary name, accompanied by the names of the species forming it, e.g., *Galeopsis tetrahit* L., adsp. *pubescens* Bess. + *speciosa* Mill. All other categories should be subordinated to the real species and Lamprecht has proposed the following designations for them: for the superspecies—*ssp.* (can be confused with the taxonomists' subspecies), e.g., *Empetrum nigrum* L. spp. *hermaphroditum* (Lge.) Hagerup ($4x$); for the mixtospecies—*mxsp.*, e.g., *Pisum sativum* L., mxsp. *abyssinicum* Braun; for the apomicts—*apom.*, e.g., *Taraxacum officinale* Web., apom. *aculeatum* Hagl. ($3x$); and for the ecotypes—*oect.*, e.g., *Lactuca canadensis* L., oect. *graminifolia* Michx. Unfortunately, only a small portion of the plant kingdom has been sufficiently investigated cytogenetically, physiologically, biochemically, ecologically and anatomically, and therefore it is difficult at present to come to a definite conclusion as to whether the nomenclatural system proposed by Lamprecht has advantages compared with the others. It seems, however, that this nomenclature cannot be considered as complete because, as pointed out by Lamprecht himself, overlapping between various categories can occur.

All definitions and concepts of species mentioned above are different but they have some substantial similarities. The comparison of these definitions reveals that their authors seem to agree that the species must consist of genetical systems of populations, which are separated from each other by complete, or at least sharp, discontinuities in morphological and physiological characteristics. These discontinuities are maintained in the following generations due to complete incompatibility or to the production of hybrids with much reduced fertility (cf. also Stebbins, 1950). I agree with Nannfeldt (1938), who says: "The scientific value of the species concept is often vastly overestimated in these discussions, for the whole hierarchy of taxonomical categories of higher and lower rank is a purely practical scheme. Nature is too rich in possibilities for allowing such definitions as leave no room to doubts or subjective opinions."

The present classification of grasses into species is based chiefly on morphological characters of the reproductive and vegetative organs. The structure and arrangement of spikelets and the great diversity in their shapes and peculiar modifications of their separate parts, especially lemmas and paleas, associated with the length of anthers, provide a greater variety of distinctive characters than the vegetative organs such as presence or absence of ligule, its type of leaf-sheath (free, with overlapping margins or tubular, with connate margins), nervation and shape of leaf-blades, peculiarities in formation of shoots (intravaginal or extravaginal), etc. In many instances, however, the morphological characters are insufficient for classification because distantly related species can possess similar spikelets, lemmas, anthers, ligules and leaf-blades. It has been proved that in some of these cases the anatomical characters of leaves can be of great value in classification. Thus, the structure of the epidermal cells of leaves, particularly the size and shape of these cells and shape
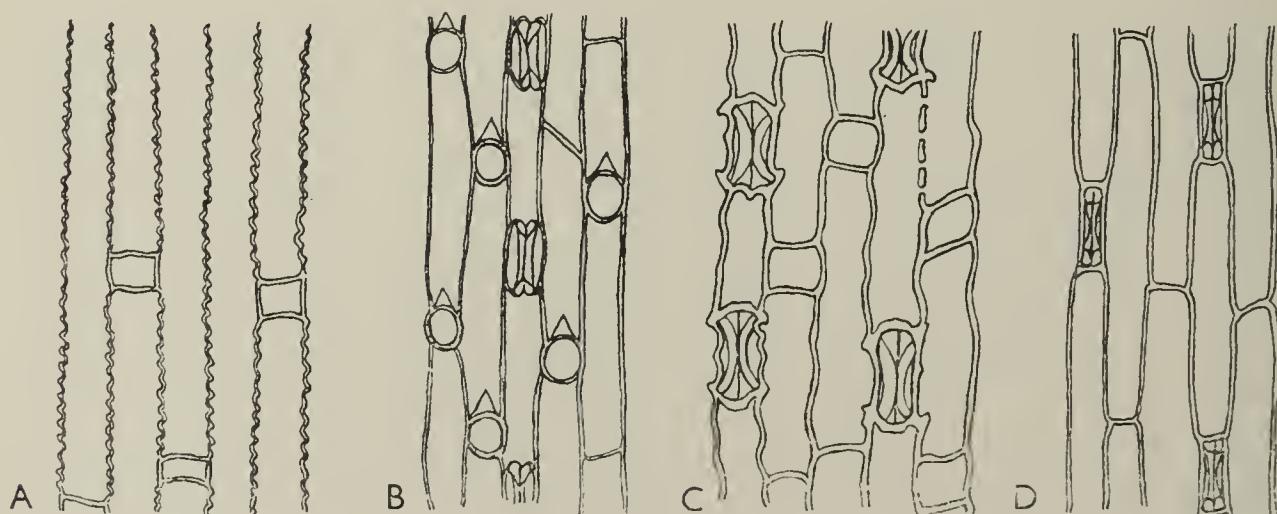
Fig. 24.

Lower epidermis of the leaf blade : A—*Hordeum secalinum* (from Bottesford, E. F. Linton, 2.viii.1877), B—*H. brachyantherum* (from Saskatchewan, A. J. Breitung, 4671), C—*Sesleria coerulea* ssp. *calcarea* Hegi (from banks of Tees A. J. Wilmott, 2020). D—*S. coerulea* ssp. *uliginosa* (from Södermanland, E. Asplund, 11.vi.1915).

of their walls, is fairly constant and characteristic in many species, e.g. of the genera *Hordeum* and *Sesleria* (Fig. 24). Also the presence or absence of paired siliceous and suberised cells and the disposition of the siliceous cells in the epidermis over the nerves can be used as distinctive characters in the separation of several species within the same genus, e.g. to separate European *Hordeum secalinum* Schreb. (*H. nodosum* L. pro parte) from the closely allied Californian *H. californicum* Covas & Stebbins and N. American *H. brachyantherum* Nevski. The arrangement of the vascular bundles and the disposition of sclerenchyma have been proved to be valuable characters to distinguish taxa in the genus *Festuca*. Results of cytogenetic research as well as data obtained in ecological and phyto-geographical studies have given agrostologists many important indications regarding the separation and relationship of species.

The value of distinctive characters in grasses, as in other plants, is measured by their constancy. A comparison of the characters used for distinguishing species shows that the taxonomic value of these characters varies from genus to genus. Those characters which are rather constant among species of one genus may be variable in species of another, particularly the absence or presence of awn or of pubescence on the lemma. Thus, species in the genera *Poa* and *Puccinellia* are awnless, but in the genera *Agrostis, Festuca, Lolium,* etc. the awned species usually have awnless forms or vice versa. In some other cases, species with typically glabrous lemmas have forms with hairy lemmas, e.g. *Bromus erectus* Huds., *B. sterilis* L., *B. secalinus* L. and *B. lepidus* Holmb., *Festuca rubra* L. and *F. ovina* L., etc. This parallelism is not confined only to the characters of the lemma, but appears sometimes also in the shape of inflorescence (panicle contracted or open), in the length of the ligule, in the presence or absence of pubescence on culms, leaf-sheaths or leaf-blades. In the older Floras such grasses aberrant in single characters were described as varieties or forms. The taxa have, however, no scientific value. A few extreme forms do not exhibit the pattern of variability sufficiently within a certain species. On the other hand, such forms may provide valuable material for genetical studies (e.g. of gene frequency or of mutation rates in nature).

During the last ten years the attention of several Scandinavian botanists has been turned to the study of variation within some polymorphic and critical genera of grasses, such as *Calamagrostis, Poa, Deschampsia, Phleum, Agrostis,* etc. Various methods of modern taxonomy have been used to solve problems involving the origin, delimitation and relationship of the species and variation within the species. Many interesting results have been obtained, on which Hylander (1953) based his treatment of corresponding genera in his recently published northern Flora. Much interest has been paid also to the study of plant distribution in Scandinavia which resulted in Hultén's (1950) comprehensive *Atlas of the distribution of vascular plants in N.W. Europe* with

maps for every species, including grasses. Data of the cytological investigations have been compiled by Löve and Löve (1948).

A short account of species problems in recent Scandinavian works on grasses, which may be of some interest in relation to those species occurring in Britain, is given below.

Calamagrostis. As shown by Nygren (1946), this genus contains amphimictic (sexual) and apomictic (producing seeds asexually) species. In Scandinavia the sexual species are the following: *C. arundinacea* (L.) Roth, *C. canescens* (Web.) Roth, *C. stricta* (Timm) Koel. (*C. neglecta* Gaertn., Mey. & Scherb.), *C. varia* (Schrad.) Host and *C. epigejos* (L.) Roth, of which the first four are tetraploids ($2n=28$), while *C. epigejos* consists of tetraploid, hexaploid and octoploid forms ($2n=28, 42, 56$). These species are characterized by usually X-shaped, dehiscent anthers with well developed pollen. They hybridize one with another and produce more or less intermediate hybrids, which can be recognized by I-shaped, indehiscent anthers with more or less badly developed pollen. They do not form seeds. The apomictic species in Scandinavia are represented by *C. chalybea* (Laest.) Fr. ($2n=42$), *C. lapponica* (Wahlenb.) Hartm. ($2n=42\text{-}112$) and *C. purpurea* (Trin.) Trin. ($2n=56\text{-}91$), which all have usually I-shaped anthers. Pollen formation has not been observed in *C. chalybea,* but occasionally or very rarely it can occur in *C. lapponica* and *C. purpurea*. According to Nygren, the apomixis within this genus has arisen as a consequence of intra- and interspecific hybridization in combination with polyploidy. He has obtained apomicts in crosses between sexual species. Thus, in *C. epigejos* ($2n=56$), an apomictic hybrid with a chromosome number $2n=42$ has been obtained. In the second generation this hybrid has given several plants with a chromosome number varying from $2n=35$ to $2n=72$. Some descendants with chromosome numbers $2n=35, 37$ and 38 resembled *C. varia* (cf. Nygren, 1948b). Another apomict with a chromosome number $2n=56$, resembling apomictic *C. purpurea,* has been synthesized by Nygren (1946, 1948a) in a cross between tetraploid *C. canescens* ($2n=28$) and hexaploid *C. epigejos* ($2n=42$). Nygren (1946) has also succeeded in obtaining *C. purpurea* by colchicine treatment of seeds of *C. canescens*.

C. purpurea is the most polymorphic species in Scandinavia. Some of its types show remarkable similarities to *C. canescens,* while others approach in some respects to hybrids between *C. canescens,* on the one hand, and *C. arundinacea, C. epigejos* and *C. stricta,* on the other. Its types with a high chromosome number produce hybrids with tetraploid sexual species (cf. Nygren, 1948a). The chromosome number in these hybrids is usually $2n=70$, which, according to Nygren, means that unreduced gametes of *C. purpurea* with 56 chromosomes have fused with reduced gametes with 14 chromosomes from a sexual species. The behaviour of these hybrids is similar to that of *C. purpurea,*

and it is very difficult to distinguish them from each other. In his further experiments with *C. purpurea,* Nygren (1949b, 1951) has discovered also some facultatively apomictic types with pollen formation in this species. They behave, however, differently with regard to their ability to produce new types. Some of them can increase the variation within the genus by self-fertilization, followed by segregation, or by hybridization with sexual species.

The origin of *C. chalybea* is not clear. According to Nygren (1946, 1948b), it may have arisen from some derivatives of the hybrid *C. arundinacea* × *C. canescens* or from a population of the Central Asiatic sexual species *C. obtusata* Trin., with which it has previously been confused in Scandinavia.

C. lapponica is more uniform than the other apomictic species but it forms some types which show a close affinity to *C. stricta* and some of its hybrids.

The situation within the genus is interpreted by Nygren (1951) as follows: "The combination of sexuality and apomixis in *Calamagrostis* makes possible a formation of a higher number of distinct forms in nature than does the usual sexual process. The facultative apomictic strains are able to perpetuate themselves by diplospory at the same time as they give rise to new biotypes by hybridizing with other facultative strains or with other species. environments different from those to which *purpurea* is adapted. to climates outside its range. When the distribution areas of the different species overlap new forms will arise which are fitted to environments different from those to which purpurea is adapted. In this way the species complex may be able to spread into new areas. In the case of *C. purpurea* it is not possible to keep the sexual and the apomictic formation of biotypes apart as has been done by several authors in other material. The two processes sometimes occur separately, but they often intermix, and in such cases great variation will be the final result."

