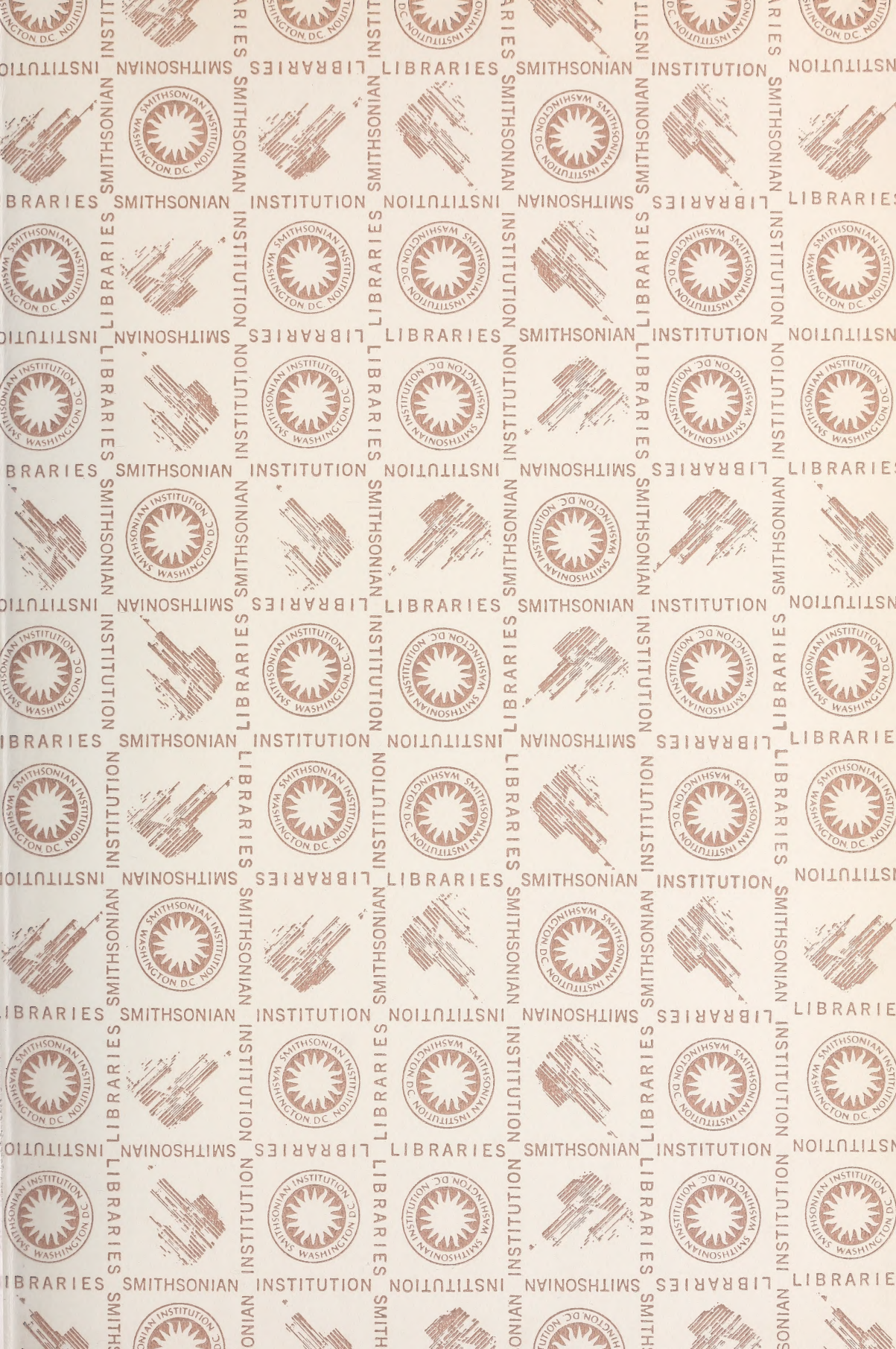
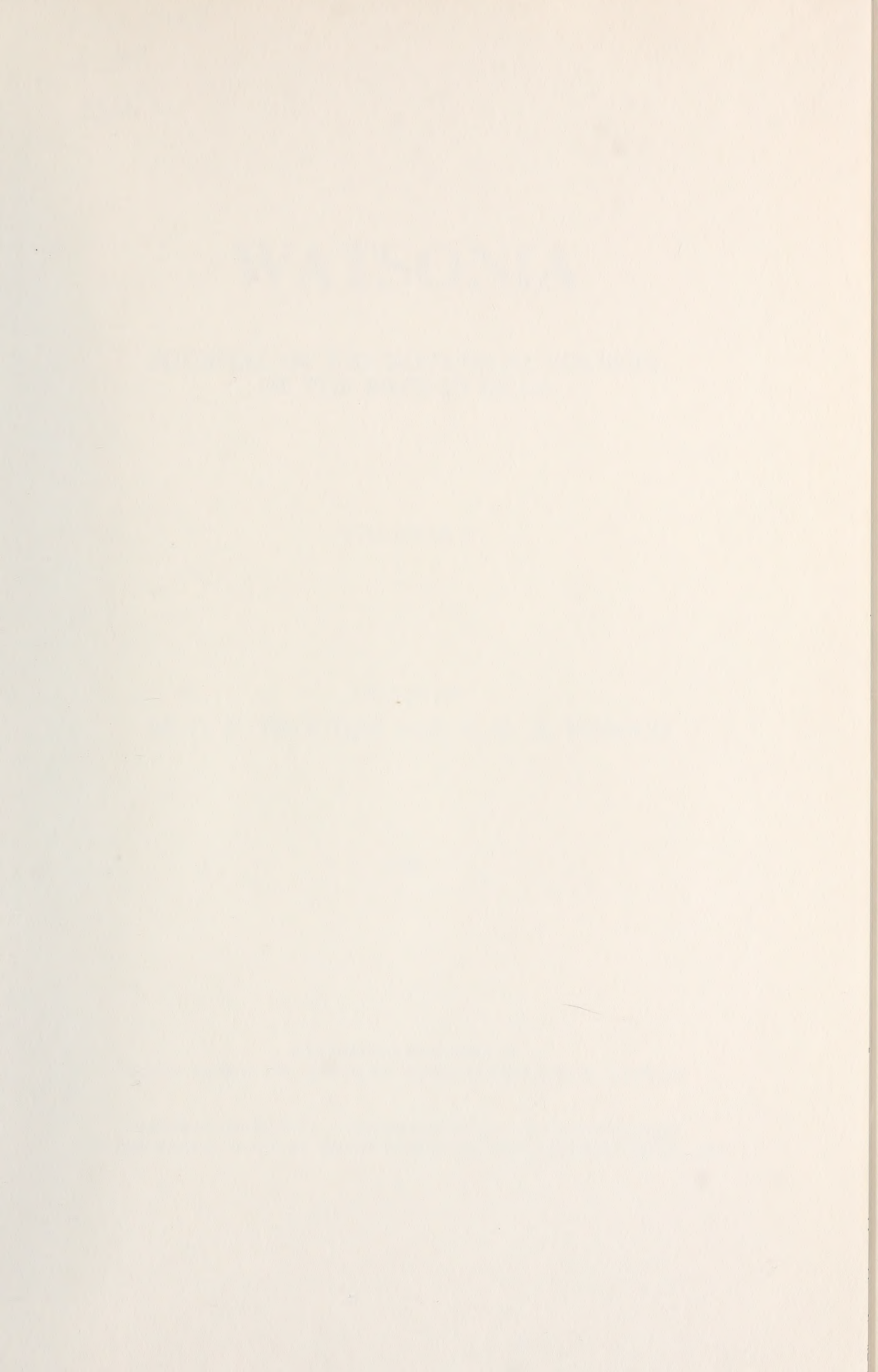










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JOURNAL OF THE BOTANICAL SOCIETY
OF THE BRITISH ISLES

VOLUME 7

EDITED BY

M. C. F. PROCTOR AND N. K. B. ROBSON

1969

PRINTED FOR THE SOCIETY BY

Headley Brothers. Ltd., London and Willmer Brothers Limited, Birkenhead

PUBLISHED AND SOLD BY THE BOTANICAL SOCIETY OF THE BRITISH ISLES,
C/O DEPARTMENT OF BOTANY, BRITISH MUSEUM (NATURAL HISTORY) LONDON, S.W.7

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Volume 7 Part 1 10 January 1969

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Editors: M. C. F. Proctor and N. K. B. Robson

Published and sold by the Botanical Society of the British Isles
c/o Department of Botany, British Museum (Natural History), London.
Price Twenty-five Shillings

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INVESTIGATIONS INTO THE PHENETIC RELATIONSHIPS BETWEEN SPECIES OF *ONONIS* L.

By R. B. IVIMEY-COOK

Department of Botany, University of Exeter

ABSTRACT

Several multivariate methods have been tested against Sirjaev's classification of *Ononis*, and their suitability for various purposes considered. It is concluded that while Association-analysis may provide the basis of a suitable key to OTUs, Principal Components Analysis offers one of the best starting points for polythetic classification. The difficulty of portraying the inter-OTU relationships can be resolved in part by using cluster analysis on the distance matrix calculated from the component specifications of the OTUs, over such a number of components as accounts for a suitable proportion of the variation within the population. Cluster analyses of distance matrices, using average linkage, calculated directly from the standardized data matrix did not, on the whole, give such satisfactory results. A comparison of weighted against unweighted cluster analyses showed in all cases that the latter seemed more appropriate.

1. INTRODUCTION

A principal aim of taxonomy must be the preparation of monographic accounts of genera. Any attempt in such monographs to discuss relationships between species ought to be made in the light of as much information as possible about the species concerned. Too often the published data are incomplete, often in material particulars. The consideration of relationships, which is a feature of many monographs, tends to be based on a limited, and often not wholly explicit, range of the more prominent characters. While it may be possible to infer phylogeny from fossil evidence in certain instances, in most cases, relationships can only be assessed between species as they occur at the present time.

The present paper enquires into the phenetic similarities between the species of the genus *Ononis* and considers these results by comparison with the arrangement presented by Sirjaev in his monograph of the genus (Sirjaev 1932); it allows some examination of the problems associated with quantitative aspects of Angiosperm taxonomy.

The tribe Trifolieae in the Papilionaceae contains 6 genera, among which *Ononis* may be distinguished by its relatively large pink, purple or yellow corolla and a legume which is neither coiled nor crescentic. Sirjaev divides the genus into two Sections; *Natrix*, which includes species with a paniculate inflorescence* and an elongated legume which is usually pendent, and *Bugranae*, whose species have a usually racemose inflorescence and an erect, rhomboid or ovoid legume. Within both Sections, a number of Sub-sections and Series are recognized (See Appendix 1, p 19).

The genus contains about 70 species, mostly distributed along both shores of the Mediterranean. The centre of distribution seems to have been southern Spain or North Africa, where nearly half the species occur. Very few penetrate north of the Alps, though 3 species occur in Britain. Several others can be found in the Middle East and south-west Asia, while *O. arvensis* is recorded as far east as India. Generally, the species flourish in fairly dry and frequently calcareous soils, but they are not especially adapted to extremes of either temperature or humidity.

There is a considerable range in the species concept within the genus. Three species in particular are very variable, *O. natrix*, *O. viscosa* and *O. spinosa*; in the last, some of

* The inflorescence in this and related genera is difficult to define. The term 'paniculate' is here used to describe an inflorescence composed of a number of axillary peduncles, which vary from 1 mm to several cm in length, each bearing 1-3 shortly pedicellate flowers. Those termed 'racemose' have no peduncle and the flowers are borne either sessile or very shortly pedicellate in the axils of the bracts, usually singly, occasionally in pairs.

the variants are commonly treated as having specific rank, but in general, the variation is recognized by the establishment of a number of subspecies and varieties. At the other extreme, there are a number of species pairs where the inter-specific distinctions are largely matters of size or other relatively minor features.

2. METHODS

Various methods can be used to assess similarities between species; these range from the intuitive (subjective) assessments of the conventional or herbarium taxonomist to the so-called objective techniques of numerical taxonomy. The basic methodology of numerical taxonomy has been set out by Sokal & Sneath (1963) and it will suffice here to outline the techniques used.

The basis of numerical methods is the unit character, which must express some aspect of the genome; such characters may be divided into a number of states, which may be expressed in any units, and the numerical values of these states provide the basis for the calculation of similarity coefficients between the species. Various statistical techniques can then be used to investigate the relationships between the species, as measured by the characters employed.

Since it is not necessary to confine the investigations to categories of the same rank, such as species, the non-committal term 'operational taxonomic unit' (OTU) is normally employed. A total of 107 OTUs of *Ononis* were considered, comprising 57 species represented by one OTU each and 10 species represented by more than one OTU. For each OTU, 64 characters were investigated and their states determined. In Appendix 2 is given a list of these characters and an indication of the range of their states.

The determination of the states of the various characters was carried out chiefly on herbarium material in the British Museum (Natural History) (BM) and in Kew (K). Most of the quantitative characters have a considerable range, not only on a single individual, but also within the OTU. Since only a single value for each character can be inserted in the data matrix, the mean of the values measured, in some cases modified in the light of those given by Sirjaev, was generally adopted.

For certain characters, particularly lengths and breadths, small differences at the low end of the range may be as significant as much larger differences at the upper end. Kendrick (1964) considers resolving this problem by coding such states on a linear scale and incrementing the code increments. This may approximate to a logarithmic transformation of the data. In the present work, logarithmic transformations have been applied to the states of certain characters where it seemed that, in the untransformed data, the values of the states at the upper end of the range would have an over-riding influence on the results. The question of data transformations of this sort is a vexed one; while it is arguable that a logarithmic transformation is not appropriate in every case, there is no special virtue in the linear scale of measurement conventionally used.

Two main approaches may be used to obtain a classification of individuals—divisive-monothetic and agglomerative-polythetic (see Williams, Lambert & Lance 1966). The divisive-monothetic approach considers the entire population and splits it up hierarchically on the basis of the presence or absence of one attribute at every step of the hierarchy. Agglomerative-polythetic methods employ indices of similarity and combine those individuals which are most similar, again hierarchically, until the original population has been reconstructed.

One divisive-monothetic method was investigated (Association Analysis, see Williams & Lambert 1959, 1960, 1961). This method has been used with considerable success in ecological investigations and can utilize one of several possible association indices. These indices have been constructed for use with presence/absence data and, to apply this method, the characters must be recoded so that the states conform to this requirement. The avoidance of logical correlations as a result of this recoding usually involves the loss of a substantial amount of information; on these grounds alone, the association index is not an especially suitable tool for the investigation of taxonomic resemblance.

Agglomerative-polythetic methods are considerably more flexible. Mostly, they allow multistate characters to be used, though one, Information Analysis, uses data in a form identical with Association Analysis. Information Analysis is described by Williams, Lambert & Lance (1966) and involves the calculation of an information statistic which gives a measure of the disorder of a group of individuals. Successive combinations involve those pairs of individuals or groups giving the least increment in the value of the information statistic.

Multistate characters may be used to obtain either a correlation coefficient or a measure of taxonomic distance. Distance may be calculated as the distance between a pair of OTUs in a Euclidean hyperspace generated by treating the character states as a set of Cartesian co-ordinates. Since these states have been measured in a variety of units, some restriction on the lengths of the character axes is required. It has been suggested that the states could be constrained within axes of unit length, but it would seem that the more conventional procedure of standardization (reduction to zero mean and unit variance) would be preferable in several respects.

The product-moment correlation coefficient can also be used to measure phenetic resemblance though Eades (1965) considers that its use is not always appropriate. Two correlation matrices can be calculated, that between characters (the R-matrix) and that between OTUs (the Q-matrix). Although the R-matrix does not, of itself, give a direct measure of resemblance between OTUs, in general its calculation is to be preferred, since it can be processed to give the required information. The calculation of the Q-matrix is again affected by the variety of units in which the character states have been measured. While it is possible to standardize the character states (as was necessary for the calculation of distance) and then to obtain correlations between the OTUs using the resulting standard deviates, the procedure is not unexceptionable nor, in this instance, necessary.

The investigation of matrices of distances or correlations for structure and relationships is complex. For distance matrices, the technique of Cluster Analysis investigates directly the relationships between OTUs, considering only those OTUs which form a cluster at any one time. The same technique is involved in the analysis of the matrix of information statistics. The results of a Cluster Analysis can usually be portrayed as a two-dimensional dendrogram, the reduction in dimensions being indicative of the extent to which information on other relationships is missing.

There are two main versions of Cluster Analysis—the *unweighted* method in which the similarity between a cluster and the remaining individuals is dependent on the number of OTUs comprising the individuals concerned, and the *weighted* method, in which the similarity is not dependent in this way, each individual, however constituted, being treated as equivalent to any other individual. The constitution of a cluster may either be confined to a pair of individuals (Pair-group method) or other OTUs may be considered for addition to the cluster initial, to form a larger cluster (Variable-group method). Such additional OTUs must meet some suitable criterion of closeness. When they first proposed the method, Sokal & Michener (1958) used an arbitrary fixed limit which applied to all clusters. This seems insufficiently flexible to be applied to different stages of the clustering process and an alternative limit of 5 per cent. above the distance between the OTUs comprising the cluster initial was tried and gave reasonably satisfactory results.

For most purposes, however, the Pair-group method is preferable to the Variable-group method, for a number of reasons. Firstly, there is no arbitrary criterion of closeness—different results can be obtained according to how this is set; secondly, it was found that if this limit was set at 5 per cent., as mentioned above, only a few groups of more than two OTUs were obtained, while if the level were raised to any extent, large variable groups tended to be formed, especially in the later stages of the clustering process; thirdly, if a group of more than two OTUs was appropriate to a particular situation, this could be expected to appear as a number of closely related pairs; fourthly, computer programming with variably sized groups is much more elaborate.

The Pair-group method of Cluster Analysis thus involves the detection of that pair of individuals which are mutually closest together. This result is recorded and a revised

distance matrix is calculated, treating the cluster as an individual, with or without weighting as appropriate. The process is repeated until one final cluster is obtained.

Quite apart from any weighting which may be involved, the calculation of distances between a cluster and the remaining individuals may be carried out in a number of ways. The one used here is by average linkage, whereby a cluster is located in the individual space by calculating, for each individual, the average of the distance between the components of the cluster and that individual. Lance & Williams (1966) have shown, however, that average linkage is only a special case of a general system in which the nature of the sorting strategy is determined by the values of four parameters; variations in these can result in different clustering patterns and the form of the cluster analysis results becomes a function of the clustering process and cannot be an inherent property of the data.

The methods available for the analysis of correlation matrices include a number coming under the general heading of Factor Analysis, one of the more widely used being Principal Components Analysis. This technique investigates the relationships between a multi-dimensional array of variables, some of which may be correlated and hence at least partially redundant. The points representing the variables form a roughly hyperellipsoidal swarm and the method extracts a set of orthogonal, and hence uncorrelated, components, these being the principal axes of the hyperellipsoid. The components are extracted in descending order of magnitude and much of the variance is accounted for by the first few components, in effect reducing the dimensions of the problem. The question of when to stop extracting components is one on which there is little agreement among the advocates of the method; in this work, all components greater than unity were extracted. Each component has associated with it a vector (the eigenvector) giving the relation between each variable and the component. These are termed the component loadings.

Principal Components Analysis only works efficiently where the swarm of variables is approximately multivariate normal. In certain cases, and especially where the variables represent OTUs, there may well be a tendency for two or more swarms to appear—*e.g.* a dumb-bell-shaped distribution which might correspond to two sub-generic taxa. Such a distribution is most likely to appear along the first component, which effectively finds the long axis of the dumb-bell. Under these circumstances, the second and subsequent components are likely to be taxonomically meaningless, as they will be constructed in the hyperspace common to the two swarms and will reflect some characters of both. This difficulty is not obvious in the matrix of component loadings when the R-correlation matrix is analysed, but these loadings do not, of themselves, give a direct measure of the similarities between the OTUs.

If the vector of component loadings so obtained is used to post-multiply the standardized data matrix, a measure is obtained of the extent to which each OTU contains characters as weighted by their representation on that particular component. These have been called the component specifications and enable the distribution of the OTUs to be plotted on the component axes.

Although Principal Components Analysis tends to reduce the dimensions of a problem by concentrating the variation in relatively few components, only rarely is it possible to consider only the first two or three components so that the results can be conveniently portrayed on paper. The results may be plotted for pairs of components as a series of scatter diagrams, but the results are difficult to visualize and unwieldy if more than four or five components are important. Such scatter diagrams are, in effect, displaying the component loadings or specifications on Cartesian co-ordinates and the results over the required number of components may be used to calculate distance matrices which can then be analysed by Cluster Analysis, as previously described.

3. RESULTS

(i) *Association Analysis*

The result of an Association Analysis between OTUs using character states as attributes is shown, in the form of a hierarchy, in Fig. 1. The characters which effect the divisions

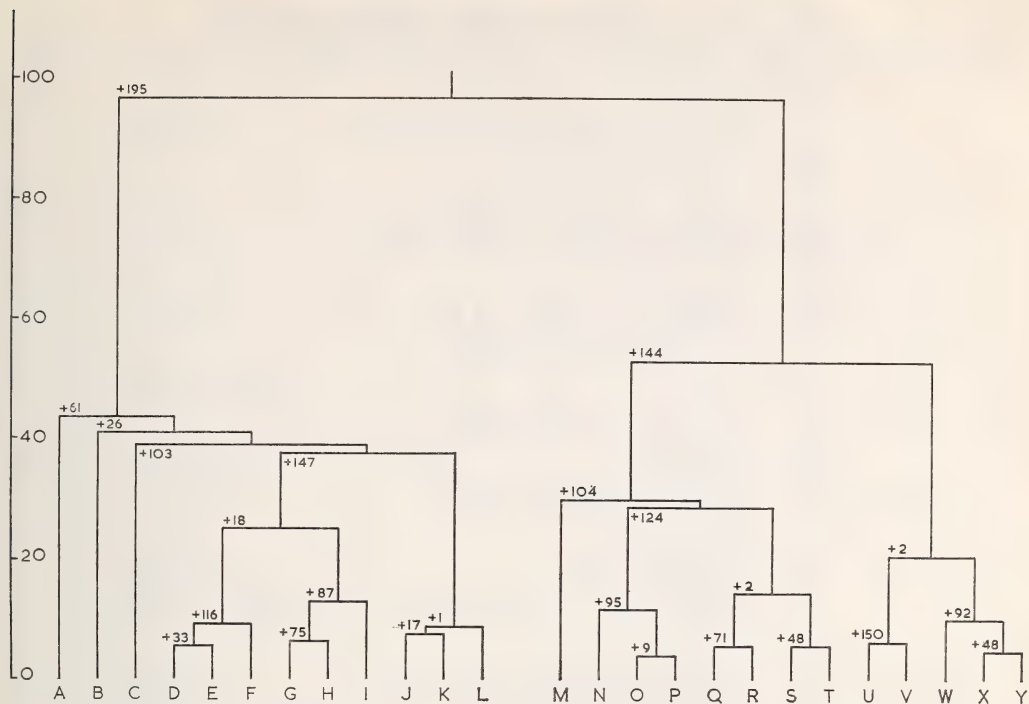


Fig. 1. The hierarchy resulting from an Association Analysis of the OTUs, using as attributes the character states as set out in Appendix 2.

at each stage are identified by the attribute number in the figure. The morphological features involved can be identified by reference to the last column of Appendix 2 and are set out in detail in Table 1. The names of the OTUs comprising the 25 final groups are set out in Table 2.

Since this method is inherently incapable of breaking down groups of fewer than 8 individuals when a 5 per cent. probability level of χ^2 is used to determine whether or not a group of individuals should be split, it is to be expected that the groups of OTUs will show varying degrees of heterogeneity. The greatest interest is likely to centre on the characters which have been chosen to effect the divisions. These characters are the attributes which when taken with every other attribute have the highest sum, over all the OTUs present, of the chosen index of association. They thus indicate the probable positions of the greatest discontinuities between the OTUs. The index of association used was χ^2/N , which theoretical considerations suggest is the most efficient. Whether it is preferable for taxonomic data has not been fully investigated. The level of maximum χ^2 at which the various divisions take place give some indications of the heterogeneity of the population under consideration, though it must be pointed out that a single significant association will suffice to cause the population to be divided.

In the standard procedure for Association Analysis, both positive and negative associations are given equal weight; in an ecological context, where the attributes are the species occurring in sample areas, a case can be made for this. Whether the same is true for taxonomic data, where the attributes represent various states of a character, is more questionable, and further investigation may show that a consideration of positive associations only may give a result which is taxonomically more meaningful.

It will be clear from an examination of Fig. 1 that the technique of Association Analysis produces a result which closely simulates a dichotomous key and since only those characters specifying the positions of the greatest discontinuities are mentioned, it is hardly to be

TABLE 1. Association analysis: subdivision characters (see Fig. 1).

195	Pod not erect
61	Leaflets with dense short hairs
26	Stipule base vaginate or infundibuliform
103	Calyx teeth with 1 nerve
147	Apex of standard not emarginate
18	Stipules longer than ca. 12 mm
116	Calyx with dense short glandular hairs
33	Petiole longer than ca. 7.5 mm
87	Arista present
75	Peduncle longer than ca. 12 mm
1	Plant not a herbaceous annual
17	Stipules longer than ca. 7.5 mm
144	Standard with glandular hairs
104	Calyx with more than 5 nerves/tooth
124	Standard purple
95	Calyx tube longer than 2 mm
9	Spines strong
2	Plant not annual
71	Bracts with 3 leaflets
48	Leaves in upper half of plant with more than 1 leaflet
2	Plant not annual
150	Standard apex not rounded, apiculate
92	Calyx not campanulate
48	Leaves in upper half of plant with more than 1 leaflet

expected that the OTUs comprising the 25 final groups are phenetically similar. If each OTU were to be replicated so that, on analysis, the final groups were composed of such replicates, then the characters chosen as division attributes should be those best suited for the construction of keys for the purposes of identification.

(ii) Information Analysis

The dendrogram constructed by the aggregation of OTUs using the information statistic as the criterion was not satisfactory. A number of groups could be detected readily, particularly groupings of subspecific taxa and some groups of closely related species, but the larger clusters did not appear to conform to any rational phenetic classification. This may reflect, to a considerable extent, the form in which the data were presented, particularly the technique used to convert quantitative data to presence/absence form; in any event, it is clear that further work will be needed before this technique can be applied to taxonomic situations.

(iii) Principal Components Analysis

This method was first applied to both the R- and Q-correlation matrices obtained from the complete 107×64 data matrix; from the former correlation matrix, the component specifications were obtained and the distribution of the OTUs plotted on the component axes. From the analysis of the Q-correlation matrix, the eigenvectors give a direct assessment of the relative positions of the OTUs. The two Sections into which *Ononis* is divided are quite readily recognizable from scatter diagrams of the OTUs plotted on the first two component axes. This is illustrated in Fig. 2 for the component specifications. Of the four OTUs which appear between the two principal groupings, *O. cintrana* (49) is recognized as being rather uncertainly placed in Section Bugranae, *O. tridentata* (2) and *O. fruticosa* (3)

TABLE 2. Association analysis: final species-groups (see Fig. 1).

A	rotundifolia tridentata	M	megalostachys
B	fruticosa cristata vaginalis	N	repens (all vars.)
C	pubescens cintrana	O	spinosa ssp. antiquorum (all vars.) spinosa ssp. leiosperma
D	sicula ssp. sicula sicula ssp. polyphylla	P	spinosa ssp. spinosa (all vars.) spinosa ssp. foetens
E	viscosa (all sspp.) crotalarioides	Q	arvensis (all vars.)
F	serotina pseudoserotina maweana natrix ssp. natrix	R	masquillieri hispida ssp. hispida hispida ssp. arborescens
G	hebecarpa polysperma ornithopodioides peyerimhoffii antennata (all sspp.)	S	diffusa (all sspp.) serrata tournefortii cephalantha villosissima
H	incisa adenotricha atlantica	T	alba monophylla
I	reclinata dentata pendula laxiflora verae thomsonii christii	U	pinnata pusilla minutissima cephalotes saxicola striata leucotricha
J	natrix ssp. ramosissima natrix ssp. stenophylla natrix ssp. angustissima natrix ssp. polyclada natrix ssp. filifolia natrix ssp. falcata	V	aragonensis reuteri speciosa
K	crispa natrix ssp. hispanica natrix ssp. mauritii natrix ssp. arganietorum natrix ssp. prostrata	W	mitissima alopecuroides baetica rosea avellana crinita
L	biflora	X	subspicata hirta cossoniana filicaulis subspicata
		Y	euphrasiifolia variegata oligophylla

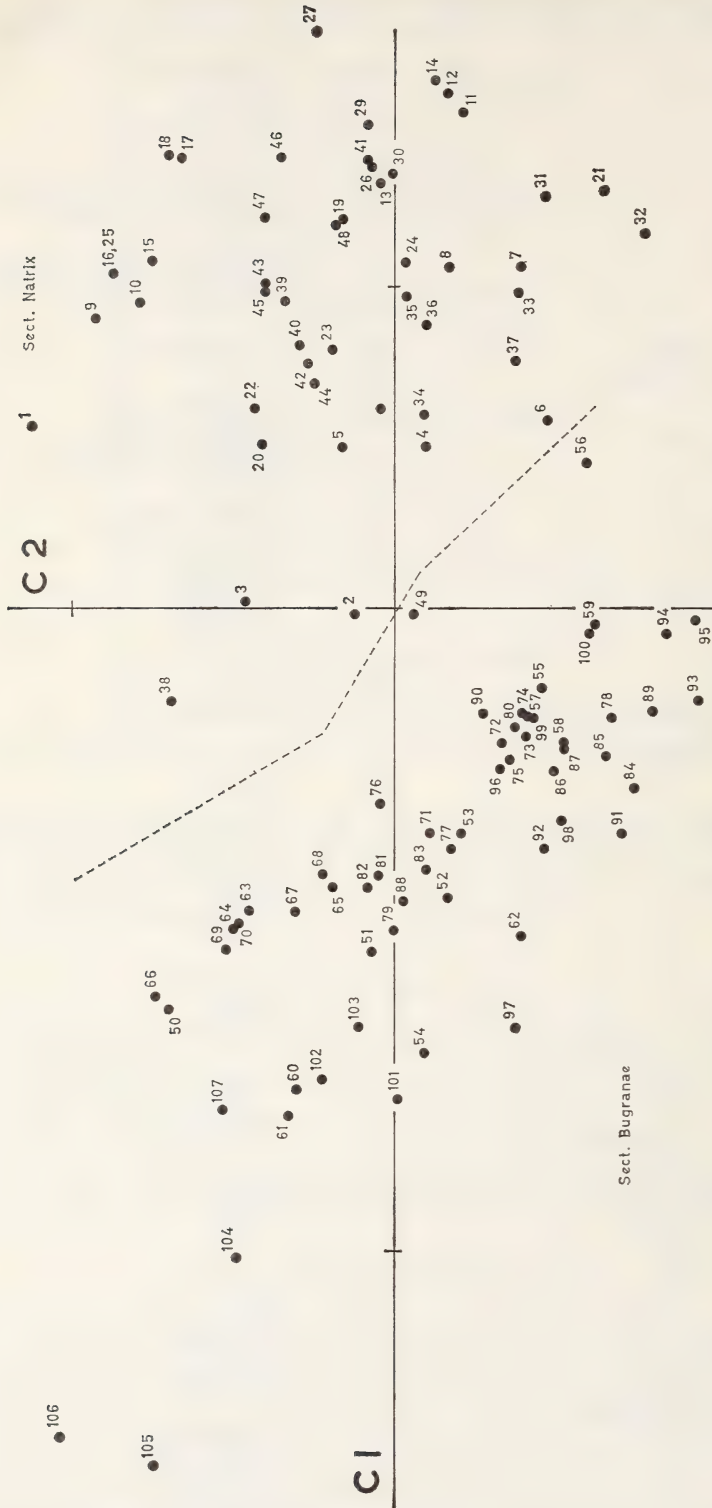


Fig. 2. A plot of the 107 OTUs on the first two component axes derived from the between-characters correlation matrix (component specifications). The two axes are drawn to the same scale and are marked at intervals of 10 units.

are classified more appropriately on component 3, as is, to a lesser extent, *O. pubescens* (38). The only species which appears misplaced in this figure is *O. minutissima* (56); again, however, it must be remembered that it is unlikely that a perfect separation can be obtained on the basis of two components which account for rather less than a quarter of the variation.

The characters which are especially involved in bringing about this separation are whether the pod is erect or pendent and the length of the peduncle, both characters which are used to differentiate the Sections. To a somewhat lesser extent, the lengths of the arista and of the calyx tube, the number of nerves in the calyx teeth and the number of seeds in a pod are all important characters in bringing about the separation along the first component. The second component is concerned chiefly with the size of the leaflets and stipules, OTUs with large foliage being found at the positive end of this axis.

Since it was felt that the immediate recognition of the two Sections would obscure the meaning of subsequent components to a considerable extent and since it was not necessary to use component analysis to make this initial separation anyway, the OTUs were split into two groups, essentially representing Section *Natrix* and Section *Bugranae*, but with a small overlap; in particular, *O. cintrana* was included in both groups.

The two groups (subsequently referred to as Group N and Group B respectively) were then re-analysed. This involved the calculation of a new R-correlation matrix for each and these were then subjected to Principal Components Analysis and the component specifications calculated. The omission of zero character scores reduced the total number of characters to 61 in Group N and 58 in Group B.

The component analyses of the two groups indicate certain differences in the shape of the hyperellipsoids. In Table 3 are given the variances of the first 12 components for Groups N and B and also, for comparison, of the original complete set of OTUs, together with the percentage of variation extracted by each component.

In Group N, the characters which contribute most to the direction of the first component are plant size, the texture and indumentum of the leaflet, the number of seeds per pod and the seed surface. The 3 OTUs from Sub-section *Chrysanthae* were included in Group N for purposes of comparison and this component very clearly separates these from the rest of the group. This is brought out very strongly in the plot of the component specifications. The characters with high loadings on the second component, and which thus are most concerned with distributing the OTUs along this axis, are the length of the stipules, the absence of long hairs on the calyx and the presence of short hairs on the stem, though quite a number of characters have loadings not much smaller than these. In Fig. 3 is shown the distribution of the OTUs along the component axes, using the component specifications for the first two components. Where a large proportion of the variation of a population is associated with the first two components, then such a diagram will give a good indication of the relationships between the OTUs. However, as Table 3 clearly shows, only about 25 per cent. of such variation has been considered and a plot of only the first two components cannot be considered an adequate representation of the distribution of the OTUs in the character space.

To investigate this distribution more adequately, the component specifications over the first 12 components were used to calculate a distance matrix which was then subjected to Cluster Analysis. Both the weighted and unweighted Pair-group methods were used and the resulting dendrograms were compared with Sirjaev's original classification using the cophenetic correlation coefficient. Values of 0.629 for the weighted and 0.635 for the unweighted methods suggest that there is little to choose between the two in this case. Fig. 4 shows the dendrogram for the unweighted method and a number of points are apparent: 1. In all cases where the OTUs are infraspecific taxa, these cluster together so that every species is eventually represented by a single stem. In the case of *O. natrix*, there is a marked distinction between a group comprising subsp. *natrix*, *ramosissima*, *stenophylla*, *angustissima*, *polyclada* and *filifolia* on the one hand and *hispanica*, *mauritii*, *arganietorum*, *prostrata* and *falcata* on the other. The best separation of these groups is found on component 3. though they are clearly distinguishable on the sizes of their leaves and stipules.

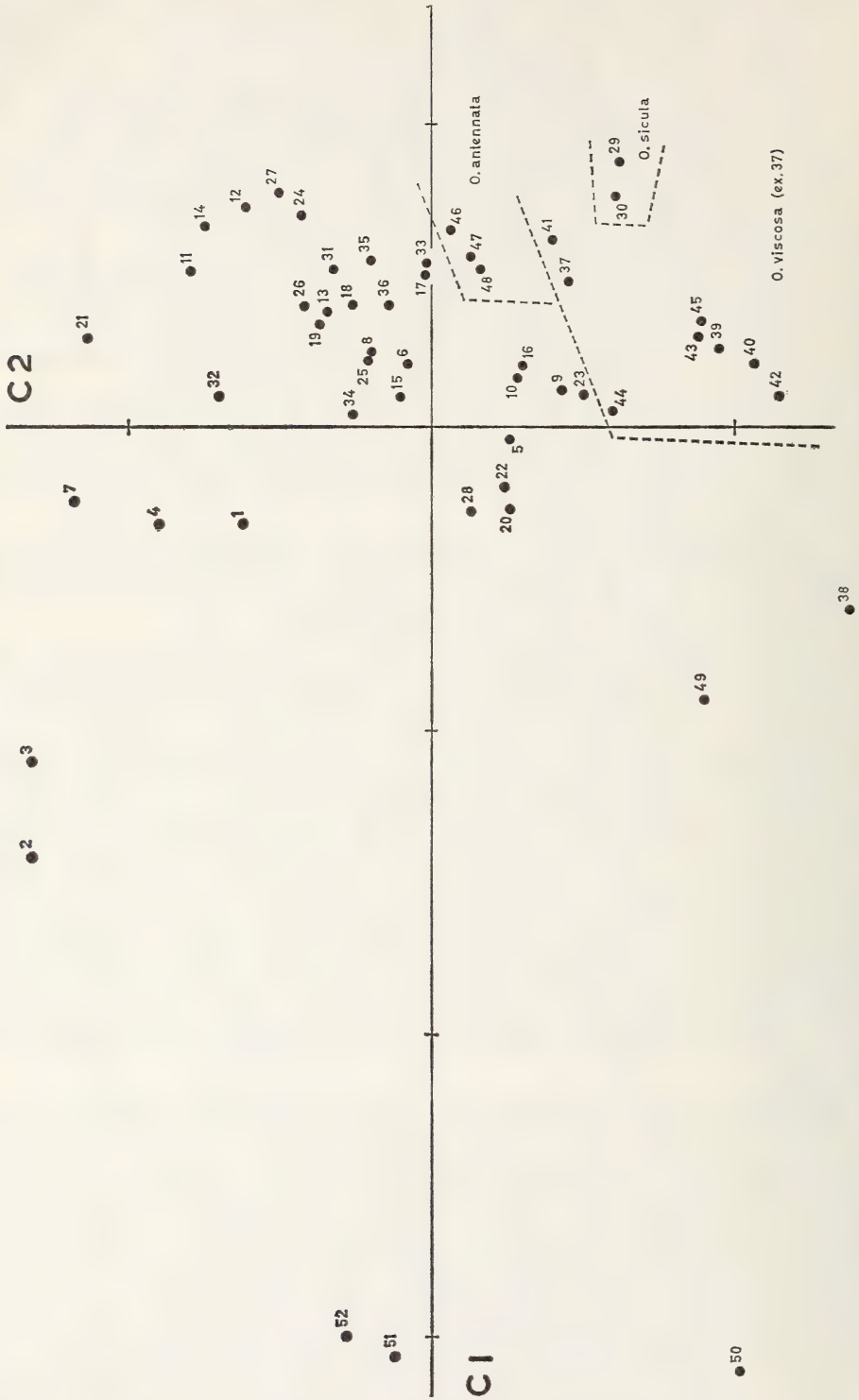


Fig. 3. A plot of the OTUs in group N on the first two component axes (component specifications). The axes are marked at intervals of 10 units.

TABLE 3. Principal Components Analysis: Variance of Components.

Component	Complete		Group N		Group B	
	Variance	Total % Variance	Variance	Total % Variance	Variance	Total % Variance
1	10.256	16.02	8.863	14.53	7.825	13.49
2	4.748	23.44	6.493	25.17	6.190	24.16
3	4.243	30.07	5.002	33.37	5.353	33.39
4	3.749	35.93	4.369	40.54	4.485	41.13
5	3.127	40.82	3.406	46.12	3.338	46.88
6	2.970	45.46	3.363	51.63	3.111	52.24
7	2.316	49.08	3.047	56.63	2.780	57.04
8	2.221	52.55	2.731	61.10	2.426	61.22
9	2.193	55.97	2.317	64.90	2.356	65.28
10	2.078	59.22	2.118	68.38	1.873	68.51
11	2.000	62.35	1.894	71.48	1.785	71.59
12	1.725	65.04	1.702	74.27	1.554	74.27
Total	41.624		45.306		43.077	

2. The recent recognition of *O. crotalarioides* (45) as a distinct species, chiefly on the basis of its much inflated pod, would not appear to be supported by these results. Overall, it seems no more dissimilar than the subspecies of *O. viscosa*, of which it was once one.

3. The most distinctive group is that comprising the 3 OTUs of Sub-section *Chrysanthae* (50–52), though the four OTUs of Sub-sections *Antiquae* and *Rhodanthae* are also well marked.

4. Sub-section *Reclinatae*, especially Series *Eu-reclinatae* (33–37) is well marked, with the addition of *O. christii* (5) and *O. thomsonii* (6) which differ chiefly in being shrubby. In

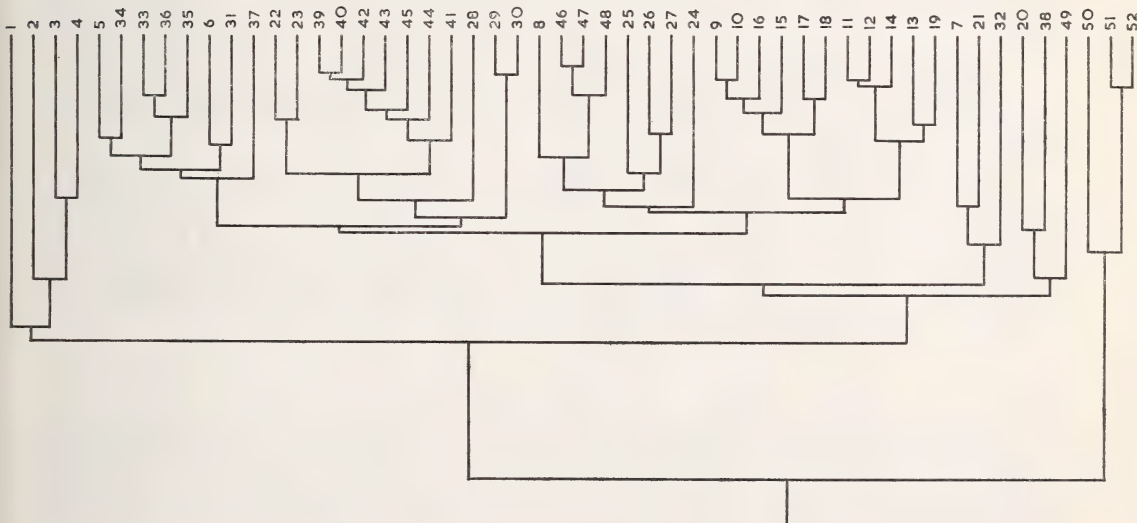


Fig. 4. The dendrogram resulting from a cluster analysis of the distance matrix calculated from the component specifications over the first 12 components, for group N. The vertical scale is indicated in distance units.

general, the aggregation of these species with the yellow-flowered *O. viscosa* group would seem not unreasonable. Although there is a tendency for flower colour to effect a separation within this group, it is clear that this is not the only significant character.