The British species of *Calamagrostis,* i.e., *C. epigejos, C. canescens, C. stricta* and *C. scotica* (Druce) Druce have not been studied cytogenetically as yet, but a similar situation may be expected also here. *C. scotica,* which is a very rare species, occurring in bogs in the northern part of Caithness (Scotland), has been the subject of discussion (cf. Hubbard, 1954). According to Bennett (1885, 1886), it was considered to be identical with Scandinavian *C. lapponica, C. stricta* or *C.* × *strigosa* (Wg.) Hartm., which is now recognised as a hybrid between *C. epigejos* and *C. neglecta.* Hackel, who saw this grass, rejected it as *C.* × *strigosa,* and Druce, therefore, referred it as a separate variety to *C. stricta* (*Deyeuxia neglecta*) (cf. Druce, 1915) and later raised it to specific rank (Druce, 1926). On examining specimens of *C. scotica* at the British Museum, the author has observed that a portion of their pollen is angular, shrivelled, lacking plasma, although many anthers are more or less X-shaped and dehiscent. Cytogenetic studies may give some valuable indications regarding the origin of this taxon. It should be noted also, that two striking forms

with features of *C. purpurea* have been collected by Mr. E. C. Wallace in Scotland (Braemar) and by Miss M. I. Tetley in Westmorland (Esthwaite). They have broader leaves than in *C. canescens*, a long ligule, shortly pubescent spikelets and narrow, yellow, I-shaped anthers with badly developed pollen. These forms, as well as those resembling a hybrid between *C. canescens* and *C. stricta* (F. E. Crackles, 1953), are in need of further critical study based on cytogenetic investigations.

Poa. This genus has been a subject of extensive studies for a long time, chiefly due to the economic importance of *Poa pratensis* s. lat. It has been found that several species have apomictic facultatively sexual and sexual types and are characterized by a very wide variation in the chromosome number* (cf. Gustafsson, 1947, for references).

As shown by Nannfeldt (1935), the section *Stoloniferae,* which in Scandinavia is represented by *P. pratensis* s. lat. and *P. arctica* R. Br. (not found in Britain), is very polymorphic and seems hardly to contain any uniform species which can be sharply distinguished. In Scandinavia the members of this section hybridize with some species of other sections, i.e., *P. alpina* L. of the sect. *Sub-bulbosae* and *P. flexuosa* Sm. of the sect. *Oreinos,* which both occur also in Britain.

P. pratensis s. lat. in Scandinavia is classified into four distinct ecological subspecies, namely ssp. *pratensis* with a chromosome number $2n = 50$-124, ssp. *angustifolia* (L.) Lindb. fil. with $2n = 50$-65, ssp *irrigata* (Lindm.) Lindb. fil. (*P. subcaerulea* Sm., *P. irrigata* Lindm.) with $2n = 48$-95 (in Scandinavian material) and ssp. *alpigena* (Fr.) Hiitonen, with $2n = 48$-92, which all are regarded by some taxonomists as separate species. British specimens of "*P. pratensis* ssp. *alpigena*", examined by the author, proved to belong to various mountain forms of *P. subcaerulea,* which is closely allied to ssp. *alpigena.* It seems that the true ssp. *alpigena* has not been recorded from Britain as yet. The glumes of *P. subcoerulea* are 3-nerved as in ssp. *alpigena,* but they are longer and more· acuminate. In addition, the inflorescence of *P. subcoerulea* is open, not contracted as in ssp. *alpigena,* and the spikelets larger. The British *P. subcaerulea,* which exists in many closely related forms occupying ecologically quite different situations such as sea-shores, dune-slacks between dunes, mountains, etc., unfortunately, has not been studied morphologically, ecologically, cytologically or embryologically as yet. The embryological situation in the British forms may be similar to that of Icelandic forms investigated by Löve (1952). The development of seeds in Icelandic *P. subcaerulea* ($2n = 82$-147), according to him, is mainly aposporous, associated with pseudogamy as in *P. pratensis.* Occasionally, possibly only in plants with a lower

*It is interesting to note that Hedberg (1952) has found a small variation in the chromosome number $2n =$ up to 42) in members of the genus *Poa* growing in East African mountains. All species there seem to be sexual in contrast to the species occurring in the boreal and arctic regions.

chromosome number, the seeds are formed also in the normal sexual way, after the fertilization of aposporous egg cells. In addition, in *P. pratensis,* egg cells with a reduced number of chromosomes are involved in the seed formation. Löve (1950) has obtained no indication that a reduction division takes place at the formation of egg cells in Icelandic *P. subcaerulea.* *P. pratensis,* on the contrary, has a reduction division, and therefore seeds can be formed also after the fertilization, either by aposporous egg cells or egg cells having a reduced chromosome number.

The polymorphic *P. arctica,* with a chromosome number $2n = 39\text{-}92$ (in Scandinavian plants), according to Nannfeldt (1940), contains only a few types with distinct and constant characters, in contrast to numerous forms with indistinct features, the limits of which are not sharply defined. These constant apomictic types were originally separated by him as subspecies, but later on (cf. Hylander, 1941, 1945) they were reduced by him to varietal rank, because the whole bulk of the forms has not been sufficiently studied to divide it into similar types. Three of them, namely var. *depauperata* (Fr.) Nannf., var. *elongata* (Blytt) Nannf. and viviparous var. *stricta* (Lindeb.) Nannf. are restricted to a limited area in Dovre mountains (in Middle Norway). Two other varieties have been found in the mountains of N. Scandinavia, i.e., var. *tromsensis* (Nannf.) Nannf. on the Mt. Fløya (N. Norway) and var. *microglumis* (Nannf.) in Signaldalen (N. Norway) and in eight localities in Lule Lappmark and Torne Lappmark (N. Sweden). Var. *caespitans* (Simm.) Nannf., occurring on Mt. Høgtinden (N. Norway) and at Nissontjårro and Kaisepakte (N. Sweden), has a wide distribution in the Arctic, from Novaya Zemlya in the East to Baffin Land and Ellesmereland in the West (cf. Nannfeldt, 1940).

Recently Nygren (1950a, b), who has studied the cytology and embryology of the Scandinavian mountain species of *Poa,* has come to some interesting conclusions regarding their polymorphy. According to him, viviparous and non-viviparous *P. alpina* have a varying chromosome number $2n = 31\text{-}57$ (in the British viviparous *P. alpina* only $2n = 35$ has hitherto been reported). The non-viviparous form has been found to be sexual. The viviparous form propagates only by bulbils, but produces pollen and can cross with the other species growing in its range (cf. Nannfeldt, 1940; Melderis, 1953). *P. flexuosa,* which has been separated by Nannfeldt (1935) from *P. laxa* Haenke of the Alps, is a sexual species with $2n = 42$ and sets very good seed. It forms with viviparous *P. alpina* a hybrid *P.* × *jemtlandica* (Almq.) Richt. which is so far recorded from Scandinavia, Scotland (Ben Nevis and Lochnagar) and Iceland. Its chromosome number $2n = 37$ (in Scandinavian material) indicates that it may have arisen by a fusion of a reduced female gamete ($n = 21$) of *P. flexuosa* with a male gamete ($n = 16$) of viviparous *P. alpina* (cf. Nygren, 1950a). This hybrid is morphologically uniform, viviparous,

sexual as to the embryo-sacs, but does not give seeds. The pollen is very poor. The embryology of non-viviparous, as well as that of viviparous *P. pratensis* ssp. *alpigena* with a chromosome number $2n = 38\text{-}81$ (recently found on Mt. Päldsa (N. Sweden)) is similar to that of the typical *P. pratensis*. The viviparous type of ssp. *alpigena* forms morphologically good pollen which is able to fertilize egg cells of non-viviparous ssp. *alpigena* or those of other species. It is possible that some hybrids in the Päldsa district may have arisen from a crossing between viviparous ssp. *alpigena* and non-viviparous *P. alpina*. A hybrid between non-viviparous ssp. *alpigena* and viviparous *P. alpina* (*P. × herjedalica* H. Smith) is not rare in Scandinavian mountains. It is viviparous and has forms with a chromosome number $2n = 47\text{-}80$. As it produces good pollen and many give seeds in a sexual or in an aposporous way, Nygren (1950a) presumes that it may be recombined in the offspring of secondary hybrids or from their derivatives. *P. arctica* var. *depauperata* and var. *elongata,* according to Nygren (1950a, b), have a chromosome number varying between $2n = 75$ and $2n = 79$ in the former, and between $2n = 68$ and $2n = 76$ in the latter. Both varieties form rather poor pollen and aposporous embryo-sacs. They cannot as mother plants give hybrids with other species of *Poa* due to a selective mechanism of an early first division of the egg cells. Var. *microglumis* with $2n = 68\text{-}82$ has well developed pollen. Although it is aposporous, the hybrids with other species can be produced with it as a mother plant. Var. *caespitans* is aposporous and sexual. It is characterized by a chromosome number $2n = 56$ and by completely barren anthers. It can give hybrids which may be persistent by propagation in an asexual way. The viviparous var. *stricta**, with a chromosome number $2n = 39$, has a sexual development of the embryo-sac. According to Nannfeldt (1940) and Nygren (1950a, b), it must be regarded as a relict of a very old sexual population which seems to have survived the last glaciation in Scandinavia. A recently discovered hybrid between viviparous *P. alpina* and *P. arctica* has a similar embryology to *P. × jemtlandica* mentioned above.

On the basis of results obtained in his studies, Nygren (1950a, b) has pointed out that polymorphy in the genus *Poa* is due to the hybridization processes accompanied by apomixis, as in *Calamagrostis,* and vivipary as well (cf. also Melderis, 1953). Numerous viviparous and non-viviparous types occurring in the Scandinavian mountains and in the Arctic have arisen from crossings between apomictic, facultatively sexual and sexual forms. The formation of new types seems to be still in progress. Repeated crossings increase the variability within the genus and level the limits between the species and types. Only pure apomicts will remain sharply differentiated. There are many types which cannot be kept apart. A portion of types arising from these processes can propagate only by vegetative means

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*Its taxonomic status has been recently discussed by Nordhagen (1954).

(bulbils, rhizomes, etc.), whilst the others reproduce by seeds formed in an asexual or in a sexual way.

In the British mountain flora, *P. subcaerulea* on the one hand, and *P. glauca* with *P. nemoralis* on the other, exhibit a great variation in their external morphology. Viviparous and non-viviparous *P. alpina, P. flexuosa* and the hybrid *P.* × *jemtlandica,* which are all rare, seem to be more uniform.

The hybridogenous origin of *P. pratensis* has been pointed out by Clausen, Grun, Nygren and Nobs (1951), when they discussed some constant new plants, resembling *P. pratensis,* which were obtained in sexual, segregating progenies of hybrids between *P. pratensis* and some American species, e.g. *P. ampla* Merr. and *P. scabrella* (Thurb.) Benth. According to them, *P. pratensis* during its evolution and distribution may have absorbed genomes from several species.

Åkerberg and Bingefors (1953) have observed from a third generation (F_3) offspring among plants with $2n = 60\text{-}78$ a sub-haploid plant with $2n = 16$. This offspring has been derived from a second generation (F_2) plant with $2n = 75$, the parents of the original cross being apomictic *P. pratensis* s. lat. with $2n = 50$ and apomictic *P. alpina* with $2n = 37$. This plant was morphologically very similar to *P. trivialis* L., and resembled another subhaploid plant with $2n = 18$ obtained by Kiellander (1942). Kiellander has indicated that *P. trivialis* may be one of the plants which have taken part in the formation of *P. pratensis.*

Nannfeldt (1940), who is also in favour of the assumption of hybridogenous origin of *P. pratensis* and *P. arctica* as well, has mentioned, on the contrary, that their parents might not be among any existing species.

It is interesting to note that the hybrid origin of another species of *Poa,* namely tetraploid *P. annua* L. (cf. Nannfeldt, 1937; Tutin, 1951), has recently been confirmed by Tutin (1953), who has synthesized tetraploid plants $(2n = 28)$ with morphological features of *P. annua* from a cross between two diploid species, viz. annual *P. infirma* Kunth $(2n = 14)$ with perennial *P. supina* Schrad. (not found in Britain as yet).

Deschampsia. The distinguishing of *D. cespitosa* (L.) Beauv. $(2n = 26)$ from *D. alpina* (L.) Roem. & Schult. $(2n = 26, 39, 41, 48, 49, 52)$ in some cases is remarkably difficult (cf. Hylander, 1953). Both have a basic chromosome number 13 in contrast to 7 in other species, e.g., *D. setacea* (Huds.) Hack. $(2n = 14)$, *D. flexuosa* (L.) Trin. $(2n = 28)$ and *D. bottnica* (Wg.) Trin. $(2n = 28)$. The characters usually given in the keys for separation of *D. cespitosa* from *D. alpina* are the following: in *D. cespitosa* the spikelets are usually non-viviparous, the awn is inserted at the base of the lemma and the branchlets of the panicle are scabrous; in *D. alpina* the spikelets are usually viviparous, the awn is inserted at about the middle of the lemma or higher and the branchlets are smooth. The occurrence of a viviparous form in *D. cespitosa*

makes them very difficult to distinguish. In metamorphosis of the spikelets in this species the awn is shifted upwards and it may occupy the position which is characteristic for *D. alpina*. Also the roughness of the branchlets in some cases is proved not to be a constant character. Thus, I have seen a viviparous *D. cespitosa* from Coire-an-Lochan in Easterness (Scotland) which has quite glabrous panicle-branchlets. The insertion of the awn in these specimens varies from the basal up to a nearly apical position in the spikelets of the same panicle.