5. The conjunction of *O. antennata* (46–48) and *O. adenotricha* (8) is interesting in that the latter species is clearly rather different from the other members of Sub-section *Natrix*. The linking of these with Sub-section *Biflorae* (25–26), *O. ornithopodioides* and *O. polysperma*, would seem to bring together a group with aristate peduncles bearing usually two $\pm$ yellow flowers and in several cases, numerous seeds in the pod. The *O. natrix* group joins on to this and there is a residue of 6 species, probably all of which, with the exception of *O. cintrana* (49), can be looked upon as having failed to cluster with their most appropriate groups. They mostly have one or a few unusual characteristics and these were probably sufficient to put them outside the range of the cluster-generating process (see p. 3).

An analogous series of operations were carried out on Group B. In this case, the characters most strongly associated with the first component are the breadth of the leaflet, the shape of the calyx and the length of the vexillum. OTUs with long vexilli, tubular or bilabiate calyces and relatively large leaflets are those in Sub-sections *Verae* and *Crinitae* and these are found at the negative end of this axis. For component 2, one character, the presence of dense glandular hairs on the vexillum, is especially prominent. Fig. 5 is a scatter diagram of the OTUs on the first two component axes, but again it is not possible to consider only the first two components in isolation and a distance matrix was calculated over the first 12 components and subjected to Cluster Analysis. The cophenetic correlation coefficient between the dendrograms and Sirjaev's classification were 0.443 for the weighted pair group method and 0.457 for the unweighted. Again, the unweighted method seems slightly preferable, though neither of these figures are high enough to be of particular significance.

Certain of the features of the unweighted dendrogram (Fig. 6) are similar to those previously mentioned; the infra-specific taxa tend to cluster together, e.g. of *O. spinosa* (69–76), *O. repens* (77–82) and *O. arvensis* (63–68). In the case of *O. spinosa*, there seems no clear-cut distinction between varietal and subspecific status—nos. 72–74 are varieties of ssp. *antiquorum* while no. 76 is ssp. *foetens*. Nos. 69, 70, and 71 are all varieties of ssp. *spinosa*. In both the other species such taxa are treated as varieties, and in general seem to be rather more different than some of the subspecies of *O. spinosa*. *O. masquillieri* (62) which has certain features, especially in the inflorescence, which distinguish it from the other members of this group, fails completely to cluster with it.

Other groups which are clearly indicated are Sub-section *Chrysanthae* (55–59) and Series *Tuberculatae* of Sub-section *Diffusae* (91–95). Smaller groups corresponding to Sirjaev's classification can also be found.

The evaluation of the larger groupings indicated in the dendrogram is rendered difficult by the fact that each tends to be formed by the addition of a reasonably homogeneous group to the population already generated. This 'chaining' tendency in the dendrogram may indeed reflect the fact that there seems to be a group of rather similar species (represented by those in the upper third of the dendrogram) while the remainder form relatively more dissimilar groups, though fairly similar within themselves.

(iv) Cluster Analysis

The application of Cluster Analysis to distance matrices calculated between the component specifications of OTUs is intended to simplify the interpretation of the results of Principal Components Analysis. The method is more usually applied to distance matrices obtained from the original data matrix, in which the OTUs are located in a character space by the values of their score for each character.

For several reasons, including those discussed under Principal Components Analysis, two separate distance matrices were calculated for the same Groups N and B, rather than a single matrix for the complete data. The results of both weighted and unweighted pair-group clustering on group N were compared with Sirjaev's classification and the cophenetic

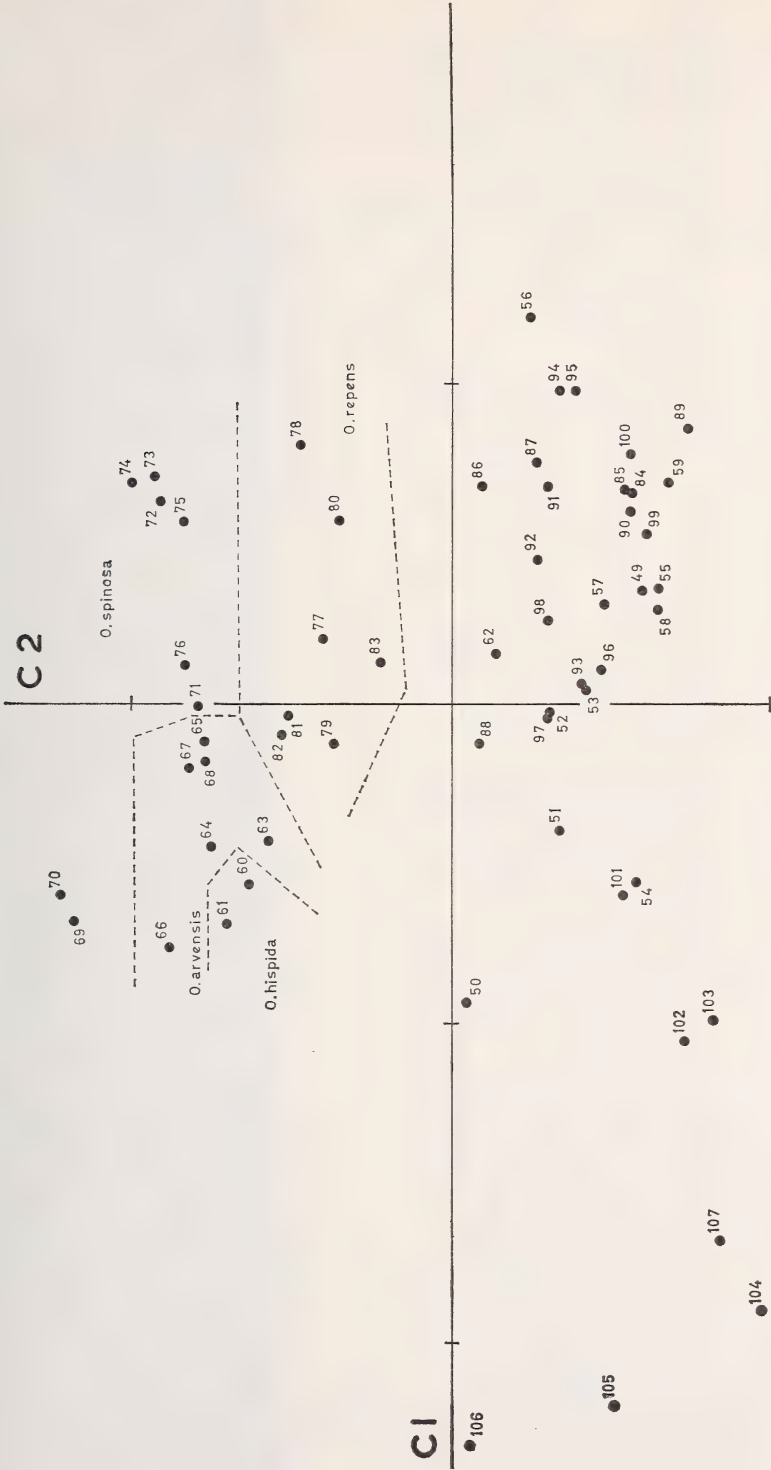


Fig. 5. A plot comparable to that in Fig. 3, but for group B.

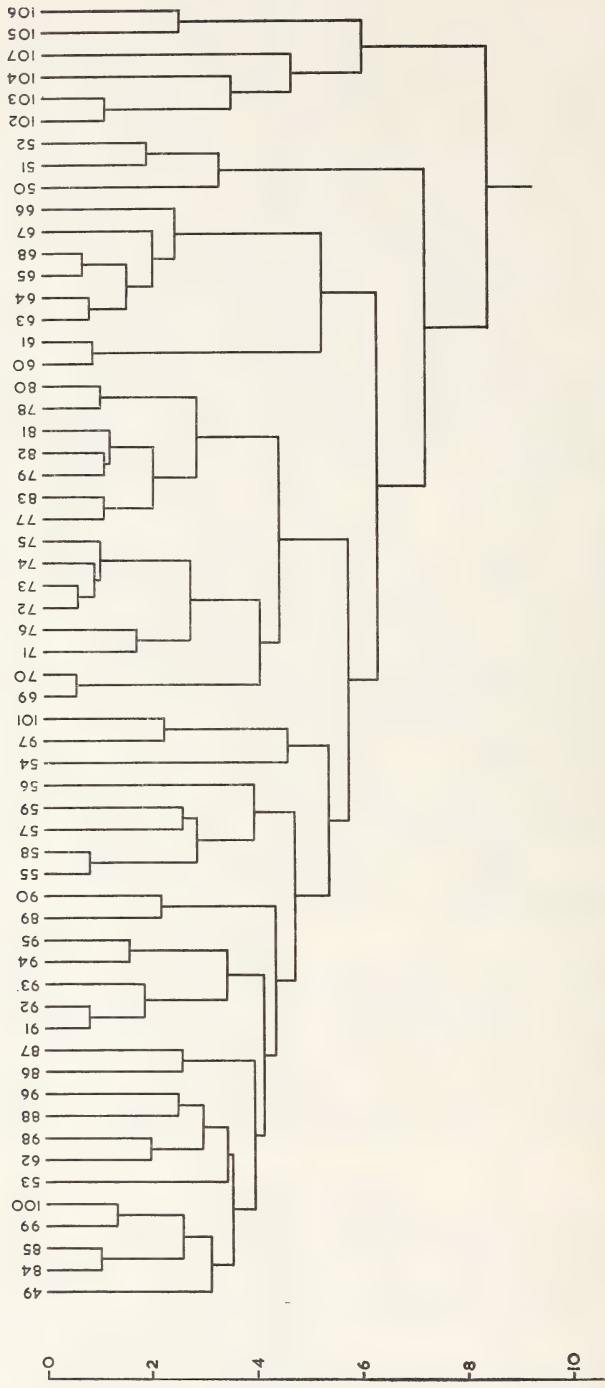


Fig. 6. The dendrogram comparable to that in Fig. 4, but for group B.

correlation coefficients were

The dendrogram obtained to that obtained from the scale and the fact that the the failure of *O. adenotric* perhaps more reasonable) residual species which must be of the method rather than when the large number of

For Group B a similar being 0.563 for the weigh

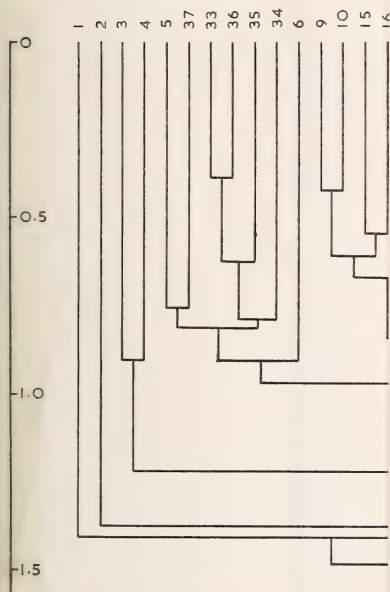


Fig. 7. The dendrogram result the standardized data matrix,

This dendrogram is significant specifications is much the aggregation of infra-species. *O. spinosa*, the appearance of OTUs 102-107. Sub-section recognition of other groups joining of these groups seem to the conclusion that the meaningful.

It is by now well recognized ability to resolve classification to it but also upon the method

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is firstly to select appropriate processes and, finally

It has been suggested taxonomy the subjective opinion. Rather, the subject in the process. It has been

correlation coefficients were 0.523 for the weighted and 0.625 for the unweighted methods.

The dendrogram obtained by the unweighted method (Fig. 7) is remarkably similar to that obtained from the component specifications. Apart from differences in the distance scale and the fact that the OTUs are in a different order, the chief features of interest are the failure of *O. adenotricha* (8) to cluster with *O. antennata* (46-48) and the different (and perhaps more reasonable) position of *O. peyerimhoffii* (31). There is also a larger group of residual species which must be looked upon as joining where they do because of the exigencies of the method rather than as indications of phenetic similarity. This is hardly surprising when the large number of dimensions of the data matrix is borne in mind.

For Group B a similar comparison was made, the cophenetic correlation coefficients being 0.563 for the weighted and 0.698 for the unweighted methods.

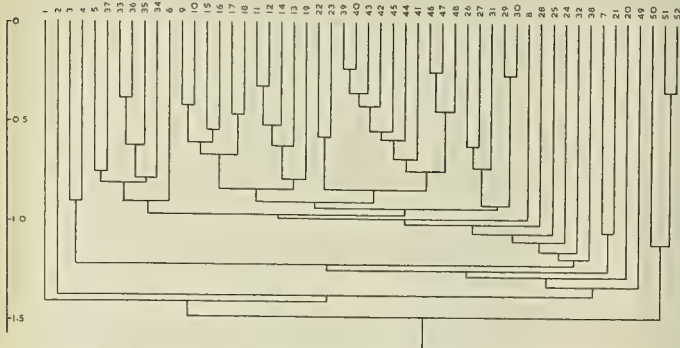


Fig. 7. The dendrogram resulting from the cluster analysis of the distance matrix calculated directly from the standardized data matrix, for group N. The vertical scale shows the distances at which the various groups cluster.

This dendrogram is shown in Fig. 8. The similarity between it and that from the component specifications is much less marked, although certain of the principal features recur: the aggregation of infra-specific taxa into species in the case of *O. repens*, *O. arvensis* and *O. spinosa*, the appearance of Sub-section Chrysanthae (50-52) and the aggregation of OTUs 102-107. Sub-section Bugranoides is represented lacking *O. striata* (59), but the recognition of other groupings is patchy, many of them being incomplete. The subsequent joining of these groups seems to have little meaning taxonomically and one is again forced to the conclusion that the clustering has taken place over too many dimensions to be meaningful.

4. DISCUSSION

It is by now well realized that a computer is but the tool of the taxonomist and its ability to resolve classificatory problems is dependent not only upon the data presented to it but also upon the method employed to analyse those data. The work of the taxonomist

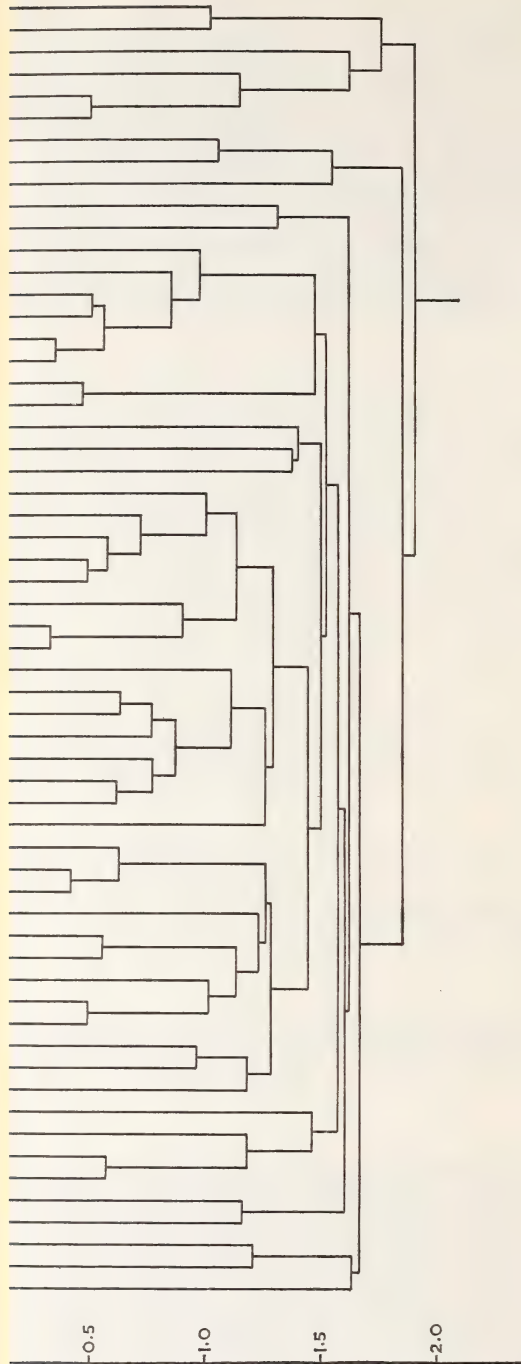


Fig. 8. The dendrogram comparable to that in Fig. 7, but for group B.

appropriate data, then to submit them to an acceptable analytical process, to interpret the results.

It is hoped that the introduction of numerical methods will remove from the element which has tended to obscure certain facets of classification. The element has been diverted, though probably reduced somewhat, to be more centred on the choice of characters from which an assessment

of the similarity between species is to be made, rather than on the assessment itself. A poor selection of characters or an unsuitable choice of character states can change the entire course of an analysis.

The 64 characters used in this investigation would seem to be a minimum for this type of work, especially as 13 of them refer to the indumentum in some part of the plant; the results of the analyses thus tend to be orientated towards indumentum, which may account for some of the more surprising conclusions. Recent work on the classification of soils suggests, however, that a smaller number of relatively uncorrelated characters may be just as effective as a large group of unselected characters (Sarkar *et al.* 1966). There seems to be no obvious justification for an arbitrary weighting of floral over vegetative or other characters, but it is, of course, possible to introduce some measure of such weighting by increasing the number of floral characters used. A more detailed examination of flower structure would undoubtedly provide a considerable number of additional characters, *e.g.* pollen grain characters, which could be usefully employed. A further consideration is the extent to which flower colour, for example, is adequately described in terms of degrees of purpleness or yellowness or whether a series of states based on a chromatographic analysis of the pigments is not more appropriate. This opens up a considerable field utilizing biochemical characters which, unfortunately, are often only available if herbarium material does not have to be used.

The choice of character states also requires considerable care for, although standardization will largely remove the effect of different units of measurement, the use of unlimited categories for characters such as length, can introduce unwanted features. This was clearly seen in a preliminary analysis when untransformed length data were used—the very large leaflets and stipules characteristic of OTUs 102–107 distorted these dimensions of the character space so that they carried a disproportionate amount of weight in the analysis.

The question of transformation of the character states is one on which there has been little constructive comment from mathematicians. Theoretically, Principal Components Analysis requires that the correlation coefficients shall have been calculated from normally distributed data. Biological data are often not normally distributed and, whereas the application of logarithmic transformations to certain growth characters and of angular transformations to characters constrained to upper and lower limits are well known, there are certain types of character state which might require the most complex transformations to bring them to normality. In any event, it is impossible to transform any type of presence/absence data, which may make up a substantial part of a taxonomic data matrix.

Of the analytical methods used, Cluster Analysis is certainly the simplest agglomerative polythetic method and the construction of a two-dimensional dendrogram presents the information in an easily assimilable form. The reduction in the number of dimensions involves the loss of a substantial amount of information—indeed, all information concerning relationships other than those expressly indicated. It is basic to the method of Cluster Analysis used here that, at each stage, a revised distance matrix is calculated, treating clusters as new individuals and the distance between two such clusters as the mean of the distances between the individuals. The shape of the clusters so formed is important in assessing the efficiency of the method. Clustering by average linkage with only pairs of OTUs being considered for each cluster can lead to the centre of gravity of a cluster moving away from other OTUs which are similar to one of the individuals, yet not sufficiently similar to join the cluster immediately. Such OTUs are liable to become completely isolated and may eventually join a cluster to which they are not especially closely related. It was to meet this difficulty that the 'variable group' method of clustering was investigated, but its arbitrary limits are open to objection. The variable group method does prevent, at least in part, the tendency for OTUs to become separated from others to which they are related, though it is not able to deal with clusters which are not approximately hyperspherical. In the case of taxonomic data, the possibility of elongated clusters is a real one, though it is difficult to devise a method which will ensure that clusters of such a shape are located accurately without including unrelated OTUs as well. It is also worth noting that in every

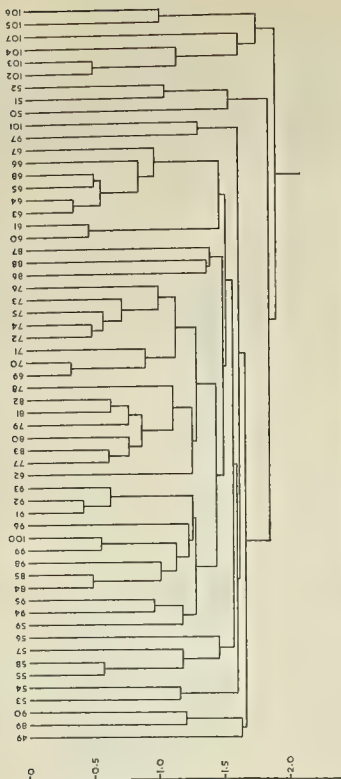


Fig. 8. The dendrogram comparable to that in Fig. 7, but for group B.

is firstly to select appropriate data, then to submit them to an acceptable analytical process or processes and, finally, to interpret the results.

It has been suggested that the introduction of numerical methods will remove from taxonomy the subjective element which has tended to obscure certain facets of classification. Rather, the subjective element has been diverted, though probably reduced somewhat in the process. It has become centred on the choice of characters from which an assessment

case the unweighted cluster analysis has given results more in keeping with the accepted classification than the weighted analysis.

One of the problems which arises when the results of different methods are to be compared is the mechanism of the comparison. The cophenetic correlation coefficient has been suggested as an appropriate measure for the comparison of dendrograms (Sokal & Sneath 1963). While this will always recognize two identical dendrograms, the amount of dissimilarity permitted before the dendrograms cease to be identical must depend on the precision of the comparison. The values of the correlation coefficient presented above were calculated on the assumption that the two Sections of *Ononis* represented taxa at the 50-phenon level and the range above this was divided into 10 parts, i.e. 5-phenon categories.

A general comparison of these results with the classification of *Ononis* put forward by Sirjaev suggests that there are few significant discrepancies. It would be unreasonable to expect a very close correlation and it is probably fair to conclude that there are few differences that need to be accounted for; this is not to say that some aspects of the classification might not be reconsidered. On the basis of the present work, which was intended chiefly to investigate methodology, it would be inappropriate to make any taxonomic changes, though a case could, perhaps, be made for the erection of two new Sections, one to contain Sub-section *Antiquae* (*O. rotundifolia*) and the other to contain Sub-sections *Salzmännianae*, *Verae* and *Crinitae*. Both new sections could be readily defined on morphological grounds and this would produce four Sections of roughly comparable standing.

A most promising method for taxonomic work would appear to be Principal Components Analysis, with the subsequent calculation of the component specifications. This seems to be more appropriate than the calculation of taxonomic distance, especially if the number of characters, and hence the dimensions of the distance matrix, is large. It also avoids the problem of the heterogeneity of column vectors. The use of Cluster Analysis to investigate the structure of the component specification matrix also seems useful and the loss of information should be considerably less than the direct investigation of the distance matrix calculated from the data, since there are many fewer dimensions to be considered.

Principal Components Analysis defines orthogonal axes; rotation of these axes can produce interesting and often useful results. Such rotation is standard practice with Factor Analysis and was employed in a taxonomic study with considerable success by Rohlf & Sokal (1962) to produce groups of individuals characterized by 'group factors' rather than the more generalized factors of the unrotated matrix. The rotation of axes defined by Principal Components Analysis has been carried out less frequently but an application to ecological data suggests that it may prove to be valuable; it has not, however, been carried out in connection with the analyses described in this paper.

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APPENDIX 1. Conspectus of the Genus *Ononis* L. (after Sirjaev 1932).

		OTU Number
NATRIX		
Raceme pedunculate, 1–3 flowered; fruiting pedicel reflexed; pod linear or oblong		
Antiquae		
Subshrub, leaves and bracts 3-foliolate; vexillum hairy; 10th stamen adnate at the base only		<i>rotundifolia</i> 1
Rhodanthae		
Shrub or perennial; leaves ternate, coriaceous; peduncle shortly aristate; vexillum hairy		
Frutescentes		
Shrub; bracts bract-like; peduncle short, 1–3 flowered		<i>tridentata</i> 2
		<i>fruticosa</i> 3
Perennes		
Perennial; bracts leafy; peduncle mucronate, 1-flowered, occasionally with 2		<i>cristata</i> 4
		(<i>cenisia</i>)
Canarienses		
Shrub; leaves 3-foliolate; peduncle short, mucous; corolla rose, glabrous; alae without teeth; seeds tuberculate		<i>christii</i> 5
Mauritanicae		
Shrub; leaves pinnate, bracts 3-foliolate; corolla rose, glabrous; alae without teeth		<i>thomsonii</i> 6
Eu-natrix		
Shrub or perennial; leaves usually 3-foliolate, but variable; bracts variable; corolla yellow, sometimes red-striped, glabrous; alae with teeth		
Atlanticae		
Peduncle spinous-aristate; stipules not connate		<i>atlantica</i> 7
Orientales		
10th stamen one-third adnate; lower leaves pinnate; peduncle usually 2-flowered		<i>adenotricha</i> 8
Polymorphae		
Peduncle unarmed; stipules not connate; 10th stamen two-thirds adnate		<i>natrix</i> 9–19
		<i>crispa</i> 20
Aegypticae		
Shrub; stipules connate; peduncle subspiny; leaves 3-foliolate		<i>vaginalis</i> 21
Serotinae		
Perennial; leaves 1-foliolate; peduncle 1-flowered, mucous or shortly aristate		<i>serotina</i> 22
		<i>pseudoserotina</i> 23
Torulosae		
Annual; corolla yellow, glabrous; pod torulose; seeds tuberculate		<i>ornithopodioides</i> 24

Biflorae

Annual; peduncle 2-flowered, aristate; corolla yellow, glabrous

Tuberculatae

Seeds tuberculate *biflora* 25

Laeves

Seeds smooth *hebecarpa* 26

Pilosae

Leaves 3-1-foliolate; corolla rose and yellow; vexillum hairy; alae without

teeth *polysperma* 27
maweana 28

Reclinatae

Annual; peduncle 1-flowered; vexillum glabrous; alae without teeth

Siculae

Corolla yellow; peduncle aristate; seeds tuberculate *sicula* 29-30

Sublaeves

Corolla yellow; peduncle aristate; seeds nearly smooth *peyerimhoffii* 31

Incisae

Corolla yellow; peduncle shortly aristate; seeds rugose; stipules incised *incisa* 32

Eu-reclinatae

Corolla rose or whitish; peduncle muticous; seeds tuberculate *reclinata* 33
pendula 34
laxiflora 35
dentata 36
verae 37

Viscosae

Annual; leaves mostly 3-foliolate; corolla yellow, glabrous; alae with teeth

Pubescentes

Upper bracts bract-like; peduncle muticous; seeds smooth *pubescens* 38

Eu-viscosae

Bracts leafy; peduncle aristate; seeds tuberculate *viscosa* 39-44
crotalarioides 45

Antennatae

Leaves all 3-foliolate; peduncle aristate; seeds tuberculate *antennata* 46-48

BUGRANAE

Peduncle absent; pod ovate, rarely reflexed

Intermediae

Annual; vexillum hairy; pod reflexed; seeds tuberculate *cintrana* 49

Chrysanthae

Shrub; leaves 3-foliolate, bracts bract-like; flowers yellow; seeds smooth

Speciosae

Leaflets subcoriaceous; raceme dense *speciosa* 50

Aragonenses

Leaflets coriaceous; raceme interrupted *aragonensis* 51
reuteri 52

Pinnatae

Annual, shrubby; leaves pinnate; corolla rose, glabrous; seeds smooth *leucotricha* 53
pinnata 54

Bugranoides

Shrub or perennial; leaves 3-foliolate; corolla yellow, glabrous *pusilla* 55
(columnae)
minutissima 56
cephalotes 57
saxicola 58
striata 59

Acanthononis

Shrub or perennial, often spiny; leaves variable; corolla rose, hairy;
seeds rarely smooth

Arborescentes

Small unarmed shrub *hispida* 60-61

Vulgares

Shrub, often spiny *masquillieri* 62
arvensis 63-68
(hircina)
spinosa 69-76
repens 77-83

Villosissimae

Annual; leaves 1-3-foliolate; corolla rose, glandular-hairy; seeds tuberculate

Trifoliatae

Leaves all 3-foliolate *filicaulis* 84
villosissima 85

Monophyllae

Leaves all 1-foliolate *monophylla* 86
oligophylla 87
alba 88

Variegatae

Annual; leaves 1-foliolate; flowers in lax racemes; corolla yellow, hairy *variegata* 89
euphrasiifolia 90

Diffusae

Annual; leaves 3-foliolate; corolla rose or white, usually hairy; raceme elongating after anthesis

Tuberculatae

Vexillum hairy; seeds tuberculate *diffusa* 91-93
serrata 94
phyllocephala
tournefortii 95

Cossonianae

Vexillum glabrous; seeds smooth *hirta* 96
cossoniana 97
cephalantha 98

Subspicatae

Vexillum glabrous; seeds tuberculate *subspicata* 99-100

Mitissimae

Annual; leaves 3-foliolate; upper bracts imbricate, coriaceous; corolla rose, glabrous; calyx tubular; seeds tuberculate *mitissima* 101

Salzmännianae

Annual; leaves 3-1-foliolate; calyx tubular; corolla rose, glabrous; seeds smooth *alopecuroides* 102
baetica 103

Verae

Annual; leaves 3-foliolate; upper bracts bract-like; calyx tubular; corolla large, rose; vexillum hairy; seeds tuberculate *rosea* 104
avellana 105
megalostachys 106

Crinitae

Annual; leaves and bracts 3-foliolate; calyx bilabiate, tubular; corolla whitish, glabrous; seeds tuberculate *crinita* 107

APPENDIX 2

	Character	No. of states	Range		Attributes*
			from	to	
1	Duration	5	herbaceous annual	shrubby perennial	1-4
2	Stature	4	erect	procumbent	5-7
3	Branch spines	3	absent	strong	8-9
4	Size (L)	5	under 15 cm	over 100 cm	10-14
5	Stipule length (L)	∞	0.5 mm	23 mm	15-19
6	Stipule shape	4	linear	rhomboid	10-22
7	Stipule base	6	free	infundibuliform	23-27
8	Stipule margin	5	entire	incised	28-31
9	Petiole length (L)	∞	1 mm	30 mm	32-34
10	Leaflet length (L)	∞	3 mm	45 mm	35-37
11	Leaflet breadth (L)	∞	1.3 mm	25 mm	38-40
12	Leaflet apex	4	acute	retuse	41-43
13	Leaflet margin	3	entire	dentate	44-45
14	Leaflet texture	3	coriaceous	fleshy	46-47
15	No. of leaflets (<i>upper leaves</i>)	∞	1 leaflet	5 leaflets	48-50
16	No. of leaflets (<i>lower leaves</i>)	∞	1 leaflet	7 leaflets	51-57
17	Short hairs on leaflet	5	none	dense	58-61
18	Glandular hairs on leaflet	5	none	dense	62-65
19	Sessile glands on leaflet	3	none	dense	66-67
20	Leaflet crisped	2	no	yes	68
21	Form of bracts	4	squamulose	3 leaflets	69-71
22	Peduncle length (L)	∞	absent	40 mm	72-76
23	Pedicel length (L)	∞	0.5 mm	10 mm	77-80
24	Flowers/peduncle	∞	1 flower	3 flowers	81-82
25	Raceme density	5	very lax	capitate	83-86
26	Arista length (L)	∞	absent	15 mm	87-90
27	Arista spinous	2	no	yes	91
28	Calyx shape	2	campanulate	tubular	92
29	Calyx teeth in fruit	3	spreading	accrescent	93-94
30	Calyx tube length	∞	1.5 mm	6.5 mm	95-96
31	Calyx teeth length	∞	2.5 mm	12.5 mm	97-99
32	Calyx teeth width at base	∞	0.5 mm	3.5 mm	100-102

Character	No. of states	Range		Attributes*
		from	to	
33 Nerves/calyx tooth	∞	3 nerves	13 nerves	103-104
34 Short hairs on calyx	5	none	dense	105-108
35 Long hairs on calyx	5	none	dense	109-112
36 Short glandular hairs on calyx	5	none	dense	113-116
37 Long glandular hairs on calyx	5	none	dense	117-120
38 Anthocyanin in petals	5	none	purple	121-124
39 Flavonol in petals	5	none	golden	125-128
40 Standard length (L)	∞	6 mm	26 mm	129-133
41 Standard breadth (L)	∞	4 mm	16 mm	134-138
42 Hairs on standard	5	none	dense	139-142
43 Glandular hairs on standard	5	none	dense	143-146
44 Shape of standard apex	4	emarginate	acute	147-149
45 Form of standard apex	2	not apiculate	apiculate	150
46 Length/breadth ratio of alae	∞	1.3	4	151-153
47 Alar tooth	2	absent	present	154
48 Length/beak ratio of keel	∞	1.0	3.0	155-156
49 Keel beak angle	3	acute	obtuse	157-158
50 Stamen adnation	∞	free	joined	159-161
51 Pod length (L)	∞	4 mm	32 mm	162-167
52 Pod breadth (L)	∞	2 mm	8.5 mm	168-171
53 Hairs on pod	5	none	dense	172-175
54 Glandular hairs on pod	5	none	dense	176-179
55 Compression of pod	5	inflated	torulose	180-183
56 Seed size (L)	∞	0.75 mm	5 mm	184-186
57 Seeds/pod (L)	∞	1 seed	40 seeds	187-189
58 Seed surface	6	smooth & shining	echinate	190-194
59 Pod position	3	erect	pendent	195-196
60 Short hairs on stem	5	none	dense	197-200
61 Long hairs on stem	5	none	dense	201-204
62 Short glandular hairs on stem	5	none	dense	205-208
63 Long glandular hairs on stem	5	none	dense	209-212
64 Calyx form	3	teeth equal	bilabiate	213-214

* These numbers refer to the attributes used in both Association and Information Analyses.

∞ No constraint was applied to the number of states of these characters and they were measured in the units stated.

(L) These character states were subjected to a logarithmic transformation before analysis of the data.

A NOTE ON FERTILE SEED PRODUCTION BY *HYPERICUM CALYGINUM*

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In a previous communication dealing with seed production and self-incompatibility of *Hypericum calycinum* (Salisbury 1963), data based upon the examination of 132 fruits were furnished which indicated an average of about fourteen fertile seeds in each capsule of this species when grown in a favourable locality. The range exhibited was from 0 to 37. Since it is known that self-incompatibility may manifest itself by a retarded rate of growth of the pollen-tubes, it was suggested (Salisbury 1963) that the proportion of fertile seeds in this normally self-incompatible species might largely depend upon the temperatures during the period of pollen-tube development. The exceptional warmth of the July temperature of 1967, after *H. calycinum* came into full bloom, afforded an opportunity of testing this hypothesis.

Capsules were therefore collected from the same plants that provided the source of the sample of 132 capsules previously examined. The location was a slope with a southern aspect. Twenty-five capsules were dissected and these yielded the following numbers of fertile seeds:

5, 16 (three examples), 19, 21, 23, 25, 28 (two examples), 29, 30 (three examples), 32, 33, 34 (two examples), 36, 39, 40, 48, 49, 50, 54.

Thus the twenty-five fruits yielded a total of 765 fertile seeds, or an average of 30.6 (standard error of mean 2.3). This compares with an average of 13.8 fertile seeds per capsule (standard error of mean 0.7) in 1962 when the temperatures at the time of pollination were lower. Furthermore the 1962 fruits exhibited a definite mode between 8 and 12 'good' seeds per capsule, whilst the 1967 fruits though only twenty-five in number exhibit a definite grouping around 30 'good' seeds.

Temperatures subsequent to pollination would then appear to be an important factor in determining the proportion of fertile seeds produced by this species. It may also be noted that the partially developed seeds to which attention was previously drawn also exhibited a significant increase compared with the 1962 sample.

In the previous paper attention was also drawn to the remarkable absence, despite careful searching, of records of seedlings from the neighbourhood of colonies of this species. An appeal made to horticulturists for observations on seedling production emphasized their rarity, but in two locations a very few seedlings were found, in both areas on cultivated loose soil adjacent to a colony where it may well be that shed seeds found immediate concealment. The seeds are oily and, both in appearance and size, resemble ants' eggs. One correspondent actually observed Tits (*Parus*) feeding upon the seeds, so that the usual absence of seedlings is most probably the result of predators upon a seed-crop that is perhaps less than one-fiftieth of what the species would produce in its native land.

REFERENCE

- SALISBURY, E. J. (1963). Fertile seed production and self-incompatibility of *Hypericum calycinum* in England. *Watsonia* 5, 368-376.

THE REPRODUCTIVE BIOLOGY AND OCCASIONAL SEASONAL DIMORPHISM OF *ANAGALLIS MINIMA* AND *LYTHRUM HYSSOPIFOLIA*

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ABSTRACT

Data are provided respecting the reproductive capacities of *Anagallis minima* and *Lythrum hyssopifolia*. In relation to their size, these species have high reproductive capacities and thus conform to the general character of species of intermittently available habitats. Experimental evidence indicates that the great majority of the seeds exhibit vernal germination which, in favourable conditions, is quasi-simultaneous in character. However, there is a variable proportion, usually small, of autumnal germinations resulting in a degree of seasonal dimorphism. The overwintering individuals, with their longer assimilatory activity, sometimes produce many times the average number of seeds. Germination, though favoured by light in adequate temperatures, was also found to occur in darkness. Though chiefly associated with non-calcareous soils, both species were found to germinate freely in calcareous as well as non-calcareous conditions. The proportion of dormant seeds of *Anagallis minima* was found to be no higher in the immature condition than when ripe seeds from the same individual were sown simultaneously.

1. *ANAGALLIS MINIMA* (L.) E. H. L. KRAUSE (*CENTUNCULUS MINIMUS* L.).

Of all the terrestrial flowering plants found wild in Britain *Anagallis minima* is one of the smallest, especially when, as so often obtains, the plants are crowded and in competition with *Radiola linoides*, with which it is almost invariably associated. The species of *Lemna* are appreciably smaller and, still more so, *Wolffia arrhiza*, but these are floating aquatics, and are not differentiated into stem and leaves and so are not biologically comparable. *Tillaea muscosa* is often as small, or even smaller, but it is restricted to more open sandy habitats. The reproductive capacity of *A. minima* is thus that of a species which must evade, rather than meet, competition. An estimate of the fruiting capacity has been based upon the aggregate of random collections from several widely separated habitats in Wales, Dorset, Hampshire and Sussex and representing more than one season. The number of capsules was counted on 589 plants, the results of which are shown in Fig. 1. It will be apparent from this graphic presentation that, though the average number of capsules upon a plant is 14, more than 54% of the entire population of plants produced fewer than 10 capsules; the most prevalent number is only 5. On the other hand, it will be noted that 17 (*i.e.* approximately 3%) were of exceptional size, producing an abnormally large number of fruits, ranging from 56 to 144 capsules. This latter figure is nearly thirty times the modal production, so that a few such individuals would have a significant effect upon a population's seasonal seed output.

It may be noted that tetramerous and pentamerous flowers can occur, intermingled, upon the same plant (Fig. 4) but these do not appear to be correlated with any constant difference in the seed content of the capsules they produce.

The seeds, which are trigonous with three prominent ridges (Fig. 4C), have a minutely granular surface and are dark brown or almost black when ripe. The average length is about 0.5 mm and width 0.3 mm to 0.4 mm. The average weight of a seed is 0.0337 mg.

The variation in the seed content of the capsules is presented, in Fig. 2, for 350 fruits. From this it will be seen that the number of seeds in a fruit may be as few as 4, or as many as 31, with an average approximately the same as the mode, namely 15. The average seed output is thus appreciable for a plant so small in size, namely 210 seeds.

Most of the seeds germinate in the spring, but a small proportion may germinate in the autumn and these can produce bushy plants branching towards the base thus forming lateral

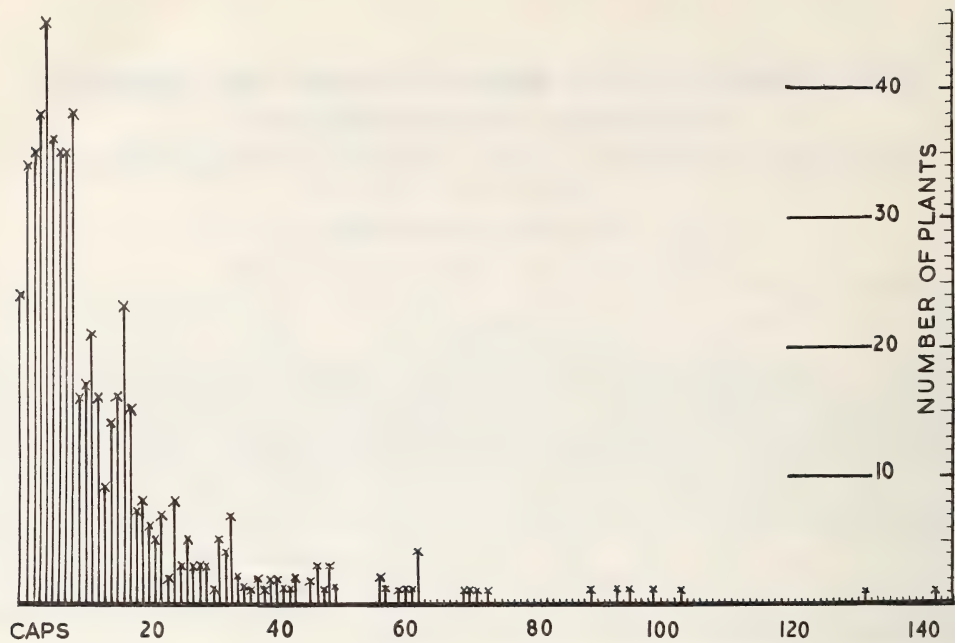


Fig. 1 Variation in number of capsules on plants of *Anagallis minima* from various localities. Ordinates, number of individual plants. Abscissae, number of capsules. Results from 589 plants; mean number of capsules per plant 14, mode 5 capsules.