According to Nygren (1949a), the vivipary is genetically fixed and its occurrence is due to a change of the normal life rhythm, e.g., variations in the length of day. It has been observed that an increase in the number of chromosomes is accompanied by an increase in the degree of vivipary. Thus, a race of *D. alpina* with $2n = 26$ from Herjedalen (Middle Sweden) is non-viviparous, sexual and produces seeds. A race with $2n = 39$ from Spitsbergen has weakly developed bulbils and can also produce seeds (cf. Flovik, 1938). Races with $2n = 41$ and more are viviparous. Nygren is in favour of the assumption that these chromosome races are polyploid derivatives of *D. cespitosa*. Non-viviparous *D. alpina* from Herjedalen, mentioned above, in its external morphology can be referred either to *D. alpina* or to *D. cespitosa*. The two species are closely allied and at present no essential characters are known for separating their viviparous forms. The British viviparous forms of *Deschampsia* have been discussed by Wycherley (1953).

Phleum. In Scandinavia this genus is represented by the same species as in the British Isles: *P. phleoides* (L.) Karst. ($2n = 14$, 28), *P. arenarium* L. ($2n = 14$), both of the section *Chilochloa*, *P. pratense* L. ($2n = 42$), *P. nodosum* L. ($2n = 14$) and *P. commutatum* Gaud. ($2n = 28$, 56), all of the section *Euphleum*. *P. commutatum* was included in older floras, both in Scandinavia and in Britain, under *P. alpinum* L. ($2n = 14$), which is restricted to the mountains of Central and South Europe and differs from *P. commutatum* in chromosome number and in the hairy awns of the glumes.

Horn af Rantzien (1946), who studied the taxonomy and distribution of *P. arenarium,* has found that this species exhibits only small variation in some morphological characters which are not essential from the taxonomic point of view. In its northern distribution this species is sharply differentiated from the other member of the same section—*P. phleoides*; but this is not so in the Mediterranean area, where many forms of various related species, showing a great ecological and morphological resemblance, have been observed.

Nordenskiöld (1945) has tried to elucidate the origin of the cultivated hexaploid *P. pratense* and its relationship to the allied species such as *P. nodosum, P. alpinum* and *P. commutatum*. All these species are morphologically closely related and they

have been treated by some authors, e.g., Ascherson & Graebner (1899), as a single collective species. Some others, e.g., Druce (1932), Ovczinnikov (1934), have divided this collective species into two species, namely *P. pratense* (incl. *P. pratense* s. str. and *P. nodosum*) and *P. alpinum* (incl. *P. alpinum* s. str. and *P. commutatum*). The interspecific crossing experiments carried out by Miss Nordenskiöld showed that these species are distinctly separated genetically. The results of the crosses are given in a table below*:

Combinations	Hybrids in F₁ (first generation)		
	Chromosome numbers (2n)	Fertility Pollen	Seed-setting
prat. 42 × *nod.* 14	28 (int.), 35 (*prat.*-like)	good	good
nod. 14 × *prat.* 42	35, 49 (both *prat.*-like)	good	good
nod. 21** × *prat.* 42	around 42 (*prat.*-like)	good	good
alp. 14 × *prat.* 42	35 (int.), 49 (*alp.*-like)	good	good
prat. 42 × *alp.* 14	——	—	—
prat. 42 × *com.* 28	35 (int.)	st.	poor
com. 28 × *prat.* 42	49 (nearly int., more like *com.*)	st.	poor
prat. 42 × *com.* 56***	49 (nearly int., more like *com.*)	st.	poor
nod. 14 × *alp.* 14	14, 21 (both *alp.*-like)	poor	poor
alp. 14 × *nod.* 14	14 (*alp.*-like)	poor	poor
nod. 14 × *com.* 28	21 (int.)	st.	st.
nod. 14 × *com.* 56***	42 (more like *com.*)	good	not abundant
com. 28 × *nod.* 14	21 (int.)	st.	st.
nod. 21 × *nod.* 14	20 (*nod.*-like)	st.	st.
alp. 14 × *com.* 28	21 (int.)	st.	st.
com. 28 × *alp.* 14	21 (int.)	st.	st.

*Abbreviations : *prat.* = *P. pratense*; *nod.* = *P. nodosum*; *alp.* = *P. alpinum*; *com.* = *P. commutatum*; int. = intermediate; st. = sterile; — = unsuccessful cross. Numbers after specific names refer to the chromosome numbers (2n). Indications of the morphological features of the hybrids are enclosed in brackets after chromosome numbers.

**Triploid *P. nodosum* (2n=21) has been obtained in the progeny of a male-sterile *P. nodosum* crossed with the typical form.

***Octoploid *P. commutatum* (2n=56) has been found in an offspring of tetraploid *P. commutatum* from Lapland (N. Sweden). It resembles the typical form, but is somewhat robust but not so tall in growth.

According to Miss Nordenskiöld, *P. pratense, P. nodosum* and *P. alpinum* give fertile hybrids in crosses with one another, provided that gametes do not possess a too deviating chromosome number. The tetraploid *P. commutatum,* which shows resemblance in some morphological features to the diploid *P. alpinum,* is the most strongly differentiated and in crosses with the other species produces highly sterile hybrids. It seems to be allopolyploid, although none of the diploid species mentioned above can be considered to have taken a part in the formation of this species. The wide geographical range of this uniform species seems to indicate that it must be very old in spite its polyploidy. Miss Nordenskiöld (1949) has also succeeded in producing a hexaploid *P. nodosum* with features of *P. pratense* by repeated colchicine treatments of seeds and young seedlings of *P. nodosum,* followed by crosses between the polyploids obtained. A cross of this hexaploid *P. nodosum* with the typical *P. pratense* gave a good seed-setting. It indicates that *P. pratense* is closely allied to *P. nodosum* and that it may have arisen from the latter.

As result of Gregor & Sansome's (1930) and Gregor's (1931) experiments and her own Miss Nordenskiöld is in favour of keeping all the species in question apart. Hylander (1953), however, has treated *P. nodosum* as a subspecies under *P. pratense,* because morphologically it cannot always be easily distinguished from *P. pratense.* As regards *P. commutatum,* he has followed Miss Nordenskiöld, but he has pointed out that the discovery of a race of *P. alpinum* with features of *P. commutatum* in the Pyrenees has complicated the separation of these two species.

Roegneria. Interspecific hybrids within this genus are not uncommon in the northern part of Scandinavia, where the distribution ranges of these species overlap, and the species come together. In the hybridization processes the following species are involved there: long-awned *R. canina* (L.) Nevski, short-awned *R. mutabilis* (Drob.) Hyl., *R. borealis* (Turcz.) Nevski and *R. fibrosa** (Schrenk) Nevski, which are all tetraploids having $2n = 28$ (cf. Hylander. 1953). These hybrids are more or less intermediate in external morphology between their parents. Some of them are found only as scattered individuals in the fringing zone between the populations of the parent species. e.g., *R. borealis* × *R. canina* and *R. canina* × *R. fibrosa.* Their pollen has been found to be completely sterile. A recently recorded hybrid between *R. borealis* and *R. mutabilis* has about 80% of sterile pollen. Hybrids with *R. mutabilis* usually grow side by side with various morphologically different types, as observed by the author in Lapland and Norrbotten (N. Sweden). Experiments with an artificial hybrid between these species revealed that it is partially sterile and by back-crossing can give

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*The chromosome number $2n = 28$ has been found by the author in *R. fibrosa* (grown at Upsala from the seeds received from the Botanical Garden in Leningrad) and in *R. behmii* (from Jämtland).

rise to a hybrid swarm. The hybrid *R. borealis* × *R. canina* on the contrary seems to be highly sterile. It did not produce seeds after back-crossing. These facts may indicate that *R. mutabilis* is more closely allied to *R. canina* than is *R. borealis*. The recently described *R. behmii* Meld. ($2n=28$), from Jämtland (Middle Sweden), is closely related genetically to *R. canina*, but differs from the latter in several essential morphological characters, such as relatively shorter and broader leaves, an erect spike, the shape of the glumes, a short awn to the lemma, etc. An artificial hybrid between them, however, has been found to be fertile, with a low proportion of badly-developed pollen. It seems that Scottish *R. doniana* (F. B. White) Meld. has the same behaviour in relation to *R. canina* as has *R. behmii*. The intermediates collected by Mr. J. E. Raven and Dr. S. M. Walters at Inchnadamph in 1953 had well-developed pollen (cf. Raven & Walters, 1954).

Agrostis. Four native species of this genus are common both in Scandinavia and the British Isles. They are: *A. canina* L., *A. tenuis* Sibth., *A. gigantea* Roth and *A. stolonifera* L. These species have been investigated cytogenetically: Scandinavian material by Björkman (1951, 1954) and British material by Davies (1953) and Jones (1951, 1953).

Cytological evidence obtained by Björkman and Jones shows that Scandinavian and British forms of *A. canina* can be divided into two larger groups, which differ in chromosome numbers, ecology and shoot morphology. These are: var. *fascicularis* (Curt.) Sincl. and var. *arida* Schlecht., which have been considered by subsequent authors, e.g. Hylander (1953) and Hubbard (1954), as separate subspecies, the former as ssp. *canina* [ssp. *fascicularis* (Curt.) Hyl.] and the latter as ssp. *montana* Hartm. Ssp. *canina*, which is diploid ($2n=14$), has thin leaves, creeping leafy stolons and occurs in damp or wet situations. Björkman (1951) has discovered also a tetraploid and a triploid form in Scandinavian material, and he has assumed that they may have arisen due to unreduced gametes. Ssp. *montana* is a tetraploid ($2n=28$) with stiffer leaves and scaly underground rhizomes, forming dense tufts. It is a plant of dry habitats, e.g. heaths, grassy hills, mountains, on sandy soil, etc. A pentaploid form has been discovered by Björkman (1951) in material from N. Sweden. According to him, some transitional forms between these subspecies have been found *in situ*, but their chromosome number does not indicate that they are hybrids. Artificial hybrids with $2n=21$ have been obtained in crosses between the two subspecies. As shown by Davies, they are completely sterile.

A. stolonifera exhibits a greater variation in chromosome number. Of 900 plants of this species from different countries examined by Björkman (1954), about 600 plants were tetraploids ($2n=28$), 160 plants proved to be pentaploids ($2n=35$) and 135 plants turned out to be hexaploids ($2n=42$). In addition 2 plants with aneuploid numbers ($2n=33$ and 41) were found. In

spite of the fact that these races are cytogenetically distinct they seem not to possess any essential character for their separation. Also the ecology does not give any clue for their classification. According to Björkman, the pentaploid and hexaploid types have been found *in situ*, growing together or separately, side by side with the tetraploids or in localities where tetraploids were absent. All three chromosome numbers have been found in plants with sim lar external morphology.

Of the other species of *Agrostis*, *A. tenuis* has been detected to be tetraploid $(2n = 28)$, and *A. gigantea* is hexaploid $(2n = 42)$.

Artificial hybrids between Scandinavian or British species of *Agrostis* obtained by Davies and Björkman are shown in the table below.*

♀ \ ♂	can. $(2n=14)$	mont $(2n=28)$	ten. $(2n=28)$	stol. $(2n=28)$	stol. $(2n=35)$	stol. $(2n=42)$	gig. $(2n=42)$	bor. $(2n=56)$	sem. $(2n=28)$
can. $(2n=14)$		+	−	−			−	+	
mont. $(2n=28)$	+		+	−			−	+	
ten. $(2n=28)$	−	+		+			+		
stol. $(2n=28)$	−	+	+		+	+	+		+
$(2n=35)$		+							
$(2n=42)$									
gig. $(2n=42)$	−	−	+	+					
bor. $(2n=56)$		+							
sem. $(2n=28)$									

As shown by Davies, a hybrid between *A. tenuis* and *A. stolonifera* sets a low proportion of seed, but the plants of the first generation (F_1) from crosses *A. tenuis* × *A. gigantea* and *A. stolonifera* × *A. gigantea* are quite fertile. A hybrid between *A. canina* ssp. *montana* and *A. tenuis* is found to be moderately

*Abbreviations : can. = *Agrostis canina* ssp. *canina*; mont. = *A. canina* ssp. *montana*; ten. = *A. tenuis*; stol. = *A. stolonifera*; gig. = *A. gigantea*; bor. = *A. borealis* Hartm. (not found in Britain); sem. = *A. semiverticillata* (Forsk.) Christens.: + = successful cross; − = unsuccessful cross.

fertile and in the next generation it produces about half the number of both parent species.