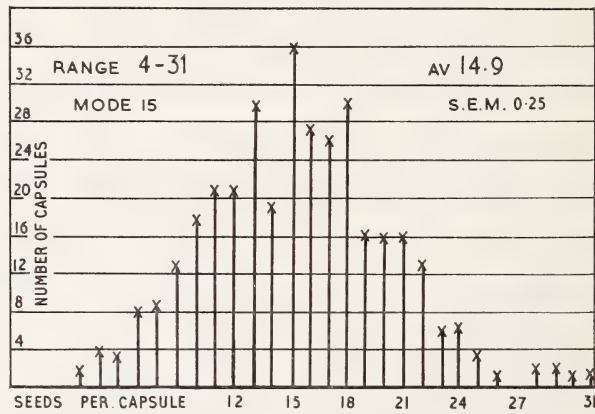


Fig. 2. Variation in seed contents of capsules of *Anagallis minima*. Ordinates, number of capsules. Abscissae, number of seeds per capsule.

shoots that may root from their lower nodes (Fig. 3A & 4B). The largest plant of this type observed was 10 cm in height. It had a spread of 15 cm with roots arising from 10 of the basal nodes. The capsules numbered 443 and a random sample, of 25 of these, exhibited a range in seed content from 11 to 24 with an average of 16.4. The abnormally large number of fruits is not, therefore, associated with any diminution in their average content. In Fig. 3 are shown drawings portraying one of these bushy autumnal plants and, for comparison, an average specimen of the vernal individuals from the same sowing. It is these autumnal plants that mostly provide the exceptionally fruitful individuals represented on the right-hand side



Fig. 3. Plants of *Anagallis minima* from the same sowing, the larger from a seed germinating in the autumn, the smaller from a vernal germination. Both seedlings drawn 22 June. Estimated seed outputs based on number of fruits and flowers c. 830 and 110.

of the graph in Fig. 1. It should, however, be added that similar, though less extreme, exuberance may be exhibited by plants derived from the vernal germination when these occur in isolation and subject to but little competition.

It is then evident that this species exhibits a measure of seasonal dimorphism. Neither the vernal nor the autumnal individuals come into flower till the short nights and long days of summer so that the vegetative life of the latter is appreciably greater than that of the vernal individuals, and the assimilatory capital correspondingly greater. (Specimens placed in Herb. Kew (K).)

The proportion of these autumnal germinating seeds appears to vary greatly. Thus from one sample of 600 seeds, harvested in 1964 and sown as soon as they were shed, only 4 germinated in September (*i.e.* 0.67%) and 45% of the remainder in April of the following year. In September 1965 a small sample of only 150 seeds yielded 5 seedlings in October (*i.e.* 3.3%), whilst 326 seeds which ripened and were sown in late October of the same year produced 8 autumnal seedlings (2.4%). Other samples yielded 0.3% and 0.7%. But yet another large sample of 1200 seeds provided no autumnal germinations whatever.

It was found that these autumnal seedlings could survive the winter conditions, probably because they have not flowered or fruited. It is known that various annuals are able to survive as perennials if flowering or fruiting be systematically prevented.

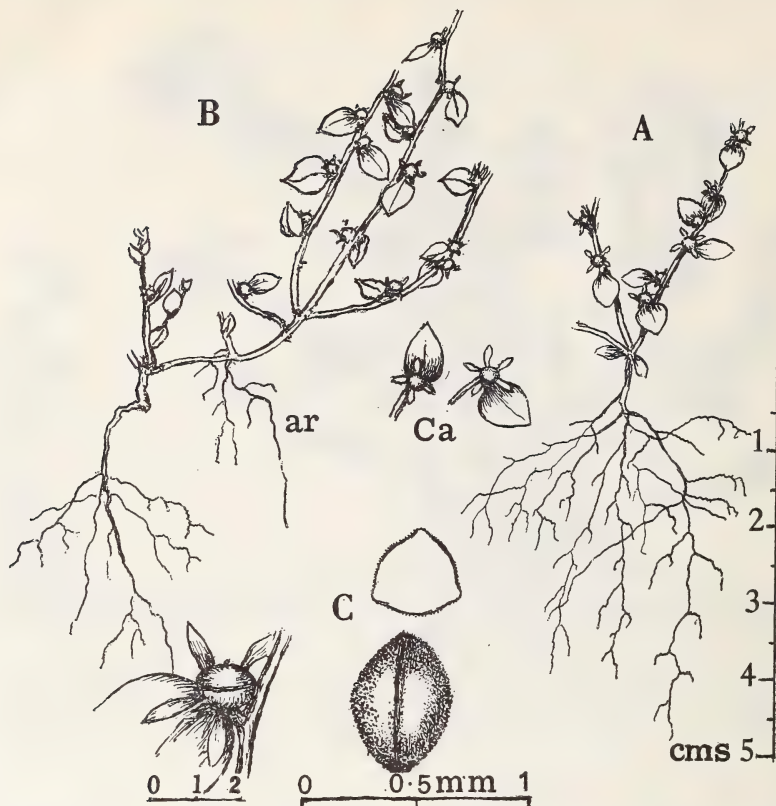


Fig. 4. A. Mature plant of *A. minima* showing depth and extent of root-system. B. Prostrate branch of large plant showing nodal rooting (ar.). Ca. A tetramerous and a pentamerous calyx from the same plant. C. A dehiscent capsule and a seed shown in side-view and in section.

Owing to the very exceptional size of the plant referred to above, with 443 fruits, it was not incorporated in the graph (Fig. 1); but that such plants can develop with an output of, perhaps, over 7,000 seeds, emphasizes the importance that such autumnal plants may have for the survival of the species. 3% of these overwintering seedlings could provide from one third to even as many seeds, as the 97% vernal individuals.

A very striking feature to which F. Townsend (1883 p. 280) drew attention and which my own experience emphatically confirms, is that *Anagallis minima* 'is much more abundant in some seasons than in others', a feature which might well be influenced markedly by the prevalence or paucity of autumnal survivors.

If there be an inhibitor, or inhibitors, in the seeds of *A. minima*, which varies in amount in the different seeds in a normal manner, it may be suggested that these autumnal-germinating seeds may in fact represent those which contain little or none, whilst the others gradually lose their inhibition and germinate when the augmenting temperature of spring permits. Sowings of seeds saved from plants that had germinated in the autumn did not give rise to populations with any apparent increase in the proportion of autumn germinations, from which one may infer that, if there be any segregating genetic component it is not normally significant.

With stored seeds I have obtained as low a proportion as 10% spring seedlings, but with freshly harvested ripe seeds sown in September the following spring germinations were obtained (Table 1).

The average spring germination, from these and other sowings, was 48.5% with a maximum of 87%. The great majority of the germinations occurred within four days after

TABLE 1. Spring germination of *Anagallis minima* seeds sown in September.

Date of sowing	Number of seeds sown	April germination
15 Sept. 1964	600	37% in 4 days (41.5% in 10 days)
1 Sept. 1964	321	48% in 12 days
19 Sept. 1965	711	37% in 25 days
19 Sept. 1965	610	63% in 12 days

the first seedlings appeared, so that, apart from the small percentage autumnal germination, there is also a marked quasi-simultaneous tendency (Fig. 6). Soon after the radicle emerges, a ring of prop-root-hairs develops around the collet, a behaviour shared by other species of this type of habitat. The roots penetrate the substrate rapidly (Fig. 5A) and the rooting depth of the adult plants, which is normally about 5 cm, is soon attained. The cotyledons are elliptical (Fig. 5B) and the first few leaves are opposite or sub-opposite (Fig. 5C) becoming more obviously alternate as the plants mature. Thus in the leaf insertion of the seedling and in the nodal rooting of the larger mature plants the resemblance to *Anagallis arvensis* is striking.

Kinzel (1927) found that immature seeds of *Anagallis minima* germinated more rapidly than the mature seeds and he concluded that the ripe seeds not only were slower but a much smaller proportion germinated in the spring although later germinations increased the percentage.

Development of the very large plants, to which reference has been made, permitted the collection of an adequate number (from 320 to 350 in each sowing) of (a) yellow-green,

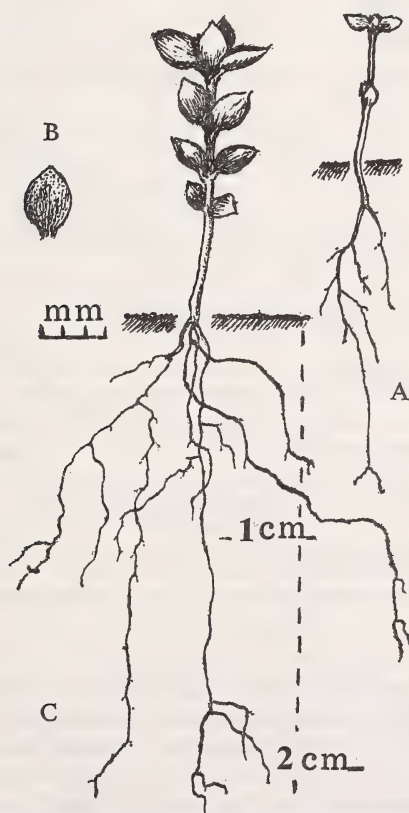


Fig. 5. *Anagallis minima*. A. Seedling. B. Cotyledon. C. Young plant showing sub-opposite leaves.

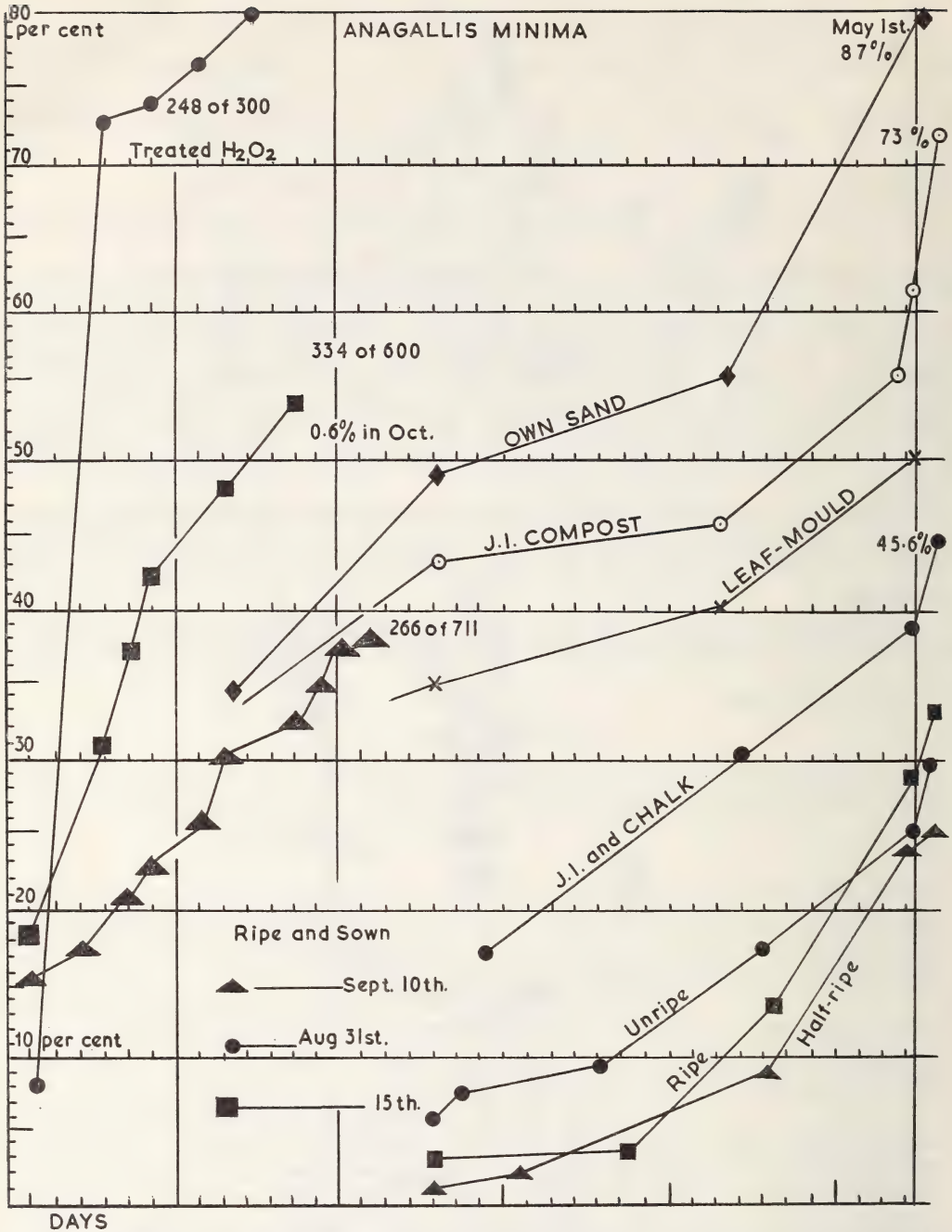


Fig. 6. Germination of *Anagallis minima* sown on various dates and various soils, also of seeds in three stages of maturity.

immature seeds; (b) half-ripe, brown seeds: and (c) purplish-black, fully mature seeds: all from a single individual plant. These were sown, immediately after harvesting them, on 10 October under identical conditions. None of the seeds germinated till March. On 23 March the immature seeds had yielded 6.2%, the half-ripe seeds 1.4% and the ripe seeds 3.2%—a difference far less pronounced than that in Kinzel's experiments but showing the same pattern. However, this was not maintained (see Fig. 6) and by 29 April the percentage

germinations were: immature seeds 30.0%, half-ripe seeds 26.3%, ripe seeds 34.4%. It is quite evident that seeds harvested in different seasons may differ greatly in the percentage germinations which they yield. Thus the maximum obtained from seeds harvested in the inclement summer of 1962 was 10.9%. Those harvested in 1964 yielded from 36.8% to 45.1% whilst some of the seeds ripened in 1965 yielded over 80%. Moreover, seeds from different plants which ripened at different times would appear to vary, not merely as to whether any germinate in the autumn and, if so, what proportion, but also as to the percentage that germinate in the spring. If the proportion of naturally dormant seeds is higher in those fruits which are formed first than in those formed later, the discrepancy in our results might be expected especially if, as seems not improbable, Kinzel's seeds were obtained from several individuals.

A series of sowings on various types of soil with seeds ripening in the late autumn yielded very few autumnal seedlings and curiously enough only on the soil exhibiting the lowest percentage germination. The germinations, otherwise, all occurred in April and the totals attained were as follows: on sandy soil (obtained from an *A. minima* locality) 87.0%: on leaf-mould 50.7%: on 'John Innes' compost 73.5%: on 'John Innes' compost plus chalk, 45.6%: on acid peat plus sand, 26.6% (Fig. 6). Since *Anagallis minima* is usually regarded as somewhat calcifuge in its occurrence, the appreciable germination on the soil to which chalk was added is noteworthy, and of especial interest in the light of Professor Good's (1948) observation that this species is not uncommon in Dorset, 'in the grassy rides of certain woods on the chalk'.

The flowers of *Anagallis minima* are self-compatible and frequently pollinated in bud so that cool, wet summers with a paucity of sunshine are unlikely to preclude the production of a normal crop of seeds. It is, however, a species which exhibits very striking fluctuations of population to which attention has already been drawn. One factor that could produce an appreciable increase in the population would be any marked augmentation of autumnal germinations leading to a larger proportion of plants with high seed yields. Nevertheless the available evidence indicates that whilst this might lead to a doubling or even trebling of the population in the following year it could scarcely account for the spectacular increase of numbers sometimes observed. At adequate temperatures, germination of the seeds can occur in darkness though it takes place more readily in light. But experiments have shown that although, occasionally, over 80% of the seeds shed in the autumn may germinate the following spring, the proportion may be as low as 10% and the average of the vernal germination is normally under half of the seeds sown in the autumn. (cf. Fig. 6). That the residual seeds are not infertile, but merely dormant, was shown by Kinzel, who found they germinated subsequently, and this is confirmed by the high percentage that can be induced to germinate in the first season by appropriate treatment. Thus I have obtained 81% germination in a period of four days after treatment of the seeds with hydrogen peroxide (Fig. 6). The germination of 98% which Kinzel obtained with immature seeds would appear to suggest that the seed coat may be involved in this natural dormancy and the response to hydrogen peroxide is not inconsistent with such an interpretation. It is not unlikely that the sudden increase in population numbers may be an outcome of the germination of an accumulation of dormant seeds, especially as this increase would appear to be normally associated with a population decline in the following season.

Anagallis minima is one of a group of species of intermittently wet habitats that have exhibited a marked diminution of frequency during the past hundred years. Counties in which this species formerly occurred but where it is now probably extinct are: Cambridgeshire, Bedfordshire, Buckinghamshire, Hertfordshire, S. Lancashire, Worcestershire and possibly Essex and also Middlesex. In addition there are 11 vice-counties in England and Wales, 10 in Scotland and 8 in Ireland for which there are no recent records. Indeed the species may have gone from about one-third of its former stations (cf. Map. p. 204. Perring & Walters 1962). Most of these areas of real or suspected loss in Great Britain are towards the drier eastern side of the country and may probably be associated with the secular fall in the water table. The causes of this declining frequency must not, however, be confused with those respon-

sible for the fluctuations in abundance that are recurrent phenomena. Nevertheless, with such an inconspicuous plant the temporary decline might readily be mistaken for a permanent trend, except where observation has extended over a period of years.

The close association with *Radiola linoides* is important in this context since although this species is also small it is, owing to its pale green colour towards maturity, quite readily recognized and exhibits similar fluctuations of abundance apparently contemporaneous with those of *Anagallis minima*. In one Hampshire locality, in 1959, *Radiola linoides* was very common and two years later abundant when it was accompanied by occasional individuals of *Anagallis minima*. Subsequently the frequency of *Radiola* diminished and during 1964 and 1966 it was only sparsely present. Diligent search in both these years failed to discover any individuals of *A. minima*, which suggests a decline that is real and not merely apparent. If the population surges be due, as suggested, to germination of dormant seeds, the following year (providing climatic conditions were favourable) might be expected to exhibit a large population derived from the seeds of the numerous individuals so that whilst the initial augmentation could be abrupt the decline might be gradual. The augmented population of *A. minima* in 1959 and its abrupt disappearance is consistent with the hypothesis that the increase was due to flushing of dormant seeds whilst renewal of the supply of these was prevented by unfavourable climatic conditions.

2. *LYTHRUM HYSSOPIFOLIA* L.

In southern England *Lythrum hyssopifolia* is commonly a summer annual, occurring usually as a casual introduced with foreign seed but, very locally, appears to have persisted in a wild condition over many years. Although, as a casual, it has been found in a diversity of habitats its more permanent stations have been in open vegetation subject to winter inundation. In common with other 'mud-species' it is liable to disruptions in the habitat but has probably been an established wild plant in a few south-eastern counties. Now, however, except as a casual, it is possibly confined to Cambridgeshire (Perring & Walters 1962, Perring, Sell & Walters 1964). *L. hyssopifolia* is thus another of the diminishing damp-habitat species, but the fact that it bears a folk-name, 'Grass Poly', would suggest that it was not uncommon before SE. England became so greatly suburbanized, when suitable habitats were widespread.

Reproduction.

Any valid estimates of fruiting capacity require to be based upon a random sample of adequate size, a stipulation that may present an obstacle when studying a rare species. Examination of only 16 individuals of average size for the species suggested a mean capsule production of 73 capsules per plant (Salisbury 1942). Since this species had become naturalized in a damp hollow in my garden in Sussex all the plants were allowed to grow untended and the entire populations of two seasons, numbering 105 plants, were examined for fruit production as a basis for estimation. For convenience of presentation, owing to the wide range of plant size, the capsule numbers have been grouped into classes of which the upper limits differ by increments of 20 capsules. The results are presented in Fig. 7 from which it is manifest that the variation curve is markedly asymmetrical. The average number of fruits borne upon a plant, based upon the whole array, is 197 capsules. If, however, we exclude the 10 exceptionally large plants with over 500 fruits this mean is approximately halved. The greater portion of the plants, about 60%, yielded between 40 and 100 capsules which would suggest that the mean, derived from the small random sample from a wild habitat, may not have been far from the norm. It is to be noted that in 1967, which was an unfavourable year for *L. hyssopifolia*, with no very large individuals, the entire population of 62 plants yielded an average of only 63 capsules.

The high average of the larger sample is attributable to the occurrence of a few very robust plants bearing between 1,700 and 3,000 capsules. Such an admixture of a small proportion of outstandingly large plants in a population of prevailingly small individuals I recall observing as a feature of this species, many years ago, in the ditches of Brittany. Such

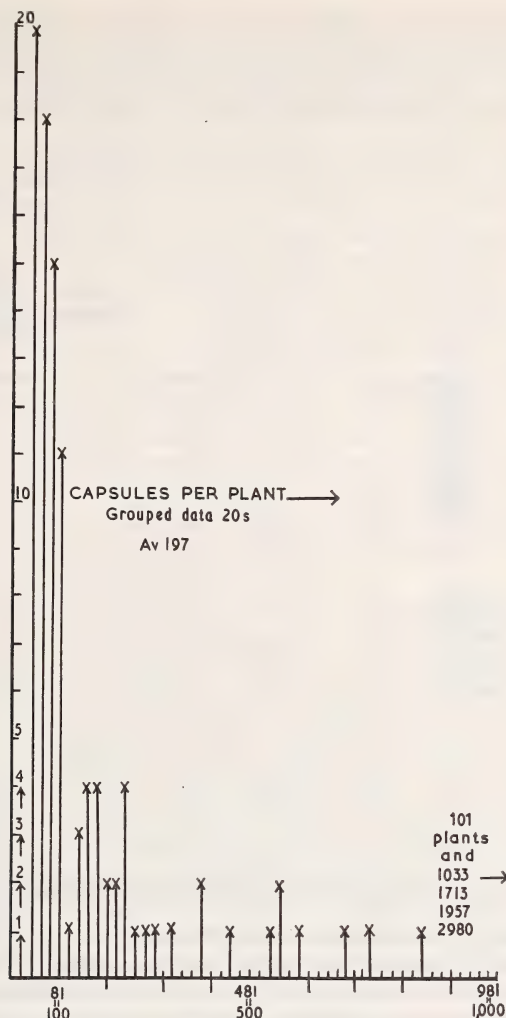


Fig. 7. Variation in the number of capsules produced upon plants of *Lythrum hyssopifolia*. Ordinates represent the number of individuals. Abscissae represent the numbers of capsules upon a plant grouped in increments of twenty capsules. Four plants bearing over 1,000 capsules are omitted from the histogram.

appears to be a characteristic in particular seasons and is a feature that becomes significant in relation to the germination behaviour to be dealt with later in this paper. One aspect of the morphology of these exceptionally large plants calls for comment. Most Floras emphasize the solitary character of the flowers of *Lythrum hyssopifolia*, a condition that is undoubtedly the prevalent one, even of the most robust specimens. However, Hegi (1927 p. 754) mentions the rare occurrence of a pair of flowers. The nodes of the major axes of the largest plants, as shown in Fig. 9, may on rare occasions bear capsules that are not only paired but even clustered, the latter condition being of especial interest since it is that which obtains in the congener *Lythrum salicaria*.

The fruits of *L. hyssopifolia* are approximately cylindrical in form, from 4 mm to 10 mm in length, containing four rows of seeds that impose a slightly nodular appearance on the ripe capsules (Fig. 8). The fruits split open at the apex, but the valves do not separate widely. The 100 capsules examined were found to contain from 13 to 37 seeds, with an average of 25.1 (standard error of mean 0.5). From Fig. 7 it will be seen that this average corresponds with the modal region of the variation curve.

The individual seeds are oval, somewhat trigonous, but with one face sometimes flattened or evenly concave (see Fig. 8), about 0.6 mm in diameter and with an average weight, based upon a number of large samples, of from 0.117 mg. to 0.133 mg. The seeds may ripen as early as September, but most ripen in October and November.

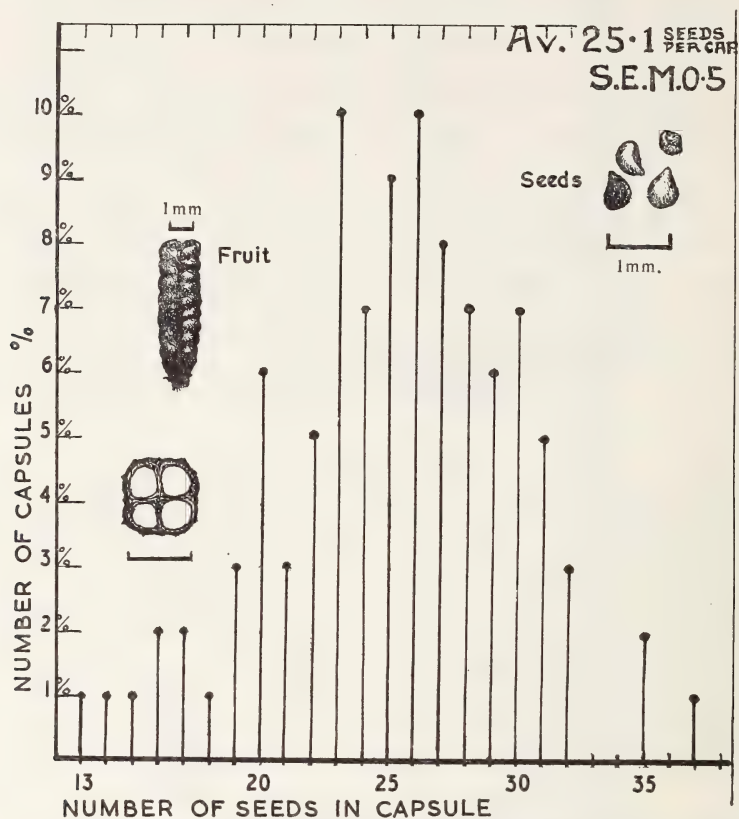


Fig. 8. Variation in the number of seeds in 100 fruits of *Lythrum hyssopifolia*. Ordinates represent the numbers of capsules. Abscissae represent the numbers of seeds. Inset are drawings showing the fruit in side view and in transverse section, also seeds viewed from the sides and end.

As shown in Fig. 9, the capsules are borne almost adpressed to the fruiting axes and, as a consequence, the seeds are not readily jerked out through the terminal aperture by gusts of wind, the less so since the plants normally grow in sheltered depressions. In fact, the seeds may be retained within the capsules until the entire plant has withered and becomes disintegrated during the late winter and early spring. From the foregoing data it would appear that in a favourable season an average output is about 5,000 seeds whereas, even in a less favourable one, an output of nearly 2,000 is suggested by the meagre sample previously reported.

Such high outputs in relation to the size of the plants conform with the very generally large potential that characterizes species of intermittently available habitats. It should be noted moreover that the productivity of the largest plants examined would range between 43,000 and 75,000 seeds! Such very prolific individuals do not, however, occur every season and, if we omit them from our estimation, the average output is about 3,200 seeds.

Germination

Since constant temperatures do not occur in natural conditions and may produce results that are grossly misleading, all germination experiments were carried out subject to

the natural daily fluctuations of temperature. Similarly, since markedly different germination behaviour may be exhibited by stored seeds when compared with those freshly shed (Salisbury 1965), and seeds of different strains of a species sometimes exhibit significantly different temporal responses (Salisbury 1962), light can only be shed upon the biology of the species under natural conditions if we sow seed that is derived from a single individual only and which has been freshly shed. In gardening practice stored seeds are the rule rather than the exception and commonly the seeds are of mixed parentage, so that experiments with such in constant temperatures can be of great practical importance (Thompson 1967) but may have little or no relevance to the natural occurrence of the species concerned.

Early maturing seeds germinated readily in the autumn when sown under conditions providing daily maxima of about 16° C. But, towards the northern limits of the species' range an absence of adequate warmth may normally preclude germination of all seeds except those that ripen precociously, until the subsequent vernal rise of temperature. Sixty years ago, I recall the plentitude of *Lythrum hyssopifolia* which, in April, occupied the floor of the shallower ditches in Brittany; some of these plants, from their size, were doubtless autumnal in origin. Here in Sussex, the small proportion of seedlings appearing in the autumn is liable to be killed in winter by the more severe frosts but, when such overwintering seedlings have survived, it was noted that they could develop into the very large plants to which reference has already been made. It is to be anticipated that the prevalence of such would diminish towards the northern limit of the species range.

One thousand three hundred and fifty seeds from freshly dehiscent capsules of a large plant, were collected and sown in November 1964 in an unheated glasshouse attaining daily maximum temperatures of about 19° C. Within one week from the first germination, nearly 900 seedlings had developed and within 10 days a total of over 70% germination was attained (Fig. 9). In the autumn of 1965 further seed samples were collected. Of these, 500 were sown on damp soil in full daylight and two batches from the same plant, of 243 seeds and 215 seeds respectively, were sown under precisely similar conditions except that they were maintained in dim light. As the curves in Fig. 10 show, the germinations under dim light were somewhat slower but the final percentages attained were not dissimilar to that in the unshaded condition. The total germination was low (42% to 45%) compared with the yield in other years, but was completed in 11 days. Furthermore, in full daylight, three-quarters of the total number of seedlings had developed within three days of the inception of germination.

Two-hundred and fifty seeds were collected and sown on 3 September 1967. 14 days later the first seedling appeared and by 1 October only 12 seeds had germinated (4.8%) which is probably indicative of the small proportion of autumnal seedlings which normally develop, but the facts mentioned show that with suitable temperatures autumnal germination can occur freely

Good germination was obtained with seeds which had been harvested in October and placed in a seed-envelope which was kept in an unheated outhouse for two months. We can therefore infer that maintenance of the moist conditions that normally obtain in the wild state is not an essential condition for the retention of viability. Since, as already stated, many of the seeds do not escape from the capsules till the spring, such retained seeds were collected from plants on 8 February and sown at once. Germination did not begin till nearly a month later, namely 6 March, but within the subsequent 9 days over 70% of the seeds had germinated. So, not only is it apparent that the belated shedding of the seeds does not impair their viability but that the quasi-simultaneous germination behaviour of the majority of the seeds is likewise unaffected.

A still later collection of seeds was obtained from capsules of dead plants, on 15 March 1967. As the number of seeds obtainable from a single plant was, at this stage, small, an aggregate from several plants was utilized and of these 500 seeds were sown in the dark and 850 in the light. No attempt was made to examine those in darkness until those exposed to light had begun to germinate, so that any germination in darkness could not be attributable to the brief exposures to illumination that examination would have necessitated. The results are shown in Fig. 11 from which it is apparent that germination began on the same

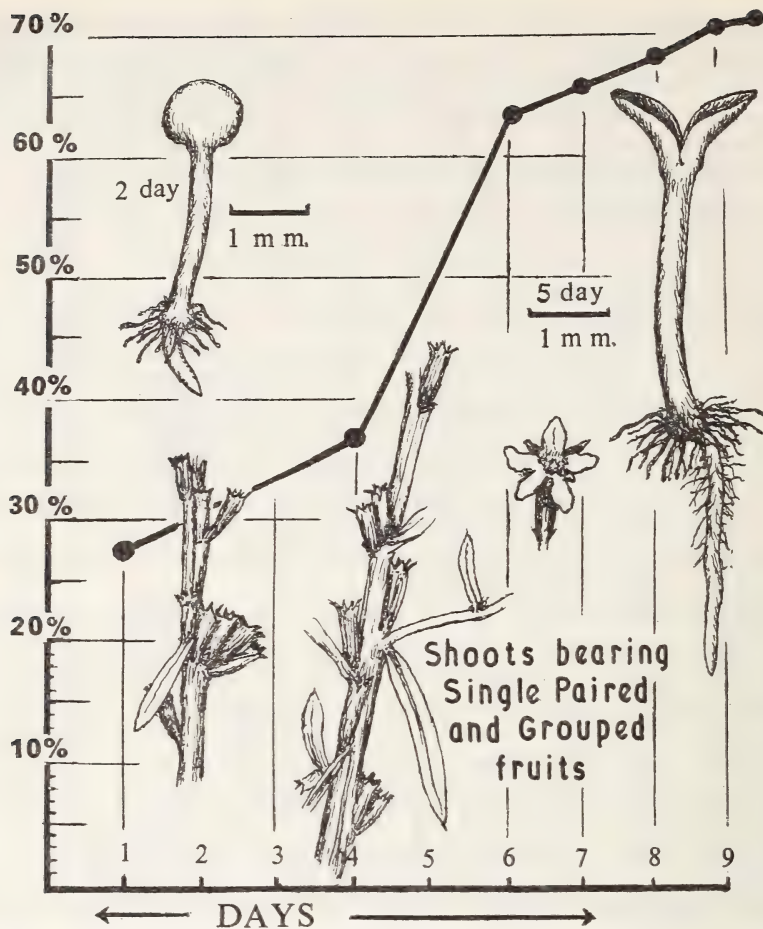


Fig. 9. Germination of 1,350 seeds from a single plant, ripe and sown November 1964. Ordinates represent percentage germination and abscissae days from first germination. Inset are shown two stages of the seedling with skirt of root-hairs upon the collet. A single flower is shown and also the paired and clustered fruits borne upon a very robust plant.

day in darkness as in light, namely 26th March, 11 days after being sown. The process, it will be noted, was far more prolonged than with the earlier harvestings but in bright light the total attained after 46 days was 93·5% and of these 75% had germinated within the first fortnight. In darkness the total attained was only 27·8% spread over a period of four weeks. As, however, no further germinations occurred in the dark during the following four weeks, the culture was transferred to full daylight whereupon, after five days, germinations were resumed and extended over a period of 15 days, though only adding 20 seedlings to the total (i.e. plus 4%). The curves in Fig. 11 indicate the fluctuations of maximum and minimum temperatures during the germination period which suggest that the magnitude of the temperature changes played little significant part in determining the course of germinations in the light, but it is noteworthy that the marked germination flushes in the dark followed abrupt rises in the maximum daytime temperatures. It is important to emphasize that, whereas in the comparatively sunless summer of 1965 the various harvestings of seed had a viability of less than 45%, the seeds of plants growing under precisely similar conditions in 1964, except climatic ones, yielded an average germination of over 70% (Fig. 9), also that the major part of the germinations occurred during the first six days. In the figures the percentages are those of the total number of seeds sown but, if the percentages are calculated on the basis of the total of apparently viable seeds, it becomes manifest that the prevailingly quasi-

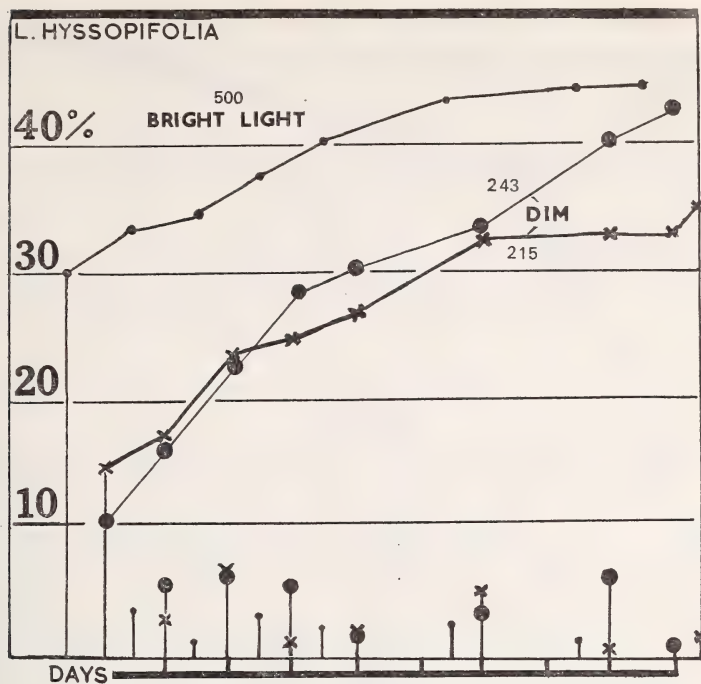


Fig. 10. Germination of *Lythrum hyssopifolia* seeds in bright light and in dim light. Seed ripe and sown 15 November 1965. Ordinates represent percentage germination and abscissae days after first germination.

simultaneous nature of the germination is very pronounced, since the percentage germinating within the first six days is, on the basis of this calculation, between 88% and 98%.

Although *L. hyssopifolia* is more especially associated with peaty and sandy conditions the seeds were found to germinate and the seedlings to grow as readily when supplied with hard tap-water as with soft rain-water. 150 seeds sown in September, on mud kept moist with tap-water, attained 43.5% in 15 days whilst the same number of seeds on mud moistened with rain-water attained 44.6% in the same period. Both yielded further germinations in the following March, amounting in each to approximately 6%. It is evident therefore that *L. hyssopifolia* cannot be classed as a calcifuge species. The average daily maxima during this experiment averaged 25° C and doubtless accounts for the high autumnal germination.

It may be noted that the seedling has cotyledons which in outline are almost circular at first (Fig. 9), although, from basal development, they become elongated later. The collet bears a conspicuous 'skirt' of root hairs, as in other mud-species such as *Limosella aquatica* (Salisbury 1967a) and *Elatine hexandra* (Salisbury 1967b).

Dry seeds shed upon the water will float but, when wet, they sink so that local dispersal is perhaps largely by rain wash. More distant dispersal is probably in mud carried upon the feet of water-birds.

Lythrum hyssopifolia is a species of central and southern Europe which occurs towards its northern limits only as a casual. As a summer annual it can evade the cold season in the seed state but its elimination as a permanent constituent of the flora further north may be because the large and prolific autumnal individuals are rarely if ever produced, so that the population fails to receive this periodic and substantial reinforcement.

DISCUSSION

The two species we have here considered both exhibit larger individuals that develop from autumnal seedlings and smaller individuals that germinated in the spring. We thus witness a measure of seasonal dimorphism which invites comparison with that exhibited by

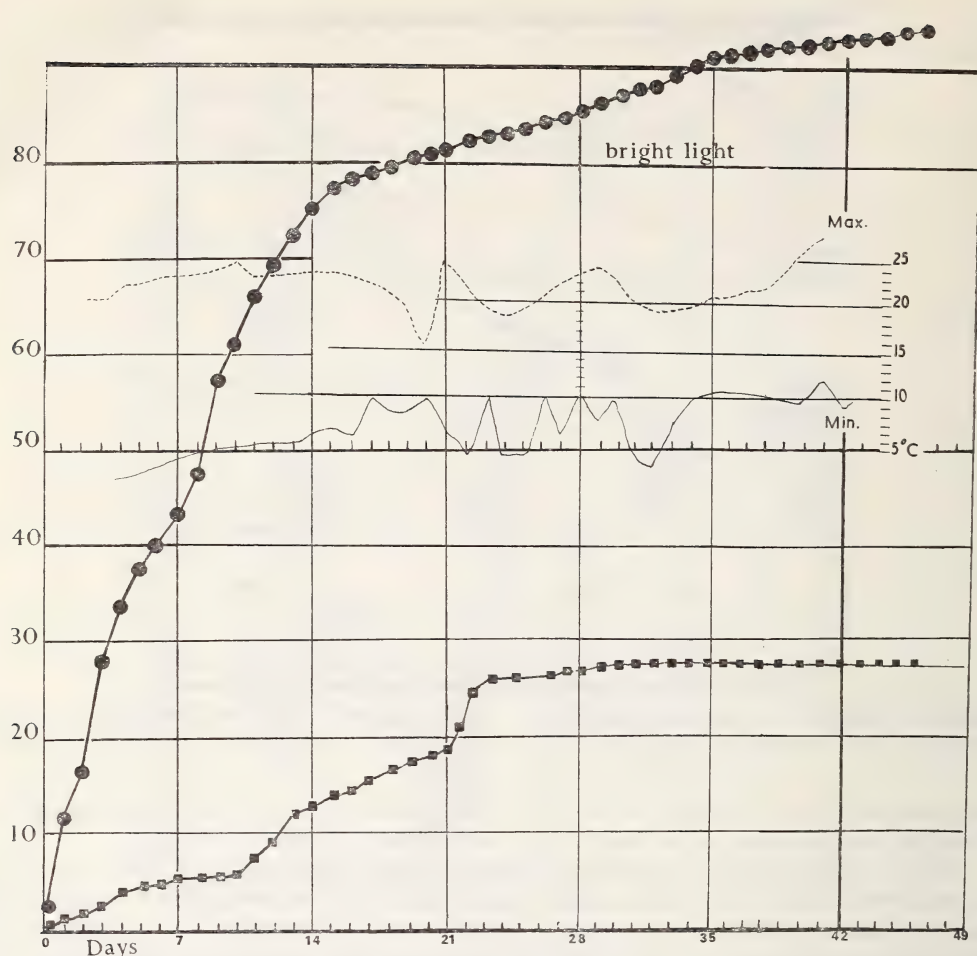


Fig. 11. Germination of late-ripening seeds retained in the capsules of *L. hyssopifolia*. Sown 15 March 1967. Ordinates represent total percentage germinations. Abscissae represent days after first germination. Upper graph percentages of 850 seeds sown in bright light. Lower graph percentages of 500 seeds in darkness. Final germinations 787 (92.6%) in light during 46 days and 139 (27.9%) in the dark during 34 days.

species of *Gentianella* and *Euphrasia*. In these genera the individuals derived from autumnal seedlings flower in the late spring and are commonly single-flowered and unbranched, or feebly so, and very few-flowered. Those derived from spring seedlings which flower in the autumn are, in contrast, usually freely branched and many-flowered as was pointed out by Wettstein (1896). Warburg (1962) expressed the view that *Gentianella baltica* and *Gentianella campestris* may well be the annual and biennial states of the same species.