The natural hybrids recorded from Scandinavia (cf. Hylander, 1953) and Britain (cf. Philipson, 1937, and Davies) are given in the following table·

Combinations	Scandinavia	Britain
A. canina × A. stolonifera	+	+
A. canina × A. gigantea	+	
A. canina × A. tenuis	+	+
A. gigantea × A. stolonifera		+
A. gigantea × A. tenuis	+	+
A. stolonifera × A. semiverticillata		+
A. stolonifera × A. tenuis	+	
A. borealis × A. stolonifera	+	
A. borealis × A. tenuis	+	
Agropogon littoralis (Sm.) C. E. Hubbard (Agrostis stolonifera × Polypogon monspeliensis)		+

Hybrids of *Agrostis* are not rare in nature and many more of them could be discovered if the wild populations were studied more carefully. Thus Björkman (1954) has found 33 natural hybrids between *A. gigantea* and *A. tenuis* in different localities, where the species grow together. Offspring of the hybrids can give rise to hybrid swarms which show great variation in the morphological pattern and in chromosome number, making the delimitation of the species difficult.

Anthoxanthum. Löve & Löve have found that *A. odoratum* L. in its northern range consists of two types which differ in minor morphological characters but are quite different in their cytology, one being diploid $(2n = 10)$ and the other tetraploid $(2n = 20 + 6f)$. They have separated the diploid type as a distinct species, *A. alpinum* Löve & Löve, from the tetraploid *A. odoratum*. *A. alpinum* has been hitherto recorded from Scandinavia, Switzerland, Iceland and Greenland (cf. Tutin, 1950). It differs from *A. odoratum* usually in narrower leaves of the vegetative shoots, shorter inflorescence, smaller spikelets, glabrous pedicels and glumes and a comparatively longer awn. *A. alpinum* from Greenland and Iceland seems to be distinct from *A. odoratum*, but according to Hylander (1953), there is some difficulty in separating these species in Scandinavian material.

It should be noted that polyploids occur rather widely among grasses in nature (cf. Stebbins, 1950; Heslop-Harrison, 1953). A portion of them is known or presumed to have arisen through hybridization by the addition of both sets of chromosomes from each parent species (amphipolyploidy, allopolyploidy), e.g.

Poa annua ($2n = 28$) from a cross between *P. infirma* ($2n = 14$) and *P. supina* ($2n = 14$) (see p. 00), *Spartina townsendii* H. & J. Groves ($2n = 126$), a product of the crossing *S. maritima* (Curt.) Fernald ($2n = 56$) and *S. alterniflora* Lois. ($2n = 70$) (cf. Huskins, 1930) and *Bromus diandrus* Roth (*B. gussonii* Parl.) ($2n = 56$) through hybridization between *B. rigidus* Roth ($2n = 42$) and *B. sterilis* L. ($2n = 14$) (cf. Cugnac & Camus, 1931); all of them are fertile.   Some other polyploids may have originated by the doubling or multiplication of the basic chromosome number in the non-hybrid plant (autopolyploidy), e.g. *Phleum pratense* ($2n = 42$) from *P. nodosum* ($2n = 14$) (see p. 152), *Dactylis glomerata* L. ($2n = 28$) from *D. aschersoniana* Graebn. ($2n = 14$) (cf. Müntzing, 1943), etc.

Morphologically, polyploids are difficult to separate from their progenitors and they differ from the latter chiefly in slight quantitative characters.   In many cases they are more vigorous in habit, darker green in colour, have larger spikelets and longer anthers.   In the identification of dried herbarium specimens size of stomata and pollen-grains often can provide valuable clues for the recognition of morphologically closely related diploids and their polyploid derivatives. Thus, e.g., according to Covas, 1949, the size of stomata in *H. secalinum* ($2n = 28$) is 44-50μ, in *H. californicum* ($2n = 14$) is 30-34μ, and in *H. brachyantherum* ($2n = 28$) is 42-48μ.   The size of pollen-grains in the same species is respecitvely 39-44μ, 32-36μ, and 39-44μ.

Genetically, on the contrary, polyploids are well distinguished: they are isolated from their progenitors usually by partial or complete sterility.   They can also be ecologically distinct.

Usually polyploids are treated taxonomically as separate species or subspecies based on the relative difference in the size of their various parts.   When it is not possible to find any essential morphological characters for their separation, polyploids are not classified as separate taxa, e.g. *Setaria glauca* (L.) Beauv. ($2n = 18$, 36, 72), *Sieglingia decumbens* (L.) Bernh. ($2n = 18$, 36, 124), *Calamagrostis epigejos* ($2n = 28$, 42, 56), *Agrostis stolonifera* ($2n = 28$, 35, 42), *Hierochloe odorata* (L.) Wahlenb. ($2n = 28$, 42, 56), *Bromus ramosus* Huds. ($2n = 14$, 28, 42), etc.

There is no doubt that experimental taxonomy greatly assists taxonomists in the solution of species problems involving delimitation, origin, relationship, etc.   Modern taxonomy must be based on close co-operation between all branches of biology.   It should be emphasized, however, that all such methods can reveal differences existing between plants but they cannot show which taxonomic rank should be given to a certain plant.   The final conclusion, which will be more objective if based on data obtained from many different sources of investigation, must be left to the taxonomist.

REFERENCES.

AKERBERG, E. & BINGEFORS, S., 1953, Progeny studies in the hybrid Poa pratensis × Poa alpina, *Hereditas*, **39**, 125-136.

ASCHERSON, P. & GRAEBNER, P., 1899, *Synopsis der mitteleuropäischen Flora*, **2/1**. Leipzig.

BENNETT, A., 1885, Calamagrostis strigosa Hartm. in Britain, *J. Bot.*, **23**, 253.

——, 1886, On Calamagrostis strigosa (Hartman) as a British plant and two Carex forms new to Scotland, &c., *Trans. & Proc. Bot. Soc., Edinb.*, **16**, 313-316.

BJÖRKMAN, S. O., 1951, Chromosome studies in Agrostis, *Hereditas*, **37**, 465-468.

——, 1954, Chromosome studies in Agrostis. II, *Hereditas*, **40**, 254-258.

CLAUSEN, J., GRUN, P., NYGREN, A. & NOBS, M., 1951, Genetics and evolution of Poa, *Carnegie Inst. Washington, Yearbook*, **50**, 109-111.

CLAUSEN, J., KECK, D. D. & HIESEY, W. M., 1940, Experimental studies on the nature of species. I. The effect of varied environments on western North American plants, *Carnegie Inst. Washington*, Publ. 520.

——, 1945, Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy, with examples from Madiinae, *Carnegie Inst. Washington*, Publ. 564.

COVAS, G., 1949, Taxonomic observations on the North American species of Hordeum, *Madroño*, **10**, 1-21.

CRACKLES, F. E., 1953, Calamagrostis stricta in S.E. Yorkshire, *B.S.B.I. Yearbook* **1953**, 54.

CUGNAC, A. & CAMUS, A., 1931, Révision du Bromus maximus Desf., d'après l'étude des peuplements naturels, *Bull. Soc. Bot. France*, **78**, 327-341.

DAVIES, W. E., 1953, The breeding affinities of some British species of Agrostis, *Brit. Agricult. Bull.*, **5**, 313-315.

DRUCE, G. C., 1915, Deyeuxia neglecta Kunth, var. scotica, *Rep. Bot. Soc. & E.C.*, **6**, 172.

——, 1926, Deyeuxia scotica Dr. in *Hayward's Botanist's Pocket-Book*. London.

——, 1932, *The Comital Flora of the British Isles*. Arbroath.

DU RIETZ, G. E., 1930, The fundamental units of biological taxonomy, *Svensk Bot. Tidskr.*, **24**, 333-420.

FLOVIK, K., 1938, Cytological studies of arctic grasses, *Hereditas*, **24**, 265-376.

GREGOR, J. W. & SANSOME, F. W., 1930, Experiments on the genetics of wild populations. II. Phleum pratense L. and the hybrid P. pratense L. × P. alpinum L., *J. Gen.*, **22**, 373-387.

GREGOR, J. W., 1931, Experimental delimitation of species, *New Phyt.*, **30**, 204-217.

——, 1944, The Ecotype, *Biol. Rev. Cambridge Phil. Soc.*, **19**, 20-30.

——, 1946, Ecotypic differentiation, *New Phyt.*, **45**, 254-270.

GUSTAFSSON, Å., 1947, Apomixis in higher plants. III. Biotype and species formation, *Lunds Univ. Årsskr.* N.F. Avd. 2, **44**.

HEDBERG, O., 1952, Cytological studies in East African mountain grasses, *Hereditas*, **38**, 256-266.

HESLOP-HARRISON, J., 1953, *New Concepts in Flowering-Plant Taxonomy*. London.

HORN AF RANTZIEN, H., 1946, Taxonomical and phytogeographical studies in Phleum arenarium L., *Bot. Notiser* **1946**, 364-386.

HULTÉN, E., 1950, *Atlas of the Distribution of Vascular Plants in N.W. Europe*. Stockholm.

HUSKINS, C. L., 1930, The origin of Spartina Townsendii, *Genetica*, **12**, 531-538.

HUBBARD, C. E., 1954, *Grasses*. London.

HYLANDER, N., 1941, *Förteckning över Skandinaviens växter*. Lund.

——, 1945, Nomenklatorische und systematische Studien über nordische Gefässpflanzen, *Uppsala Univ. Årsskr.*, **7**.

——, 1953, *Nordisk kärlväxterflora*. Stockholm.

JONES, K., 1951, Autotetraploidy in Agrostis canina, *Nature*, **169**, 159-160.

——, 1953, The cytology of some British species of Agrostis and their hybrids, *Brit. Agricult. Bull.*, **5**, 316.

KIELLANDER, C. L., 1942, A subhaploid P. pratensis L. with 18 chromosomes and its progeny, *Svensk Bot. Tidskr.*, **36**, 200-220.

LAMPRECHT, H., 1949, Systematik auf genetischer und zytologischer Grundlage, *Agri. Hort. Genetica*, **7**, 1-28.

——, 1953, Petunia axillaris (Lam.) B.S.P. und ihre Synonyme P. violacea Lindl. und P. inflata R. Fries, mit Betrachtungen zum konventionellen und naturbedingten Artbegriff, *ibid.*, **11**, 83-108.

LÖVE, A., 1952, Preparatory studies for breeding Icelandic Poa irrigata, *Hereditas*, **38**, 11-32.

LÖVE, A. & LÖVE, D., 1948, Chromosome numbers of Northern plant species, *Reykjavik Univ. Inst. Appl. Scien., Dep. of Agron. Rep. Ser. B.*, **3**, 1-131.

MELDERIS, A., 1953, Some parallels between the British and Scandinavian mountain floras, in *The Changing Flora of Britain*, (edit. J. E. Lousley), 89-104.

MÜNTZING, A., 1943, Characteristics of two haploid twins in Dactylis glomerata, *Hereditas*, **29**, 134-140.

MÜNTZING, A., TEDIN, O. & TURESSON, G., 1931, Field studies and experimental methods in taxonomy, *Hereditas*, **15**, 1-12.

NANNFELDT, J. A., 1935, Taxonomical and plant-geographical studies in Poa laxa group, *Symb. Bot. Upsal.*, **1/5**.

——, 1937, The chromosome numbers of Poa, sect. Ochlopoa A. & Gr. and their taxonomical significance, *Bot. Notiser*, **1937**, 238-254.

NANNFELDT, J. A., 1938, Poa maroccana Nannf. n. sp. and P. rivulorum Maire & Trabut, two more tetraploids of sect. Ochlopoa A. & Gr., and some additional notes on Ochlopoa, *Svensk Bot. Tidskr.*, **32**, 295-321.

——, 1940, On the polymorphy of Poa arctica R.Br., with special reference to its Scandinavian forms, *Symb. Bot. Upsal.*, **4**.

NILSSON, HERIBERT, N., 1930, Synthetische Bastardierungsversuche in der Gattung Salix, *Lunds Univ. Årsskr. N.F. Avd. 2*, **27/4**.

NORDENSKIÖLD, H., 1945, Cyto-genetic studies in the genus Phleum, *Acta Agricult. Suecana*, **1**, 1-138.

——, 1949, Synthesis of Phleum pratense L. from P. nodosum L., *Hereditas*, **35**, 190-202.

NORDHAGEN, R., 1954, Apologi för Poa stricta Lindeb., *Svensk Bot. Tidskr.*, **48**, 1-18.

NYGREN, A., 1946, The genesis of some Scandinavian species of Calamagrostis, *Hereditas*, **32**, 131-262.

——, 1948a, Further studies in spontaneous and synthetic Calamagrostis purpurea, *Hereditas*, **34**, 113-117.

——, 1948b, Some interspecific crosses in Calamagrostis and their evolutionary consequences, *Hereditas*, **34**, 387-413.

——, 1949a, Studies on vivipary in the genus Deschampsia, *Hereditas*, **35**, 27-32.

——, 1949b, Apomictic and sexual reproduction in Calamagrostis purpurea, *Hereditas*, **35**, 285-300.

——, 1950a, A preliminary note on cytological and embryological studies in arctic Poae, *Hereditas*, **36**, 231-232.

——, 1950b, Cytological and embryological studies in Arctic Poae, *Symb. Bot. Upsal.*, **10**.

——, 1951, Form and biotype formation in Calamagrostis purpurea, *Hereditas*, **37**, 519-532.

OVCZINNIKOV, P. N., 1934, Phleum, in Komarov, V. L., *Flora URSS*, **2**, 127-135.

PHILIPSON, W. R., 1937, A revision of the British species of the genus Agrostis Linn., *J. Linn. Soc. Lond. Bot.*, **51**, 73-151.

RAVEN, J. E. & WALTERS, S. M., 1954, The Inchnadamph Roegnerias, *Proc. Bot. Soc. Br. Isl.*, **1**, 88-89.

STEBBINS, G. L., Jr., 1950, *Variation and Evolution in Plants*. London.

TURESSON, G., 1922a, The species and the variety as ecological units, *Hereditas*, **3**, 110-113.

——, 1922b, The genotypical response of the plant species to the habitat, *Hereditas*, **3**, 211-350.

——, 1929, Zur Natur und Begrenzung der Arteinheiten, *Hereditas*, **12**, 323-333.

——, 1931, The geographical distribution of the alpine ecotype of some Eurasiatic plants, *Hereditas*, **15**, 329-346.

TUTIN, T. G., 1950, A note on species pairs in the Gramineae, *Watsonia*, **1**, 224-226.

——, 1951, Origin of Poa annua L., *Nature*, **169**, 160.

——, 1953, Poa annua and its parents, *B.S.B.I. Yearbook* **1953**, 60.

WYCHERLEY, P. R., 1953, Proliferation of spikelets in British grasses, *Watsonia*, **3**, 41-56.

THE CONFLICT OF CATEGORIES

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The year 1953 marked the 200th anniversary of the publication of Linnaeus's *Species Plantarum,* the work taken as the starting point, for the purposes of priority, of the present system of nomenclature for the higher plants. One of the principal reasons for accepting the *Species Plantarum* as a starting point is that in this work Linnaeus employed consistently binomial nomenclature, a system used sporadically by several of his predecessors, but not before exploited in a uniform and logical manner. This crystallisation of the system of nomenclature for living organisms is significant in a way not often stressed, for it indicates that the Linnaean concept of the species, itself leading back to that of Ray, has, on the whole, satisfactorily stood the test of time, and has proved applicable in a vastly greater field of organisms than was ever contemplated by Linnaeus himself.

Indeed, it is a matter of considerable biological interest that through two centuries the Linnaean taxonomic system should, with the occasional interpolation of intermediate categories, have served fairly adequately the needs of systematics. This in itself is an indication that the actual pattern of organic variation is for the most part of a form which can be fitted into a classificatory system composed of a hierarchy of categories. As various biologists have recognised, this means that a basic feature of the variation of living organisms is the existence of discontinuities at various levels. In Dobzhansky's words (1941), ". . . . the living world is not a single array of individuals . . . . but an array of more or less distinct separate arrays, intermediates between which are absent or at least rare. Each array is a cluster of individuals, usually possessing some common characteristics and gravitating to a definite modal point in their variations. Small clusters are grouped together into larger secondary ones, these into still larger ones, and so on in a hierarchical order."

Until relatively recently, systematists on the whole have simply accepted this state of affairs, and have not been seriously concerned with re-examining the basic assumptions about organic variation upon which their work depends. Energy has been devoted to the completion of the primary survey of the living kingdoms using the traditional methods, and discussion has been mainly directed towards the problems of codifying the rules governing nomenclature rather than towards any reassessment of fundamental principles. In the last half century, however, methods other than those of comparative morphology have been applied to the analysis of natural variation. Geneticists, cytologists and others, initially basing their investigations on

existing taxonomic arrangements, have not infrequently found these unsatisfactory, and have on occasions come to question the whole existing basis of taxonomic methodology (cf. Darlington, 1951). This has been particularly true in alliances where the rigid taxonomic framework does not fit too well, and where the criteria of classical taxonomy, derived mainly from comparative morphology, produce groupings at variance with those exposed by the methods of the newer disciplines.

It is naturally at and about the level of the average Linnaean species that these problems have mostly come into prominence—the level of variation with which the present conference is concerned. In this contribution, I wish to focus attention primarily upon one matter: how desirable or practicable it is for the basis of orthodox nomenclatural taxonomy to be modified to accommodate the newer conceptions of the sources and nature of organic variation. In the literature of the last two or three decades two divergent tendencies are apparent. Broadly these are as follows:—

1. To attempt to give the word "species" a particular genetical or biological meaning in sexual groups, and to convert the basis of orthodox (nomenclatural) taxonomy to establish the unit so defined as the sole one to bear the binomial, even if this should lead to the abandonment of some of the classical criteria of taxonomy;

2. To serve the ends of experimentalists by the formation of various special purpose classifications with distinctive categories and criteria wherever such are required within the framework of orthodox taxonomy, allowing the latter to develop and adapt its methods and species criteria to absorb such of the experimental data as may prove compatible with its functions and facilities, without necessarily abandoning its basis of comparative morphology.

The popularity of the first of these approaches is considerable, albeit mainly among non-taxonomists. The logic of the argument lying behind it is certainly persuasive, and indeed in some ways incontrovertible. In essence it runs as follows:—

(a) The taxonomic system currently in use, consisting of a hierarchy of categories, is workable only because of the existence of variational discontinuities in the array of living organisms.

(b) These variational discontinuities arise from certain genetical causes, the bulk of which appear now to be understood in some detail.

(c) The road, therefore, to a more "perfect" taxonomy is to take cognisance of the existence of this knowledge of causes, and to *define* taxonomic categories—particularly the fundamental one, the species—in terms of the basic biological properties which, in effect, provide the mandate for the existence of the variational units which are fitted into them.

The difficulty is, of course, that there is little or no agreement as to which biological property shall be given primary importance. Attempts at "genetical" definition of species are in no way new,

nor for that matter have they all arisen within the half-century life of the science of genetics. A primary attribute required of a species is that it "breed true", a genetical property as meaningful to Theophrastus as to any modern Drosophilist. However, if the requirement of genetical uniformity within a species, both between the individuals existing at a given time and in the lineage, is pushed to the extreme, the result is that the homozygous biotype becomes the only variational unit which can bear the name. This is the outcome of one line of reasoning, and preposterous as it may seem to us to-day, it was seriously put forward by one of the most distinguished geneticists of the early part of this century, Lotsy (1918). Such a concept is, obviously, untenable in any general application. There are no doubt many taxonomic plant species which fulfil the requirement, being essentially homozygous through many generations of autogamy; examples are to be found among our critical species of ephemerals, in *Capsella, Stellaria* and the like, in some annual groups, e.g., *Euphrasia* and probably *Salicornia,* and also among perennials like autogamous *Epipactis* and *Ophrys.* But with allogamous organisms, a genetical species concept such as that of Lotsy can have no meaning, for the processes of gene segregation and recombination ensure that all individuals will in effect be genetically different to some extent.

With these sexual outbreeding organisms, the species of taxonomy normally embraces an assemblage of morphologically similar but not necessarily identical individuals. The Lotsyan concept not being applicable to this situation, the geneticist naturally enquires what property these groups possess which preserves their unity and distinction from others. The answer generally found is, of course, some level of reproductive isolation. The idea that the limits of the morphologically recognisable species coincide largely with the boundaries beyond which hybridisation is impossible or productive of sterile offspring is also certainly an ancient one. It was apparent enough to Linnaeus, and Lindley, rather more than a century ago, penned a definition of the species in which this notion was given prominence.

This concept, also, can be given an extreme interpretation, and has indeed been given such by some workers in the last half century, primarily by geneticists who have accepted "specific differences" between two groups of organisms as being indicated only by a total—or practically total—*inherent* sterility barrier. Winge (1938) gives as a geneticist's species concept, ". . . individuals are specifically different when they are unable to hybridise or when, by crossing, they produce more or less sterile progeny". Where limitations on interbreeding exist as a normal feature in a plant population due to incompatibility mechanisms, dioecism, etc., strict application of a principle as bald as this would result in the segregation as different species

of two individuals of the same sex, or of the same incompatibility group!

A related viewpoint has recently been upheld by the Swedish geneticist, Lamprecht (1944, 1948) who, on the basis of extensive experiments with legumes, considers that a strict genetical definition can be given to the species. In effect, Lamprecht's view contains a development of one stated by Winge (1938), that all species are characterised by genes which cannot be transferred in interspecific crosses or which behave as lethals. In *Phaseolus,* Lamprecht states that free recombination is possible for all of the genes governing differences between the species *P. vulgaris* and *P. coccineus* except for those governing the position of the cotyledons during germination and the form of the stigma. These genes cannot be recombined in fertile offspring, and for this reason Lamprecht refers to them as "primary species-separating". Generalising from this finding, he argues that the only true species in nature are those which are separated in this manner, and arrives at a definition of the species as ". . . a unit including all biotypes which differ from all others by at least one common interspecific gene".

Lamprecht's is probably one of the most radical of the species concepts currently held by geneticists, but a viewpoint almost as extreme has been expressed by Clausen, Keck and Hiesey (1939). These investigators, in developing their "experimental concept of the species", are prepared to accept only those ". . . internal barriers that are of a genetic-physiologic nature" as species-separating; those, in other words, which prevent the production of offspring even after artificial cross-pollination, or lead to the sterility of any progeny produced. Where such barriers do *not* exist between two forms, they must be considered as belonging to the same species, whatever the taxonomist may have done with them. Acting on a principle of this sort, some workers have actually attempted taxonomic revisions of flowering-plant groups and have degraded forms lacking inherent isolating mechanisms from species to lower taxonomic rank. Thus, because they show high interfertility in cultivation and are not therefore to be considered "biologically different species", D. Löve (1944) has down-graded the taxonomic species *Melandrium rubrum* Garcke and *M. album* Garcke to subspecies of *M. dioecum* (L.) D. Löve.

There can be no doubt that these thorough-going genetical concepts of species limits, initially attractive because of their apparent simplicity and infallibility, have fallen into some disrepute, mainly because as laboratory or experimental garden concepts they simply do not relate in every instance to the situation in nature, at least in the manner their authors assert.

A more subtle approach is that of those who have recognised that barriers other than internal-genetic may operate in nature, and who seek to establish a "biological" species concept. Proponents of the biological species have, naturally, much common

ground with the advocates of the genetical species. They point
to the fact that it is characteristic of outbreeding sexual organ-
isms that they form discrete or almost discrete groups in nature,
these being the species, and argue that the formation and con-
tinued independent existence of these species requires the origin
and maintenance of *some* form of reproductive isolation. While
the latter may not necessarily be of an inherent genetical nature,
it must be a biological attribute of all true species. The type
of species definition arising from these considerations is well
illustrated by Mayr's formulation (1940): "A species consists of
a group of populations which replace each other geographically
or ecologically and of which the neighbouring ones intergrade
or interbreed wherever they are in contact or which are potenti-
ally capable of doing so (with one or more of the populations)
in those cases where contact is prevented by geographical or
ecological barriers.

Or shorter: Species are groups of actually or potentially inter-
breeding populations, which are reproductively isolated from
other such groups."

Biological species definitions such as this one of Mayr have
been criticised from various viewpoints, often on the grounds
of the general ambiguity or indefiniteness of the terms employed,
and also because examples can always be quoted where the
application is obscure. This would seem to be inevitable because
of the nebulous nature of the concept of reproductive isolation
once there is a departure from the relatively secure basis of the
"inherent genetical barrier". Dobzhansky has used the phrase
"reproductive isolation" in a sense synonymous with "physio-
logical isolation" to imply that the factor inhibiting the cross-
breeding of two forms is not solely their geographical separation
from each other. A limitation of this nature is necessary, since
two colonies separated by a major topographical feature are of
course as effectively inhibited from gene exchange as they would
be by any inherent genetical barrier, and all such colonies would
have to be given "specific" rank if the simple criterion of *actual*
inter-breeding or non-interbreeding were assumed. For this
reason, definitions like that of Mayr quoted above have to incor-
porate such phrases as ". . . actually or *potentially* interbreeding
populations . . ."

But it is just this introduction of the idea of potential capacity
for interbreeding which creates difficulty. It disallows, for
example, one form of inherently-determined isolating factor which
is certainly of considerable importance in the plant kingdom. An
inherent genetical difference between two groups, itself concerning
in no direct manner the processes of reproduction, may neverthe-
less act as a reproductively isolating factor through the *agency*
of spatial isolation when it determines differences in habitat pre-
ference. This is the basic aspect of "ecological isolation", which,
while appreciated by most botanists, seems to be incomprehensible
or unacceptable to many zoologists, no doubt as an outcome of

the greater motility of the organisms with which they deal. In such instances, the *potentiality* of gene exchange exists while the actuality is absent, and its absence is not due to the fortuitous existence of a geographical hiatus in range, but to distributional differences arising from innate dissimilarity in habitat predilections. The British flora provides several examples of forms which are reproductively isolated largely if not entirely by ecological differences. The most fully investigated case is undoubtedly that of *Silene vulgaris* and *S. maritima,* studied in detail by Turrill and Marsden-Jones (1928-51). Others were discussed by Clapham at the 1948 Conference of the Society, and by Valentine at the Conference of 1950.