This reversal of the prevailing habit compared with the species *Anagallis minima* and *Lythrum hyssopifolia* is associated with the fact that the Euphrasias and Gentians referred to flower in relation to the long-nights and short-days, so that whereas the autumnal seedlings of *Euphrasia* which flower in late spring or early summer, are short-lived and consequently small, the vernal seedlings do not come into flower till the days shorten in the autumn and hence have a much larger assimilatory capital which enables the freely-branched and bushy habit to be attained. The photoperiodic stimulus for flower production of the two species here considered is the short night and long day but the response is essentially comparable. In *Anagallis minima* the distinction between the two states would appear to be to some extent intrinsic since, however favourable the environmental conditions, the percentage of seeds

that would germinate in the autumn always proved to be small. *Lythrum hyssopifolia*, however, appears to be largely, perhaps entirely, extrinsically determined and in some degree accidental. We have seen that ripe seeds of *L. hyssopifolia* removed from the capsules in September and subjected to high daytime temperatures will germinate freely, but in natural conditions the seeds are in fact commonly retained in the capsules and shedding is so delayed that in our latitudes, for most of the seeds, the conditions requisite for germination do not obtain till the rise of temperature in the spring, and in consequence the proportion of large, autumnal, plants is small or absent and such as may occur are at risk from severe frost. It is, perhaps, such plants of *Lythrum hyssopifolia* with a more prolonged period of vegetative activity to which Jepson (1923) refers as attaining 'even 60 cm' in California. We may also note that *Anagallis minima* reaches up to 12·5 cm in the same region.

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A NEW SPECIES OF *HIERACIUM* IN DERBYSHIRE

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ABSTRACT

A new species, *Hieracium naviense*, in Section *Oreadea*, is described from two limestone cliffs in Derbyshire. It is related to *H. subbritannicum* and *H. britannicum*.

An unfamiliar *Hieracium* was first noticed on a limestone cliff in Winnats Pass, Derbyshire, in 1961 and has been under observation since then. Careful search has revealed only two colonies, on adjacent cliffs, growing both on turfey ledges and in cracks in the bare rock, and associated with *H. cymbifolium*. Its obvious affinities are with the *H. dicella* group (Sell & West 1963), but Mr. Sell and Dr. West agree that it belongs to no known British species, so it is described as a new species and named from a nearby Roman site which is known only in the ablative as *navio*. It most closely resembles *H. subbritannicum*, which grows on the limestone of South Wales and adjacent parts of England. Disjunct distributions are common in the genus *Hieracium*, so a root of the new plant, and one of *H. subbritannicum*, have been grown beside one another in the author's garden in Manchester and the plant has been grown from seed both in Manchester and in Cambridge; the distinctive characters persist in cultivation. The capitulum is smaller than those of other species in this group, though it becomes somewhat larger in cultivation, and the phyllaries are shorter and notably paler owing to the much sparser clothing of simple hairs. Fig. 1 shows the type specimen. In its native habitat it has never been observed to follow the habit usual among *Hieracia* of developing secondary growth later in the year, often somewhat different in form from the characteristic first growth. In cultivation it is more vigorous, reaching 40 cm in height, with up to 8 capitula, and produces secondary growth; a specimen with larger, subentire, elliptical-obovate leaves with cuneate base has been observed in August and has even flowered for a third time in October, whereas in its native habitat by August nothing remains but a few radical leaves and dried-up stems and receptacles.

The precise terminology introduced by Sell & West (1965), and awaiting publication, has been adopted to describe this plant.

In sectione *Oreadea* Zahn

***Hieracium naviense* J. N. Mills, sp. nov.**

Ab *H. subbritannico* (A. Ley) Sell & C. West et *britannico* F. J. Hanb. capitulis minoribus, pilis glanduliferis, squamis capitulorum brevioribus et viridioribus differt.

Holotype: Rock ledges on limestone cliffs in Winnats Pass, V.C.57, Derbyshire, G.R.43/134827, 19 June 1966, J. N. Mills no. 66/34 (CGE). Planta phyllopoða. Caulis ad 30 cm altus, inferne nonnumquam purpureus, pilis stellatis inferne paucis, superne numerosis, aliis simplicibus superne nullis vel saepe paucis brevibus vestitus. Folia caesia, interdum subtus purpureotincta; basalia 3-8; primigenia ovata, obtusa, basi subtruncata, dentibus paucis parvis; cetera ovata vel longe ovata, nonnumquam oblonga vel obovata, dentata vel e basi raro inciso-dentata, dentibus saepe mammiformibus, variabilibus basalibus patulis vel retrorsis; caulinum 0-1, plerumque minus lanceolatum vel lineare, petiolatum, raro majus dentatumque basalibus simile; omnia superne glabra vel pilis simplicibus subsetiformibus paucis, margine aliis simplicibus densis, inferne pilis simplicibus mediocribus, saepe in costa densioribus, nonnumquam pilis stellatis costa inferna vestita. Anthela cymosa, capitulis 3-5, ramis acladium parce superantibus; pedunculi mediocres, divaricati, pilis aliis stellatis, plerumque densis, aliis glanduliferis paucis obscuris brevissimis, aliis simplicibus raris brevibus obscuris vestiti. Involucra squamæ 10-12 mm longae, circa 1 mm latae, ante anthesin porrectae, virides, interiores marginibus pallidioribus, lineari-



Fig. 1. *Hieracium naviense* sp. nov. Holotype.

lanceolatae, acutae, pilis aliis stellatis densis in marginibus, aliis glanduliferis nigris minimis, aliis simplicibus paucis brevibus vel mediocribus pallidis vestitae, apice attenuato glabro. Ligulae pallide luteae. Styli lutei. Receptaculi alveoli margine breviter dentati. Cypselae obscurae, 3–3.5 mm longae.

Phyllopodous. Stem to 30 cm, commonly purple below, nearly glabrous, with sparse stellate hairs increasing upwards and usually a few short simple hairs above. Radical leaves caesious, sometimes purple tinted below, primordial ovate, obtuse, with a subtruncate base and a few small teeth; the later ones ovate-oblong or obovate, obtuse or acute, unequally dentate, the basal teeth patent or often retrorse or even decurrent on the petioles; cauline 0–1, lanceolate or linear, petiolate, occasionally large and dentate like the basal

leaves; all glabrous or with sparse medium subsetiform hairs above, dense on the margins, with sparse medium simple hairs below, commonly more numerous on the midrib, stellate hairs sometimes present. Inflorescence usually simply cymose with 3-5 capitula, the lower barely reaching the acladium, peduncles medium, divaricate, with usually dense stellate hairs, very short black glandular hairs, and occasional short simple hairs. Phyllaries 10-12 mm long, 1 mm wide, linear-lanceolate, acute, porrect in bud, with stellate hairs, abundant on the margins, very short black glandular hairs, and usually very few short or medium pale simple hairs, tapering to a glabrous apex. Ligules pale yellow. Styles yellow. Margins of receptacle pits shortly dentate. Cypselae dark, 3-3.5 mm long.

ACKNOWLEDGMENTS

My thanks are due to Mr. P. D. Sell and Dr. C. West for multifarious help and advice, and to my wife for the figure.

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BOOK REVIEWS

Plants, Man and Life. Edgar Anderson. Pp. 251. University of California Press, Berkeley & Los Angeles; Cambridge University Press, London. 1967. Price (paperback edition) 19s. 6d.

A warm welcome is sure to be given to this paperback edition of Edgar Anderson's classic work, which first appeared in 1952 and discusses in a very interesting and amusing way various aspects of the interaction between Man and the plants (both wild and cultivated) which occur in close proximity to him. Those who did not read this book when it first appeared now have an opportunity to repair this omission, while those to whom it is already familiar may well wish to have it in its new format. For this edition a short epilogue and some recent references have been added.

N. K. B. ROBSON

Taxonomy. Richard E. Blackwelder. Pp. 698. John Wiley & Sons, New York, London, Sydney. 1967. Price £8 15s. 0d.

At first reading this book seems to have little coherence; it appears to be a series of discussions of different aspects of zoological taxonomy loosely connected and without a clearly defined theme. It is intended as a text and reference book, of course, covering a wide field, so heterogeneity is inevitable. Almost seven hundred pages with very few figures make a large volume, a plethora of facts and ideas which might have been better arranged. The detailed Contents pages at the beginning of each Part are only of limited help.

The introductory matter deals with preliminary definitions and the organization of taxonomy professionally. It includes a reference list predominantly of American institutions and an interesting section giving many examples of the practical value of taxonomy. One is surprised that the author considers such a thorough justification of this value to be necessary, until one realizes that the evidence demonstrates particularly the need for synthetic taxonomic schemes rather than intensive speciation studies. After a rather cursory review of the practical routines of taxonomy, which nevertheless includes some astute observations on collecting and cataloguing, there follows an unusual pair of chapters on the diversity of animal life. Although the matter is familiar here, it is brought together in very readable fashion. The reasons for the different types of diversity are discussed; influences are classified; those of sex, climate, development, reproductive cycles and so on. The author seeks to show how little the museum taxonomist need be constricted by the non-living nature of his specimens.

The heart of the work is Part IV; this mostly concerns the practical aspects of classification and includes lists for reference use, as well as a sophisticated discussion of the formation of groups and advice on the use of literature and even on latinization. An important section deals with the type concept, and its relationship to the lower categories of the taxonomic hierarchy is carefully analysed. Even in this Part, theory comes in: the methodological chapters 10 and 11 are short but interesting and, significantly, their bibliographies (pp. 618-639) are the longest of any. The emphasis is on data and its elucidation, and the overriding theme is the author's concern for comparison rather than mere recognition. The one chapter which all biologists should read is Chap. 11: although not entirely new, the discussion of the nature of species and subspecies may provide the necessary stimulus towards the eventual clarification of their distinction. As Prof. Blackwelder explains, species have a validity which subspecies lack and it is the former with which taxonomists should be primarily concerned.

Methodology proper is dealt with rather shortly in Part V. The two interesting though somewhat didactic chapters present the author's conviction of the primacy of comparative studies in taxonomy, and especially those of structure. He advocates recognition of the biological wholeness of nature, but denies that the search for 'biological species' is the business of the taxonomist. This Part is another presentation of the author's omniscient method: to consider *all* the data and use it selectively and critically to construct a taxonomic scheme (*cf.* Blackwelder 1964). The discussion of the confusion of 'categories' with 'groups' is a very worth-while contribution to the linguistics of taxonomy: one must agree with the author that taxonomists have overlooked the probability of improvement that would follow from semantic refinement of their concepts.

The remaining two-fifths of the book deals with the Code of Zoological Nomenclature, its development and use. There is much critical matter here also, but the text mainly offers practical help to working zoologists. Although this reviewer is a botanist, he judges that the quotations from the 1961 Code together with the author's interpretation and criticism will be of great help to those who wish to present their work appropriately within the complicated framework of zoological nomenclature.

This book is an important contribution on the subject of taxonomy, because Professor Blackwelder speaks from the experience of over thirty years of actual taxonomic practice combined with a real concern

about theoretical principles. This rare combination ensures that a great deal of useful basic information has been brought together and enlivened by higher level criticism. The author has tried to arrange the matter suitably but one feels that the loose organization reduces the book's general utility; scientific philosophy and elementary practice alternate irregularly. It may become a bedside book: a kind of intellectual lucky-dip; there are pearls of wisdom here but the general reader may not enjoy hunting for them.

REFERENCE

BLACKWELDER, R. E. (1964). Phyletic and Phenetic *versus* Omnispective Classification. In *Phenetic & Phylogenetic Taxonomy*, ed. by V. H. Heywood & J. McNeill, pp. 17–28. Publication No. 6 of the Systematics Association. London.

JOHN LEWIS

Systematic Embryology of the Angiosperms. Gwenda L. Davis. Pp. viii+528. John Wiley & Sons Ltd., New York and London. 1966. Price £9 4s. 0d.

It is most unusual to find a newly-published biological text wholly lacking in illustrations; this book is such a rarity. Obviously intended for the specialist—there is no attempt to define or explain the technical terms utilized—the work is a *sylloge* of embryological data for all the families of flowering plants.

It has three sections. The first is a succinct introduction, which does not attempt to be a comprehensive review of the subject. A systematic catalogue of features abstracted from the literature makes up a middle portion occupying rather less than half the book. This is followed by an almost equally lengthy bibliography, which lists about 5,000 references. The systematic account is based upon the families as circumscribed by Hutchinson in *Families of Flowering Plants*, ed. 2 (1959), and their order is alphabetical. It is not surprising that some of his small, segregate families are still embryologically unknown, though these are just the families where information on the development of anthers, ovules, embryo-sacs, endosperm and embryos might be of special value to systematists.

The family accounts have a disadvantage in lacking any indication of the genera that have been studied by the authorities cited at the end of each family. The unfortunate effects of this can be readily appreciated by examining a large family such as the Compositae: anyone interested only in agamospermy in *Taraxacum* or *Hieracium* is presented with a list of more than 300 citations of scientific papers for the family. There are no clues to indicate which genera have been examined by the authors cited; each must be looked up separately in the bibliography to yield such relevant information as the title of the paper may (or may not) enshrine—a herculean task.

Though many will undoubtedly share the view of Alice in wondering 'What is the use of a book without pictures or conversations?', for specialists in those fields, the *Systematic Embryology of the Angiosperms* is a valuable compendium.

B. M. G. JONES

Flora of Hertfordshire. J. G. Dony. Pp. 112 with a coloured frontispiece, 16 plates and 56 pages of maps. Hitchin Museum, 1967. Price £2 2s.

Dr. Dony's *Flora of Hertfordshire* is one of the most beautifully produced and most skilfully written county Floras of our time. The firm pages, the clarity of the printing and the excellent frontispiece make a most attractive book, though the small type may be trying to some eyes. Besides the coloured photograph of the Chiltern Gentian, which is the first thing we see when we open the book, there are sixteen pages of black and white photographs in the middle. These are carefully chosen views of the Hertfordshire countryside and will attract not only readers to the book but visitors to the county. There is a short historical introduction and at the end of the book a bibliography and a single comprehensive index, which makes the book easy to use and places the botanists among the flowers where they ought to be.

The body of the Flora is in three parts. First we have a series of 109 habitat studies, a feature with which readers of Dr. Dony's *Flora of Bedfordshire* are familiar. These studies are word pictures of great value. They fix the ever-changing scene for the benefit of future generations. If only botanists a hundred years ago had had the wit or the opportunity to describe the vegetation of their counties in this exact manner, how greatly we should have valued their work now.

The second part of the Flora is a condensed account of the species in their scientific sequence. A good deal could be said about this. At first sight the compression appears to be too drastic. But we must judge a book in the light of its author's intentions. Where information is plotted on a map it is not generally necessary to reproduce it in words and Dr. Dony had to consider also the heavy cost of printing in our day. He decided therefore not to reproduce all the work of his predecessors, especially as this work has been published and is available to students, but to summarize it. The new *Flora of Hertfordshire* is more than a supplement to Pryor's Flora of 1887, but it does not supersede it: both are necessary for a full view of the past and present vegetation of Hertfordshire.

It is evident that Dr. Dony has read Pryor's *Flora* carefully and checked the geographical references. For example, the apparently simple account of *Potentilla palustris* masks a good deal of work and is an admirable summary of Pryor's longer statement. It is necessary to read both books side by side to appreciate the skill with which the new *Flora* has been written. There is, of course, a loss of bedside reading for those who like to dream about the past. No summary, for example, however scientifically adequate, can compensate us for the loss of Pryor's record of *Gentiana germanica*, 'About a mile through Tring, on the east of a cart road through ripening barley . . .' We could wish that Dr. Dony had relaxed his rule from time to time to include some of these picturesque statements. For imaginative readers they have the value of coloured illustrations.

But this does not mean that the new *Flora* is without colour altogether. The observation that *Linum usitatissimum* often sprang up where birdcatchers dropped their seed is reproduced and Dr. Dony tells us that the yellow sap of *Chelidonium majus* is still thought to be a cure for warts. Nor must we overlook the notes of the author himself, as, for example, that the white-flowered form of *Raphanus raphanistrum* is most often seen on arable land and the yellow-flowered form on newly-made roadside verges. Many of Dr. Dony's entries are splendid examples of the *Flora*-writer's art. What could be better than his accounts of the Juniper and the Box? It is the excellence of such entries as these that whets the appetite. Would not the story of *Euphorbia lathyris* be improved if we were told that the copse near Goldings was once called *Euphorbia* copse and that thousands of plants of Caper Spurge sprang up when the underwood was cut in the winter of 1841-2? Sometimes the addition of a date is all that is needed. For example, the pleasure of the botanist who is fortunate to see the single surviving plant of *Vicia sylvatica* in Wain Wood would be increased, if he knew that it was first found there in 1843.

The value of first records has sometimes been doubted but they are always interesting and many readers will be grateful to Dr. Dony for introducing Isaak Walton to them as a botanist. How fitting it is that he should be the first to record the Bluebell and the Cowslip for Hertfordshire, though he would be surprised to know it. But if first records are to be included in a *Flora* the author's search into the past should be thorough. In the light of Dr. Dony's work it is surprising how many of Pryor's earliest dates are incorrect. Another pleasing feature of the new *Flora* is the inclusion of the latest date on which a species presumed to be extinct is known to have been seen. This may often be more reliable than the earliest date, but of the two it is the one we should most like to prove wrong!

The third part of the *Flora* consists of distribution maps of 696 species. This is a novel and excellent feature. Doubtless the shape of the book was determined by the shape of the county as there are fifteen maps to a page. These are rather small but so clear that nothing is lost. Only the rarest species are without a map, so that for the first time in a county *Flora* we can see at a glance how each species is distributed. This is a great convenience. The map of *Silene dioica*, for example, which takes the place of a page of records in Pryor's *Flora*, not only saves much space, but it affords a much clearer view of the peculiar distribution of this species than a long list of place names. It may be said that maps of species like *Bellis perennis*, which has been recorded for every square, and of others, which are known to occur in nearly every square, are unnecessary and that Dr. Dony could have saved six pages by their omission. This is true. But we may be glad he did not prune his book in this way. The full maps are valuable as a contrast to the others and increase the pictorial attraction of the pages. The maps are the cream of the book. They summarize the field work that has been done by Dr. Dony and his helpers and show how thorough that work has been. They offer us a picture of the flora of Hertfordshire as it is at the present day, owing nothing at all to past work in the county. Their simplicity and clarity will do more than many words to popularize the 'tetrad' method of recording.

The maps, however, tell us nothing about the location of the rarest species and the treatment of these species in the textual part of the *Flora* is uneven. All the recent records are published, but the old records in accordance with the author's general policy are usually summarized. But the old records of species which have diminished during the years are particularly interesting. Dr. Dony gives a full account of *Orchis militaris*. Why should we not have complete accounts also of, say, *Herminium monorchis* and *Drosera rotundifolia*? Where there are too many old records for verbal reproduction, a special series of maps could have been drawn, using hollow circles to indicate unconfirmed records. Maps showing the former distribution of *Parnassia palustris* and *Hottonia palustris* would be instructive.

Dr. Dony's *Flora of Hertfordshire* reflects its author's interest in alien species and garden escapes. They are all there, even *Ligustrum ovalifolium* which 'does not appear as a wild plant'. By contrast the author has little direct interest in the so-called critical species and seems to welcome the opportunity which the *Flora Europaea* gives him of combining the plants we used to distinguish as *Sagina apetala* and *S. ciliata*. This makes recording in the field much easier, but it reduces the value of the book.

The treatment of the genus *Rubus* could hardly be more meagre. Dr. Dony is right to say that a mere list of uncertain names would not be worth printing, but there is a solid nucleus of uncontroversial species

which deserve full recognition. Besides *Rubus ulmifolius*, species like *R. lindleianus*, *R. vestitus* and *R. echinatus* can be recognized at a glance and are widespread. Maps of a dozen or even a score of these could have been made as easily as maps of non-critical species, if anyone who knew the brambles had been willing to spend a fortnight in the county. Perhaps the writer of this review ought not to say more about this. But in his view the poor treatment of the critical species is the one major weakness of Dr. Dony's Flora.

There are those who say that a county Flora is not the place for a detailed account of critical plants, but Dr. Dony's motive was probably to save space and time. To have enlisted sufficient expert help would have delayed the publication of the Flora and the extra pages would have increased its cost. But we can't help asking for more. We are Oliver Twists only because the gruel is so good. Four more pages would probably have been ample for a satisfactory account of the Hertfordshire *Rubi* and if the size of the book could have been increased by thirty pages, not only could all the critical species have been fully recorded, but there would have been room to print longer accounts of the rare species and to include some of the picturesque old records in the summaries of the common ones.

But if we repine for what is not, it must not be supposed that we are ungrateful for what we have. We are very grateful indeed. The new *Flora of Hertfordshire* is a masterpiece of planning and probably contains more information to the page than any other Flora. And as we peruse its pages we feel that what we read is reliable.

E. S. EDEES

Sub-Antarctic Sanctuary: Summertime on Macquarie Island. Mary Gillham. Pp. 223, with 32 photographs and 46 line drawings in the text. 1967. Victor Gollancz Ltd., London. Price £2 5s. 0d.

The author of this book is a botanist with an intimate knowledge of sea-birds. She has pursued this interest on islands around the coasts of Britain, and of Australia and New Zealand. It was therefore appropriate that she should have the distinction of being one of the first four women scientists to visit an Australian National Antarctic Research Expedition's base. The book is an account of this visit, and of the general natural history of Macquarie Island. It is full of observations and information ranging over a wide spectrum of biological interest, from seals and sea birds—albatrosses, cormorants, skuas, gulls, terns, petrels and penguins—to tussock grass, herbfield, feldmark, fen and bog. Naturally in a book of this kind, the animals and birds receive most attention, but the author ensures that a variety of aspects of plant life are represented—indeed, it is no surprise to find that she is often at her most interesting when discussing the impact of animal and bird colonies on the plant cover.

One of the appendices consists of a list of 38 vascular plants recorded on the Island, of which a few such as *Stellaria media* and *Poa annua* are introductions. A previously misidentified fern is named as *Cyclophorus serpens*, but owing to its very dwarf habit the author expresses herself as only 'pretty certain' of the determination. The accompanying list of 42 mosses and 4 hepatics must be a very much less complete indication of the representation of these groups.

A botanical reader familiar with the Antarctic flora may detect some errors. For example, after mentioning the occurrence of *Colobanthus crassifolius* and *Deschampsia antarctica* on the coasts of the Antarctic continent, the author continues '... no flowering plants occur on any Sub-antarctic islands in more favourable latitudes until we get as far north as Macquarie Island ... and South Georgia ... The plantless, icebound islands include Balleny ... , South Shetlands ... , South Orkneys ... , South Sandwich and Bouvet Oya ... ' In fact, both of the species mentioned occur in the South Shetlands and South Orkneys, while *Deschampsia antarctica* is recorded from South Sandwich. Furthermore, the implied inclusion of all these islands under the heading 'Sub-antarctic' does not accord with the usual distinction, where vegetation is concerned, between a Sub-antarctic zone (e.g. Macquarie and S. Georgia) and a Maritime Antarctic or Low Antarctic zone (e.g. the other islands named) as discussed by Wace (1965) and Holdgate (1964). Different again is the oceanographers' use of the term, adopted in the map on p. 23, for the region of sea extending from the Antarctic convergence to the Sub-tropical convergence, which excludes even South Georgia.

Apart from these details and some unnecessarily dogmatic statements ('The theory of continental drift is untenable ...'), the book will appeal to naturalists and will pleasantly recall much that is familiar to any who have visited some part of the Antarctic. It is illustrated by a large number of really excellent photographs and a series of generally pleasing sketches. While the publisher's claim that it is a 'must' for the specialist in several fields is not to be taken very seriously, we can agree that the general reader will find it attractive and interesting.

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C. H. GIMINGHAM

Nordisk Kärlväxtflora II. Nils Hylander. 4 February 1966. Almquist and Wiksell, Stockholm. Price Sw.kr. 58.

This second volume of the *Nordisk Kärlväxtflora* is long awaited by all who have made use of the first volume and by those who know the value of Dr. Hylander's well-considered and experienced opinions. But the first volume was published in 1953 and there are many younger botanists to whom Volume II will be an introduction to this detailed and all-embracing work. The Flora, then, covers a wide area, namely Sweden, Norway, Denmark, Faeroes, Iceland, Finland and Russian Fennoscandia. It is very unfortunate that the map showing the provinces used in the Flora is not reproduced again in Volume II. There is, however, an additional map, that showing botanical districts in Denmark. The volume contains accounts of Cyperaceae (11 genera, 150 spp.), Orchidaceae (24 genera, 48 spp.), Salicaceae (2 genera, 49 spp.), Polygonaceae (6 genera, 56 spp.), and the smaller families of Myricaceae, Juglandaceae, Corylaceae, Betulaceae, Fagaceae, Ulmaceae, Cannabiaceae, Urticaceae, Santalaceae and Loranaceae. The descriptions are detailed and often long and the vital differences may well be lost in a text describing the subtle variation. Detailed distributional data are given and references for literature records are usually given in full. The keys are indented and in many cases short and to the point, requiring only a scanty knowledge of Swedish in order to use them; in other genera, e.g. *Carex*, the many variations of the characters used make heavy going, but on the whole this key to 113 species is commendable. There is at the end of the book a chapter on 'Taxa and nomina nova' validating the new taxa and new combinations mentioned in the body of the work. The volume lacks an index to species (except in the case of *Carex*, on pp. 43–46); a generic index is given on the front inside cover but this does not include all synonyms. There are no page heads to guide the user and the fact that the family headings are in the same 12-point bold typeface as the genera does little to alleviate the situation of quick reference. There is also a sizeable 'Appendix to Volume I' and a list of general literature. The latter is confusing: all references are indexed according to the full title given in the text. Thus 'D. P. Young' is listed along with 'Dandy [J. E.]'; more bewildering, A. Löve is found in the 'A's, whereas 'Löve [A.] and Löve [Doris]' is in its rightful place following 'Lönnqvist'.

Naturally this is a reference book for all who are working on or interested in the flora of Europe. It will be widely used as this and should be in all University and research libraries. But what of its use to the individual botanist who is interested in the Scandinavian flora as a whole but not fully conversant with the Swedish language? In my opinion the keys, descriptions and distributional data make the book a usable handbook. There could have been more illustrations to help clarify the finer points. But as Dr. F. A. Stafleu has said in a review elsewhere, 'The treatment is critical to such an extent that if one finds something "different" it is better to hesitate twice and investigate, before one disagrees with the author'. To the present reviewer this sums up the reason why this Flora is so valuable: if Hylander has not followed a well-known classification, arrangement or concept, there is a considered reason. In *Carex*, and one may be forgiven in referring so frequently to that genus as it takes up almost one-third of the book, the first thing that is 'different' is the arrangement of the species and the circumscription of the Sections into which they are placed. The relationship of the species to one another is a problem which besets all regional monographers of this large genus; and it will not be solved until the genus is monographed again on a world basis. However, it is interesting to see Hylander's views.

He places *C. lasiocarpa*, *C. hirta*, *C. pseudocyperus*, the *vesicaria* group and *C. riparia* and *acutiformis* in one Section, the *Paludosae*. They are placed at the end of the genus and presumably considered the most advanced, an opinion with which I agree as they all show a specialized inflated utricle to aid water dispersal of the seed. I do not understand on the other hand why *C. dioica* and *C. parallela* (Sect. *Dioicae* Tucker.) are placed in subgenus *Vignea* and not subgenus *Carex*, or why subgenus *Primocarex* is maintained for the *pauciflora*, *capitata*, *pulicaris* and *rupestris* groups.

At the species level the 'differences' are not so outstanding. It is interesting to note that *C. polyphylla* is placed as a subspecies of *C. divulsa* [subsp. *leersii* (Aschers. and Graebn.) W. Koch], and indeed there is much to be said for this. I feel if this policy is taken then perhaps both *C. spicata* and *C. polyphylla* should be subspecies of *C. muricata*. Hylander describes a new subspecies of *C. muricata* (which he calls *C. pairaei* F. W. Schultz), namely subsp. *borealis* Hyl. It is more robust than the type with a wider leaf and larger inflorescence. The most distinguishing difference is the colour of the female glumes which are a darker brown with a green midrib and which show up against the paler green immature utricle. It appears to replace subsp. *pairaei* (i.e. *C. muricata* subsp. *muricata*) in the northern part of the species range.

What has been said for *Carex* could be said similarly for Orchidaceae and the other big genera. Hylander's concept of genera in orchids is not always consistent. *Hammarbya* is recognized as distinct from *Malaxis*, but it is doubtful whether, had the author seen material referable to *Malaxis* from a world-wide range, he would have singled out *M. paludosa* as a distinct genus. Yet on the other hand he includes *Lysichiton* and *Limnorchis* in *Platanthera*. Hylander makes several new combinations and new taxa at varietal and

formal level, in *Dactylorhiza*, *Betula* and *Populus* especially; one wonders if all are worthy of taxonomic recognition, especially where nothomorphs of the *Betula* hybrids are concerned.

Hylander follows a Code of Nomenclature which is not always that followed by other botanists and he states his differences in the preface. This is unfortunate but in spite of it the next volume of the *Nordisk Kärleväxtflora* will be awaited eagerly and all must hope that there will not be as long to wait between that and the present volume as between Volumes I and II.

A. C. JERMY

Tropical Plant Types. B. G. M. Jamieson and J. F. Reynolds. The Commonwealth and International Library. Pergamon Press, Oxford 1967. Price in U.K. £2 10s. (hard cover), £2 (paper).

A taxonomist should not be misled into thinking this book deals with type-specimens. It is in fact a traditional type of botany textbook 'to meet the requirements of the Cambridge Overseas Advanced Level Biology Examination', as the Preface states, with many of the examples taken from the tropics. Its qualities need to be judged in relation to this declared aim of providing students in tropical countries with tropical species to study in their own neighbourhood.

The object is achieved to a large extent and it is good to find real attention being paid to the tropics. Even so, one has the feeling that the text is written from a temperate point of view with tropical examples substituted for temperate species. Several temperate types remain; for instance *Fucus*, and not *Sargassum*, is taken as the type of the Phaeophyta, *Psalliotia hortensis*, and not *Volvariella volvacea*, as a Basidiomycete; *Ranunculus* is used for the anatomy of the root instead of a typical tropical genus, and the only example of heterostyly given is that of *Primula* even though it is stated that 'heterostyly is remarkably widespread and has been shown to occur in seventeen families'—it would have helped teachers if some of these such as Rubiaceae (e.g. *Mussaenda*, *Psychotria*) had been mentioned.

Several incorrect botanical names have slipped through in the text such as *Bougainvill(a)ea* and *Encephar(c)tos*.

The beautiful illustrations by Miss P. Fawcett are a great asset to the book. They are technically accurate and skilfully drawn but it is unfortunate that some of them have been over-reduced, such as Figs. 54 and 55 of *Dryopteris* where the real beauty is lost, and others where the points of interest are so small as to be hard to see.

It is to be hoped that students will be encouraged to look around and to make their own investigations on the fascinating wealth of morphological adaptations available in tropical plants. Much of this basic work remains to be recorded (as is shown by the recent paper by J. Jenik, in *J. Linn. Soc. (Bot.)* 60, 25–29 (1967), on root adaptations in West African trees) and if Jamieson and Reynolds' text-book stimulates the reader in this way, as well as enabling him to pass examinations, it will have more than succeeded.

F. NIGEL HEPPER

Index to Botanical Monographs. D. H. Kent. Pp. xi+163. Academic Press, London and New York (for B.S.B.I.). Price £2 2s. 0d.

Since Dandy's *List of Vascular Plants* displaced Druce's *British Plant List* as the authoritative check list of British plants, botanists have lacked two sources of information found in the latter work—the lists of casual aliens and the list of critical papers on the British flora. Mr. Kent's publication now replaces the latter and will be very welcome, especially to amateur botanists. Whether it will really be widely used by 'botanists undertaking a taxonomic revision', as claimed by the front flap, is doubtful; most botanists undertaking taxonomic revisions do so either because no previous monograph exists or because they are familiar with such as do exist and have found them to be manifestly inadequate. My own view of this book is that it will be tremendously useful to botanists attempting to name plants which they have collected. I cannot help but feel, incidentally, that the fact that the botanical monographs listed apply to British wild plants should have been made clear on the dust cover as well as on the title page. The word 'wild' has been interpreted in the sense of 'not deliberately cultivated', and thus the publication will be a 'must' for the alien-hunter—a breed obviously well to the fore in Mr. Kent's mind when making his compilation.

It is, of course, always easy to find omissions in such a work, and the compiler is as aware of this fact as anyone. Nevertheless, one has the impression that had Mr. Kent's typescript been circulated a little more widely before going to press, there could have been far fewer of these than there are at present. The omission of some references to well-known and useful papers on British native plants is odd—for example Elliston Wright's *Journal of Botany* papers on *Sagina*. Important papers or revisions very relevant to aliens are missed. For example, Davis' 'Revision of the genus *Calotis*' is included, but not Anderson's 'Revision of the Australian species of *Bassia*' (an equally frequent genus of wool aliens), also in *Proc. Linn. Soc. New South Wales* (Vol. 48, pp. 317–355; 1923). Jaubert and Spach's monograph of *Cicer* is cited but not the much

more recent one of Popov, in *Bull. Appl. Bot., Genetics & Plant Breeding*, Leningrad 21:3–239 (1929). Dudley's very useful paper on *Alyssum* sections *Meniocus* and *Psilonema* in *Journ. Arnold Arboretum* 46:181–217 (1965) differentiates numerous annuals occurring in Britain as casuals, but is omitted; while Nyárády's work on the perennials of section *Odontarrhena* (in papers difficult of access) is included, although rarely if ever likely to be used by British botanists. Other similar examples spring to mind during a casual browse through the book.

Errors are few; however, it might have been as well, in equating *Kohlruschia* with *Petrorhagia*, to add *Tunica* also—for although Dandy transferred *Dianthus saxifragus* L. to *Kohlruschia*, this naturalised species is still perhaps best known to amateur botanists as *Tunica saxifraga* (L.) Scop. Misprints are likewise few and obvious, ranging from the Welsh-sounding 'Pesga llinaceus' on p. 43 to 'Onagearum' on p. 77, which sounds like a group of hybrids between willowherbs and wild donkeys!

Finally, it is a pity that Mr. Kent does not indicate in his Introduction whether in fact he 'closed his books' on 31 December, 1966, so that one might know at what point any future supplement is to begin.

The price will appear high to all still unaccustomed to the blatant excesses of certain continental publishers, but the compiler is presumably not to blame for this, and we can only offer him our thanks for a time-consuming and rather tedious task performed with characteristic diligence.

C. C. TOWNSEND

Deadly Harvest. John M. Kingsbury. Pp. 128. George Allen & Unwin Ltd., London, 1967. Price £1 1s. 0d.

The purpose of this book is summed-up by the author in his introduction: 'To mount a small campaign for better understanding of poisonous plants; to create a better-informed public so that poisonings may occur with less frequency despite the move to suburbia; to make the dimensions of the problem more generally known; to encourage the undertaking of significant research.' This, it should be said at once, was written in the U.S.A.—the book is an English reprint of one published in the States in 1965. To judge from the evidence presented, plant poisoning, of humans no less than animals, is a bigger problem there than here. Nor need we be surprised. We benefit from a few thousand years of tradition based on experience of the plants around us; the Americans are still colonizing into lands where most of the plants have only received names in the past couple of centuries. The mobility of the human population over a vast area with a vast flora must also create problems unknown to us with our cosy little 2,000-odd species.

This having been said, it will be appreciated that parts of this book will be common knowledge to English readers, other parts will be read with no more than general interest or even amused detachment. But is a good little book and worth reading. It reviews the hazards of plant poisons ('plant' here including fungus) under various headings, with constant reference to particular species, many of which will be familiar to readers in this country. As befits one who has already published a systematic textbook of toxic plants, the author writes in a scholarly and accurate manner, marred by only occasional slipshod terminology—'plant' where he means 'genus', and 'molecule' for 'compound'. His admitted preoccupation with poisoning unfortunately shuts out any reference to the beneficial uses of poisonous plants in medicine. Yet surely it is no accident that these same plants yield valuable drugs: for a compound, or a plant containing it, that is not fairly toxic is, *ipso facto*, bereft of pharmacological activity. The book is attractively illustrated with many small but good plant drawings; the few photographs are almost indecipherable.

D. P. YOUNG

The Elements of Biometry. Kenneth Mather. Pp. x+193. Methuen & Co. Ltd., London, 1967. Price £1 15s. 0d.

The term biometry was introduced some 35 years ago to cover the statistical treatment of measurements on organisms. Since that time, and especially within the last decade, there has been a great increase in the use of mathematical techniques for the evaluation of biological data. Many of these modern applications are concerned not so much with the analysis of experimental data and the testing of hypotheses, as with the use of quantitative data to assess similarities or other functions with a view to improving on an intuitive judgment; what might be termed the quantification of biology.

It could be argued that such aspects properly come within the province of biometry, though there is a substantial body of opinion which still prefers to restrict the use of this term to the statistical or probabilistic approach. Although Professor Mather defines biometry as 'quantitative biology', it is clear that he holds this latter view.

The first half of his book is concerned with the analysis of variance. This is a very readable account which sets out clearly the mechanism of the process. The worked examples should facilitate the interpretation of the procedure for any set of comparable data. A further 30 pages are devoted to the design of experiments

and the methods which can be used to assess the various results obtained from replication, randomization and factorial designs. It is unfortunate that no indication is given of how to deal with missing data, since this is not especially complicated and is one of those problems which an experimenter is likely to meet. The discussion of the relationships between two variables is essentially confined to simple regression and it is surprising that no mention is made of the correlation coefficient; indeed, covariance is hardly mentioned. Although multiple regression is expressly excluded, it is a pity that reference could not have been made to recent works where this and other multivariate techniques are discussed in some detail.

Methods for the analysis of frequency data cover the use of χ^2 where there are several categories for the variable and the author derives the special case of the 2×2 contingency table. The book continues with a chapter on the estimation of parameters. While it is true that in certain aspects of biology this can be an important topic, this section involves by far the most advanced mathematics of the entire text, and its inclusion at the expense of other aspects is rather surprising. One could, for example, have included a brief discussion of ranking methods.

The author draws a considerable number of his examples from genetics, a field in which the statistical applications of biometry are of considerable importance; certain of the terms used may well cause a non-geneticist to reach for his glossary! There are also a number of instances of rather casual phraseology. The paragraph on p. 28 introducing the data on *Primula sinensis* is a case in point, where the words 'pin' and 'thrum' are used where the usual expressions are 'pin-eyed' and 'thrum-eyed'; while 'pin-flower' may be acceptable, surely 'pin-plant' (Fig. 5, legend) is not. Although the word 'family' is used here in its genetical connotation, it would seem that the situation could be explained more clearly if it were stated exactly what groups of plants were being dealt with. It would seem improbable that there is any chance of 'a progeny being pin and thrum'; this type of phrase in a different context appears also on p. 139. One must deprecate the phrases 'more strictly correct' (p. 139) and 'work to be expended' (p. 177). It seems unfortunate that it was not possible to ascertain the specific epithet of *Pharbitis* in the examples on pp. 146 and 162. *Pharbitis*, as the name of a genus, is not a plant (p. 146) and it is difficult to see how it can have a genetic complement.

Typographical errors are few; most are self-evident, though it may take a few minutes to discover that $= 2yB3$ in Table 7 should presumably read $+ 2yB3$. The index is not very efficient, chiefly because of a tendency not to index the paragraph headings. Thus the first reference to 'Normal distribution' is to p. 13, though the paragraph and introductory discussion commence on p. 10. It is surely undesirable to use Σ for summation instead of the conventional Σ ; there is a failure to distinguish between logarithms to base 10 and to base e (especially on p. 132). In a book clearly aimed at beginners, it would surely have been possible to have indicated somewhere the pronunciation of the Greek letters used—how many could read the equations on p. 133?

By taking a restricted view of biometry, Professor Mather has written a book which is in direct competition with a number of texts on the simpler aspects of biological statistics which have appeared in recent years, most of which go rather further into the subject than he does. It may well be that his book will be found sufficient for those biologists, especially in schools and on some undergraduate courses where the concern is chiefly with the experimental aspects of simple populations and a few variables. For many, however, especially those with leanings towards ecology and taxonomy, where it is necessary to consider more elaborate methods adapted to deal with more variables and where comparisons are of more importance than tests of significance, this book will serve as only a very limited introduction to biometry. It is the more unfortunate that there are not even any indications where this additional information may be found.

R. B. IVIMEY-COOK

Vascular Plants: form and function. F. B. Salisbury and R. V. Parke. Pp. 184. Macmillan & Co. Ltd., London. 1964. Price 12s. 6d.

Reproduction, Heredity and Sexuality. S. A. Cook. Pp. 117. Macmillan & Co. Ltd., London. 1964. Price 12s. 6d.

Plants and Civilization. H. G. Baker. Pp. 183. Macmillan & Co. Ltd., London. 1964. Price 12s. 6d.

These books are three volumes out of a series of seven known as the 'Fundamentals of Botany Series' which were originally published in the U.S.A. and which aim, between them, to provide an introduction to all the main aspects of plant science. Each volume is complete in itself, yet there is very little overlap between the volumes as a whole, and it must be said that they achieve a very consistent level of presentation. Each volume is freely illustrated, though in some the photographs could be of a higher standard e.g. the illustrations on pp. 58, 59 in *Vascular Plants*.

American botany books naturally draw their examples from American flora and fauna, and this limits the use of the books in other countries. *Ranunculus adonaeus*, for example, is a buttercup unknown to Great Britain and a genus like *Hymenoxys* is equally unheard of. Similarly words like 'corn' are used which do

not have the same meaning in the U.S.A. and Great Britain, while there are others like 'forb' that are rarely used here. Incidentally, *Drosophila* does not 'rise in clouds from over-ripe fruit left in the kitchen or garbage can' in this country.