Also with the two *Melandrium* species quoted above ecological isolation is certainly important (Baker, 1948), but here the specialisation of the flowers for different pollen vectors and a difference in time of anthesis contribute to some extent. An example like this reveals a further difficulty which arises whenever a species definition such as that of Mayr is taken as a precept for action as apart from simply an interesting concept for academic discussion. In any particular instance, when it comes to the point of actually determining whether two allopatric populations are "potentially interbreeding", what tests are to be applied? With plants, one can, of course, grow representatives together in the experimental garden. Artificial cross-pollination, such as practised by Clausen, Keck and Hiesey, simply short-circuits some of the subtle barriers which effectively separate some breeding populations in nature, just as growing the plants together eliminates the spatial isolating factor. In actual fact there is no clear level at which the intervention of the experimenter must cease. In one instance, cultivation in close proximity will be sufficient to promote crossing; in another cross-pollination may be necessary; in a third, cross-pollination plus an operation to reduce style length; in yet a fourth, perhaps artificial culture of the F_1 embryo. Any of a large number of techniques is indeed available to test the "interfertility" of two forms, and each will, of course, give a result valid within its own context. But as to what level shall be taken as marking the end of "potential capacity for interbreeding", there can be no unequivocal rule. This part of so-called biological species definitions can, therefore, hardly be effectively translated into practice.

Proponents of such definitions have to some extent realised this. Mayr, for example, states that reproductive isolation can be an immediate practical test only for sympatric, synchronically reproducing species, and admits that it is often impossible for practical reasons to test to what extent reproductive isolation actually exists between geographically isolated populations. He goes on to suggest that "the conspecificity of allopatric . . . forms, which depends on their potential capacity for interbreeding, can be decided only by inference, based on a careful analysis of the morphological differences of the compared forms". This he con-

siders feasible because " . . . the biological gap between species
(reproductively isolated groups) is, in general, correlated with
certain morphological differences". With plants, however, this
principle can hardly be regarded as generally applicable. In-
stances from the British flora in which morphologically well-
defined forms retain complete interfertility have been quoted
above, and several others could be cited to illustrate the reverse
—the intersterility of morphologically closely similar forms.
Cardamine pratensis is an interesting case. In this Linnaean
species several chromosome races exist, some of which are yet to
be sorted out as morphologically distinguishable units (Lovkvist,
1947). Professor Tutin will, I believe, be telling us of intersterile
races within *Glyceria fluitans*, barely recognisable morphologically
from each other; here the barrier appears to be on a genic or
chromosomal-structural level rather than chromosome-numerical.
The case is thus similar to that of *Datura stramonium*, a species
in which morphologically similar, intersterile "sectors" exist, the
intersterility being due to the presence of chromosomal inversions
and translocations.

Even although it cannot be regarded as a general truth that
reproductive isolation and morphological divergence are neces-
sarily correlated, the fact that resort has to be made to such a
proposition in developing the "biological" species concept has
interesting implications. It is clear that the idea of the species
advocated by Mayr and his followers is quite a different matter
from the experimental concept of the species laid down by such
workers as Clausen, Keck and Hiesey. While ostensibly based
upon the principle that specific distinction depends upon repro-
ductive isolation, it does not assert that species limits can, or
necessarily should, be determined by experimental tests for
sterility or fertility. It does indeed ultimately admit for allo-
patric forms what is essentially an orthodox interpretation of
what shall be taken as constituting a species, based upon degree
of morphological difference; this is so, in spite of Mayr's argu-
ment that degree of morphological difference is only to be em-
ployed as a yardstick in cases where the presence of reproductive
isolation cannot be directly determined.

In fact, it seems that in sexual groups as we move away from
the crude interpretations of what are species which arise from
the acceptance of unmitigated genetical criteria, adding proviso
after proviso in the attempt to attain a broader biological basis,
the units defined become more and more congruent with the
morphological species of orthodox taxonomy. Ultimately bio-
logical species definitions cease to become definitive altogether:
they provide no absolute criteria for circumscribing species, and
in effect simply describe some of the biological properties of the
"good" species of taxonomy. And this, I think, is generally a
sign of their success.

The effect of the abandonment of any strict basis of experi-
mental delimitation by proponents of the biological species

concept is, simply, to re-establish personal judgment as a primary factor in species discrimination. In a doubtful situation, decision is made by reference to a complex mental framework in which considerations of comparative morphology, ethology, distribution, etc., all play a part. The units of a classification based upon this sort of complex foundation, in which the same criteria have different significance in different contexts, are unlikely to be in any way uniform in their genetical properties. The need for special purpose sub-classifications based upon single criteria would still arise, as it does against the present background of a primarily morphologically based taxonomy.

The construction of special genecological (or "experimental taxonomic") classifications is the second current tendency which I referred to at the outset. It is perhaps desirable for a moment to consider the philosophical implications of this sort of approach, for it is misunderstanding of these which has led to doubts and suspicions in the minds of taxonomists, and to some misinterpretation of the significance of their activities to taxonomy on the part of the experimentalists themselves. I hope I will not overlap too much here with Mr. Gilmour, who has already discussed some of these matters elsewhere (Gilmour, 1940, 1951).

All would, I think, concede the need for a general classification of the living kingdoms, and would to this extent accept the principle laid down in the International Codes of Nomenclature that all organisms should find a place in the general classification. Further, without entering upon the debatable matter of the place of phylogenetical speculation in classification, it appears to be true to state that most satisfactory form of general classification is one based upon maximum correlation of attributes of the organisms and groups of organisms involved; this is certainly the most "natural" in the original sense of Linnaeus and de Candolle, since it allows the greatest number of inductive generalisations to be made about the groupings produced.

But "maximum correlation" does not mean "complete correlation" of attributes. It is self evident that, even in the most natural of arrangements, groups placed together may for some characteristics resemble each other less than they do other, more remote groups. A cross-classification based upon these features is always possible, and may for some purposes be desirable. The fact that we may wish to make it is in no way an attack on the original "natural" arrangement. We may take, for example, the matter of latex production. That a text-book of economic botany places together as latex plants representatives of *Compositae, Moraceae, Asclepiadaceae* and *Euphorbiaceae,* is not a criticism of the taxonomic arrangement which separates these plants rather widely in the general scheme of classification. The same principle of cross-classification can be widened indefinitely; ecological classifications for the whole Phanerogamae are possible, and have indeed been formed, based, for example, on life

form.   The classifications of so-called experimental taxonomy
can be looked upon in a similar sense, as giving recognition to
specific attributes of organisms which, in certain contexts, are
of special importance.

It is at the point where experimentalists assert that their
classifications are necessarily the most "natural" and are
tempted upon such grounds to challenge orthodox taxonomic
arrangements that their activities become suspect.   As with an
economic classification of plants, there is simply no inherent need
to expect or require that classifications based upon special criteria
such as degree of interfertility should coincide with those of
orthodox taxonomy, and certainly no justification in insisting
that the latter be brought into line where the agreement is low.

It is perhaps unfortunate that one of the earliest and best
known approaches to the "experimental" treatment of the
natural variation of plants, that of Turesson, began with a set of
categories two of which bore names based upon the root
"-species".   It may be largely due to this simple fact that so great
a measure of confusion about the concepts involved in this type
of classification has arisen.   On the one hand, some taxonomists
have reacted against the whole scheme, disconcerted perhaps by
the suggestion that one kind of species, the coenospecies, could
contain several whole taxonomic genera, or that another, the
ecospecies, could be composed simply of a morphologically un-
differentiated local race characterised perhaps by a chromosome
inversion.   On the other hand, some enthusiasts have seen in the
Turessonian system the foreshadowing of doom for orthodox
taxonomy, and have hastened to demand nomenclatural recogni-
tion of the new categories.

Knowing that Mr. Gilmour will be taking this matter of the
relationship of nomenclatural and experimental categories con-
siderably further, I do not propose to pursue it, except to state
that I find myself in full agreement with what I believe he is
going to say.   I think in the present state of our knowledge, there
is nothing whatever to be gained by an attempt to incorporate
genecological, biosystematical, experimental taxonomic, or what-
ever they may be termed, category concepts in the formal
taxonomic system.   There is a motion to open the door to this
before the Eighth International Botanical Congress to be held
in Paris this year: I can only hope that its sponsors will think a
little more carefully of what they are proposing to do before press-
ing ahead with it.

These remarks extend also to variational categories below the
rank of species.   The case concerning these has been well expressed
by our leading genecologist, Dr. Gregor, in his Presidential Address
to the Botanical Society of Edinburgh of 1948, and I recommend
all botanists interested in these problems to read it.

Before leaving the matter of the experimental classification of
plants, a word or two on the methods and purposes of this activity
may not be out of place.   Since the original proposals of Turesson

and Danser were put forward, now more than a quarter of a century ago, there has been a considerable development of outlook. Following upon a phase of optimistic attempts to improve the precision of the criteria used in experimental classification, there has been an increasing realisation that the complexity of natural variation is such that no absolute standards can be established for defining the experimental categories, any more than for the categories of the orthodox taxonomic system. It has become clear that several different and equally valid classifications of the same groups of populations may be possible using experimental criteria, so far are the latter from establishing the ultimate relationships. In recognition of this, some of us (Gilmour & Heslop-Harrison, 1954) have been seeking recently to establish a terminological system which would be sufficiently flexible to allow a whole sequence of properties and inter-relationships.

However, currently developing among genecologists and evolutionists there is a belief that an "experimental taxonomy" as such may not be required at all. As Gregor has suggested, genecological classifications tend to be summaries of experimentally or cytologically determined facts about natural plant populations which bear upon their origin, structure and properties. To express this information, it may not be necessary to resort to a classificatory approach, and certainly no nomenclatural system is required. It may even be that the carrying over of taxonomic concepts seen in the tendency to define 'types' and 'species' is actually an impediment to genecological research. An example of this may perhaps be seen in the early history of the ecotype, for there is no doubt that here the overstressing of the 'type' aspect long tended to conceal the existence of ecologically conditioned clinal variation.

The problems of genecology are the problems of the inter-relationship and interaction of organism with organism, and organism and population with the secular environment, all in the continuum of time. Taxonomic typification has little to do with such a study, for the recognition of stages is but a poor substitute for the investigation of processes.

In conclusion I feel obliged to add a word or two on what Dr. Turrill terms the synthetic approach to taxonomy, lest it be thought from the foregoing that I am advocating a retention of the *status quo* in the science.

I began with the postulate that since the Linnaean method had persisted in its essentials for two centuries and had seen a fair measure of success in that period, the presumptions upon which it was based could hardly be fundamentally incorrect. Modern population theory does little to contradict this in any general manner; it does, in fact, provide an explanation for the pattern of variation which fits reasonably well a taxonomic system composed of a hierarchy of categories.

The essentially Linnaean species concept which is the basis of our present nomenclatural taxonomy is not, of course, without

its defects in practice. Perhaps it is hardly necessary to specify the evidence for this to the present audience: it lies in any flora. A day or two ago, while pondering on the topic of this conference, I dipped at random into the new *Flora of the British Isles,* and leafed through a page or two from the one I first encountered. In six openings, I struck eight families. All told, in the vicinity of the pages I hit upon, almost half of the genera listed bore some indication of confused taxonomy. In several instances, the evidence was of man-made nomenclatural confusion, but in the remainder the problems were inherent in the plants themselves. In about one-third of the cases, the trouble arose from apomixis: one could, of course, hardly avoid hitting *Rubus* or *Hieracium* at least once. In one genus, the difficulty arose apparently from autogamy, in another from possible hybridity.

This small study was informative, and an analysis of the entire flora on these lines would no doubt be highly illuminating. It illustrates the interesting point that the bulk of the problems of plant taxonomy *in a geographical region the size of ours* arise from special forms of reproductive behaviour which, while not peculiar to the higher plants, are much more prevalent among them than, say, among the higher animals. In apomictic and autogamous groups, the species concept of nomenclatural taxonomy certainly needs overhauling. I have deliberately refrained from discussing these groups in this paper, for in what direction an improvement is to be sought I am not prepared to say. But I commend the whole topic of the reproductive biology of British plants to the Society as a possible subject for a future conference or symposium.

A striking feature is that for the sexual forms in our flora there is on the whole surprisingly little confusion. Where it does arise, there are two primary sources of discord; firstly, vertically in the taxonomic hierarchy, over the matter of the taxonomic ranks to be awarded to groups of low degrees of differentiation, and secondly, horizontally in the hierarchy, over the number and position of the lines of demarcation in alliances where there is some degree of intergrading variation due to imperfect differentiation or hybridity.