The classification of the plant kingdom given in *Vascular Plants* may well be unfamiliar to British readers, and in the accompanying text there is confusion between members of a genus and the generic name itself, as in passages like '*Ephedra* (a shrub . . .)' and '*Araucaria* (the Monkey puzzle tree . . .)'. The possible evolutionary relationships of the angiospermous families are taken from the work of Bessey, and include the lumping of several families into the *Amentiferae*, an arrangement now usually abandoned. But these are minor blemishes on a book which succeeds in relating structure to function exceedingly well and giving, at the same time, an excellent account of many of the most important aspects of plant physiology. There is a good account of the primary and secondary plant bodies, their growth and differentiation, as well as an introduction to cell structure. Chapters follow on the ascent of sap and transpiration, translocation and the activity of the root. The structure of the flower is described together with the physiology of flowering, and there are chapters which deal with the fruit and seed and the physiology of germination. The book also manages to include, here and there, brief mentions of some of the experimental work on which many of the modern views are based.

Reproduction, Heredity and Sexuality commences with a sound introduction to Mendelian principles, and follows it with an account of the gene and its mode of action. The role of recombination in sexual reproduction and its importance in evolution is stressed. The part played by asexual reproduction and apomixis in the life of plants is covered in a further chapter. Finally, the control of recombination and the evolution of genetic systems is briefly outlined. The book draws its examples widely, ranging from the bacteria and fungi to the higher plants. Concisely written, the book covers a wide field yet concentrates on the essentials. More illustrations and some expansion of nature of the evidence for the statements written would have enhanced the value of this book.

Plants and Civilization is a fascinating introduction to the uses of plants by man from prehistoric times down to the present day. It is particularly valuable to the English reader for the frequent mention it gives of early agricultural practices in the Americas. The vast amount of archaeological knowledge of the Old World is, in consequence, a little neglected, but this is well documented elsewhere. There are chapters concerned with major grain crops like wheat and maize. The account of maize is particularly good, for it gives a complete picture, describing its probable origin, genetics and modern development. Wheat genetics are also mentioned, and in this way the book is linked with the others in the series. There is, however, little link with any biochemistry or plant physiology; here an opportunity has been missed. Further chapters give account of the origins of the chief beverages, the uses of trees and the preparation of drugs and dyes. The book ends with a mention of possible future uses of plants and a plea for the conservation and right use of the world's plant resources.

Each book is well indexed and there are good glossaries and lists of books for further reading.

C. T. PRIME

The Biology of Aquatic Vascular Plants. C. D. Sculthorpe, Pp. xviii+610. Edward Arnold. London. 1967. Price £6 6s. 0d.

In 1920 the Cambridge University Press published a book by Agnes Arber entitled *Water Plants, a study of aquatic angiosperms*. This book has become a classic and is often considered to be the best book written on a botanical subject, an opinion borne out by the fact that it was reprinted in 1963 and still continues to sell. Since 1920 an enormous quantity of work on aquatic plants has been published which has sometimes shown parts of Arber's book to be in need of revision. Mr. Sculthorpe has wisely not attempted a revision of Arber's book, but has written on almost the same subject a completely new treatise which in 15 chapters attempts to cover the morphology, physiology, breeding mechanisms, geography, ecology and applied aspects of aquatic vascular plants.

The first chapter, entitled 'The salient features of aquatic vascular plants', is the worst in the whole book, and in many ways it is a pity it was included as it contributes very little to an otherwise very useful book. The first part of this chapter is devoted to avoiding any precise definition of aquatic vascular plants; it is pointed out, however, that emergent plants of saline habitats, such as *Salicornia* and the mangroves, are excluded. The next part of the chapter is an account of the various classifications of vascular hydrophytes according to life forms and growth forms. Hejný's 1960 classification is rejected because only three groups (euhydatophytes, hydatoaerophytes and tenagophytes) were recognized. This, unfortunately, is not correct: Hejný (1960) recognized no less than 10 major and about 50 minor groups and, in my opinion, produced by far the most practical and useful ecological classification of hydrophytes. After dismissing Hejný in one sentence the author then suggests a classification of his own (with 4 major and 3 minor groups) in which

species such as *Eichhornea crassipes* (Mart.) Solms and *Ceratopteris cornuta* (Beauv.) Lepr. could be placed in each of his major groups. The next part of the first chapter is called 'zonation of aquatic vegetation' but is largely a list of names of phytosociologists; page 13, for example, contains 94 reference citations to ecological (phytosociological) work but without any indications as to which of these references are worth reading—no claims are made that this list is complete. The last part of this chapter is on the systematic distribution of vascular hydrophytes and is, perhaps, the least satisfactory part of the whole book. Extracting information on systematics is not difficult, but a critical evaluation is needed and this is just what is not provided; a little time spent looking at herbarium specimens in one of the major herbaria would have enabled the author to avoid many of the more obvious pitfalls. For example, the Elatinaceae and Haloragaceae would never have appeared in the list of exclusively aquatic families. The latter family comes in for an extraordinary circumscription: 'The Haloragaceae *sensu stricto* (i.e. without the gigantic *Gunnera*).' This presumably means that the author chooses to recognize the Gunneraceae Endl. as a separate family (not stated in the text), and not that *Gunnera tinctoria* (Molina) Mirbel (the best candidate for the gigantic *Gunnera*) is to be excluded from the Haloragaceae while the other 32 smaller species of *Gunnera* are to be left in (most species of *Gunnera* are small prostrate herbs).

The second chapter is very much better than the first and deals with the salient features of the aquatic environment. Useful conversion tables are given on pages xi and xii for readers unfamiliar with the metric measurements adopted in the text, some of which, for example metric tons per hectare and cubic metres per minute, are not yet widely accepted in English language publications. The next four chapters discuss the structure and physiology of emergent, floating and submerged plant organs. These are then followed by one chapter on the free-floating habit and another on vegetative polymorphisms. Sexual and asexual reproduction are dealt with in the next two chapters. These nine chapters, the central core of the book, cover a very large amount of information and this has been achieved by adopting a very terse style of writing which requires a considerable amount of concentration by the reader.

The eleventh chapter is on the geography of aquatics. It suffers from some of the same faults as the first chapter, namely, that there are too many statements based on inadequate taxonomy. Perhaps the worst feature is that it is not pointed out to the reader when doubts among taxonomists exist. One must not assume that the latest publication is necessarily the best. A good example is the treatment of the genus *Lemna* where the author has accepted piecemeal the taxonomy of Daubs (1965). As a taxonomist I have no confidence in this work and prefer to follow the much earlier monograph by Hegelmaier; but until taxonomists start criticizing each other's work a little more publicly it is difficult for a newcomer to a particular plant group to know which treatment to adopt.

The last four chapters of this book I found the most interesting and readable. The first of these deals with productivity in hydrophyte communities and the interactions between hydrophytes, their environment and other aquatic organisms. This chapter is followed by two on aquatic weeds and their control. The sections on *Eichhornea crassipes*, *Salvinia auriculata* Aubl. and the problem of sudd obstacles are particularly well presented. The final chapter is a short summary of the aesthetic and economic value of aquatic vascular plants. In many ways I feel that it is a pity the last four chapters were not enlarged and presented as a separate book.

The information in this book is taken almost entirely from published work, with the consequence that many fallacies are reiterated without alteration. For example, on page 131 there is a section on the lack of lacunae in the Podostemaceae; to me this lack seemed unreasonable so I cut some sections of *Apinagia richardiana* (Tul.) van Royen and *Mourera fluviatilis* Aubl. which I have in my own collection and found them both to have well developed lacuna systems. It must, however, be admitted that the much smaller species *Tristicha triflora* (Bory) Spreng. appeared to be without lacunae. Also the generalization that the Podostemaceae have 'minute aerial flowers' (page 283) is not true. *Brasenia* which the author places in the Nymphaeaceae is somewhat misunderstood: firstly, it is apocarpous (page 272), secondly, it is not 'confined to primitive tropical rain-forests and swamps' (page 273) and thirdly, the illustration of its leaf (page 74) is not representative. The condensed style of writing often leads to controversial but unqualified statements; an example is: 'some members of the Pontederiaceae show a trend towards zygomorphy and heterostyly'. This may well be true but I am sure the evidence presented by the genera *Heteranthera* and *Zosterella* is that the trend is away from zygomorphy and heterostyly.

The price is very reasonable for a specialist book of this length and quality. There are many photographs and line drawings which, on the whole, are excellent. The presentation of the book is very good and it is remarkably free from misprints. This does not mean that the book is free from mistakes but most mistakes are not primarily those of the author but of the workers he quotes. Except, perhaps, for the last four chapters the material contained in this book is not really reviewed—it is presented as a collection of summaries and as such it is valuable, but it is rarely stimulating. Very little detailed information can be obtained from the text without recourse to the original references, but the bibliography, which runs to 57 pages, is

absolutely magnificent. To anyone with an interest in aquatic plants this a source-book *par excellence* and in this respect without equal, but I hesitate before recommending it to general biologists or amateur botanists.

REFERENCES

- DAUBS, E. H. (1965). A monograph of Lemnaceae. *Illinois Biol. Monog.* **34**, 1–118.
 HEJNÝ, S. (1960). *Ökologische Charakteristik der Wasser- und Sumpfpflanzen in den slowakischen Tiefebene(n) (Donau- und Theissgebiet)*. Slovak. Akad. Wissen. Bratislava.

C. D. K. Cook

Since writing the above review two highly critical reviews of Daubs's (1965) Monograph of Lemnaceae have come to my notice. They are:

- CLARK, H. L. & THIERET, J. W. 1966. *Sida* **2** (6): 437–438.
 DEN HARTOG, C. 1967. *Blumea* **15** (2): 575–576.

Britain's Green Mantle: Past, Present and Future. A. G. Tansley. Second Edition, revised by M. C. F. Proctor. Pp. 327, with 12 line drawings, 72 plates with reproductions of 140 photographs in black and white, and frontispiece in colour. George Allen & Unwin Ltd., London. 1968. Price £2 10s. 0d. (in U.K. only).

Britain's Green Mantle, first published in 1949, was written by the late Sir Arthur Tansley for non-technical readers. He included as much of the material in his classic *The British Islands and their Vegetation* as 'might be of interest to all who love our wilder countryside', and provided a popular account of the more important plant communities in these islands.

The rapid changes during the past twenty years necessitated thorough revision for the second edition, and it is greatly to the credit of the editor that this has been done so skilfully that it still remains essentially the same book, and few readers are likely to detect the additions. The most obvious changes are in the printing and illustrations, and in both respects the new edition is a great improvement. The book first appeared under post-war austerity conditions with 294 pages of crowded print on yellowish paper, but the new volume printed by Jarrolds in 11 point Baskerville type is a first-class production. The photographic illustrations show a comparable advance. Those in the first edition were mainly familiar pictures used to illustrate early ecological works and fell short of modern technical standards. Fortunately it proved impossible to trace copies of the original photographs and a new set of illustrations had to be found; many were provided by the editor himself. These rank amongst the best pictures which have ever been used for an ecological work in this country. Regrettably some of them have been printed so that it is necessary to turn the book sideways, and there is even ambiguity in some captions (*e.g.* page 176), and very few give the scale. To readers unfamiliar with the species portrayed these are serious disadvantages.

In the text the most extensive changes are in the chapter on mountain vegetation (where Dr. Proctor seems more at home than Sir Arthur did), and the new chapter on Conservation and the Future which has replaced one now hopelessly out of date. The first edition appeared in the same year as the Royal Charter establishing the Nature Conservancy, of which Sir Arthur Tansley was the first chairman, and the great progress in conservation since then is a tribute to his pioneer efforts.

It is unfortunate that this book, which is unlikely to be superseded for very many years, should appear at a time when the nomenclature of the flowering plants occurring in Britain is in a more chaotic state than ever before in living memory. Dr. Proctor states that he has used the names in the second edition of the *Flora of the British Isles*, 1962, but he is not consistent, and users of that work will look in vain for such a then well-known name as *Chamaenerion angustifolium*. In any case there have been so many changes in the last six years that many names in that work already seem unfamiliar. At the present time writers are faced with the choice between the *British Plant List* with amendments in the *Proceedings of the B.S.B.I.*, the second edition of the *Excursion Flora*, *Flora Europaea* so far as it has appeared, the *Critical Supplement to the Atlas of the British Flora* and the innovations in other recent books such as Dony's *Flora of Hertfordshire*. While these conditions prevail it is perhaps wiser for writers on ecology to take their names from a descriptive flora where the meaning will always be clear, rather than to adopt the latest name which may prove to have only a brief currency.

Britain's Green Mantle was written for the benefit of the general public but a considerable knowledge of the British flora is essential if it is to be understood. The work is of the greatest value to field botanists who are not primarily ecologists, and to students of ecology who require a short general account of our main communities. To these readers this well illustrated and up-to-date second edition is to be most warmly recommended.

J. E. LOUSLEY

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Keys should be in one of the generally accepted forms; *Flora of the British Isles* by Clapham, Tutin and Warburg (ed. 2, Cambridge, 1962) and *Flora Europaea* (Vol. 1, Cambridge, 1964) provide suitable patterns.

Names of genera and species should be underlined, but any other typographical indications should be inserted lightly in pencil. Names of British vascular plants should normally follow the *List of British Vascular Plants* by J. E. Dandy (British Museum (NH) and BSBI, London, 1958), and may then be cited without authorities. Otherwise, authors' names must be cited, at least on the first occasion where they appear in the text. Authors must follow strictly the *International Code of Botanical Nomenclature* (Utrecht, 1966). Synonyms should be cited in chronological order; misapplied or illegitimate names should be placed in square brackets. Examples will be found in recent parts of *Watsonia*.

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**Journal of the Botanical Society
of the British Isles**

Volume 7 Part 2 2 June 1969

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STUDIES ON BRITISH POPPIES

I. SOME OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF THE BRITISH SPECIES OF *PAPAVER*

By STELLA ROGERS

Department of Biology, Queen Elizabeth College, London

ABSTRACT

The breeding mechanisms of the British species of *Papaver* have been re-investigated and it has been confirmed that *P. rhoeas* is self-incompatible and that the other species, *P. dubium*, *P. lecoqii*, *P. argemone* and *P. hybridum*, are all self-compatible.

The proportion of self- to cross-fertilized seed in the capsules of the self-compatible species is generally related to aspects of their floral biology such as anther height, flowering period, attractiveness to insect visitors, etc. In *P. dubium*, however, there is also evidence of considerable variation in the degree of inbreeding which is not dependent upon the quantity of self pollen reaching the stigmas, and which would therefore appear to be genetically determined.

INTRODUCTION

Bud pollination is a well-known characteristic of the poppies and it was not unreasonable for observers to assume that this resulted in self-fertilization, especially in a genus where there were no obvious features of floral morphology which might be associated with self-sterility. The work of McNaughton & Harper (1960a) has clarified the situation by showing that *Papaver rhoeas* is self-incompatible and *P. dubium*, *P. lecoqii* and *P. argemone* self-compatible. These workers were, however, primarily concerned with the end result of the reproductive process, that is with the quantity of seed set; it is the object of the present paper to fill in some of the relevant detail.

METHODS

Compatibility within and between the British species of *Papaver* was investigated by determining:

- (1) the germination of self, cross and hybrid pollen on the stigmas and the penetration of the pollen tubes into the transmitting canal;
- (2) the quantities of seed set following self, cross and open pollinations.

Germination of the pollen and subsequent growth of the pollen tubes was observed on cut emasculated flowers kept in a dark incubator at 22° C for 18–24 hours (Lewis 1947), then fixed in acetic alcohol and stained in light green/acid fuchsin.

Self-pollination was either allowed to occur naturally by auto-deposition or was aided by brushing the self pollen over the stigmas to ensure that the amount of seed set was not limited by the amount of pollen reaching the stigmas. Cross-pollinations were carried out twenty-four hours after emasculation and all emasculated and pollinated flowers were enclosed in pollen-proof bags. Open-pollinated flowers were allowed to pollinate naturally and were bagged after the petals had fallen, to avoid loss of seed as the capsules matured and to ensure that the capsules developed under the same conditions as capsules pollinated by the other methods.

RESULTS

1. *Homogamy*

According to Clapham (1962) the species under consideration are all homogamous and bud pollinated. Observations on the self-compatible species *P. dubium*, *P. lecoqii*, *P. argemone* and *P. hybridum* show that the self pollen will germinate freely on its own stigmas immediately following anther dehiscence, indicating that the pollen is mature by this stage. Pollen is normally shed while the buds are still in the drooping position, that is, about two

days before the opening of the flower. In *P. rhoeas* there is no immediate germination of the self pollen within the bud after anther dehiscence and in the following forty-eight hours only a few pollen-tubes develop. That this behaviour is not due to the immaturity of the stigmas may be shown by emasculation before anther dehiscence and subsequent pollination with mature cross pollen. The results, summarized in Table 1a, show that the stigmas are already receptive at the time of dehiscence of the anthers. If not pollinated they remain receptive for about a week although seed-setting is not consistent after about five days. The

(a) Stigma receptivity.

TABLE 1. *Papaver rhoeas*.

Days after emasculation		0	1	2	3	4	5	6	7	8
Pollen germination	Number of attempts	21	16	15	13	13	9	4	6	3
	Number of successes	13	14	8	11	12	6	3	5	1
Seed set	Number of attempts	15	14	16	14	10	10	9	5	—
	Number of successes	14	14	16	14	7	6	1	0	—

(b) Pollen Maturity.

No. of Flow- ers examined	Position of Bud	Condition of Anthers		Condition of Pollen	
		dehiscd	undehisced	Starch present	Starch absent
22	Drooping	16	6	22	nil
18	Horizontal	18	nil	18	nil
18	Vertical	18	nil	5	13
36	Opening	36	nil	4 very little	32

time-sequence of pollen development in this species would appear to be rather different from that in the self-compatible species. In the latter, the pollen is starch-free at anther dehiscence and will germinate freely in both 5% and 10% sucrose solutions as well as on the stigmas. It is thus capable of germination prior to the opening of the flower. In *P. rhoeas*, the pollen is still starchy at anther dehiscence and will not germinate in sucrose until the starch has disappeared. This has normally happened by the time the bud opens. The flower is therefore effectively homogamous (Table 1b).

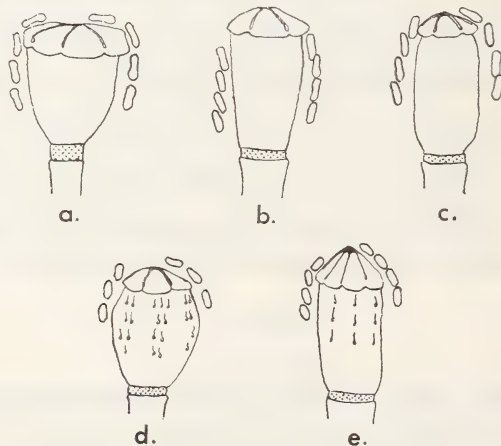


Fig 1. Floral biology in the British Poppies (a) *Papaver rhoeas* (b) *P. dubium* (c) *P. lecoqii* (d) *P. hybridum* (e) *P. argemone*.

The anther level on the right represents the maximum height attained; on the left the normal height.

2. Anther position

The significance of anther position in relation to the amount of self pollen reaching the stigmas can be seen from Fig. 1. In *P. rhoeas* and *P. lecoqii* the anthers cover at least one half of the stigmatic disc, and in the latter species the inmost anthers are often firmly wedged between the stigmatic rays so that the pollen comes into intimate contact with the stigmatic papillae at anther dehiscence. *P. argemone* and *P. hybridum* are characterized by having the filaments dilated at the apex and, in the case of the inmost stamens, these filaments may be held by the strong upwardly-directed hairs on the ovary wall, thus maintaining close contact between their anthers and the stigmatic rays. *P. dubium* differs from the preceding species in that the anthers never cover any part of the stigmatic disc and only rarely touch the extreme edge of the stigmatic rays. At anther dehiscence pollen is deposited on the ovary wall, and, since the bud is still then in the drooping position, some may fall on to the ray edges.

3. Gynoecial structure

The morphology of the *Papaver* gynoecium has been described by Arber (1938). Pollen is deposited on the stigmatic papillae and upon germination the tubes penetrate between the papillae and into the stigmatic grooves where they grow horizontally until they reach the transmitting canal. This is also lined with papillae, among which the tubes grow vertically downwards into the ovary (Fig. 2a). It follows therefore that pollen tubes arising from grains deposited near the outer edge of the disc must grow appreciably further than those originating from grains nearer the centre of the disc. The tubes are readily identified in the stigmatic grooves and transmitting canal but since the papillae are numerous, it is not possible to follow an individual tube for any distance between them.

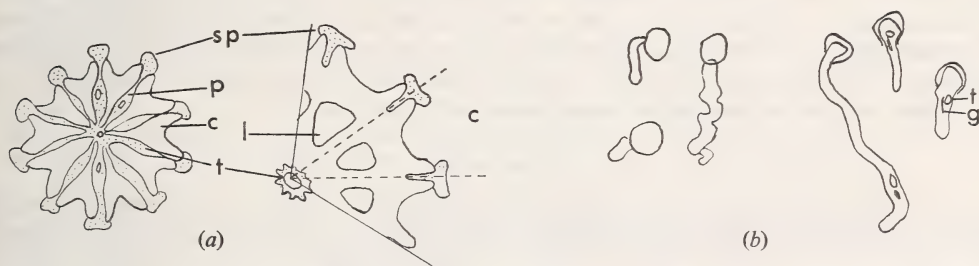


Fig. 2(a). *Papaver rhoeas* stigmatic disc T.S. c = carpel, l = loculus, p = papillae lining stigmatic grooves, sp = stigmatic papillae, t = transmitting canal.

(b) *Papaver rhoeas* pollen germination. Left, self pollen tubes after two days on the papillae. Right, pollen germinated in sucrose. t = tube nucleus, g = generative nucleus.

4. Pollen behaviour

As already noted, pollen germination in the self-compatible species follows rapidly upon anther dehiscence and the self pollen tubes thus have a considerable time advantage over tubes developing from grains brought by pollinating insects after the flower opens. In *P. argemone*, *P. hybridum* and *P. lecoqii* self pollen tubes may be found along the stigmatic grooves by the time the flower opens and in the latter two species appreciable numbers have also penetrated into the transmitting canal. The relatively small number of self pollen grains reaching the stigmatic papillae in *P. dubium* makes observation of their behaviour more difficult, and their position on the extreme edge of the disc necessitates the pollen tubes traversing the entire length of the stigmatic grooves; thus the time advantage is appreciably less than in those species where the self pollen falls more centrally on the disc. From the above observations it would seem that the degree of inbreeding in *P. dubium* is limited by the position of the stamens and the consequent scarcity of self pollen on the stigmas. This does not appear to be borne out, however, by the results of seed setting experi-

ments described in the next section. In *P. rhoeas*, the development of any self pollen which germinates is arrested at a very early stage. The tubes are often much twisted and distorted and may have swollen ends. There is no evidence of their penetration between the stigmatic papillae or into the stigmatic grooves.

Pollen behaviour in the cultivated Shirley poppy differs from that of wild *P. rhoeas* in that the self tubes grow to a considerable length without obvious distortion or swelling of the tips. There is, however, no observable penetration into the stigmatic grooves and the self-incompatibility barrier is complete. The Mediterranean species *P. apulum* was included inadvertently in one of the trials and, like *P. rhoeas*, it is completely self-sterile (see also McNaughton & Harper 1960a). Its sequence of pollen development resembles that of wild *P. rhoeas* but, as in the Shirley poppy, any self tubes produced are straight and relatively long. Compared with self pollen, unrelated pollen in *P. rhoeas*, the Shirley poppy and *P. apulum* germinates very rapidly on receptive stigmas and numerous tubes may be seen within eighteen hours of pollination. These tubes penetrate straight between the stigmatic papillae and two days after pollination may be found in the transmitting canal. The pollen grains of *P. rhoeas* are binucleate, and when germinated in 5% or 10% sucrose solution the generative nucleus does not divide either within the grain or early in its passage down the pollen tube (Fig. 2b).

5. Pollen germination of stigmas of other species

It was found by trial that the pollen of each species will start to germinate freely on the stigmas of all other species. Penetration of the pollen tubes into the stigmatic grooves was not investigated in this experiment. However, long straight tubes were frequently observed penetrating between the papillae and the fact that some interspecific hybrids can be obtained is evidence that the tubes may sometimes achieve the complete journey. Hybrids between *P. rhoeas* and *P. dubium* were included in the trial, though since they were completely male-sterile they could be used only as the female parent. Pollen of all species germinated on the stigma of hybrids having *P. rhoeas* as the female parent. The results for the reciprocal cross are incomplete owing to lack of material.

6. Seed setting

The experimental results are summarized in Tables 2 and 3. For the self-compatible species, seed production by self-pollination is expressed as a percentage of the total seed output and as an inbreeding/outbreeding ratio $\frac{\text{inbred seed}}{\text{total} - \text{inbred seed}}$.

P. rhoeas. The self-sterility barrier is effectively complete and no evidence was obtained of the pseudo-compatibility reported by Philp (1933) although plants from many different

TABLE 2a. Summary of seed setting experiments.

Pollination Method	<i>P. rhoeas</i>		<i>P. dubium</i>		<i>P. lecoqii</i>		<i>P. argemone</i>	
	% success	Average seed no.	% success	Average seed no.	% success	Average seed no.	% success	Average seed no.
Self	8.1	4	84	591	88	918	73	143
Aided self	5	1	85	455	—	—	64	184
Controlled cross	86	not esti- mated	—	—	—	—	45	212
Open	92	not esti- mated	100	1,434	100	1,695	53	274
Inbred	—	—	5	260	100	395		

TABLE 2b. Inbreeding in the self-compatible species.

	<i>P. dubium</i> (all data)	<i>P. lecoqii</i>	<i>P. argemone</i>
Inbred/total seed %	41	61	64
Inbreeding/outbreeding ratio	0.7:1	1.18:1	1.97:1

The differences between (1) self and aided self (2) controlled cross and open pollinations were not significant at the 5% level.

The differences between self and cross pollinations were significant at the 0.1% level in *P. dubium* and *P. argemone* and at the 1% level in *P. lecoqii*.

Within sample variations are taken into account throughout.

TABLE 3. *Papaver dubium*: Seed set by autodeposition and open pollination.

	Population		
	1. Kent	2. E. Suffolk	3. W. Norfolk
Self pollination			
Minimum seed no. per capsule	1	31	117
Maximum seed no. per capsule	1,240	1,228	1,922
Av. seed no. per capsule	232	518	1,026
Open pollination			
Av. seed no. per capsule	1,576	1,344	1,827 (10 capsules only)
Inbred/total seed no. %	14.7	38.5	56.15
Inbred/total seed average for species (1,434) %	16.2	36	71.5
Inbreeding/Outbreeding ratio (based on species average for open pollination)	0.19	0.56	2.51

Allowing for within-sample variation, the differences in average self seed number between populations 1 and 2, and 1 and 3 were significant at the 0.1% level and between populations 2 and 3 at the 1% level.

sources were grown. *P. rhoeas* thus resembles *P. nudicaule* in which Fabergé (1943) established that the bud pollination was completely ineffective. As no comparisons could be made between the quantities of seed set following self- and cross-pollinations, estimations of seed numbers were not made for this species. The degree of cross-compatibility is high, indicating that a considerable number of alleles is involved in the incompatibility system. Of 162 controlled cross-pollinations, 139 were successful and most of the failures could be attributed either to the use of old and probably non-viable pollen or to the pollination of very young buds whose stigmas may not have been receptive. All recorded reciprocal crosses were compatible in both directions.

P. dubium. Open-pollinated capsules of this species yielded an average of 1,434 seeds. This is rather less than the number given by Salisbury (1942), but since unset seed was rarely found in the capsules, it may be taken as representing a full seed set. Capsules set by auto-deposition contained an average of 591 seeds. This represents 41% of the average number set by open pollination and is a result higher than anticipated in view of the scarcity of self pollen on the stigmatic papillae. That the expected increase in the amount of seed set when self pollen was rubbed over the stigmas was not obtained may be seen from the graph in Fig. 3. The percentage frequency curves for seed numbers following self- and aided self-pollinations are almost identical and the differences between them are not significant statistically. Combining the two sets of data, 30% of the capsules produced by self-pollination contain less than 250 seeds but 7.6% exceed the average number of 1,434 set by open pollination. The very wide range of seed numbers per capsule resulting from self-pollination suggests that individuals may vary in their degree of inbreeding. Unfortunately

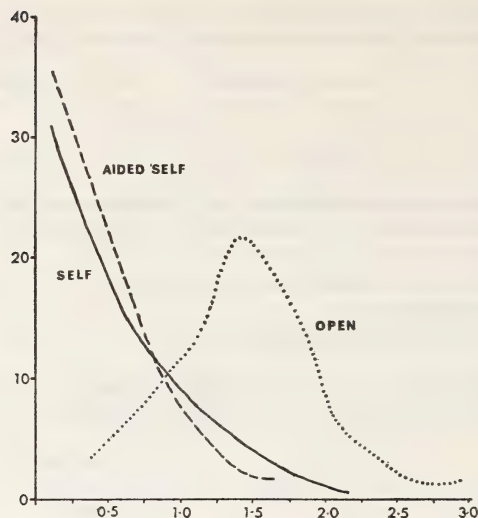


Fig. 3. *Papaver dubium* seed yields resulting from different methods of pollination. Horizontal axis—seed number (in thousands), vertical axis—percentage frequency.

data for replicated self-pollinations on individual plants were not obtained but some evidence that the degree of inbreeding may vary in different populations was found and is summarized in Table 3. The difference in average seed number set by auto-deposition is significant at the 1% level between the east Suffolk and west Norfolk populations, and between these and the Kent population at the 0.1% level. There is also some variation in the average seed set by open pollination, but this is not significant in the case of populations 1 and 2 and it makes little difference to the inbreeding/total seed percentage whether the self seed average is related to the open pollinated seed average of the population or of the species as a whole. In the case of population 3, both the self- and open-pollinated seed averages are considerably above the species averages, though the open-pollinated data were obtained from only ten capsules. Calculated from either open-pollinated average, however, the inbreeding/total seed percentage is obviously high in this population.

P. lecoqii. The average number of seeds set by self-pollination in this species was 61% of the open-pollinated average (Table 2). This result is appreciably lower than that reported by McNaughton & Harper (1960c) but the data are consistent and would therefore seem to be reliable for plants growing under field, rather than greenhouse, conditions. Flowers which are functionally cleistogamous are not uncommon on otherwise apparently normal plants of this species. The condition results from the failure of the sepals to separate so that the petals do not expand and the stamens remain closely applied to the stigmatic disc. This enforced autonomy is apparently less effective than normal self-pollination. The capsules recorded contained only 38% of the seed number set by open pollination and the difference between the average numbers for self and cleistogamous pollination is significant at the 1% level.

P. argemone. All methods of pollination yielded very variable results in this species and capsules having a low seed number invariably contained unset seed indicating that fertilization was incomplete. No statistically significant increase in seed set was obtained by rubbing the self pollen over the stigmas—a result anticipated in view of the higher level of the anthers in the flower when compared with *P. dubium*. Controlled cross-pollination gave an increased seed yield and the results obtained did not differ significantly from those obtained by open pollination. Combining the results whose differences were non-significant, the average seed number for open pollination is significantly greater than that for self pollination (at the 0.1% level) and the inbred/total seed percentage calculated on these results is 64%.

The failure of many of the open-pollinated capsules to set fully may be associated with the very short flowering period and the scarcity of insect visits. The flowers open early in the morning and by midday most of the petals and stamens have fallen so that the maximum flowering period is only about six hours. The flowers are not conspicuous when compared with those of *P. rhoeas*, *P. dubium* or *P. lecoqii* and the results of McNaughton & Harper (1960a) for bee flights among plots of the five British *Papaver* species show relatively few visits to *P. argemone*.

DISCUSSION

In the British species of *Papaver*, a store of genetic variability exists within the self-incompatible species *P. rhoeas* and the phenotypic variability of this species in the field is obvious. The self-compatible species exhibit much less phenotypic diversity and their variation pattern can be correlated with their degree of inbreeding. The proportion of self- to cross-fertilized seed in a capsule is determined by:

- 1) the biology of the flower, including the time of maturity of the pollen and stigmas, the quantity of self pollen deposited on the stigmas, the flowering period and the number of insect visits;
- 2) the nature of the genetic mechanism controlling the compatibility reaction.

The significance of floral biology and ethological factors is apparent from the studies of McNaughton & Harper and from the present work. The necessary background for an incompatibility system is present in the genus and has been shown to operate effectively in at least three species at the diploid level, *P. rhoeas*, *P. apulum* and *P. nudicaule*. For the last species Fabergé (1943) has shown by the reciprocal nature of the incompatibility that the system is gametophytic rather than a sporophytic one, and it seems reasonable to assume that this applies to all self-incompatible species in the genus. In other genera and families which have been extensively investigated, the same system has been found to operate in all the self-incompatible species studied. Thus pollen control is gametophytic in Rosaceae whereas in Cruciferae all investigated species yield data consistent with sporophytic control (Bateman 1955). Brewbaker (1957) associates late division of the generative nucleus in the pollen grain with gametophytic pollen control in self-incompatible species, and he notes that members of the Papaveraceae have binucleate pollen grains. This is in agreement with the observations made in the present work that division of the generative nucleus does not occur early in the germination of the pollen and supports Fabergé's conclusion that pollen control is gametophytic. On the other hand, Bateman (1955) associates the very early inhibition of self pollen in Cruciferae with sporophytic control and a similar correlation appears to hold in Compositae (Hughes & Babcock 1950, Crowe 1954). Pollen behaviour in the self-incompatible species of *Papaver* is similar to that reported in *Brassica* (Kakizaki 1930), *Capsella* (Riley 1936), *Raphanus* and *Iberis* (Bateman 1955) and indicates that the inhibitory reaction takes place on the surface of the stigmatic rays. It would seem that in the case of *Papaver* this early inhibition is associated with the unusual form of the stigma rather than with the type of pollen control. In other species where a gametophytic incompatibility system operates, the stigmatic surface is separated from the ovary by a style and the inhibitory reaction is generally between the pollen tube and the stylar tissues. In *Papaver* both the stigmatic grooves and transmitting canals are open ducts lined by papillae and, although the pollen tubes grow among the papillae, the same intimate contact between pollen tube and sporophyte cells may not be achieved as when there is a cellular style. Also, the distance traversed by the pollen tubes arising from grains lying centrally in the disc is relatively small so that the inhibition reaction must occur rapidly if it is to be effective.

Self-compatibility in the genus occurs at the diploid, tetraploid and hexaploid levels though the information regarding breeding behaviour at the higher levels of polyploidy is incomplete (Table 4).

In common with other genera which contain both self-incompatible and self-compatible

TABLE 4. Polyploidy and compatibility in the genus *Papaver*.

Species	Compatibility	Chromosome number	Author
<i>P. alpinum</i>	SC	14	Fabergé, 1944
<i>P. apulum</i>	SI	12	Sugiura, 1936
* <i>P. commutatum</i>	?	14	Philp, 1933
<i>P. hybridum</i>	SC	14	Clapham, Tutin & Warburg, 1952
<i>P. rhoeas</i>	SI	14	Lawrence, 1930
<i>P. lecoqii</i>	SC	28	McNaughton, 1958
<i>P. pinnatifidum</i>	—	28	Sugiura, 1940
<i>P. argemone</i>	SC	12	Beale, 1939
		42	Sugiura, 1940
<i>P. dubium</i>	SC	28	Ljungdahl, 1922
		42	Löve & Löve, 1944
<i>P. lapponicum</i>	—	56	Horn, 1938
<i>P. relictum</i>	—	70	Horn, 1938

— no information available

* *P. commutatum* is stated to be naturally cross fertilizing but nevertheless phenotypically uniform and presumably therefore highly homozygous. This requires verification.

species, the pollen behaviour of the British species of *Papaver* does not conform to Lewis & Crowe's rule (1958) that 'in the four possible combinations in crossing self-compatible and self-incompatible species, pollen tube growth is uninhibited except in the cross self-incompatible style—self-compatible pollen, where it is inhibited similarly to self-incompatible germination'. Since these authors argue that all the exceptional genera and species have a recent history of self-compatibility, these observations may be accepted as evidence for the recent self-compatibility in *Papaver*.

The results obtained for *Papaver dubium* are of interest in that they suggest that individuals of this species may vary in their degree of compatibility from almost self-incompatible to fully self-compatible. A rather similar situation is described by Grant (1956) in *Gilia capitata*, where the different taxonomic subspecies show variation in their degree of self-compatibility which can be inversely correlated with their phenotypic variability. Data obtained for *Papaver dubium* indicate that some populations exhibit more phenotypic variability than others in certain characters, though it would not be possible to differentiate discrete taxa on this basis. Variation in the degree of inbreeding has also been reported in both *Petunia* and *Nicotiana* (Mather 1943). In the latter genus, the S-alleles which determine the incompatibility system vary in efficiency and the weakest, when homozygous, will permit the free set of self seed. Such a system may operate in *P. dubium*. The alternative is to suggest a parallel between the hybrid *Nicotiana* × *sanderana* and the species *P. dubium*. The former shows marked pseudo-compatibility in spite of the fact that both its parents are self-incompatible. In Mather's view this pseudo-compatibility results from a breakdown in the efficiency of the S-alleles due to polygenic unbalance in the hybrid. Observation of bivalent formation in the hybrid *P. rhoeas* × *dubium* suggests considerable homology so that at least one self-incompatible species may have been involved in the ancestry of *P. dubium*.

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STUDIES ON BRITISH POPPIES

II. SOME OBSERVATIONS ON HYBRIDS BETWEEN *PAPAVER RHOEAS* L. AND *P. DUBIUM* L.

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ABSTRACT

The observations reported here on interspecific hybrids between *Papaver rhoeas* and *P. dubium* are in general agreement with those given by McNaughton & Harper (1960b). Irregular germination of the hybrid seed is thought to be due to poor embryo development. The total failure of the F_1 hybrids to produce viable gametes would seem to preclude the possibility of any gene-flow between the two species. Observations of meiotic behaviour in the hybrids, however, suggests that the two species may have a genome in common, though its members appear to have undergone structural changes in the two species. No evidence has been obtained regarding the identity of the other *P. dubium* genomes, but the species seems likely to be of hybrid origin.

INTRODUCTION

In spite of the fact that *P. rhoeas* and *P. dubium* frequently occur together in the same habitat, gene interchange between them seems unlikely on account of their differing levels of polyploidy and an effective discrimination shown by the principal pollinating insect, *Apis mellifera* (McNaughton & Harper 1960a).

Presumed hybrids are however reported from time to time and artificial hybrids have been raised both by McNaughton & Harper (1960b) and by the present writer in an attempt to ascertain whether gene flow between the two species is possible.

METHODS

Parent plants were raised in an unheated greenhouse using seed collected from wild populations. Emasculations and pollinations were carried out in a similar manner to that described by McNaughton & Harper (1960b).

<i>Pollinations</i>	<i>Attempted</i>	<i>Successful</i>
<i>P. rhoeas</i> $\times$ <i>dubium</i>	41	10
<i>P. dubium</i> $\times$ <i>rhoeas</i>	14	3

For cytological observations, the Feulgen technique (Darlington & LaCour 1950) was used, following 1:3 acetic alcohol fixation. Hydrolysis times were 9 minutes in the case of root tips and a maximum of 6 minutes for pollen mother cells.

SEED GERMINATION AND EMBRYO DEVELOPMENT

Contrary to the result reported by McNaughton & Harper (1960b), germination of the hybrid seed was poor and the subsequent seedling mortality rate high, only 16 out of 48 seedlings ultimately developing to maturity.

Embryos were examined from some of the hybrid seed to ascertain whether their development might account for its poor germination. Fifty embryos were dissected out from the seeds resulting from three separate crosses, all having *P. rhoeas* as the seed parent. Twenty-six of these had very small or rudimentary embryos with the cotyledons not or barely differentiated. Eleven had small but fully differentiated embryos, and in the remaining thirteen the embryos were well developed though smaller than those of *P. rhoeas*. Some typical examples are illustrated in Figure 1a. There was insufficient seed to examine

embryos resulting from the reciprocal cross. Variation in the size of hybrid embryos has been reported by Valentine (1953) in *Primula* where it is also associated with poor seed germination.

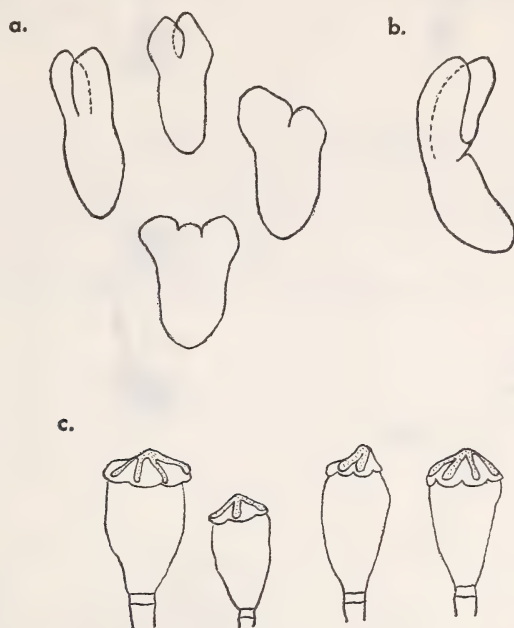


Fig. 1.

A. Embryos from ripe seed of *Papaver rhoeas* $\times$ *dubium*.

B. *P. rhoeas* embryo for comparison.

C. Capsules *P. rhoeas* $\times$ *dubium*. (a) and (b) $\times$ 50, (c) $\times$ 2.

GROWTH OF THE HYBRID PLANTS

Similar abnormalities to those reported by McNaughton & Harper (1960b) were observed in the growth of the young hybrid plants. The foliar distortion and chlorosis became less marked with age and the plants ultimately flowered. All were male sterile, though in some the anthers were well developed and contained recognizable but shrivelled pollen grains. The ovary was intermediate in form between those of the parents having a length/breadth ratio between 1.7 and 2.2 (Fig. 1c).

CYTOLOGICAL OBSERVATIONS

Root tip squashes from both *P. rhoeas* $\times$ *dubium* seedlings and the reciprocal cross gave chromosome counts of $2n = 28$, thus confirming the hybrid nature of the seedlings (Fig. 2a).