It is here that our orthodox taxonomy has a clear opportunity, and indeed an obligation, to develop and adapt its methods, and to make use if necessary of experimental data to produce a superior *orthodox* taxonomic arrangement. It is here, indeed, that the attitude urged by the proponents of the 'biological' species concept is likely to be the fruitful one.

In dipping into the new flora, I encounter *Ranunculus aquatilis.* Here there are listed five subspecies, all accepted as species in other recent critical treatments of the genus in Britain, if under different names. Here is an example of variation of treatment in both dimensions of the taxonomic system, and this is surely an instance of an alliance the taxonomy of which would benefit from experimental studies. How much clearer the varia-

tion pattern would be with some comprehensive and reliable data on phenotypic plasticity, chromosome numbers, reproductive biology and the like.

Another example worth considering is that of *Salix*. Here there is every evidence of a wealth of hybridisation among our native forms. Perhaps no orthodox taxonomic treatment will ever be adequate for this genus throughout the Palearctic region, but at least our knowledge of the source of the variational complexities in the group should guide our attempts to produce one, and should certainly guard us against the excesses into which some essentially non-biological systematists have been led. Chromosome numbers point to where to look for variational foci; population studies offer a method of detecting them, and biometrical techniques a means for expressing our findings. Knowledge of breeding behaviour and the extent and effects of hybridisation, already available in the work of Heribert-Nilsson, should warn us against slavish attempts to apply a 'type' concept of the species. They should certainly check—or at least throw into disrepute—the activities of the name conjurers, whose species limits are set by the finest morphological differences they can detect—or fancy they can detect—upon herbarium sheets, and who are accordingly prepared to continue to describe and name hybrid segregates as long as they can persuade botanical journals to publish them.

REFERENCES.

BAKER, H. G., 1948, Stages in invasion and replacement demonstrated by species of Melandrium, *J. Ecol.*, **36**, 96-119.

CLAPHAM, A. R., 1948, Ecology and critical groups, in *British flowering plants and modern systematic methods* (ed. A. J. Wilmott). London.

CLAUSEN J., KECK, D. D. & HIESEY, W. M., 1939, The concept of the species based upon experiment, *Amer. J. Bot.*, **26**, 103-106.

DARLINGTON, C. D., 1951, Do the chromosomes fit the species? *Nature*, **167**, 662-3.

DOBZHANSKY, T., 1941, *Genetics and the origin of species.* New York.

GILMOUR, J. S. L., 1940, Taxonomy and Philosophy, in *The New Systematics* (ed. J. Huxley). London.

——, 1951, The development of taxonomy since 1851, *Adv. Sci.*, **8**, 70-74.

GILMOUR, J. S. L. & HESLOP-HARRISON, J., 1954, The deme terminology and the units of micro-evolutionary change, *Genetica*, **27**, 147-161.

GREGOR, J. W., 1948, Some reflections on infraspecific ecological variation and its classification, *Trans. & Proc. Bot. Soc. Edinb.*, **34**, 378-91.

LAMPRECHT, H., 1944, Die genisch-plasmatische Grundlage der Artbarriere, *Agri Hort. Gen.*, **2**, 75-142.

——, 1945, Intra- and inter-specific genes, *Agri Hort. Gen.*, **3**, 45-60.

Lotsy, J. P., 1918, Qu'est-ce qu'une espèce?, *Arch. Néerl. Sci. Nat.*. Ser. 3b, **3**, 57-110.

Löve, D., 1944, Cytogenetic studies on dioecious Melandrium, *Bot. Not.*, **1944**, 125-213.

Lovkvist, B., 1947, Chromosome studies in Cardamine, *Hereditas*, **33**, 421-422.

Marsden-Jones, E. M. & Turrill, W. B., 1928-1951, Researches on Silene vulgaris and S. maritima, *Kew Bull.*, **1928-1951**.

Mayr, E., 1940, Speciation phenomena in birds, *Amer. Nat.*, **74**, 249-278.

——, 1942, *Systematics and the origin of species*. New York.

Valentine, D. H., 1950, Geographical distribution and isolation in some British ecospecies, in *The Study of the Distribution of British plants* (ed. J. E. Lousley). Oxford.

THE SPECIES CONCEPT AND EXPERIMENTAL TAXONOMY

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Yesterday Dr. J. Heslop-Harrison outlined two opposed tendencies at present evident in attempts to deal with the problem of the relationship between the species concept and modern knowledge of micro-evolutionary change, as revealed by the discipline usually known as "experimental taxonomy". He put forward strong reasons, both scientific and practical, for keeping the term "species" for a unit based mainly upon comparative morphology, rather than attempting to re-define it genetically, cytologically or on inter-fertility criteria; as a corollary to this course he advocated the use of independent and non-nomenclatural categories for classifying variational units of importance in micro-evolutionary change.

Today, I shall attempt to back up Dr. Heslop-Harrison's arguments from a rather different point of view and to discuss a little more fully the type of independent categories that might be used.

In the first place, it is important to bear in mind the basic point that every classification should have a purpose extraneous to itself. Failure to realise this may lead to confusion. Frequently one classification is described as "better" than another without specifying for what purpose it is "better". Such usage implies that there is some intrinsic and universal aim of classification as such, whereas, in fact, the speaker will have a particular, undeclared, aim in mind which may well be quite different from the aim (also undeclared) recognised by another taxonomist with whom he is arguing; confusion inevitably results.

If we accept this point of view, let us start by trying to define the aims respectively of what is sometimes called "orthodox taxonomy" (i.e., classification into the categories embodied in the International Code), and "experimental taxonomy"—the aims, that is to say, as revealed by the actual practice of those working in these disciplines.

The criteria used by "orthodox" taxonomists are basically the phenotypic (largely morphological) characters of the organisms concerned, coupled with their distribution, and the aim of their work is to produce a broad "map" of the phenotypic diversity of the plants and animals distributed over the globe. The units they construct are of use not only to general biologists but also to the many groups of people such as horticulturists, agriculturists, anthropologists and so on, who have occasion to deal with living organisms.

"Experimental taxonomists", on the other hand, take at once a more limited and a more dynamic view of plants and animals. Their aim, as revealed by their work, is to discover the units of importance in micro-evolutionary change and to study how these units came into existence and their relationship with one another. The criteria they use for defining their units are mainly genetical, cytological, ecological, and distributional, leading to the construction of units differentiated largely on grounds of inter-fertility or inter-sterility.

It is clear from these considerations, then, that the aims of the two disciplines are essentially different, and *prima facie* it would seem desirable to keep the terminology of their respective categories distinct, otherwise confusion may result.

At this point it may be helpful to illustrate the differences in aim and terminology between "orthodox" and "experimental" taxonomy by an analogy with the classification of books. For general purposes, the basic classification of books is into "titles", or, more colloquially (though confusingly!) into "books"; thus "Barnaby Rudge" is a different "book" from "War and Peace". This classification is useful for a wide variety of purposes and corresponds broadly to a classification of living things into species. For the special purpose, however, of studying the physical evolution of particular "books", it is quite inadequate, and a whole set of separate terms must be pressed into service, such as edition, state, issue, printing, impression, and the like. These special bibliographical terms, with their special purpose, correspond in function and aim to the special terminology for experimental taxonomy advocated above. Both require the basic terminology of "species" or "books" as a background; both should be kept separate from this basic terminology if they are not to be confused with it.

In addition to what may be called loosely the philosophical arguments for keeping the two terminologies separate, there are two more practical reasons which should be mentioned. Firstly, as I have said, the categories of "orthodox" taxonomy are used by a wide variety of people. The majority of these are not interested in the evolutionary history of the units concerned, but mainly in their phenotypic characters, both morphological and physiological. Their need is for a stable classification and nomenclature, based on the characters in which they are interested, and this cannot be provided if the species concept (and consequently the species names) is subject to constant changes in an attempt to make it conform with the changing ideas on evolution. It is surely in the interests of everyone that the "basic map" should remain relatively stable, while our rapidly developing knowledge of evolutionary change should be embodied in a flexible system of categories specially constructed for the purpose.

The second point arises from the past history of the term "species". Until the middle of the nineteenth century it was, of

course, almost universally regarded as a specially created and
unchanging entity, and there is no doubt that, unconsciously,
this idea still clings to the word, and colours our thinking on the
species question. If, therefore, the term species is pressed into
the service of "experimental taxonomy", even in the form of a
compound word such as ecospecies, there is a danger that the
"clouds of glory" that it inevitably trails may interfere with clear
thinking on the construction of units for the expression of evolu-
tionary change. This tendency can be detected in a good deal
of recent writing on the species question.

If, therefore, we accept the thesis that separate categories
should be used for "experimental taxonomy", what form should
these take? Recently a small group of botanists have been dis-
cussing this problem and a paper by Dr. Heslop-Harrison and
myself is in the press embodying their views*. Broadly speaking.
there are three courses open: (1) to try to produce an ordered
and coherent scheme out of the existing mass of terms that have
been proposed, defined, and re-defined during the last thirty
years, (2) to construct a completely new scheme, or (3) to take
some of the existing terms as a basis and to expand them. We
have chosen the last course and have adopted the word *deme*
(Gilmour & Gregor, *Nature,* **144**, p. 333, 1939) as a basic root to
which prefixes can be attached to indicate different kinds of
demes. The root *deme* is defined as "a term, always used with a
prefix, denoting any group of individuals of a specified taxon";
it is thus a completely "neutral" term, not implying, in par-
ticular, any spatial relation between the individuals concerned.
A considerable number of prefixes are set out in the paper, but
the following five will give an idea of the scope and method of
the terminology: —

  (1) gamodeme: a deme composed of individuals which are
       so situated spatially and temporally that, within the
       limits of the breeding system, all can interbreed.
  (2) ecodeme: a deme occurring in a specified kind of
       habitat.
  (3) topodeme: a deme occurring in a specified geographical
       area.
  (4) genodeme: a deme differing from others genotypically.
  (5) genecodeme: an ecodeme differing from others geno-
       typically.

The sponsors of this proposed terminology have put it for-
ward in the hope that their fellow biologists interested in experi-
mental taxonomy will test it on the particular groups on which
they are working, and that eventually it may develop into a flex-
ible, yet coherent, system to replace the present confusing and
unco-ordinated series of terms.

*Now published as "The Deme Terminology and the Units of Micro-evolutionary
    Change" in *Genetica.* **27**, 147-61, 1954.

Dr. W. B. TURRILL said that he was puzzled and hesitant about some of the points raised. Dr. Heslop-Harrison in his paper (see pp. 160-172) described and set out two tendencies, and now Mr. Gilmour gave three. He thought Mr. Gilmour should define what he meant by morphological characters—did he include such characters as colour of flowers and colour of leaves? These could hardly be considered apart from bio-chemistry and habitat. There was a tendency to draw a line between morphology and physiology but it seemed to him that there should be an attempt at synthesis and not too much analysis.

Mr. Gilmour said that when making a classification we should be clear as to the purpose, but he thought this should be in the plural—purposes. He was not clear how different demes were to be designated. If we used letters and referred to Gamodeme A, Gamodeme B., etc., our alphabet would not go far—perhaps we should use Chinese characters—there are more of them!

Mr. GILMOUR replied that he would not propose to lay down any hard and fast rule, as the method to be used for designation must depend on the nature of the investigation and the number of demes involved. He would deprecate any attempt to set up any formal nomenclature and especially any nomenclature employing Latin which would be liable to confusion with existing Latin names. Numbers as well as letters could be used.

Dr. HESLOP-HARRISON said that we should not attempt to produce a classification of these particular units. Such statements as "the chalk ecodeme of x", and "*Dianthus gratianopolitanus* is a topodeme in the British Isles" present a cross classification.

In further reply to Dr. Turrill, Mr. GILMOUR said that he quite agreed that there should be reasons, rather than a reason, to justify a classification. He also agreed that morphology was an undesirable shorthand term, and that characters used in orthodox taxonomy might be physiological as well as the conventional "morphological".

Prof. D. H. VALENTINE pointed out that the term "species" had proved to be a flexible concept. He agreed that the characters represented by the "deme" terminology should be kept separate but at the same time it was important to avoid any possible effect of separating the research of orthodox from that of experimental taxonomists. It must be remembered that International Congresses were not divinely inspired and the categories they laid down should not be regarded as fixed for all time.

Mr. GILMOUR said that he entirely agreed with the great importance of preserving co-operation between orthodox and experimental taxonomists, and that it was advisable to keep the term "species" as flexible as possible.

Dr. R. W. BUTCHER suggested that characters referred to as morphological would be better described as "ocular"—what was really intended was what we could see.

THE FUTURE OF SYNTHETIC TAXONOMY

W. B. TURRILL (Royal Botanic Gardens, Kew).

This is the penultimate communication of five sessions which were daily broken only by tea and lunch intervals. You are praying that I keep well within my time. Your prayers will be answered. My remarks will be concise to the danger limit of seeming to be dogmatic and are under three headings: —

1. Introductory.   2. Appreciative of the papers we have heard, with some criticisms.   3. Suggestions for future researches.

1. *Introductory.* In any statements I make or any conclusions I reach it must be clearly understood that I am not "running down" herbarium taxonomy, or morphological taxonomy, or nomenclatural taxonomy, or any kind of taxonomy. On the whole, plant taxonomists have done and are doing excellent work, the results of which are indispensable for research in any and every branch of botany. Partly for historical reasons but partly also for interesting technical and philosophical reasons, which we must not now stay to discuss, taxonomy has been built up largely on the basis of gross structural characters, i.e., of morphology as studied by the naked eye or up to about × 20 magnification with a hand lens. However, our Conference Programme is headed "The Species Concept in its relation to the British Flora". I do not suggest that our knowledge of the gross morphology of the British flora is complete but it is relatively well known when compared with, say, that of the flora of the Amazon Basin or of Uganda. In other words, I contend that we should introduce more and more into our taxonomy of the British Flora criteria additional to those provided by gross morphology. I repeat, we have gratefully to thank our taxonomic predecessors but if they, in the intervals of botanizing in the Elysian fields, glance at the activities of us, their successors on earth, they will justly criticize us if we do not advance and this we can only do by improving and enlarging our methods with due regard to the purposes our classifications are to serve.

2. *Appreciative, with some criticisms.* It is impossible in a brief time to summarize the papers we have been privileged to hear. Those dealing with named taxa—genera or species—from *Fucus* or ferns amongst the cryptogams, to grasses, *Salicornia, Arum, Stellaria, Erica, Euphrasia, Caltha,* and *Centaurium* amongst seed plants are extremely valuable because they provide the kind of data which must be considered in the formulation of broader and better schemes of classification than we have at present. I will refer to this matter later, for I hold strong views on

it. Those of us who are, at least mainly, phanerogamists welcome the experiences of our colleagues who specialize in fungi, bryophytes, ferns, and fossil plants. It is still polite to consider them as botanists, with some doubt as to whether the fungi are not best accepted as a kingdom of their own and mycologists thereby altered in status. There are left for consideration six more general papers. Adequately to discuss any one of these would more than occupy the rest of my time. I am, therefore, forced here to refer very briefly, though perhaps somewhat critically, to two only, the one by Dr. Heslop-Harrison and the other by Mr. Gilmour.

If I may somewhat modify Dr. Heslop-Harrison's first statement in his summary I would agree with it. If instead of "classical taxonomic species" (whatever the phrase means) he would write "what have by one taxonomist or more than one taxonomist been accepted as species" have been shown, during the past half-century, to correspond with biological units of many different sorts, I accept the statement. I do not agree that one is limited to the two "tendencies" he enumerates in attempting to improve the situation. There is a third possibility, which, in my opinion, may provide a much more satisfactory scheme than any we have at present. That is to determine how many "kinds" of taxa, amongst what are now called species, it is best to recognise and then to label them either by accepting grades of "species" or inventing other taxon designations. By the methods of synthetic taxonomy, and only by these methods, a considerable number of so-called species in some genera of the British flora can be shown not to be species in any stable sense but segregating hybrids, as in *Centaurea*. These should be eliminated as "species". A special group are the apomicts, as in *Hieracium* and *Taraxacum*. One or more groupings of "microspecies" will probably be found desirable and "aggregate species" may be a useful conception. "Species in the making" may have to be recognized. Problems of polyploidy have never, to my knowledge, been fully and properly considered taxonomically. We may have to accept some dynamic and some elastic concepts. Here then is a concrete suggestion that taxonomists, and especially those who know the value of synthetic methods, should experiment with enlarging the number of taxa round about and within what are now often called "species". There is, however, a "but" and a big "but". We may propose a scheme, but have we yet sufficient data to propose a reasonably complete one, even for the British flora? I think not and, therefore, I am prepared to accept tentatively and temporarily a part of what Dr. Heslop-Harrison places as a second "tendency" and which was dealt with again by Mr. Gilmour. There is only one test of such a scheme—the pragmatic one. I suspect that the proposed scheme may be found useful in parts and I have faith that all that is good in it will ultimately be absorbed by synthetic taxonomy. I am very much averse to opposing "experimental taxonomy" to "herbarium taxonomy" or to "morphological taxonomy" or to pretending that the latter alone is

taxonomy proper. As a taxonomist, I am not going to be ordered, even by an International Code, to use only (or mainly) morphological characters. I shall use any and every kind of character, any and every kind of datum I can find, beg, buy, borrow or scrounge, which, in my considered opinion can help me to make a more widely useful classification of this or that group of plants. The only exception to this generalization is in forming special classifications, or cross-classifications as Dr. Heslop-Harrison called them, with deliberately limited functions. The "deme" scheme comes into the category of special classifications and, as a scheme whose value remains to be determined by application, it must be welcomed since its use may add data and interpretation to some aspects of synthetic taxonomy.

3. We must quickly turn to my third heading: *suggestions for future researches*. There is one possible criticism of this conference. That it has been too academic and professional. The speakers, with a few exceptions, are university or government employees. I do not wish to suggest we are "players" opposed to "gentlemen", but one does wonder if there may not be a risk that this Society will fail, along the lines it is now tending to follow, adequately to encourage the amateur botanist, using "amateur" in the sense only of one who studies plants for love of them and earns his livelihood independently of botany.

I would like in my final remarks to address myself to those who have the advantages of choosing their botanical interests independent of academic needs or government directions. As we have already noted, within the limits of gross morphology alone, one can say that the taxonomy of the British flora is now fairly well worked out. It seems rather a waste of energy to go over the same ground again and again. There is, however, a great deal to be done by using the methods of synthetic taxonomy. I wish there were time to discuss these in some detail. They have not yet been fully written up and published. You will find some guidance in Huxley, *The New Systematics*; Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy*; Turrill, *British Plant Life*; and for practical instructional details on the experimental side of plant taxonomy (an important part but by no means the whole of synthetic taxonomy) in Turrill, Methods of the Experimental Ground in Relation to Taxonomy, in *Kew Bulletin*, **1952**, 427-37.

In my opinion, there are a large number of taxonomic problems in the British flora that cannot be solved except by applying the methods of synthetic taxonomy. One welcomes the *Biological Flora* in course of publication by the British Ecological Society. This is providing much new and valuable information, especially ecological, which has to be absorbed by synthetic taxonomy. It does not cover, certainly in sufficient detail, the whole range of synthetic taxonomy and its present rate of publication is very slow.

I have listed genera and species of the British flora which need investigation by the methods of synthetic taxonomy. Work is in progress on a few of these. The list is too long to consider here in detail. A few examples must suffice. Genera or groups of species include *Thalictrum* (especially the *T. minus* group), *Polygonum, Atriplex, Erodium* (especially the *E. cicutarium* group), *Polygala, Arctium, Gentianella, Melampyrum, Rhinanthus, Symphytum,* and *Mentha*. Species pairs are *Papaver rhoeas* and *P. dubium, Arenaria serpyllifolia* and *A. leptoclados, Vicia sativa* and *V. angustifolia, Prunus spinosa* and *P. insititia, Betula verrucosa* and *B. pubescens,* and *Sonchus asper* and *S. oleraceus*. A small selection of species is: *Anemone nemorosa, Ranunculus flammula, Stellaria media, Spergula arvensis, Malva sylvestris, Fragaria vesca, Chamaenerion angustifolium, Convolvulus arvensis, Origanum vulgare, Calamintha ascendens, Salvia horminoides, Jasione montana, Achillea millefolium, Matricaria maritima, Bellis perennis, Endymion nonscriptus,* and *Allium vineale*.

The inclusion of some of these taxa in such a list may cause surprise. For several I can give further particulars since my colleague, Mr. Marsden-Jones, and I made preliminary studies on them in our experimental grounds at Kew and Potterne.

The studies one has in mind include determination of the following: degree and kind of plasticity; whether contrasting phenotypic characters are due to genetic differences or only to differences of environment; the kind and number of variations; the correlation of characters and character variations; characters often ignored in taxonomic accounts, such as germination, seedling structure and behaviour, rate of growth, phenological behaviour, vegetative multiplication, dispersal, and so on; pollination mechanisms; compatibility and incompatibility; hybridization; range and distribution of variants and hybrids. All of these lines of research, and others, have been proved to lead to taxonomy that better fulfils its purposes. Those of us who have to work on foreign and very inadequately known floras with a limited number of dried specimens and very incomplete data, know, by contrast with the results obtained by using synthetic methods on a few British taxa, how essential field and experimental data are if more than a very tentative taxonomic scheme is to be prepared. Herbarium or morphological taxonomy is extremely important, but it is the beginning not the end of synthetic taxonomy.

Finally, in suggesting to members of the Botanical Society that they specialise in one or a few taxa of the British flora by the methods of synthetic taxonomy, may I point out that there are many advantages in such research. It combines field work and experimental investigations with indoor research in herbarium, laboratory, and library. One or other aspect can be carried on throughout the whole year. It does not necessarily require expensive apparatus or a large amount of room. It is

surprising, for instance, what can be done in a small garden with no more than ordinary horticultural tools. It is healthy and exciting since there are great chances of making new discoveries. What more can one want?

———

Dr. R. W. Butcher remarked that from his own work he quite agreed with Dr. Turrill's recommendation that the *Thalictrum minus* group was in need of investigation by the methods of synthetic taxonomy and he would add the Batrachian *Ranunculi* to the list. He felt that a word of warning was necessary before recommending *Convolvulus* species for cultivation in the garden!

Dr. J. Heslop-Harrison said he thought that Dr. Turrill and he were trying to achieve the same ends from slightly different angles. Dr. Turrill in going through the British *Flora* started from page one, and worked right through to the errata sheet. He preferred to do a little statistical sampling! The position as he saw it was that there were two extreme possibilities—either to retain orthodox taxonomy, or to use orthodox taxonomy steadily improved by the results of experimental taxonomy.

He agreed with Dr. Turrill that there had been far too much mention of chromosomes at this Conference and it must be remembered that they are not the answer to all our problems. Amateur botanists are not in a position to work on cytology but there is a wide field of research on floral biology, insect visitors, incompatibility and similar subjects open to them. The Society offered extraordinarily fine facilities for the publication of their results.

Prof. T. G. Tutin said he would go farther than Dr Turrill. He thought it doubtful if any species could be found in the British flora which would not repay investigation.

Dr. E. F. Warburg remarked that amateur botanists should not be put off by the prospect of big research projects. We also needed snippets of information—short notes on individual observations which, if published, could collectively add up to a valuable addition to our knowledge.

CONCLUDING REMARKS BY CHAIRMAN

Dr. R. W. Butcher, who was in the Chair at the final session, said he felt that the Conference had been an outstanding success. We were in the middle of a revolution in the study of systematic botany. Botanists were turning from making collections to the study of the plants themselves, and then to the study of intimate details of species. Students now tended to study a lot about a little, instead of a little about a lot as in the past. We should be extremely grateful to the heroes and heroines who had boldly tackled our most difficult groups and read papers on them to the Conference. He thought that one of our objects should be to make such discoveries and investigations intelligible to as many people as possible.

Dr. Butcher said that about 240 members and guests had attended the Conference and suggested that all concerned—and especially the Meetings Secretary—should be congratulated on the very smooth way in which all the arrangements had been carried out. This was received with acclamation.

Mr. J. OUNSTED proposed a vote of thanks to Professor Tutin, Dr. Butcher and Mr. Lousley for taking the Chair at the various sessions. He thought the Conference had been most successful and enlightening and his only regret was that there had been no paper on the species concept by a wild flower enthusiast. He suggested that the views of "Benthamites", "Butcherites" and "Tutinites" and their various outlooks might have added something of value.

THE DISTRIBUTION MAPS SCHEME

The Distribution-Maps Scheme is a project for collecting data concerning the distribution of plants on a scale not previously known to botanical science in this country, and the Conference provided an opportunity of bringing the work to the notice of members and the public.

Throughout both days there was a demonstration by Powers-Samas of working machines of the types to be used for preparing and sorting the punched cards to be used in collecting the data, and for the automatic printing of the distribution maps. The sources to be used in obtaining records were also illustrated. This took place in a room adjoining the lecture hall and the demonstration was inspected by most of the members and guests present and by additional visitors who came to the open meeting on the evening of April 9th. The information given by Professor A. R. Clapham and Dr. S. M. Walters in their addresses to this evening meeting is summarised, with some additional matter and illustrations, in *B.S.B.I. Proceedings,* **1**, pp. 121-130, 1954.

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B.S.B.I. CONFERENCE REPORTS

No. 1. BRITISH FLOWERING PLANTS AND MODERN SYSTEMATIC METHODS.

Being the report of the Conference on " The Study of Critical British Groups " arranged in 1948. Edited by A. J. Wilmott, pp. 102 + 18 half-tone plates. Price 10/-, plus postage 4d.

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