Examination of the pollen mother cells showed that both the first and second divisions of meiosis are negotiated. The onset of meiosis is simultaneous in all the pollen mother cells in an anther, but proceeds at different rates so that both 1st division metaphases and tetrads may be found within the same anther, a condition frequently encountered in interspecific hybrids.

Observations of diakinesis and metaphase I indicate that between three and seven bivalents are formed, the residual chromosomes remaining unpaired (Fig. 2b, 2c). There is also evidence from the configurations at diakinesis that chiasmata are established between the pairing chromosomes, indicating a certain degree of homology. The unpaired chromosomes at anaphase I fail to get on to the spindle and form two groups of irregular numbers near the poles of the spindle. There is no evidence of a precocious division of the unpaired chromosomes at this stage and they all appear to become incorporated in the interphase

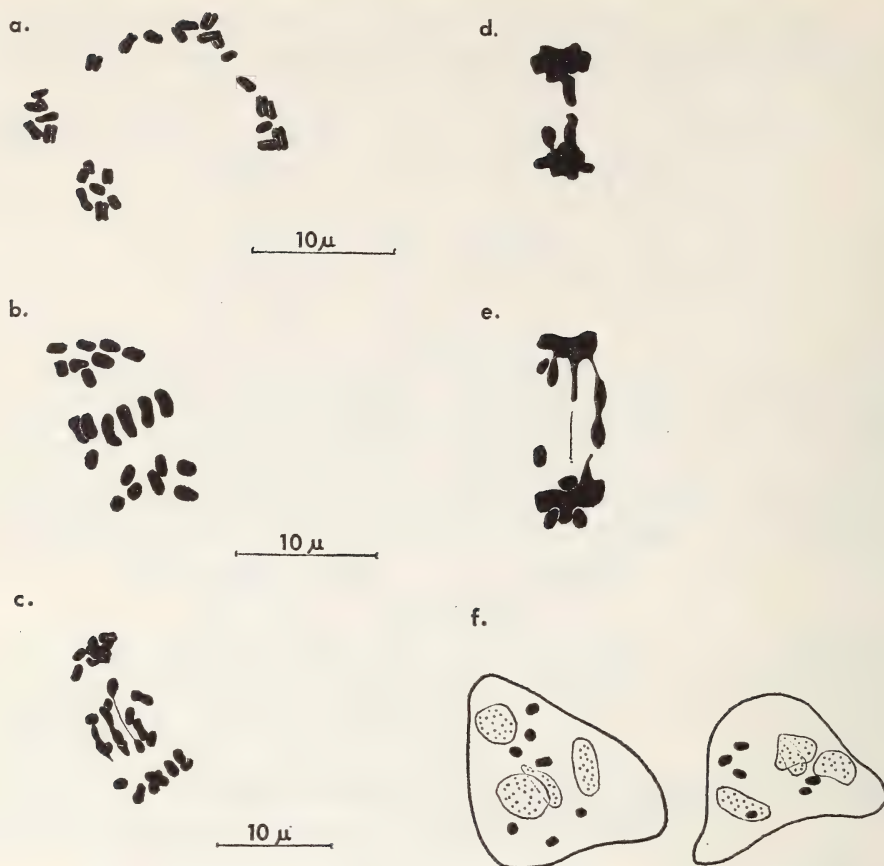


Fig. 2. *Papaver rhoeas* $\times$ *dubium*

(a) Root tip squash $2n = 28$.

(b) Meiosis in pollen mother cells: 6 bivalents and 16 univalents.

(c) 7 bivalents separating and 13 univalents.

(d) and (e) Anaphase bridges.

(f) Uneven nuclei and excluded chromosomes at the end of the second division.

nuclei and thus enter the second division. Anaphase bridges occur in many nuclei when the bivalents separate (Fig. 2d, e) and this not only provides further evidence of the establishment of chiasmata but also indicates that the pairing chromosomes differ structurally. In the majority of the pollen mother cells the second division is completed and tetrads are produced. The nuclei of these are of very uneven size (Fig. 2f) and invariably some chromosomes are excluded from them. The 'tetrad stage' frequently contains only two or three nuclei and in these cases there are many excluded chromosomes.

The meiotic behaviour here described indicates strongly that there is homology between the chromosomes of *P. rhoeas* and one of the genomes constituting the hexaploid *P. dubium*. The formation of a maximum of seven bivalents could only be explained otherwise as being the result of pairing between members of two of the *P. dubium* genomes. In this case the formation of tri- and quadrivalents and the consequent irregularities in meiosis and reduction of fertility would be expected in populations of *P. dubium*. Observations of meiosis and pollen development in *P. dubium* provide no evidence of this. The formation of anaphase bridges indicates that the common genome has undergone structural modification within the two species which result in its constituent chromosomes not being homologous along their entire length.

While no evidence has been obtained regarding the identity of the other *P. dubium* genomes, a hybrid origin for this hexaploid does not seem unlikely and might provide an alternative explanation to the possession of weak incompatibility alleles, for the partial self-compatibility in this species.

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AN ANALYSIS OF POPULATIONS OF IRISH *EUPHRASIA* L.

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ABSTRACT

Data from population samples of Irish *Euphrasia*, selected as representative of homogenous morphological types, were projected on horizontal axes in a natural ordering for 34 characters. The 32 wild populations so treated were found to occur in groups, with varying degrees of proximity, along the gradients of several characters.

The characters were investigated for their diagnostic value in delineation of groups of populations. The resulting groups were analysed for their degree of separation and were found to relate to the following species: *E. micrantha*, *E. scottica*, *E. tetraquetra*, *E. nemorosa*, *E. brevipila*, *E. rostkoviana*, *E. confusa*, *E. salisburgensis*, *E. pseudokernerii*.

All characters except one, glandular hairs, were continuously variable; the majority of characters tested were stable in cultivation. For most species, habitat appears to have been an important factor in speciation and is often an aid in identification.

Variation within this section of the genus is essentially continuous and intermediate populations are of frequent occurrence; nevertheless, narrowly separated but 'good' species have emerged from the study.

INTRODUCTION

Euphrasia, as suggested by Webb (1963), 'is a difficult genus, in which the delimitation of species and their distribution in Ireland are still subject to much uncertainty'. The purpose of this study was to investigate the nature of the variation within the genus as represented in Ireland, and to delineate the taxa present.

Pugsley's (1930) revision of the British *Euphrasiae*, based on Wettstein's (1896) monograph, is the most recent taxonomic treatment of the section of the genus occurring in the British Isles. The species of the British Isles all belong to Section *Semicalcaratae* Benthham of the type Subgenus *Euphrasia*. The section consists of four subsections, two of which include species of the British Isles, Subsection *Angustifoliae* Joergensen which includes one species in the British Isles, and Subsection *Ciliatae* Joergensen. Subsection *Ciliatae* consists of eight series; four of these include species of the British Isles: Series *Nemorosae* Pugsl., Series *Latifoliae* Pugsl., Series *Brevipilae* Pugsl., Series *Hirtellae* Pugsl. (Pugsley 1930).

Pugsley admitted 24 species and several varieties to the British *Euphrasiae*. One additional species was included in the British Flora (Warburg 1962) which follows the treatment of Pugsley. A total of fifteen species are recorded for Ireland; Webb (1963) treated thirteen species.

Among the twenty species Yeo (1954) considers indigenous to the British Isles, only two chromosome numbers occur, the diploid, $n = 11$, which occurs in five species, and the tetraploid, $n = 22$, which is common to all other species. Barriers to hybridization are essentially lacking and there are numerous records of hybrids as well as reports of successful cross-fertilizations in cultivation (Yeo 1959, 1966). Apomixis is considered not to be involved in reproduction of *Euphrasia* (Yeo 1966).

One of the difficulties in the determination of species of *Euphrasia* is due to the lack of certainty of the diagnostic value of the characters. An initial step, therefore, in this study, was a biometric analysis of characters in the Irish *Euphrasia*. This resulted in the structuring of groups of morphological types which finally were related to previously described species.

METHODS

Samples, ranging from 37 to 70 plants with an average of 58 plants, were taken from each of 32 wild populations (Table 1), and 21 characters of each plant were measured. An effort was made to sample as widely and completely as possible the total range of

TABLE 1. Population numbers, localities and sample size.

<i>Population</i>	<i>Locality</i>	<i>Sample size (n)</i>
A1	Stepaside, Co. Dublin	60
A2	Ballyknockan, Co. Wicklow	43
A3	Ballyknockan, Co. Wicklow	68
A4	Caherconnell, Co. Clare	55
A5	Carron, Co. Clare	66
A6	Forth Mountain, Co. Wexford	60
B1	Kilcoole, Co. Wicklow	70
B2	Gort, Co. Clare	70
B3	Ballin straw, Co. Wexford	60
C1	Mannin Bay, Co. Mayo	53
C2	Achill, Co. Mayo	60
C3	Ballyvaughan, Co. Clare	60
C4	Lady's Island, Co. Wexford	60
C5	Lady's Island, Co. Wexford	60
C6	Lady's Island, Co. Wexford	60
D1	Caherconnell, Co. Clare	37
D2	Caherconnell, Co. Clare	60
D3	Caherconnell, Co. Clare	47
E1	Poulsallagh, Co. Clare	51
E2	Lackagh, Co. Galway	58
E3	Baur, Co. Clare	46
F1	Aghavannagh, Co. Wicklow	40
F2	Malahide, Co. Dublin	60
G1	Glencree, Co. Dublin	60
G2	Lough Bunny, Co. Clare	60
G3	Oughterard, Co. Galway	50
H1	Taum, Co. Galway	70
H2	Ballinrobe, Co. Clare	70
H3	Corranroo, Co. Clare	60
J1	Portmarnock, Co. Dublin	60
J2	Lahinch, Co. Clare	70
J3	Roadford, Co. Clare	70

variation within the genus as represented in Ireland, and in so doing to include all the taxa reported for the country. This resulted in collecting in all the habitats recorded for the Irish *Euphrasia*, with the exception of mountain tops. Only those populations were sampled that were considered to be homogeneous, that is, composed of one morphological type. Populations which appeared to consist of more than one type or species, and those in which intermediate forms occurred, were not sampled. Two populations of one morphological type were sampled; all other morphological types were represented by samples of at least three populations.

Each population studied was paced systematically and collections of five plants were made at approximately every five metres. In collecting, an effort was made to reduce the variation caused by grazing, host establishment, and age of plant. Grazed plants if inadvertently collected were subsequently eliminated after inspection of dried material. Plants obviously weak and poorly developed, possibly due to inadequate or late host

establishment (Yeo 1959) were not collected. At the same time an effort was made to avoid gathering only the large most vigorous plants. Gatherings were made of plants at the same stage of maturity in that they were in full flower and had set seed in the lower capsules.

In measuring each plant as large a sampling of morphological structures was made as was practical with the proposed statistical methods. Twenty-one characters of each plant were measured and, in addition, combinations of these direct measurements, including ratios, differences between the measurements of pairs of characters, and correlations of pairs of characters, were investigated. In the selection of characters an effort was made to include those used by previous workers, to quantify characters previously used subjectively and finally to include characters not formerly used but which as a result of field studies were suspected of having some diagnostic value (Table 2).

TABLE 2. Characters selected for analysis (* = original measurement).

*1. Number of glandular hairs per 1.5 mm
*2. Length of longest glandular hair
*3. Plant height
*4. Plant width
5. Plant height/width
*6. Length of stem to first branch
*7. Length of stem to first flower
8. Length of stem to first branch/plant height
9. Length of stem to first flower/plant height
*10. Number of primary branches
*11. Angle of branching
12. Number of primary branches/plant width
13. Angle of branching/plant width
*14. Number of flowers and capsules
15. Number of flowers and capsules/plant height
*16. Leaf width
*17. Leaf length
18. Leaf length/width
*19. Leaf teeth
20. Leaf width/number of teeth
*21. Lower corolla lip width
*22. Lower corolla lip plus tube length
*23. Upper corolla lip width
*24. Upper corolla lip plus tube length
25. Flower size (lower corolla lip width $\times$ lower corolla lip plus tube length)
26. Lower corolla lip plus tube length/width
27. Lower/upper corolla lip plus tube length
*28. Flower colour
*29. Capsule width
*30. Capsule length
*31. Capsule apex indumentum
*32. Calyx length
33. Leaf length minus calyx length
34. Calyx length minus capsule length

All measurements of the plants were made after they were pressed and dried. Means and standard deviations were calculated and means for each character then were plotted on histograms, with the populations arranged along the horizontal axis in ascending order of the means (Bobear 1964). These diagrams were then examined for discontinuities in the range of variation and for repeated occurrence in proximity of the same populations. As a result of this examination certain groups of populations were found to cluster consistently for several characters.

The groups* of populations were further analysed and tested for their overall affinities. Populations which proved at the conclusion of the study to have clustered for several characters were considered to be of similar morphological type and are here assigned a letter, indicating the group to which they belong, and a number representing the population number within the group (Table 1).

Seed from the plants of wild populations used in the study was planted in November of the year in which collections were made. All pots were placed in cold frames at the time of planting and were moved out of doors in April. Adventive species were retained as host plants of *Euphrasia*. The work on the semi-parasitic habit of *Euphrasia* by Yeo (1959, 1961) and Wilkins (1958, 1963) indicates non-specificity of host preference and therefore steps were not taken to provide particular hosts.

The cultivated plants were harvested and pressed in July and August, care being taken that they were collected in a stage of development similar to that of the wild populations; that is, they were in full flower with some mature capsules. Thirteen cultivated populations were examined in detail and an average of 21 plants for a population were measured for the same characters and in the same manner as were the wild populations.

RESULTS—CHARACTERS

As a result of analysis of the variation of characters, four categories of characters were established. Category I consists of characters exhibiting discontinuities in variation for groups of populations similar for several other characters. In category II are those characters continuous in variation but resulting in clustering, along the gradient, of several groups of morphologically similar populations. Category III consists of characters continuous in variation and resulting in clustering of one or very few populations of similar morphological type. The distinction between Categories II and III is necessarily somewhat arbitrary. Category IV consists of characters most of which show little if any clustering of populations which occur in proximity in the variation for other characters. Characters of this category are considered of little or no diagnostic value.

A degree of genetic stability of characters in all categories was indicated through cultivation results, with three exceptions, plant width, capsule length, number of primary branches. Correlation coefficients were calculated between wild and cultivated populations for fourteen characters as given in Table 3.

TABLE 3. Correlation coefficients (r) and corresponding probabilities (P) for means of characters in wild and cultivated populations.

Character	r	P
Number of glandular hairs	+0.9537	<0.001
Capsule width	+0.8545	<0.001
Plant height	+0.7034	<0.01
Plant width	+0.1159	>0.10
Lower corolla lip width	+0.8426	<0.001
Lower corolla lip plus tube length	+0.8832	<0.001
Upper corolla lip width	+0.6928	<0.01
Upper corolla lip plus tube length	+0.8870	<0.001
Leaf width	+0.8426	<0.001
Leaf length	+0.7652	<0.001
Calyx length	+0.6928	<0.01
Capsule length	+0.3672	>0.10
Number of primary branches	+0.1792	>0.10
Angle of branching	+0.7242	<0.01

*To simplify the presentation, the 'Groups' which emerged at the conclusion of the analysis have been referred to freely in the following sections on character variation. See p. 85.

(a) CHARACTERS OF CATEGORY I

The only characters of Category I, those having discontinuities in variation, are related to features of glandular hairs: their presence or absence, if present their length and number.

Number of glandular hairs

The presence or absence of glandular hairs has been considered a useful but variable character in distinguishing species of *Euphrasia* (Pugsley 1930).

In this study data for the character were obtained through sampling of the relative abundance of glandular hairs by counting the glandular hairs present along a 1.5 mm segment of the mid-vein on the dorsal surface of the leaf measured.

Discontinuities occurred in the variation of populations measured for number of glandular hairs, as seen in Fig. 1, first in the presence or absence of the hairs. A second discontinuity occurs between the mean of population means of 13.04 hairs/1.5 mm representing Group A, and the mean of population means of 5.93 hairs/1.5 mm representing Group B. These two groups are separated from all others and from each other. The character proved of little value for those groups of low mean for number of glandular hairs since variation within this portion of the range for the character is continuous (Fig. 1a).

Based on the number of glandular hairs, four morphological types are distinguishable.

Numerous glandular hairs ($\bar{x} = 13.04$)	—Group A
Less numerous glandular hairs ($\bar{x} = 5.93$)	—Group B
Scarce glandular hairs ($\bar{x} = 1.12$)	—Groups C and D
No glandular hairs	—Groups J, G, F, E, H

Length of glandular hairs

A second measurement of glandular hairs was made, the length of the longest glandular hairs among those counted. Two distinct mean lengths were found. Mean length of $\bar{x} = 0.60$ mm distinguished Group A, and $\bar{x} = 0.20$ mm was found in all other populations bearing glandular hairs.

There was a correlation in length and number of glandular hairs in that populations at the highest end of the range for number of glandular hairs were also at the highest end of the range for the length of glandular hairs. Group A was thus separated from other types by a discontinuity of variation for both number and length of glandular hairs (Fig. 1a).

(b) CHARACTERS OF CATEGORY II

Eleven characters constitute the second category in which the variation is continuous but several groups of populations originally believed to be similar occur in proximity within a relatively limited range of the gradient. The characters of this category were found to have diagnostic value for several morphological types.

Capsule width

Capsule width, not formerly used as such but apparently included in descriptions of capsule shape, was measured at the widest section of a matured capsule which had not yet dehisced. The measurements were small and therefore the differences were slight, but capsule width proved a successful character in distinguishing six of the nine morphological types, Groups E, A, C, H, B, D respectively (Fig. 1b).

Plant height

Plant height has been consistently used by previous workers and frequently precise measurements have been given (Wettstein 1896, Townsend 1897, Bucknall 1917, Pugsley 1930, Warburg 1962, Yeo 1962).

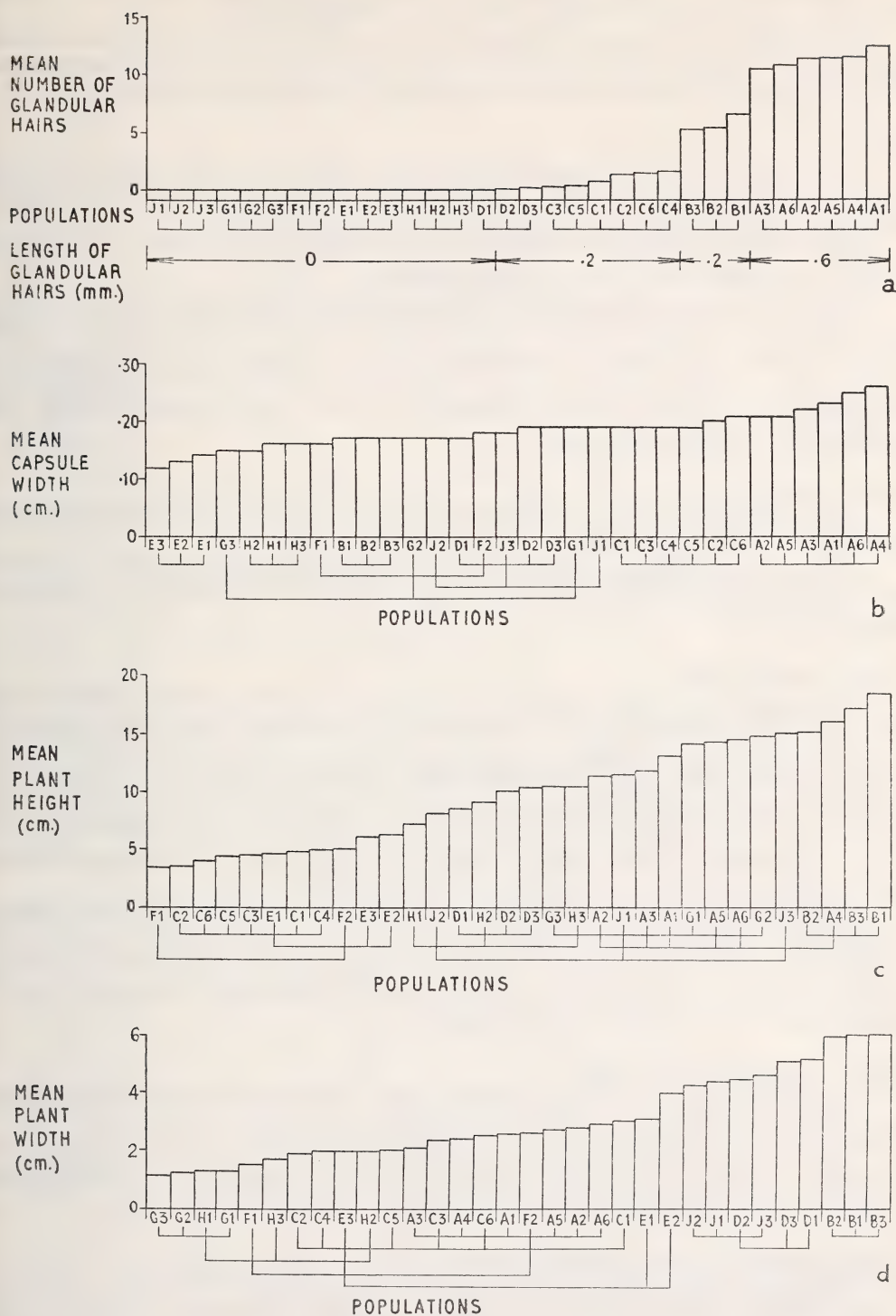


Fig. 1. Histograms of characters of Category I (a) and Category II (b, c, d).

The measurement of plant height was here made from the base of the stem, indicated by withered cotyledons or their scars, to the tip of the floral spike.

The members of six groups of populations, Groups C, E, F, B, A, D, similar in other morphological characters were similar also in plant height (Fig. 1c). In addition tall meadow forms remained tall and low-growing pasture plants remained low in cultivation.

Plant width

Plant width has not been directly used by other workers, although reference has been made by Pugsley (1930) to 'slender' plants and his and Wettstein's (1896) 'early summer habit' and 'late summer habit' usually included the width of the plant.

Plant width was measured at the widest point of the plant, which was in most cases between the extremes of the most spreading branches.

Plant width varies continuously but the populations of three Groups, B, D, J, consistently occurred at the high end of the range and two Groups, G and H, occurred so at the low end, while a sixth group of populations, Group A, clustered in the centre of the gradient (Fig. 1d). Plant width was one of three characters that did not remain stable in cultivation; nevertheless it proved a consistent character in geographically isolated wild populations of similar morphological type.

Plant height/width ratio

Plant height/width ratio was not found to have been used in the past as a quantitative character but was generally referred to in description of habit.

For this ratio, six Groups, G, H, A, C, D, B, of morphologically similar populations were distinguishable for their clustering within the gradient. Group G was discretely distinct (Fig. 2a).

Lower corolla-lip width

Floral characters being considered of importance have been used in various ways. Wettstein (1896) divided the Section *Semicalcaratae* into three Series based on the elongation of the corolla tubes, a characteristic later not considered of value (Chabert 1902, Pugsley 1930). Bucknall (1917) considered corolla-length variable and unreliable as a diagnostic character, while Pugsley accepted the importance of overall corolla size. Yeo (1962, 1966) and Wilkins (1958) both used floral characters, especially those of the lower corolla lip.

All measurements in this study were made on a flower chosen from among the largest on each plant and believed to have recently dehiscent anthers.

The width of the lower corolla-lip was measured at the widest part of the lip. Plotting of the means of populations for this character resulted in seven groups of populations occurring in proximity. Groups D, A, and B, respectively, were at the high end of the range, and Groups G, E, F, H, at the lower, with Group J in the centre of the range. Group C proved most variable for this character (Fig. 2b).

Lower corolla-lip plus tube length

The measurement of the lower corolla-lip plus tube length was taken from the base of the tube to the tip of the middle lobe of the lower corolla lip.

The distinguishing of groups in the gradient for length of lower corolla-lip plus tube is similar to that for the lower corolla-lip width in that the same six groups are found to occur in proximity but there is slightly less variation in the latter character (Fig. 2c).

Lower corolla-lip plus tube length/width ratio

This ratio, not previously used, proved useful in the sorting of the large-flowered forms with small differences in length and width at one extreme of the range, Groups D, A, B, and the small-flowered forms with large differences in the two measurements at the other end of the range, Groups G, E, F. Six groups then were proximal for this ratio. One, Group C, was conspicuously varied for length-width ratio of the lower corolla (Fig. 2d).

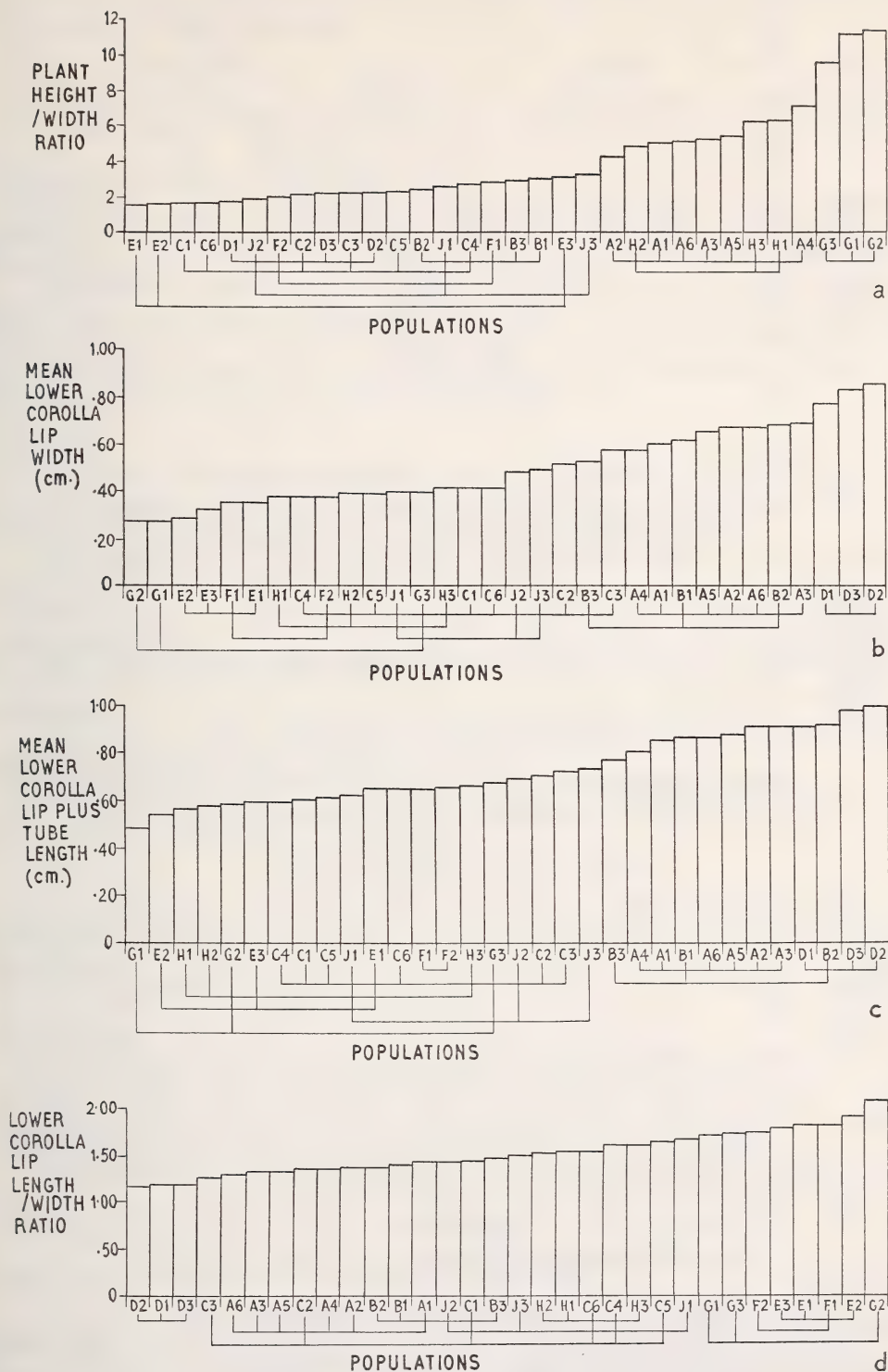


Fig. 2. Histograms of characters of Category II.

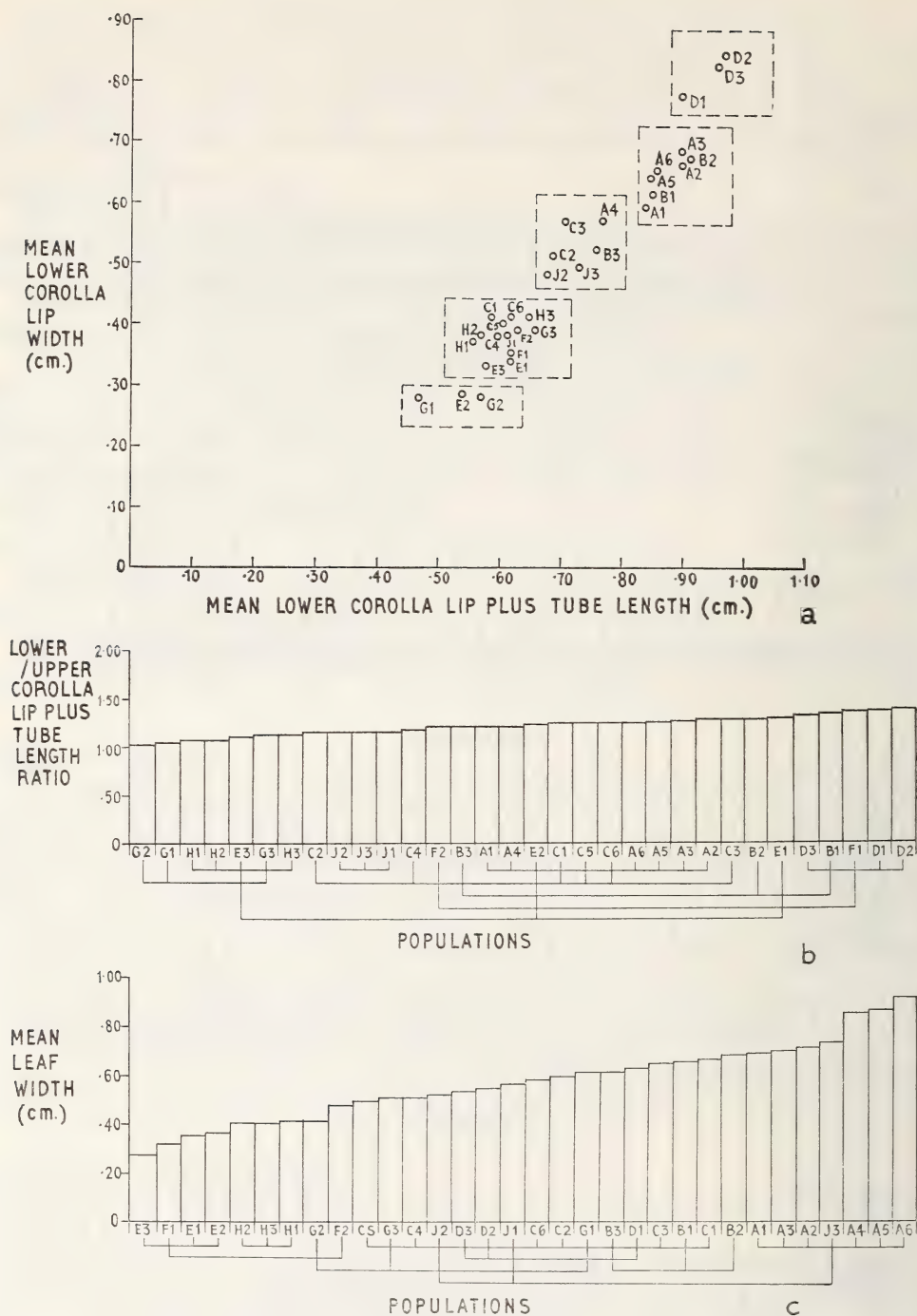


Fig. 3. Scatter diagram and histograms of characters of Category II.

Lower corolla-lip width $\times$ lower corolla-lip plus tube length (Flower Size)

Lower corolla-lip width and lower corolla-lip plus tube length were plotted against each other on rectangular axes, and were used as an estimate of flower size (Fig. 3a).

The continuous nature of the variation of the characters is apparent as well as the positive correlation between the two characters, but such an arrangement of data is useful

in revealing three categories of groups of populations, which may be distinguished by flower size, small, medium and large. There is also a small degree of discontinuity in mean measurements for the three groups:

<i>Lower corolla-lip</i>	<i>Small</i>	<i>Medium</i>	<i>Large</i>
<i>Mean length</i>	0.47–0.66 cm	0.68–0.91 cm	0.90–0.97 cm
<i>Mean width</i>	0.28–0.41 cm	0.47–0.68 cm	0.77–0.82 cm

Lower/upper corolla-lip plus tube length ratio

The relative lengths of the lower and upper corolla-lip plus tube were consistently used by Pugsley (1930) in his descriptions of the British *Euphrasiae*, and it appears in both the British and Irish Floras (Warburg 1962, Webb 1963), but without quantification.

The difference in length of the two corolla-lips is useful for two groups, G and H, of similar populations with small differences for the ratio; and for one group, Group D, with a large difference for the ratio. Two groups of populations, J and A, near the centre of the gradient are also proximal but this character is not as useful in distinguishing these groups as it is for those at the extremes of the range (Fig. 3b).

Leaf width

Leaf shape has been used by previous workers as a diagnostic character with measurements often given for leaf length (Bucknall 1917, Pugsley 1930, Warburg 1962). Leaf width has been used in relation to the length with an approximate ratio.

The leaf selected for measurement was the one subtending the capsule measured; it was measured at its widest point including the teeth.

Leaf width is a useful character resulting in the distinguishing of six groups of morphological types, Groups E, H, F at the lower end of the gradient, and Groups A and B at the upper end, with Group D populations proximal near the centre of the gradient (Fig. 3c).

Leaf length

Leaf length was measured along the mid-vein from the leaf base or point of attachment to the stem, to the tip of the leaf.

Leaf length is similar to leaf width in its value as a diagnostic character in that the same six groups are proximal for leaf length, Groups H, E, F, A, B, D (Fig. 4a).

(c) CHARACTERS OF CATEGORY III

The third category of character variation consists of seven characters for which the clustering of morphological types within the continuous gradients of variation is infrequent. The characters are of less diagnostic value than those in the preceding two categories, since fewer morphological types are distinguishable by use of the following characters.

Capsule length

Capsule shape, with some measurements given for capsule length (Pugsley 1930) has been previously used as a diagnostic character.

Capsule length was measured from the base to the tip of the capsule, not to the central notch. The capsule measured was the one also measured for capsule width.

When arranged in order of population means for capsule length, Groups E and H were proximal at the lower end of the range, Groups B and F at the upper centre. The character proved variable for all other morphological groups (Fig. 4b).

Upper corolla-lip width and upper corolla-lip plus tube length

The width of the upper corolla-lip was measured at the widest part of the lip. The length was measured from the base of the tube to the tip of the lobes of the upper lip.

For the gradient of both characters populations of similar morphological type occur within proximity for five groups, but these characters of the upper lip proved less efficient in distinguishing groups than did comparable measurements of the lower lip (Figs. 4c, 4d).

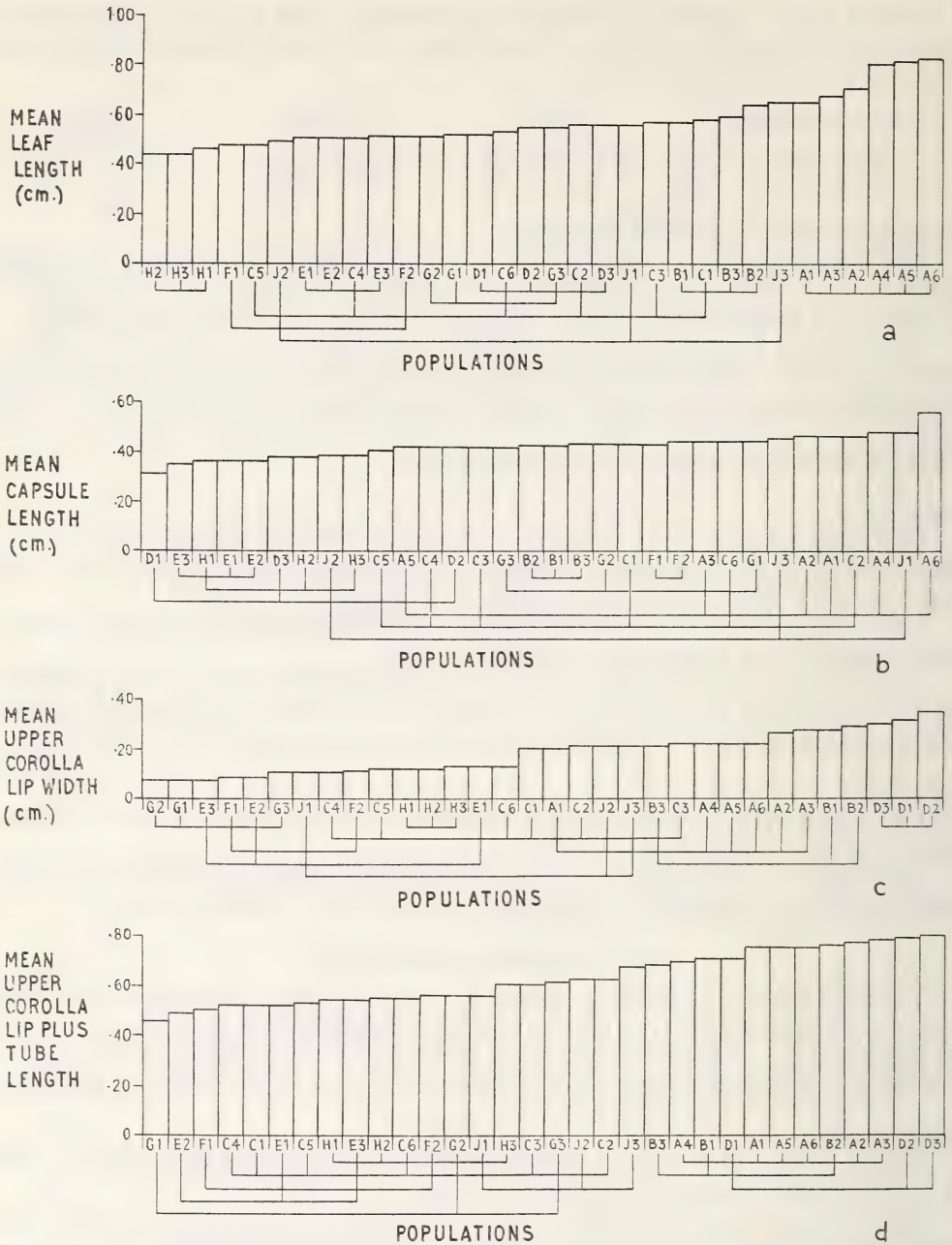


Fig. 4. Histograms of characters of Category II (a) and Category III (b, c, d).

The saccate shape of the upper lip (which did not press well), and variations in the tendency of the margins to curl in drying, rendered the upper lip of the corolla less amenable to measurement than the lower lip.

Leaf length/width ratio

Leaf length/width ratio has been considered of value (Pugsley 1930) as a distinguishing character, although numerical values have not been given.

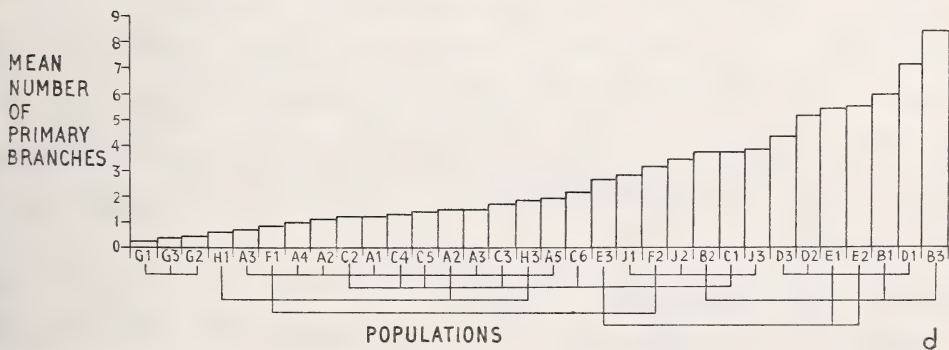
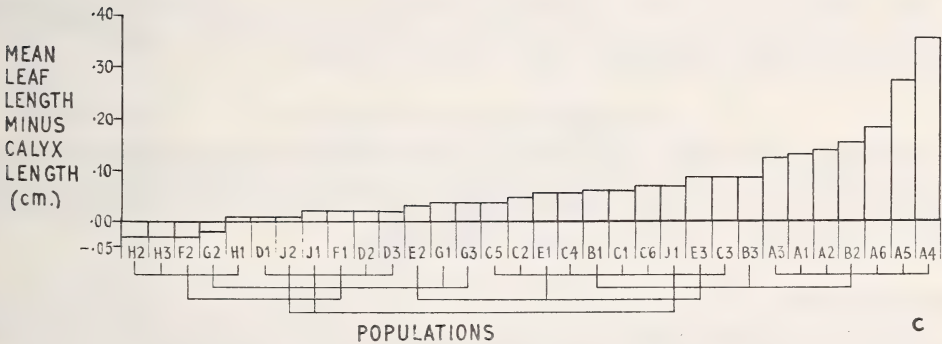
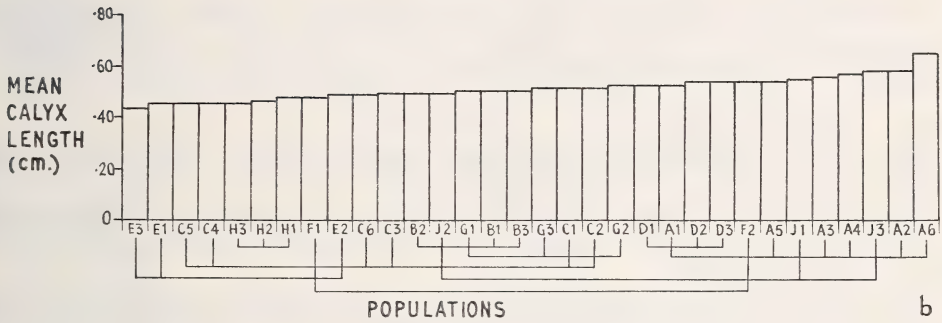
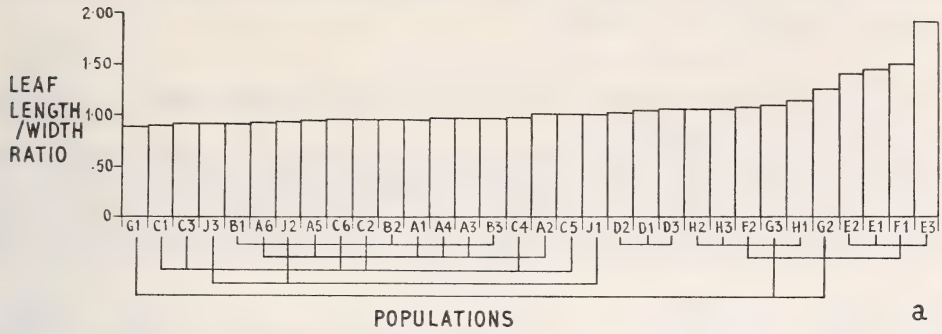


Fig. 5. Histograms of characters of Category III.

The leaf length/width ratio was here found useful as a distinguishing character for four morphological types, Groups E, H, D, F. The character was variable in the remaining five groups of populations (Fig. 5a).

Calyx length

Calyx length appears in Pugsley's (1930) work as being shorter, longer, or as long as either the capsule or subtending leaf.

It was measured, for this study, from the base of the calyx to the tip of the calyx teeth.

Five groups demonstrate varying degrees of clustering for this character. Two groups, B and G, were overlapping in the centre of the range and the variation of groups at either end of the gradient, Groups E, H, A, was greater than in most preceding characters (Fig. 5b).

Leaf length minus calyx length

The difference in length of leaf and calyx has been expressed as calyx 'exceeding greatly' or 'equalling or exceeding' (Pugsley 1930).

In this study the character was found to be continuous in variation with three groups of populations proximal within the gradient, Groups H, A, D. The character therefore is of value for three morphological types (Fig. 5c).

Number of primary branches

The degree of branching had been found useful by Pugsley (1930) and has been expressed as 'few branches' or 'bushy habit'.

The mean number of primary branches was found to be consistently less than one for Group G, and relatively high for Groups D and B. The character has diagnostic value for these three groups (Fig. 5d).

The number of primary branches is a character which appeared as a result of cultivation trials to lack stability (Table 3); but, as with plant width, it was consistent in wild material.

Plant width and the number of primary branches were found to be strongly correlated as demonstrated by plotting of mean values on abscissa and ordinate, and also by calculation of the correlation coefficient, $r = +0.8306$ ($P < 0.001$).

(d) CHARACTERS OF CATEGORY IV

The characters of category IV have the least diagnostic value since groups of populations occurring in proximity for other characters show considerable variation for the following characters. In some other cases two characters were found to be too closely correlated for both to be of value as individual diagnostic features.

Angle of branching

Angle of branching, implied in the terms 'erect' or 'ascending' or 'suberect', has been used by Pugsley (1930) and those who followed his treatment of the genus.

An estimate of the average angle of branching was obtained by laying a protractor on the plant and reading the angle common to the majority of branches.

Within the continuous variation of means of populations for angle of branching two groups, G and A, cluster at the lower end of the range and two, Groups B and D, at the upper centre. The total range of variation of angle of branching is small and the character is difficult to apply except for Group G at the lowest end of the gradient (Fig. 6a). A plotting of values for angle of branching and width of plant revealed a lack of correlation between the two characters.

Calyx length minus capsule length

Pugsley (1930) consistently referred to the relative lengths of the calyx and capsule as a descriptive feature of each species.

Plotting of the means for this difference resulted in the proximity of one group of populations at the upper end of the continuous gradient, Group D, and two groups, C

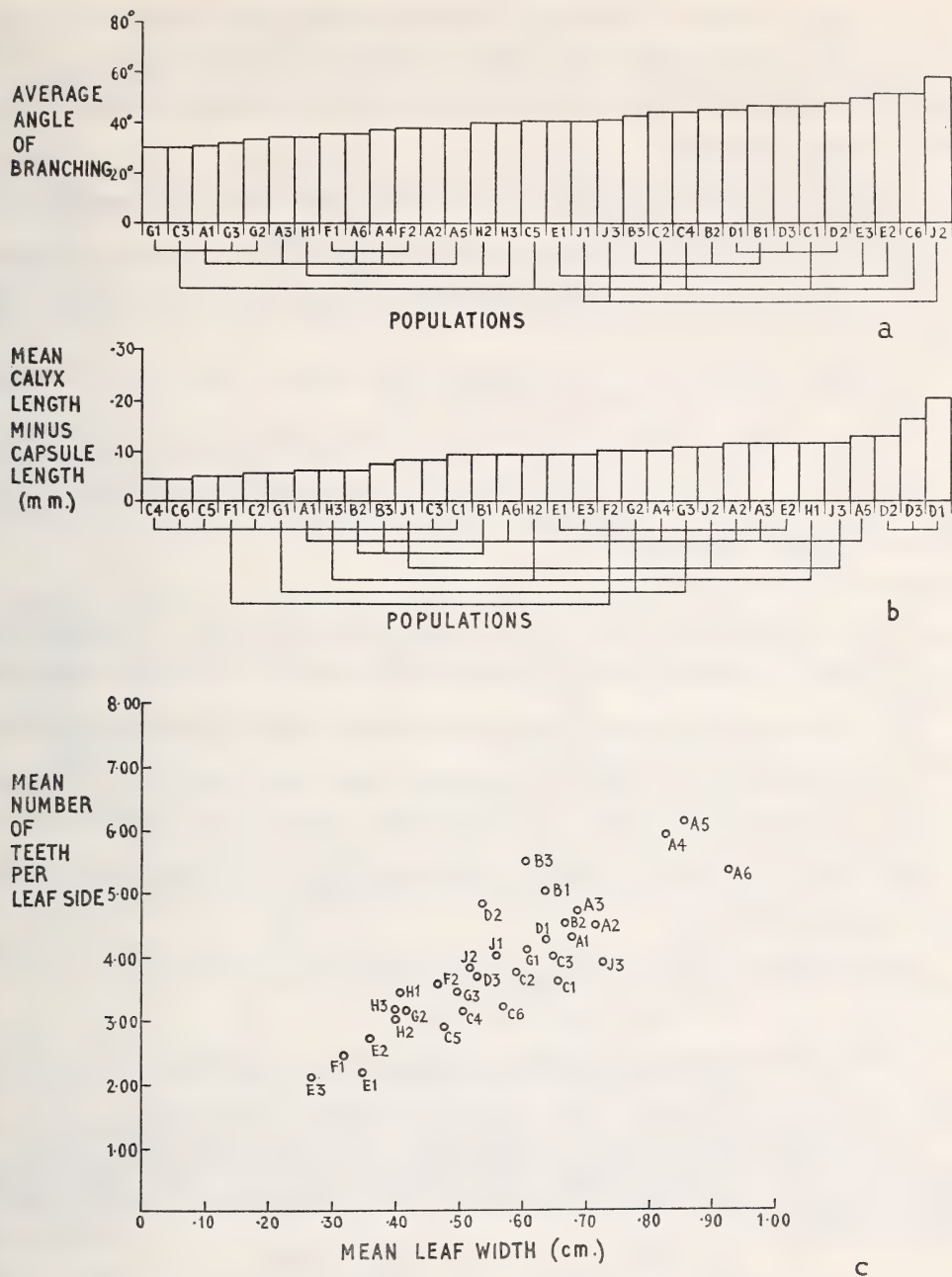


Fig. 6. Histograms and scatter diagram of characters of Category IV.

and B, near the lower end. All other groups showed considerable variation for this characteristic. The results are not unexpected since variation within groups was high for both capsule and calyx lengths (Fig. 6b).

Leaf teeth

The number of leaf teeth on a side of a leaf appeared in each of Pugsley's (1930) species descriptions.

The number of teeth on a side were plotted (abscissa) against the width (ordinate) of the leaf. The two characters were found to correlate with a value of $r = +0.8659$ ($P < 0.001$). The few populations which appeared to deviate from the general trend of correlation of the majority, belonged to several different morphological groups (Fig. 6c).

Length of stem to first branch

The height of branching was frequently used and referred to as being near the base or the midpoint of the stem (Pugsley 1930). Warburg (1962) refers to the number of the node at which branching commences.

In this study the length of the stem to the first branch was measured from the base of the stem to the first branch. This was considered to be a more reliable quantification of height of branching than a counting of nodes which may be difficult to determine with precision.

Populations of Group G were conspicuously clustered at the upper end of the range and Groups F and C were proximal at the lower end.

Plotting of length of stem to first branch (ordinate) against plant height (abscissa) indicates that the characters are positively correlated. The populations of Group G are the only ones of a single group that consistently demonstrate lower branching for their height. This character then is of particular value in characterizing Group G, while all others correlate with plant height (Fig. 7a).

Length of stem to first flower

Length of stem to first flower is and has been a frequently used character. Pugsley (1930) used the number of the pairs of leaves at which flowering begins. The node at which flowering begins is commonly used by Warburg (1962) to indicate the length of stem to the first flower.

This character was determined here by measuring the length of stem from its base to the first flower or capsule of each plant.

Variation is essentially continuous for length of stem to first flower with populations of Group B clustering at the upper end of the gradient, Groups D and E at upper and lower ends of centre respectively, and Groups C and F at the lower end (Fig. 7b).

While these five groups did occur in proximity, plotting of the mean values of plant height (abscissa) against length of stem to first flower (ordinate) revealed a correlation of the two characters (Fig. 7b).

The correlation coefficient between the two characters is $r = +0.8887$ ($P < 0.001$). The height of flowering appears to have minimal diagnostic value.

Flower colour

Pugsley (1930) recognized variability of flower colour, but thought it to be useful in providing 'some indication of species'. It was used by him in his key as well as in descriptions and has appeared in subsequent floras based on his treatment of the genus.

In the present study, in order to render colour of flower more amenable to biometric treatment, a colour scale of three values was prepared. Flowers of each plant were compared with the colours of the chart and were scored using a combination of the two elements of the following key:

I - white	U - upper lip only
II - light purple	L - lower lip only
III - dark purple	UL - both lips

Flower colour has the same pattern of continuous variation as is typical of all but one other character examined in *Euphrasia*. Flowers within individual populations may range from white to dark purple. Three populations were composed entirely of plants with white flowers, and one entirely of plants with dark purple flowers. The majority of populations, however, were varied from all white through varying degrees of purple and white on single flowers to all dark purple flowers. Even in the flowers of an individual plant, there is often considerable variability in colour. In general, populations found to be related in respect to other characters were not distinguished by flower colour.

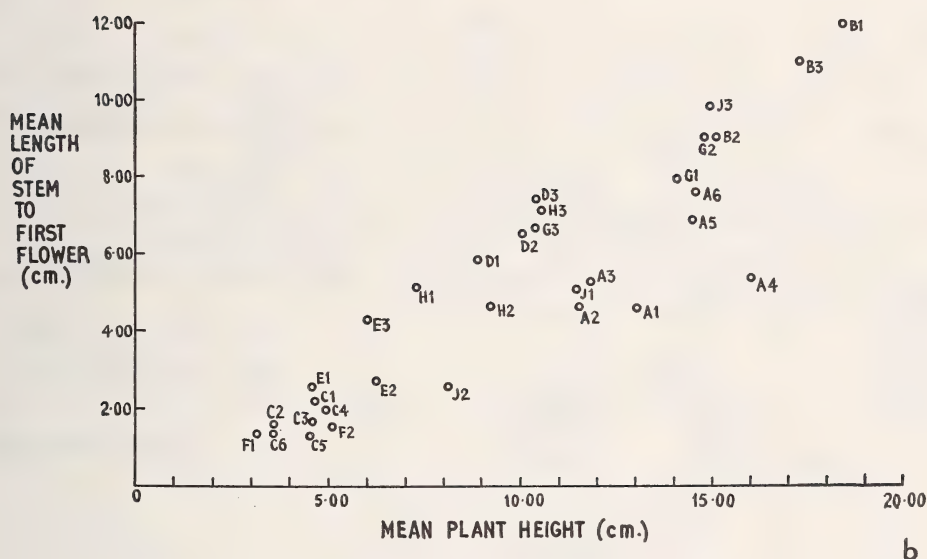
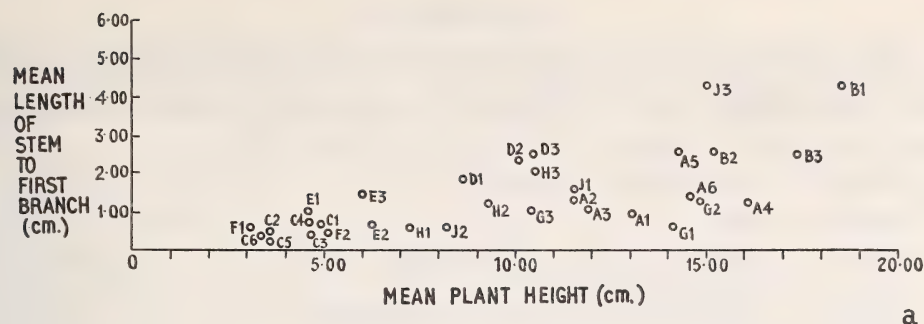


Fig. 7. Scatter diagrams of characters of Category IV.

The flower colour patterns of wild populations were unchanged by cultivation.

Flower colour appears to have little diagnostic value, with the exception of one morphological type which is predominantly white flowered. Also, the one all dark purple population studied occurred within the group for which this flower colour has frequently been reported.

Number of flowers and capsules

The number of flowers and capsules were counted to discover, in particular, whether this characteristic in relation to plant height would be a distinguishing character of a low-growing form of *Euphrasia* from an exposed habitat. While populations of this morphological type did occur in proximity at the upper end of the gradient, the difference was not sufficiently distinct from other low-growing forms for this relationship to be of diagnostic value.

Capsule-apex indumentum

The capsule apices of all plants were examined and found to be ciliate with the exception of a single morphological type, Group E, in which they were glabrous.

(e) HABITAT

While ecological studies were not a part of this work, some recordings were made of soil pH, height of sward, and associated species. In analysing this data it was discovered that the populations of seven of the groups were consistent in habitat to the following degree. Classification of vegetation follows that of Tansley (1939).

Group G — wet habitat (fen and flush)

Group H — heath

Group E — limestone pasture (average height of sward 7 cm)

Group C — dune grassland (grazed)

Group A — meadow (average height of sward 46 cm)

Group D — meadow

Group B — meadow

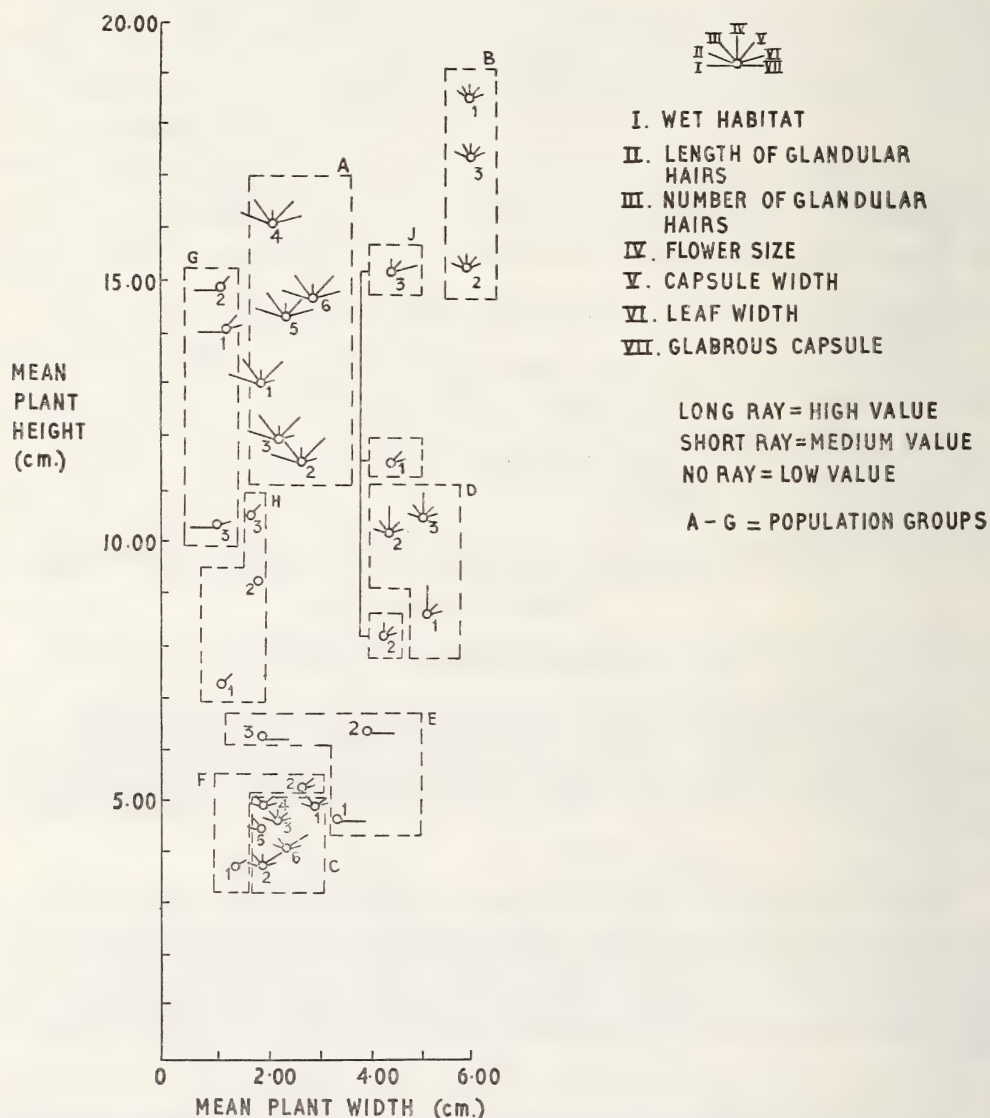


Fig. 8. Populations diagrammed for 9 characters.

RESULTS—GROUPS

As a result of the preceding analysis of characters, nine of the characters which appeared likely to be most informative as to the composition of possible population groups were selected for investigation on a co-variation diagram (Fig. 8) as described by Anderson (1957).

On the basis of the results as revealed by the diagram and the additional evidence of character variation presented above but not included on the diagram, nine morphological types are distinguishable. These groups of populations, Groups A to J, were identifiable at this stage of the study, although they have been used, in this paper, in the preceding section on character variation and in Table I, for simplicity of presentation.

In order to determine further the relative importance of differences between groups, *t*-tests were performed between the mean values of adjacent groups for six of the most discriminating characters. The points of interest which emerged were the predominantly continuous variation in the mean values of groups for the characters considered, and secondly the inconsistency in occurrence of significant differences between the same pairs of groups for different characters. The results of the *t*-tests are illustrated in a diagram of the type developed by Roberts (1961).

In the diagram (Fig. 9), groups are arranged vertically for each of the six characters in order of magnitude of the mean values, the high values being uppermost. Discontinuities in the variation of each character are indicated by interruptions in the columns. The variation of characters for groups enclosed within resulting blocks is continuous. The lines connecting blocks indicate the position of each group within the gradient for each character.

The reticulate pattern of variation of the groups for the six characters is evident. However there is indication that the characters do not vary independently; some co-variation is evident through the number of parallel lines linking groups between characters.

Group B is the most sharply differentiated group; Groups A, E, H, G, D are also differentiated from each other and remaining groups. Groups C, F, J are less well differentiated but can be defined in terms of particular ranges of values for several continuous variables.

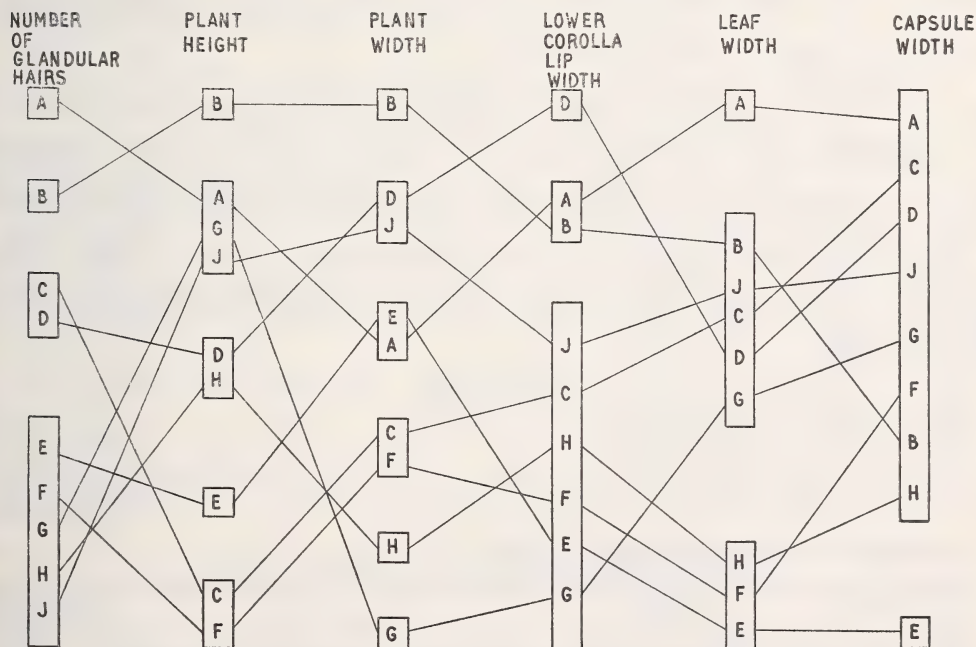


Fig. 9. A natural ordering from high to low value of Groups of populations (A-J) for six characters.

RESULTS—TAXONOMIC

Fifteen species of *Euphrasia* have been recorded for Ireland (Hart 1887, 1898, Stewart & Corry 1888, 1938, Colgan 1904, Praeger 1909, 1934, Scully 1916, Pugsley 1930, Bruncker 1950, Warburg 1962, Webb 1963).

Examination of the whole of the data considered above indicates the following relationships between the previously described species and the nine morphological groups recognized in this investigation.

<i>E. micrantha</i> Reichb.	Group H
<i>E. scottica</i> Wettst.	Group G
<i>E. tetraquetra</i> (Bréb.) Arrondeau (<i>E. occidentalis</i> Wettst.)	Group C
<i>E. nemorosa</i> (Pers.) Wallr.	Group J
<i>E. brevipila</i> Burnat & Gremli	Group B
<i>E. rostkoviana</i> Hayne	Group A
<i>E. confusa</i> Pugsley	Group F
<i>E. salisburgensis</i> Funck	Group E
<i>E. pseudokernerii</i> Pugsley	Group D
<i>E. frigida</i> Pugsley	
<i>E. curta</i> (Fr.) Wettst.	
<i>E. borealis</i> Wettst.	
<i>E. anglica</i> Pugsley	
<i>E. hirtella</i> Jord. ex Reuter	
<i>E. montana</i> Jord.	

The semi-alpine habitat of *E. frigida* was not visited. Localities reported for *E. curta* were investigated but *E. brevipila* was always found. No collections fitting the descriptions of *E. borealis* were discovered and all herbarium material seen could either be placed in *E. nemorosa* (one specimen), or, except for the lack of glandular hairs, could be identified as *E. brevipila*.

One population studied was found to exhibit in some degree the lower node of first flowering, wider leaves, smaller corolla and wider capsules described (Pugsley 1929) for *E. anglica*, but it was not sufficiently distinct from the others of Group A to justify its separation as a discrete morphological type.

E. hirtella and *E. montana* have been distinguished (Pugsley 1930) from *E. rostkoviana* by an unbranched habit which was found to be characteristic of all populations of Group A. These two species were also distinguished by leaf and flower size, characteristics of considerable variation in Group A. No single populations of Group A could be separated from the others on the basis of Pugsley's (1930) descriptions for these two species. It appears possible that the variation of populations of Group A included that of *E. hirtella* and *E. montana*.

The following key and descriptions were prepared for the nine species as delineated by this study. Each description includes only those characters which were most efficient diagnostically for particular species, while the asterisk (*) indicates the characters of greatest diagnostic value.

Key to Species

- Glandular hairs present, at least on some plants 2
Glandular hairs lacking 5
- Glandular hairs maximum length 0.60 mm; mean number of glandular hairs per 1.5 mm c. 13 *E. rostkoviana*
Glandular hairs maximum length 0.20 mm 3
- Glandular hairs present on all plants; mean number of glandular hairs per 1.5 mm c. 6 *E. brevipila*
Glandular hairs not always present on all plants; mean number of glandular hairs per 1.5 mm < 2 4

4. Mean plant height *c.* 5 cm; mean lower corolla-lip width <5 mm; mean number of glandular hairs per 1.5 mm 1.98 *E. occidentalis*
 Mean plant height *c.* 10 cm; mean lower corolla-lip width *c.* 8 mm; mean number of glandular hairs per 1.5 mm 0.16 *E. pseudokerneri*
5. Capsule apex glabrous *E. salisburgensis*
 Capsule apex ciliate 6
6. Mean plant height *c.* 4.5 cm *E. confusa*
 Mean plant height >7 cm 7
7. Mean plant width *c.* 4 cm; mean lower corolla-lip width >4 mm *E. nemorosa*
 Mean plant width <2 cm; mean lower corolla-lip width *c.* 3.5 mm 8
8. Mean lower corolla-lip width *c.* 3 mm; habitat fen or flush *E. scottica*
 Mean corolla lip width *c.* 4 mm; habitat heath *E. micrantha*

Euphrasia rostkoviana Hayne (Group A)

Character	Mean	Range
* Length of longest glandular hairs	0.60 mm	
* Number of glandular hairs per 1.5 mm	13.04	7-24
Plant height	13.61 cm	5.50-31.50 cm
Plant width	2.59 cm	0.60-15.00 cm
Plant height/width ratio	5.28	
Number of primary branches	1.27	0-10
* Capsule width	0.23 cm	0.15- 0.32 cm
Lower corolla-lip width	0.63 cm	0.40- 1.00 cm
Lower corolla-lip plus tube length	0.85 cm	0.52- 1.25 cm
* Leaf width	0.78 cm	0.40- 1.00 cm
Leaf length	0.74 cm	0.40- 1.40 cm
Leaf length/width ratio	0.95 cm	
Leaf length minus calyx length	0.19 cm	
Habitat—meadow		

Euphrasia brevipila Burnat & Gremli (Group B)

Character	Mean	Range
* Length of longest glandular hairs	0.20 mm	
* Number of glandular hairs per 1.5 mm	5.93	1-14
* Plant height	16.98 cm	7.60-35.00 cm
Plant width	5.93 cm	0.60-21.00 cm
* Number of primary branches	5.91	0-17
* Capsule width	0.17 cm	0.11- 0.26 cm
Lower corolla-lip width	0.60 cm	0.40- 1.00 cm
Lower corolla-lip plus tube length	0.84 cm	0.52- 1.40 cm
Leaf width	0.64 cm	0.30- 1.20 cm
Leaf length	0.60 cm	0.40- 0.90 cm
Leaf length/width ratio	0.94	
Habitat—meadow		

Euphrasia tetraquetra (Bréb.) Arrondeau (Group C)

Character	Mean	Range
* Length of longest glandular hairs	0.20 mm	
* Number of glandular hairs per 1.5 mm	1.98	0-10
* Plant height	4.70 cm	2.00-10.60 cm

Plant width	2.20 cm	0.80– 6.00 cm
Plant height/width ratio	1.64	
Number of flowers and capsules/plant height	4.78	
* Capsule width	0.19 cm	0.13– 0.30 cm
Lower corolla-lip width	0.44 cm	0.26– 0.72 cm
Lower corolla-lip plus tube length	0.63 cm	0.42– 0.90 cm
Leaf width	0.57 cm	0.24– 1.00 cm
Leaf length	0.54 cm	0.35– 0.83 cm
Leaf length/width ratio	0.95	
Habitat—sand dunes		

Euphrasia pseudokernerii Pugsl. (Group D)

Character	Mean	Range
Glandular hairs usually lacking, but if present:		
Length of longest glandular hairs	0.20 mm	
Number of glandular hairs per 1.5 mm	0.25	0–2
Plant height	9.74 cm	5.00–14.80 cm
Plant width	4.84 cm	0.80–17.00 cm
* Plant height/width ratio	1.70	
Number of primary branches	5.57	0–25
Capsule width	0.18 cm	0.13– 0.30 cm
* Lower corolla-lip width	0.81 cm	0.50– 1.00 cm
* Lower corolla-lip plus tube length	0.94 cm	0.62– 1.20 cm
* Lower lip plus tube length/width ratio	1.16	
* Lower/upper lip plus tube length ratio	1.21	
Leaf width	0.56 cm	0.36– 0.90 cm
Leaf length	0.54 cm	0.40– 0.82 cm
Leaf length-width ratio	1.03	
Calyx length minus capsule length	0.17 cm	
Habitat—meadow		

Euphrasia salisburgensis Funck (Group E)

Character	Mean	Range
* Capsule apex glabrous		
Glandular hairs lacking		
Plant height	5.73 cm	2.90–10.10 cm
Plant width	2.93 cm	0.40– 9.00 cm
Plant height-width ratio	2.14	
* Capsule width	0.13 cm	0.10– 0.22 cm
Capsule length	0.35 cm	0.26– 0.50 cm
Lower corolla-lip width	0.32 cm	0.20– 0.50 cm
Lower corolla-lip plus tube length	0.58 cm	0.40– 0.80 cm
* Lower corolla-lip plus tube length/width ratio	1.79	
Flower colour—high percentage of white flowers		
* Leaf width	0.33 cm	0.10– 0.70 cm
Leaf length	0.50 cm	0.30– 0.70 cm
* Leaf length-width ratio	1.57	
Habitat—limestone pasture		

Euphrasia confusa Pugsl. (Group F)

Character	Mean	Range
Glandular hairs lacking		
* Plant height	4.40 cm	2.00– 9.00 cm
Plant width	1.97 cm	0.50– 6.00 cm

Plant height/width ratio	2.37	
Capsule width	0.17 cm	0.12– 0.22 cm
* Capsule length	0.44 cm	0.30– 0.60 cm
Lower corolla-lip width	0.36 cm	0.24– 0.60 cm
Lower corolla-lip plus tube length	0.62 cm	0.50– 0.90 cm
* Lower corolla-lip plus tube length/width ratio	1.73	
Leaf width	0.39 cm	0.20– 0.64 cm
Leaf length	0.44 cm	0.35– 0.70 cm
Leaf length minus calyx length	0.02 cm	
Habitat variable—sand dunes, acidic pasture		

Euphrasia nemorosa (Pers.) Wallr. (Group J)

Character	Mean	Range
Glandular hairs lacking		
Plant height	11.59 cm	5.00–24.00 cm
Plant width	4.25 cm	0.30–14.30 cm
Capsule width	0.18 cm	0.12– 0.26 cm
Lower corolla-lip width	0.44 cm	0.30– 0.70 cm
Lower corolla-lip plus tube length	0.67 cm	0.45– 0.90 cm
Leaf width	0.60 cm	0.30– 1.00 cm
Leaf length	0.56 cm	0.35– 0.90 cm
Leaf length/width ratio	0.94	
Habitat variable—sand dune, basic meadow		

Euphrasia scottica Wettst. (Group G)

Character	Mean	Range
Glandular hairs lacking		
Plant height	13.19 cm	6.00–24.70 cm
Plant width	1.16 cm	0.60– 4.60 cm
* Plant height/width ratio	10.67	
* Number of primary branches	0.29	0–4
Length of stem to first branch	5.56 cm	2.40–10.00 cm
Number of flowers and capsules	11.42	2–43
Capsule width	0.17 cm	0.13– 0.30 cm
Lower corolla-lip width	0.31 cm	0.20– 0.58 cm
Lower corolla-lip plus tube length	0.56 cm	0.38– 0.80 cm
* Lower corolla-lip plus tube length/width ratio	1.80	
Lower/upper corolla-lip plus tube length ratio	1.04	
Flower colour—may have high percentage of all white		
Leaf width	0.51 cm	0.20– 1.20 cm
Leaf length	0.53 cm	0.30– 0.80 cm
Habitat—wet, fen or flush		

Euphrasia micrantha Reichb. (Group H)

Character	Mean	Range
Glandular hairs lacking		
Plant height	8.99 cm	2.80–15.70 cm
Plant width	1.60 cm	0.40– 7.00 cm
Plant height/width ratio	5.70	
Number of flowers and capsules	12.72	3–52
Capsule width	0.16 cm	0.12– 0.20 cm
Capsule length	0.36 cm	0.22– 0.49 cm
Lower corolla-lip width	0.39 cm	0.20– 0.60 cm
Lower corolla-lip plus tube length	0.59 cm	0.42– 0.83 cm

Lower/upper corolla-lip plus tube length ratio	1.05	
Flower colour may be dark purple		
Leaf width	0.40 cm	0.20– 0.62 cm
Leaf length	0.44 cm	0.30– 0.70 cm
* Leaf length minus calyx length	(—) 0.02 cm	(—) 0.03– 0.00 cm
Habitat—heath		

CONCLUSIONS

The characters of *Euphrasia* were found, with the exception of glandular hairs, to be continuously variable and also inconsistently variable within each species. That is, a character such as lower corolla lip width was variable within a large range for some species and within a small range for others. Therefore characters were found to have diagnostic value for varying numbers of species, some being useful for several, others for only one or two species. No single character was consistently useful for all morphological groups.

Vegetative characters were efficient in distinguishing species. Plant height was consistent for particular morphological types in both wild and cultivated populations. Plant width, while unstable in cultivation, proved a reliable character in wild populations, a fact which appears consistent with Davis & Heywood's (1963) observation that 'adaptive characters will remain stable as long as the environmental conditions to which they are adapted remain constant'. This is particularly applicable to *Euphrasia*, most species of which appear to be specific for habitat.

It is interesting that, while the indications are that *Euphrasia* demonstrates ecological specificity, this at the same time usually fails to function as a barrier to hybridization, since habitats themselves are continuously variable, permitting spatial proximity of differing morphological types. Interbreeding is apparently of frequent occurrence, isolating mechanisms being virtually lacking (Yeo 1966), and yet it seems characteristic of the genus that, despite apparent lack of barriers to gene flow, segregation does occur.

It was found that data for many individuals from homogeneous populations disclosed the existence of morphological types distinct in their particular combination of correlating characters. However it is clear that species of *Euphrasia* are less well separated than would be desirable for efficient taxonomic handling of the group. It must also be accepted, as has been long recognized (Anderson 1949, Clausen 1951, Heslop-Harrison 1960, Davis & Heywood 1963), that the use of relatively large population samples rather than a few individuals is necessary for a realistic approach to identification.

ACKNOWLEDGMENTS

Sincere appreciation is expressed to Professor D. A. Webb, Trinity College, Dublin, under whom this work was initiated and completed. I am also grateful to many friends in the British Isles, especially Miss M. J. P. Scannell, National Museum of Ireland, for use of herbarium material, help in the field, and for her interest and encouragement; Miss Evelyn Booth, Bunclody, Co. Wexford, for her support and introduction to the *Euphrasiae* of Counties Wicklow and Wexford; Dr. P. F. Yeo, University Botanic Gardens, Cambridge, for his interest and information on the cultivation of *Euphrasia*; Mr. J. P. Brunner for the use of his material determined by Pugsley.

I also wish to acknowledge the State University College at Brockport, New York, for grants of leave of absence and sabbatical salary; and the Research Foundation of the State University of New York for Grant-in-Aid.

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THE ORIGIN OF *CARDAMINE FLEXUOSA* WITH EVIDENCE FROM MORPHOLOGY AND GEOGRAPHICAL DISTRIBUTION

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ABSTRACT

The morphology and geographical distribution of *Cardamine flexuosa* and some closely related species have been examined. The data obtained suggest that *C. flexuosa* arose by allopolyploidy from *C. impatiens* and *C. hirsuta*.

INTRODUCTION

C. flexuosa is a tetraploid which may have arisen by autoploidy or allopolyploidy. Species which, on morphological grounds, may have been involved in its origin are: *C. hirsuta* L., *C. impatiens* L., *C. parviflora* L., *C. caldeirarum* Guthnick and *C. trichocarpa* Hochst.

TABLE 1. Chromosome numbers of some *Cardamine* spp. which are related morphologically to *C. flexuosa*.

Species	2n	Reported by:
<i>C. hirsuta</i>	16	} Several authors, see Löve & Löve (1961)
<i>C. impatiens</i>	16	
<i>C. parviflora</i>	16	
var. <i>arenicola</i>	22,24	Smith 1938, Mulligan 1965
<i>C. caldeirarum</i>	?	Rollins 1966
<i>C. trichocarpa</i>	32	Not counted
<i>C. flexuosa</i>	32	Morton 1961 (as <i>C. hirsuta</i>)
		Several authors, see Löve & Löve (1961)

C. hirsuta appears to have been closely concerned in the evolution of *C. flexuosa*. Morphological resemblances are so strong that it is sometimes difficult to distinguish the species, especially when only winter rosettes are available. Indeed, in the Floras of many European countries it is only in the present century that the species have been distinguished, and as recently as 1943 they were recombined (under *C. hirsuta* L.) by Biswas (1943).

The hybrid *Cardamine flexuosa* $\times$ *hirsuta* (*C. zahlbrucknerana* O. E. Schulz) is known from the wild. It was reported by Schulz (1903) as occurring naturally in Austria and there are specimens in the collections of the British Museum (BM) from localities in the Basses Pyrénées and Montgomeryshire. These specimens have been overlooked until recently, which may indicate that the hybrid has often not been recognized in the wild. It has been synthesized by Benoit (1957) and on separate occasions by both of the present authors.

C. flexuosa does not at first sight appear to be as closely related to any other species of *Cardamine* as it is to *C. hirsuta*. Several hybrids were reported by Schulz (1903) but only *C. flexuosa* $\times$ *hirsuta* and *C. flexuosa* $\times$ *pratensis* have been proved by synthesis (Lövkvis 1957). Possible origins of *C. flexuosa* may be summarized as in Table 2.

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TABLE 2. Possible origins of *Cardamine flexuosa*.

ALLOPOLYD ORIGIN		(Doubling of chromosome complement $2n = 16 \rightarrow 32$)	CARDAMINE FLEXUOSA
1. <i>Cardamine hirsuta</i> × <i>C. caldeirarum</i>	}		
2. <i>Cardamine hirsuta</i> × <i>C. impatiens</i>			
3. <i>Cardamine hirsuta</i> × <i>C. parviflora</i>			
AUTOPLOYD ORIGIN			
4. <i>Cardamine hirsuta</i>	}		
5. <i>Cardamine parviflora</i>			
6. <i>Cardamine impatiens</i>			

When *C. hirsuta* and *C. flexuosa* are compared they are seen to differ in several characters. If *C. flexuosa* is of hybrid origin between two species then the characters of the unknown parent can be predicted as in Table 3. The characters used are taken from Jones (1964).

TABLE 3. Predicted characters of the other species involved in the origin of *C. flexuosa*.

Character	<i>C. hirsuta</i>	<i>C. flexuosa</i>	Unknown Parent
1. Growth habit	annual	annual and biennial	biennial
2. Height	7-30 cm	10-50 cm	13-70 cm
3. Stem hairs	absent	present at base of stem	present throughout stem
4. Numbers of pairs of leaflets on basal leaves	1-3	3-6	5-9
5. Shape of leaflets	obovate to orbicular	ovate	ovate to elliptic
6. Leaf margin	crenate	crenate to dentate	dentate
7. Number of cauline leaves	2-4	4-10	6-16
8. Number of pairs of leaflets on cauline leaflets	2-5	5+	5-9
9. Number of stamens	6 (4)	6	6
10. Siliqua size	18-25 × 1 mm	12-25 × 1 mm	12-25 × 1 mm
11. Style size	0.5-1.0 mm	1-1.5 mm	1.5-2.0 mm
12. Diploid chromosome number	16	32	16
13. Seed size	0.9-1.0 × 0.7-0.8 mm	1.0-1.2 × 0.8-0.9 mm	1.1-1.4 × 0.9-1.0 mm

The predicted characters of the putative parent are compared with the characters of *C. caldeirarum*, *C. impatiens* and *C. parviflora* in Table 4.

Banach (1950) suggested that *C. flexuosa* might be an autotetraploid derivative of *C. hirsuta*. This suggestion was made because of the close morphological resemblance between the species. The assumption made (that an autotetraploid derivative closely resembles the diploid) appears to be supported by evidence from other plant species, but here we are dealing with a diploid and a tetraploid which differ in a significant number of features, and this invalidates Banach's conclusion. In fact, as will be clear from the data given later in the paper, the synthesized autotetraploid resembles diploid *C. hirsuta* more closely than *C. flexuosa* and bears out this point. According to Stebbins (1957) there is a correlation between autopolyploidy and outbreeding, and between allopolyploidy and inbreeding in all published examples. It is worth noting that *C. flexuosa* is inbreeding; if Stebbins' correlation holds in this case, we would expect the plant to be an allopolyploid.

TABLE 4. Comparison of the characters of possible parent species with those predicted from a comparison of *C. hirsuta* and *C. flexuosa*.

Character (as Table 3)	<i>C. caldeirarum</i>	<i>C. impatiens</i>	<i>C. parviflora</i>
1	2	1	0
2	1	2	0
3	1	0	0
4	1	0	2
5	1	2	2
6	1	2	0
7	—	—	—
8	1	2	2
9	2	2	2
10	0	1	2
11	—	—	—
12	—	2	2
13	—	2	0
Total	10	16	12
Total possible	18	22	22
% affinity	55%	72%	54%

Explanation of scoring

2 = corresponds to predicted character.

1 = $\pm$ corresponds to predicted character.

0 = does not correspond to predicted character.

$$\% \text{ affinity} = \frac{\text{Actual score}}{\text{Total possible}}$$

The morphology of *C. flexuosa* and *C. hirsuta*, introduced into New Zealand, has been studied by Pritchard (1955, 1957) who reports differences between the species similar to those seen in European material.

Experimental investigation was confined to *C. flexuosa*, *C. hirsuta*, *C. hirsuta* autotetraploid, the F_1 hybrid *C. flexuosa* $\times$ *hirsuta* and *C. impatiens*. All observations have been made on plants cultivated under similar conditions.

LEAF MORPHOLOGY

C. flexuosa and some apparently closely related species show leaf polymorphism. For comparison of leaf characters, samples were taken from the rosette and from the lower and upper parts of the flowering stem. In *C. flexuosa* and *C. impatiens* these three categories of leaf could be easily distinguished. In *C. hirsuta*, some samples showed three main leaf types, but in others it was possible to distinguish only rosette and cauline leaves.

In the synthesized F_1 hybrid between *C. flexuosa* and *C. hirsuta*, only small differences were observed between the lower and upper cauline leaves.

The characters which were analysed statistically are: leaf length, number of pinnae per leaf and the dimensions of the terminal leaflet. The means of these characters are summarized in Tables 5–7. The number of measurements made in each sample was twenty except for the *C. hirsuta* autotetraploid where the extremes of the ranges of variation were estimated. More precise estimates cannot be given because each tetraploid plant possesses comparatively few leaves.



Fig. 1. Leaf morphology of *Cardamine impatiens*, *C. flexuosa* and *C. hirsuta*.

Fig. 2.

		<i>C. impatiens</i>		<i>C. hirsuta</i>		<i>C. flexuosa</i>				<i>C. hirsuta</i> x <i>C. flexuosa</i>		<i>C. hirsuta</i>	
		S70	S76	S27	Lip	P2	P16	6647	6609	Lym	F1	4x	
<i>C. impatiens</i>	S70		0	4	0	1	3	3	3	3	1	2	
	S76			5	6	7	3	2	5	4	3	5	
	S27		% 10.4		4	7	7	6	6	6	4	5	
	Lip			% 48.6		6	2	6	5	5	4	8	
<i>C. hirsuta</i>	P2						1	2	1	1	2	8	
	P16							5	8	7	2	0	
	6647		% 25.0		% 22.5				11	10	6	5	
	6609						% 70.0			10	5	4	
<i>C. flexuosa</i>	Lym										6	3	
	<i>C. flexuosa</i> x <i>C. hirsuta</i>		% 8.3		% 27.0			% 39.6					2
	<i>C. hirsuta</i>		% 16.6		% 54.0			% 25.0			% 16.6		
	4x												

TABLE 5. Dimensions of rosette leaves. N = 20 for leaf measurements.

Species	Mean	Standard deviation	Range in sample
(i) Leaf length (cm)			
<i>C. impatiens</i> S70	19.11	4.30	11.70-23.20
<i>C. hirsuta</i> S76	6.45	0.68	4.30-9.70
„ S27	7.42	1.50	4.90-11.00
„ P2	4.20	0.72	3.50-6.30
„ Lip.	5.41	1.45	4.11-9.20
<i>C. flexuosa</i> P16	15.70	2.60	10.00-19.40
„ 6647	12.91	2.22	7.80-16.60
„ 6609	13.36	2.31	7.15-17.70
„ Lym.	9.93	2.10	5.70-14.10
<i>C. hirsuta</i> × <i>flexuosa</i> F ₁	9.25	1.71	7.75-14.50
4x <i>C. hirsuta</i>	—	—	5.00-5.80
(ii) Pinnae per leaf			
<i>C. impatiens</i> S70	14.55	1.62	13-17
<i>C. hirsuta</i> S76	6.10	1.16	3-7
„ S27	7.37	1.09	3-9
„ P2	6.50	1.90	3-7
„ Lip.	6.40	1.67	3-7
<i>C. flexuosa</i> P16	12.70	1.71	11-15
„ 6647	10.82	2.48	9-15
„ 6609	12.25	2.13	11-15
„ Lym.	10.00	1.00	8-13
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	9.25	1.71	5-11
4x <i>C. hirsuta</i>	—	—	7-8
(iii) Length of terminal leaflet (mm)			
<i>C. impatiens</i> S70	19.40	5.15	10.50-27.00
<i>C. hirsuta</i> S76	7.77	1.81	5.50-13.00
„ S27	13.10	2.48	9.00-18.00
„ P2	6.70	0.90	3.50-9.80
„ Lip.	7.6	1.13	5.30-10.20
<i>C. flexuosa</i> P16	17.27	2.19	14.50-20.0
„ 6647	12.55	1.99	10.50-16.50
„ 6609	11.33	3.71	9.00-24.00
„ Lym.	12.00	2.20	11.80-16.45
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	11.62	1.93	8.00-13.50
4x <i>C. hirsuta</i>	—	—	6.00-10.00
(iv) Breadth of terminal leaflet (mm)			
<i>C. impatiens</i> S70	13.49	3.94	10.00-19.00
<i>C. hirsuta</i> S76	9.37	1.62	7.00-13.00
„ S27	16.10	3.53	8.00-18.50
„ P2	9.47	2.00	7.50-15.20
„ Lip.	7.70	1.80	5.70-14.60
<i>C. flexuosa</i> P16	16.22	2.27	12.00-22.00
„ 6647	12.85	3.00	8.50-21.00
„ 6609	15.55	2.71	10.00-21.00
„ Lym.	12.00	1.40	11.50-16.50
<i>C. hirsuta</i> × <i>flexuosa</i> F ₁	9.55	1.87	7.00-13.00
4x <i>C. hirsuta</i>	—	—	8.00-11.00

TABLE 6. Dimensions of lower cauline leaves. N = 20 for leaf measurements.

Species	Mean	Standard deviation	Range in sample
(i) Leaf length (cm)			
<i>C. impatiens</i> S70	10.59	2.60	7.30-14.00
<i>C. hirsuta</i> S27	6.50	1.35	3.60- 7.20
„ P2	4.20	0.77	2.85- 5.20
<i>C. flexuosa</i> P16	7.14	1.51	4.50- 9.90
„ 6647	3.94	1.69	3.30- 6.25
„ 6609	4.02	1.40	2.52- 7.20
„ Lym.	6.56	3.40	3.16-10.36
4x <i>C. hirsuta</i>	—	—	3.2 - 4.00
(ii) Pinnae per leaf			
<i>C. impatiens</i> S70	14.12	1.12	13-16
<i>C. hirsuta</i> S27	6.77	1.09	5- 8
„ P2	5.90	0.99	5- 7
<i>C. flexuosa</i> P16	10.50	1.46	7-13
„ 6647	10.45	1.29	9-13
„ 6609	10.21	0.83	9-13
„ Lym.	9.00	1.41	6-12
4x <i>C. hirsuta</i>	—	—	6- 4
(iii) Length of terminal leaflet (mm)			
<i>C. impatiens</i> S70	13.00	2.32	10.00-16.50
<i>C. hirsuta</i> S27	19.00	3.65	13.50-23.50
„ P2	7.90	1.80	6.10-11.50
<i>C. flexuosa</i> P16	15.67	4.58	11.00-22.00
„ 6647	8.16	2.59	4.50-12.00
„ 6609	11.33	2.64	7.83-16.33
„ Lym.	14.20	1.53	11.20-18.70
4x <i>C. hirsuta</i>	—	—	8.00-12.00
(iv) Breadth of terminal leaflet (mm)			
<i>C. impatiens</i> S70	6.50	0.92	5.00- 8.00
<i>C. hirsuta</i> S27	7.27	1.65	5.50-10.00
„ P2	7.40	0.99	5.40-10.13
<i>C. flexuosa</i> P16	11.25	2.81	7.00-15.50
„ 6647	7.09	2.50	4.50-12.00
„ 6609	9.42	1.89	6.21-15.82
„ Lym.	9.90	1.23	7.40-13.60
4x <i>C. hirsuta</i>	—	—	4.00- 6.00

These characters can be divided into those which are the same in two or more samples, indicating affinity, and those significantly different, indicating distinctness. Fig. 2 indicates: (i) the number of characters common to any two of the samples studied, and (ii) percentage affinity between the taxa studied.

There are distinct differences between *C. flexuosa*, *C. hirsuta* and *C. impatiens* in six of the twelve leaf characters studied. These are leaf length and number of pinnae per leaf for rosette, lower cauline and upper cauline leaves. In all these characters *C. flexuosa* is intermediate between *C. hirsuta* and *C. impatiens*.

Stomatal guard cell sizes were measured on rosette leaf terminal leaflets obtained from herbarium specimens. Guard cell length and breadth were measured by means of a camera lucida. The mean sizes are summarized in Fig. 3.

TABLE 7. Dimensions of upper cauline leaves. N = 20 for leaf measurements.

Species	Mean	Standard deviation	Range in sample
(i) Leaf length (cm)			
<i>C. impatiens</i> S70	6.43	1.30	4.15- 8.00
<i>C. hirsuta</i> S76	3.07	0.61	1.45- 4.80
„ S27	3.60	1.10	2.40- 5.20
„ P2	3.30	1.48	1.80- 3.67
„ Lip.	1.98	0.75	1.25- 4.10
<i>C. flexuosa</i> P16	3.26	1.00	2.10- 5.70
„ 6647	2.86	1.86	1.60- 8.70
„ 6609	4.02	1.40	2.00- 8.30
„ Lym.	3.44	1.52	2.05- 7.90
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	3.28	0.82	2.10- 4.70
4x <i>C. hirsuta</i>	—	—	1.80- 2.20
(ii) Pinnae per leaf			
<i>C. impatiens</i> S70	15.10	2.09	11-17
<i>C. hirsuta</i> S76	4.50	0.84	3- 6
„ S27	6.50	3.33	5- 7
„ P2	5.28	0.71	4- 7
„ Lip.	6.60	0.84	5- 7
<i>C. flexuosa</i> P16	7.75	1.16	5- 9
„ 6647	8.13	1.54	8-13
„ 6609	8.11	1.42	5- 9
„ Lym.	7.40	0.84	5- 9
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	7.85	1.08	7-10
4x <i>C. hirsuta</i>	—	—	4- 7
(iii) Length of terminal leaflet (mm)			
<i>C. impatiens</i> S70	18.30	3.78	12.50-22.00
<i>C. hirsuta</i> S76	10.20	3.01	5.50-15.50
„ S27	14.83	3.66	10.50-21.00
„ P2	9.20	0.50	8.00-10.70
„ Lip.	7.15	0.29	6.50- 8.20
<i>C. flexuosa</i> P16	12.00	3.24	8.00-18.00
„ 6647	9.59	4.05	5.00-19.50
„ 6609	11.33	2.64	7.00-11.00
„ Lym.	10.60	1.19	7.30-13.80
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	8.07	2.81	4.00-15.00
4x <i>C. hirsuta</i>	—	—	7.00- 9.00
(iv) Breadth of terminal leaflet (mm)			
<i>C. impatiens</i> S70	6.64	1.04	6.00- 9.00
<i>C. hirsuta</i> S76	4.15	1.59	2.00- 7.00
„ S27	2.16	0.81	1.00- 3.00
„ P2	4.19	0.45	3.25- 6.02
„ Lip.	2.57	0.19	1.80- 3.24
<i>C. flexuosa</i> P16	5.83	1.49	3.00-10.00
„ 6647	6.68	2.00	2.00-12.50
„ 6609	5.55	1.84	3.00- 5.50
„ Lym.	5.80	0.23	5.20- 6.70
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	5.20	0.66	2.50- 8.50
4x <i>C. hirsuta</i>	—	—	1.50- 2.50

FLORAL MORPHOLOGY

The floral morphology of *C. flexuosa*, *C. hirsuta*, *C. impatiens* and the F₁ hybrid *C. flexuosa* × *hirsuta* was examined. The numbers of floral parts observed were usually sepals four, petals four, stamens six, and ovary one, but in diploid *C. hirsuta*, individuals

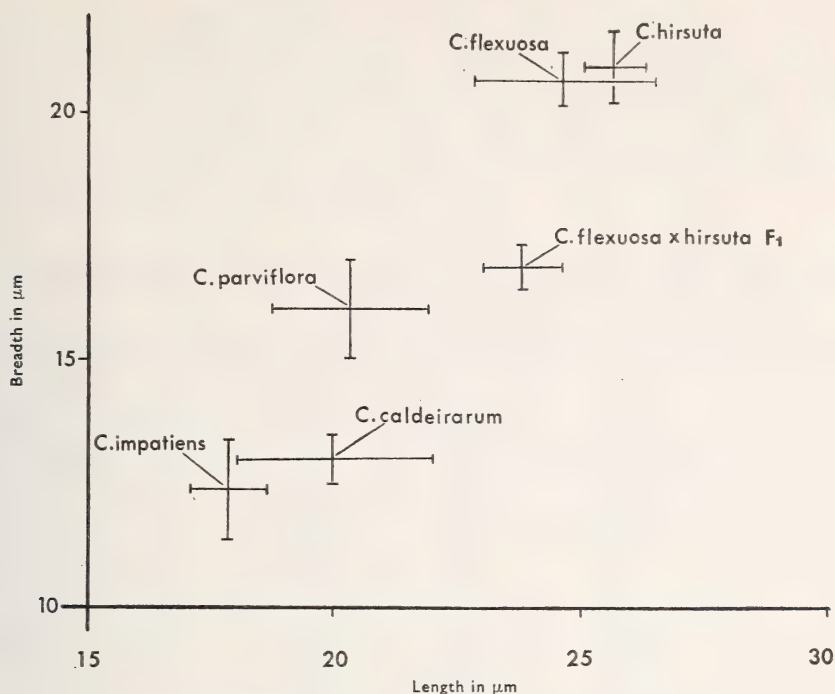


Fig. 3. Sizes of stomata, means $\pm$ twice standard error of the mean.

with only four stamens were occasionally observed, while in autotetraploid *C. hirsuta*, four stamens were consistently observed. One of eleven collections of *C. impatiens* studied was apetalous.

Measurements of sepals, petals and stamens were made on flowers which had opened and which possessed stigmas capable of pollination, by photographing the dissected flower parts and measuring images produced by projecting the negative. This was judged by observing stigmatic papillae which on young stigmas have not developed and which on older stigmas wither. Between these stages, stigmatic papillae are prominent for a period of about two days and experimental pollination is possible. In the Cruciferae, the six stamens are normally arranged in two pairs of long and one pair of short stamens. The longer and shorter stamens were separated for analysis.

C. flexuosa was found to be intermediate in sepal size but larger than *C. impatiens* and *C. hirsuta* in petal and stamen size. When compared with autotetraploid *C. hirsuta*, *C. flexuosa* was seen to have smaller sepals and anthers while the petals were the same size. Autotetraploid *C. hirsuta* had larger floral parts than the diploid.

Differences observed between the shape of the stigma in the mature fruit in *C. hirsuta*, *C. impatiens* and *C. flexuosa* are summarized in Fig. 4.

POLLEN SIZE

Pollen shape was found to vary between ellipsoidal and spherical depending on the degree of dehydration, when examined without mountant, or with concentration of the mountant, e.g. glycerine. Changes of size were noted at the same time as the changes of shape. For these reasons all measurements were made on pollen mounted in acetocarmine in 45 per cent. acetic acid. The diameters of the pollen samples measured are summarized in Table 8. Mean pollen volume was calculated from half the mean diameter for each sample.

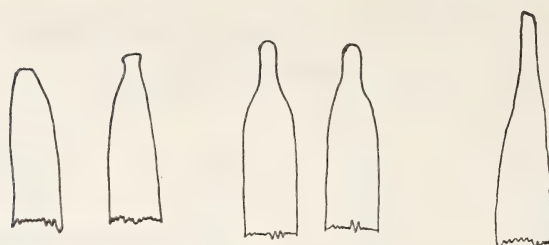
Fig. 4. Stigma shape in mature pod; (left to right) *C. hirsuta*, *C. flexuosa*, *C. impatiens*.

TABLE 8. Pollen diameters.

Species	Sample reference	Number in sample	Mean diameter in μm	2 $\times$ Standard error of mean	Pollen volume ($\times 10^3 \mu\text{m}^3$)
<i>C. flexuosa</i>	Lymington	500	23.58	0.18	6.86
	P30	400	29.33	0.15	13.21
	Coimbra	300	25.07	0.82	8.25
<i>C. flexuosa</i> (male sterile)	6609	260	20.21	1.04	4.32
<i>C. impatiens</i>	S70	412	18.83	0.19	3.50
<i>C. hirsuta</i>	S27	104	29.20	1.66	13.04
	Frome	201	23.86	0.62	7.11
Synthetic <i>C. hirsuta</i> $\times$ <i>flexuosa</i>	F ₁ hybrid	108	21.90	1.84	5.50
	F ₂ hybrid	100	21.76	0.91	5.39
<i>C. hirsuta</i> (4x), synthetic autotetraploids	S27C3	180	31.60	0.28	16.52
	S27C23	64	36.09	0.99	24.61
	S27C6	278	40.43	1.10	34.60

GEOGRAPHICAL DISTRIBUTION

The geographical ranges of these species cited by Schulz (1903) in his monograph of *Cardamine* indicate that the most widespread species have well differentiated regional morphological types; some of these are treated as species in more recent accounts (e.g. Hultén 1958). *C. hirsuta* is commonly anthropochorous. It seems that the very widespread *C. flexuosa* is not of recent origin, and from their present distributions *C. caldeirarum* and *C. trichocarpa* are unlikely to have been involved in its origin.

TABLE 9
Geographical distribution of *C. flexuosa* and related species.

Species	Distribution
<i>C. flexuosa</i> subsp. <i>flexuosa</i>	Europe, Asia Minor and possibly native in Eastern N. America.*
<i>C. hirsuta</i> subsp. <i>hirsuta</i>	Cosmopolitan in the north temperate zone and widespread in the tropics and southern hemisphere.** (The species is a successful anthropochore whose region of origin is uncertain.)
<i>C. impatiens</i>	Europe; W. & C. Asia.
<i>C. parviflora</i> subsp. <i>parviflora</i>	Europe; Algeria; Iran; Siberia; China.***
<i>C. caldeirarum</i>	Açores.
<i>C. trichocarpa</i>	E. African mountains; Ceylon; Assam.

* Other subspecies and allied species in E. Asia and N. America.

** Other subspecies in N. America and E. Asia.

*** Subsp. *virginica* in N. America.

Hultén (1950) in his classification of Scandinavian plants into migrational groups and distribution types considers *C. flexuosa*, *C. hirsuta*, and *C. impatiens* to be in the same migrational group—that of southern plants adapted to conditions of north-west Europe.

His maps show that *C. impatiens* and *C. hirsuta* do not have such a widespread or northerly distribution as *C. flexuosa* in Scandinavia. *C. impatiens* is primarily a species of moist woodlands and *C. hirsuta* of open, drier habitats; *C. flexuosa* is ecologically diverse, and occupies a wide range of intermediate habitats.

DISCUSSION

The impression that *C. flexuosa* and *C. impatiens* have morphological affinities has been confirmed by closer examination. However the lack of data concerning *C. parviflora* and *C. caldeirarum* does not allow the relationship of these species to *C. flexuosa* to be fully established. The chromosome number of *C. caldeirarum* has never been determined. The mean stomatal guard cell size of this species and *C. parviflora* is close to *C. impatiens*, indicating the possibility that they are diploids (see Fig. 3). The pollen volume of *C. caldeirarum* is similar to that of *C. hirsuta*. *C. caldeirarum* is morphologically similar to *C. flexuosa* and if it is a diploid the possibility that *C. flexuosa* is an autotetraploid derivative of it cannot be excluded on the present evidence. The morphology of *C. impatiens* and *C. parviflora* seems to be sufficiently distinct from *C. flexuosa* to preclude the possibility that they may have given rise to it by autotetraploidy.

Comparison of the leaf morphology of *C. flexuosa* with *C. hirsuta* and *C. impatiens* shows that the affinity of *C. flexuosa* with either species is of the same order. In both cases about 25 per cent. of the characters of *C. flexuosa* are shared with *C. hirsuta* and *C. impatiens*. Autotetraploid *C. hirsuta* and the F_1 hybrid *C. flexuosa* $\times$ *hirsuta*, on the other hand, show a greater affinity with one of the species or the other. Autotetraploid *C. hirsuta* shares about 50 per cent. of characters with *C. flexuosa*. *C. flexuosa* $\times$ *hirsuta* F_1 shares about 40 per cent. of characters with *C. flexuosa* but only 27 per cent. with *C. hirsuta*. These facts are in accordance with the hypothesis that *C. flexuosa* is not autotetraploid *C. hirsuta*, but is intermediate between *C. hirsuta* and *C. impatiens*, and arose by allopolyploidy. This is further supported by the fact that, in the characters which show statistically significant differences, *C. flexuosa* is intermediate between *C. hirsuta* and *C. impatiens*.

Floral morphology varies less than leaf morphology and may be related to the prevalence of inbreeding. This contrasts with the diversity of flower size, shape and colour seen in the outbreeding *Cardamine pratensis*. *C. hirsuta*, *C. flexuosa* and *C. flexuosa* $\times$ *hirsuta* F_1 shared five of the six flower characters studied. *C. flexuosa* and autotetraploid *C. hirsuta*, and *C. impatiens* and *C. hirsuta* (both diploid and autotetraploid) shared three characters. In contrast, the shape of stigmas from mature pods varies considerably (see Fig. 4) and *C. flexuosa* is again seen to be intermediate between *C. hirsuta* and *C. impatiens*.

Apart from the characters examined statistically, the general impression gained is that, under the conditions of experimental cultivation, *C. flexuosa* is morphologically intermediate between *C. hirsuta* and *C. impatiens*. This is so for example in growth habit, where *C. hirsuta* is short and upright and *C. impatiens* tall and lax, and in the features of the margin of the leaflets (see Fig. 1). It is also the case in occurrence of stipules, which are present in *C. impatiens*, absent from *C. hirsuta* and 'vestigial' in *C. flexuosa*. These differences are not so apparent in herbarium material, or in plants in the wild.

The pollen-volumes of the plants examined present an interesting problem. The synthetic autotetraploid of *C. hirsuta* has pollen twice the volume of diploid *C. hirsuta*. However, the wild tetraploid *C. flexuosa* has pollen of a similar volume to that of *C. hirsuta*. This is circumstantial evidence which supports the hypothesis, based upon external morphology, that *C. flexuosa* did not arise as an autotetraploid of *C. hirsuta*. A possible explanation may lie in the low pollen volume of *C. impatiens*, the other putative diploid parent of *C. flexuosa*: although *C. impatiens* and *C. hirsuta* both have $2n = 16$, the pollen-volume of the former is half that of the latter species. A hybrid between these two might be expected to have pollen of an intermediate size, and the 'raw' allopolyploid derivative

should have pollen somewhat larger than that of *C. hirsuta* (Table 10). The observation of pollen volumes for *C. flexuosa* rather lower than expected on the assumption that tetraploidy doubles the pollen-volume, may be due to intergenomic segregation of genetic factors determining pollen size and to selection subsequently favouring small microspores. *Nasturtium officinale* sensu lato presents a parallel case. *N. microphyllum* is an allo-octoploid, one of whose parents is the tetraploid *N. officinale* sensu stricto (Howard & Manton 1946).

TABLE 10. Comparison of observed and predicted pollen volumes.

Species	Genotype	Predicted pollen volume $\times 10^3 \mu\text{m}^3$	Observed means of pollen volume $\times 10^3 \mu\text{m}^3$
(i) <i>Diploids</i>			
<i>C. impatiens</i>	AA	—	3.5
<i>C. hirsuta</i>	BB	—	7.1–13.0
<i>C. impatiens</i> $\times$ <i>hirsuta</i> F ₁	AB	5.3–8.2	—
(ii) <i>Triploids</i>			
<i>C. flexuosa</i> $\times$ <i>hirsuta</i> F ₁	ABB	6.2–10.6	5.5
(iii) <i>Tetraploids</i>			
Tetraploid	AAAA	7.0	—
derivatives of	BBBB	14.2–26.0	16.5–34.6
above diploids	AABB	10.6–16.5	—
<i>C. flexuosa</i>	AAAA AAAB AAAB	* } 7.0–16.5	6.9–13.2

* = hypothetical genotypes, refer to text for explanation.

The pollen volumes for the two species, calculated from the data of Green (1955), are $8.2\text{--}14.2 \times 10^3 \mu^3$ and $4.1\text{--}9.2 \times 10^3 \mu^3$ respectively. Here also the upper limits of the range of the allopolyploid pollen volumes is rather less than might be expected from a doubling of the tetraploid pollen volume. The same explanation may be given for the fact that the stomatal guard-cells of *C. hirsuta* and *C. flexuosa* are statistically indistinguishable in size (Fig. 3).

As there are taxonomic difficulties in these species, the reported geographical distributions do not allow reliable conclusions to be drawn about the 'centre of origin' of the group. However, the distribution of the species in Scandinavia is significant; there is a difference between the more southerly and restricted diploids and the tetraploid which is more widespread and extends farther north. *C. hirsuta* and *C. flexuosa* show a similar and widespread distribution in the British Isles (Perring & Walters 1962). *C. impatiens* is rarer and restricted to a narrower range of habitats, mainly on limestone.

The differences in the relative distribution of the diploid and tetraploid species in Scandinavia and Britain may exist for several reasons. The glaciation of Scandinavia was more extreme than in Britain and present day climates are more severe in Scandinavia. Differences in distribution may therefore reflect differences in genetic variability and hence adaptability, i.e. ability to invade new habitats and to diversify genetically in developing vegetation types. This makes the allopolyploid origin for *C. flexuosa* more likely than an autopolyploid origin whose long-term consequence would be the stabilization of existing genotypes.

CONCLUSIONS

C. flexuosa is morphologically distinguishable from both diploid and autotetraploid *C. hirsuta*, and it does not appear likely to have arisen from *C. hirsuta* by autopolyploidy. Lack of evidence does not allow comment on the possibility of autotetraploid origin from

C. caldeirarum. At the same time the available evidence concerning the morphology of *C. hirsuta* and *C. impatiens* suggests that *C. flexuosa* may have arisen by hybridization of these diploid species followed by doubling of the chromosome complement.

The similarity in pollen volume and stomatal guard cell size between the tetraploid *C. flexuosa* and the diploid *C. hirsuta* is most easily explained by the origin of the tetraploid species from the hybridization of *C. hirsuta* with another diploid species characterized by smaller guard cells and microspores; *C. impatiens* has such features.

The geographical distribution of the species in Scandinavia also supports this hypothesis: the tetraploid has a wider ecological amplitude than either of its presumed parents, but the habitats lie, in most respects, between the extremes of the putative parent species.

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APPENDIX

Sources of material. (Collections of wild origin, except where indicated)

<i>C. impatiens</i> S70	Berlin Botanic Garden, Germany.
<i>C. hirsuta</i> S76	Yalta Botanic Garden, U.S.S.R.
„ S27	Palermo Botanic Garden, Sicily.
„ P2	Wisley, England.
„ Frome	Frome, England.
„ Lip.	Liphook, England.
<i>C. flexuosa</i> P16	Denmead, nr. Portsmouth, England.
„ Coimbra	Coimbra Botanic Garden, Portugal.
„ 6647	Lac du Gaube, Hautes Pyrénées, France.
„ 6609	L'Hospitalet, Pyrénées Orientales, France.
„ Lym.	Lymington, England.
„ P30	Lock's Bridge, Sussex, England.
<i>C. flexuosa</i> × <i>hirsuta</i> F ₁	Experimentally produced hybrid between <i>C. flexuosa</i> P16 and <i>C. hirsuta</i> S76.
<i>C. hirsuta</i> 4x S273	Experimentally induced autotetraploids from <i>C. hirsuta</i> S27.
„ S276	
„ S2723	

A NEW COMBINATION IN *DACTYLORHIZA*

My attention has been drawn to the fact that the new combination *Dactylorhiza majalis* subsp. *cambrensis* (R. H. Roberts) R. H. Roberts, *Watsonia* 6, 261 (1966) was not validly published, because the exact page where the basionym occurred was not given. The opportunity is now taken to make the new combination valid according to the International Code of Botanical Nomenclature.

Dactylorhiza majalis (Reichb.) P. F. Hunt & Summerhayes subsp. ***cambrensis*** (R. H. Roberts) R. H. Roberts **comb. nov.**

Basionym: *Dactylorchis majalis* (Reichb.) Vermeul. subsp. *cambrensis* R. H. Roberts, *Watsonia* 5, 41 (1961).

I am grateful to Dr. R. K. Brummitt for bringing this error to my notice.

R. H. ROBERTS

BOOK REVIEWS

The Flora of Greenland. Tyge W. Böcher, Kjeld Holmen and Knud Jakobsen. Pp. 312, with 66 text figures, 2 coloured plates and a map of Greenland with floristic provinces and districts. Illustrated by Ingeborg Fredriksen. Translated from Danish by T. T. Elkington and M. C. Lewis. P. Haase & Sons, Copenhagen. 1968. Price £5.

Greenland is considered to be the largest island in the world, having an area of 850,000 square miles which is about nine times as big as that of the British Isles. Its flora of vascular plants, however, consists only of about 500 species (including microspecies), whilst the number of native species of vascular plants in the British Isles is about 2,180 (including microspecies). This is due to the fact that Greenland is situated mainly in the Arctic, where a low summer temperature and a short growing season affect the vegetation. In addition, except for a coastal fringe of varying width up to 95 miles, it is covered by a huge continuous ice cap, rising to a height of several thousand feet at its centre.

Much attention has been devoted to study of the Greenland flora and vegetation, because the growing conditions near the ice cap or on nunataks (small ice-free summits of rocky mountains protruding through the ice cap) are similar to those which prevailed in Europe and N. America during the glacial period. The Greenland flora has also provided an interesting subject for the study of the relationship between the North American, Icelandic and Scandinavian floras and of their origin, because Greenland is located between the Canadian Eastern Arctic (being separated only by some narrow straits in the North-West, and by the wide Baffin Bay in the West), Iceland (separated by the Denmark Sea in the South-East) and Svalbard (separated by the Greenland Sea in the North-East).

Although the investigation of the Greenland Flora commenced about 200 years ago, the first scientific Flora of Greenland, *Conspectus Florae Groenlandicae*, was published by J. Lange in 1880, with two supplements in 1887 and 1892, where 371 species of vascular plants were recorded. Subsequently very extensive botanical explorations were carried out, and they have resulted in *Grønlands Flora*, produced in 1957 by T. W. Böcher, K. Holmen and K. Jakobsen, well-known Danish experts on the Greenland flora. This first edition (in Danish) embodied the results of critical study of many difficult groups and contained 485 species of vascular plants. For those not familiar with Danish there was a short English Guide, together with translated abbreviations of plant occurrence and frequency. The second edition appeared in 1966. It was slightly modified, but enlarged and much revised, especially in respect of some critical groups in the following genera: *Dryas*, *Potentilla*, *Papaver*, *Cerastium*, *Stellaria*, *Campanula*, *Carex*, *Trisetum*, etc. Twelve figures, each containing illustrations of several species, were added, making 62 figures showing habit and morphological detail of about 290 species, as well as four figures of leaf-shapes, diagrams of flowers and types of inflorescence. As a result of recent discoveries the number of species dealt with was considerably increased.

The English translation of the second edition of Böcher, Holmen & Jakobsen's *Grønlands Flora*, now being reviewed, is well done by two British botanists, Dr. T. T. Elkington of the University of Sheffield, and Dr. M. C. Lewis of the University of Birmingham. The two versions of the second edition are nearly identical, except that the introductory chapter dealing with botanical terminology in the Danish version is omitted in the English one, where it is replaced by a glossary of botanical terms at the end of the book. The book contains 496 species, few of which are adventive or introduced. Of these species about a quarter are natives of Britain, some of these being represented in Greenland by a different variety or subspecies. Several species are new, being endemics to Greenland, e.g. *Hieracium trigonophorum* Oskarss., *Taraxacum amphiphrons* Böch., *Sisyrinchium groenlandicum* Böch., etc. *Rhododendron vanhoeffenii* Abrom., found at Karajak Nunatak in Continental West Greenland, is possibly a good species according to the authors, but may be an intergeneric hybrid between *Ledum palustre* L. and *Rhododendron lapponicum* L. The Greenland '*Equisetum* × *trachyodon* A. Braun', which has been reported from Qagssiarsuk at Igaliko Fjord in SW Greenland, also offers a problem. *E.* × *trachyodon* is supposed to be a hybrid between *E. hyemale* L. and *E. variegatum* Schleich. ex Weber & Mohr. As *E. hyemale* has not been found in Greenland, the occurrence of *E.* × *trachyodon* has been explained by its introduction there by Norsemen settlers in the past. However, examination of material referred to *E.* × *trachyodon*, collected in the above-mentioned locality and preserved at the British Museum (Natural History), revealed that it shows a remarkable resemblance to *E. variegatum* var. *wilsonii* (Newm.) Milde, occurring in Kerry. The late A. H. G. Alston, who examined Rosenvinge's specimen of *E. hyemale* var. *doellii* Milde, on which the Greenland record of *E.* × *trachyodon* was based, came to a conclusion that it is not *E.* × *trachyodon*, but represents a form of *E. variegatum* (cf. Polunin 1959). The Flora also contains 30 distinct hybrids, of which two are supposed to be intergeneric hybrids, between *Leucorchis albida* var. *straminea* (Fern.) Á. Löve and *Platanthera hyperborea* (L.) Lindl., and between *Agropyron violaceum* (Hornem.) Lge. and *Elymus arenarius* subsp. *mollis* (Trin.) Hult. A considerable number of changes in nomenclature are made, some for taxonomic reasons, by raising some minor taxa to specific rank, e.g. *Lycopodium dubium* Zoega and *Carex boecheriana* Löve, Löve & Raymond, or by sinking some species to a lower rank, e.g. in *Draba*; others owing to misapplication of a name, e.g. *Thymus drucei* Romm. is replaced by *T. praecox* subsp. *arcticus* (Dur.) Jalas and *Campanula rotundifolia* L. by *C. gieseckiana*

Vest; and still others for purely nomenclatural reasons, bringing the nomenclature more up to date, e.g. *Euphrasia arctica* Lge. ex Rostr. is replaced by *E. frigida* Pugsley.

With regard to the pteridophytes, the generic names follow *Flora Europaea*, except for *Thelypteris phegopteris* (L.) Slosson, which in the first edition was treated as *Lastrea phegopteris* (L.) Bory and in the second as *Phegopteris connectilis* (Michx.) Watt. The generic limits in the phanerogams in some cases are different from those adopted by British botanists. Thus, *Comarum* is kept apart from *Potentilla*, *Melandrium* from *Silene*, *Viscaria* from *Lychnis*, and *Elytrigia* and *Roegneria* from *Agropyron*, but *Chamaepericlymenum* is united with *Cornus* and *Arctous* with *Arctostaphylos*. The correct spelling of the generic name of the Sea Sandwort is *Honkenya*, not *Honckenya*. Some specific names of the first edition familiar to the British botanists have been replaced by names rejected in Dandy's *List of British Vascular Plants* and in recent British Floras, e.g. *Callitriche intermedia* Hoffm. by *C. hamulata* Kütz. and *Carex curta* Good. by *C. canescens* L. Some further discrepancies are as follows: *Atriplex latifolia* Wbg. is used instead of *A. hastata* L., *Calamagrostis neglecta* (Ehrh.) G., M. & S. instead of *C. stricta* (Timm) Koel., and *Phleum commutatum* Gaud. instead of *P. alpinum* L. *Potamogeton pusillus* subsp. *groenlandicus* (Hagstr.) Böch. should be referred to *P. berchtoldii* Fieb.

We are told in the Preface which sections of the book were done by the three Danish authors. The first chapter 'Earlier accounts of the Greenland Flora' deals with a history of exploration of the Greenlandic vascular plants, giving an account of published species lists and Floras. It is accompanied by a list of references. The chapter 'The occurrence and distribution of the species' shows the vegetational belts in Greenland and floristic provinces. Special attention has been directed to the descriptions of the most important types of Greenland plant communities, such as copse; herb slopes; snow-patches; grassland slopes; arctic-subarctic steppe; dwarf-shrub heath or heather moor; fell-fjeld; communities on solifluction soils; beaches and dunes; saltmarsh; bog; fen, marsh and wet flushes; and freshwater lakes. The descriptions are brief, but they characterize each type of habitat well, and include a mention of some of the most characteristic plants of each habitat. The main part is devoted to a taxonomic treatment of pteridophytes and phanerogams. It is well done and easy to use. The arrangement, with some modifications, is similar to that adopted by Clapham, Tutin & Warburg's *Flora of the British Isles*, where pteridophytes are placed at the beginning and monocotyledons at the end. There are keys to major groups, families, genera and species. Descriptions of all taxa are given with clear characters, followed by the chromosome number (based mainly on Jørgensen, Sørensen & Westergaard's cytological studies on the Greenland plants), by details of habitat, distribution of the species in Greenland, information about references to distributional maps published in other books or periodicals, and particulars about the total range of species. It is a pity that a key to all species of *Taraxacum* has not been produced, species of the sect. *Spectabilia* being left out. Of 17 species belonging to the Section, 14 are not supplied with descriptions. The taxonomical part is followed by a good glossary of botanical terms, a bibliography of works dealing with the distribution of plants occurring in Greenland, a carefully prepared index, and a map of Greenland with floristic provinces and districts.

The book is an excellent work, well produced; misprints are rare. Any adverse criticisms do not diminish its scientific value. The illustrations prepared by Miss Ingeborg Fredriksen are of a high standard, both from a scientific and an artistic point of view, and they will be of great assistance.

It must be mentioned that Greenland is still an open field for scientific exploration. Firstly, many areas in that vast country have not been visited, and it is possible to discover plants which may be new to Greenland or may provide new records for a particular area. Secondly, visitors could study its fascinating plant life, especially near the ice cap or on nunataks. Thirdly, many plant groups still need careful study from the cytotaxonomic point of view, e.g. *Cochlearia*, *Papaver*, *Salix glauca* L. agg., *Stellaria*, *Hieracium*, *Taraxacum*, *Poa*, and species related to *Agropyron pauciflorum* (Schwein.) Hitchc. e.g. *Roegneria virescens* (Lge.) Böcher, Holmen & Jakobsen.

The *Flora of Greenland* will be of great value to all who are interested in the Greenland flora and in arctic botany in general. Unfortunately, it is rather expensive.

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A. MELDERIS

Excursion Flora of the British Isles. A. R. Clapham, T. G. Tutin and E. F. Warburg. Second Edition. Pp. xxxv + 586. Cambridge University Press. 1968. Price £1 10s.

Six years have elapsed since the publication of the second edition of the *Flora of the British Isles*, and in that time many advances have been made in the study of British plants. Much, but not all, of this is reflected in the pages of the new edition of the *Excursion Flora*. As in the first edition, the descriptions are concise but adequate, and the keys practical and workable. The completely revised treatment of the ferns including comparatively recent revisions in *Dryopteris* and *Polypodium* is in line with modern thinking, though taxonomists still tend to disagree on the correct delimitations of taxa in the latter genus.

The main weakness of the work is I feel, in the inconsistent treatment of certain genera. Jonsell's excellent revision of the north-west European species of *Rorippa* is adopted, but the equally competent revision of *Ranunculus* section *Batrachium* by Cook is ignored, as is Nilsson's work on *Claytonia*, Nordborg's revised treatment of *Sanguisorba* and Harley's recent findings on *Mentha*.

There are the usual number of inevitable changes in nomenclature, e.g. *Erodium cicutarium* L. subsp. *bipinnatum* (Willd.) Tourlet for *E. glutinosum* Dumort. and *Agrimonia procera* Wallr. for *A. odorata*, but *Petrorhagia prolifera* is surely a slip for *P. nanteuillii*, the former species being absent from the British Isles where it is replaced by the latter. It is, however, easy to criticize and the revision of a national Flora is a major task. The present book may therefore be considered the most up-to-date account of the flora of our islands, and in view of its compact size and moderate price is certain to find its way into the hands of all those interested in British botany.

D. H. KENT

Evolutionary Biology. Edited by Th. Dobzhansky, M. K. Hecht and W. C. Steere. Vol. I. Pp. xi + 444. Appleton-Century-Crofts, New York. 1967. Price \$14.

This is the first volume of a serial publication designed to provide expert reviews in the wide and growing field of evolution. It contains eight articles, and an idea of their range may be given by quoting some of their titles, e.g. 'Chemical Evolution', 'Variation and Taxonomy of the early Hominids', 'Permanent Heterozygosity'. There are three articles which are likely to be of special interest to readers of *Watsonia*. The first of these, on the 'Use of Computers in Studies of Taxonomy and Evolution', is by D. J. Rogers, H. S. Fleming and G. Estabrook. This is easily the best article on this subject which we have ever read. It is clear, cool and critical. It describes what can and cannot be done with the aid of a computer, and it makes an excellent analysis of known applications under the two main headings of data processing and data correlation. Particularly important is the point made by the authors that rarely can a single person perform an operation of this kind successfully; the biologist will generally need the help of a mathematician, so that the problem under investigation can be properly programmed, and the results correctly interpreted.

The second article to be discussed is that on 'biochemical systematics' by the late R. E. Alston. This again is of very high quality and it is also extensive (100 pages). Alston points out that the main work in this field so far has been on secondary compounds such as the phenolics, and that these often provide illuminating information about taxonomy at the level of the species or the genus. But above the level of the genus, Alston does not see that the use of such compounds as criteria of evolutionary relationship is likely to be of much importance, though there are some notable exceptions, as for example in the work of McClure on the Lemnaceae. He sees the use of information about macromolecules, such as proteins and nucleic acids, as showing most promise in the future for the student of evolution.

The third article to which we would direct attention is that of G. L. Stebbins on 'Adaptive Radiation and Trends of Evolution in Higher Plants'. Stebbins points out that botanists have not recognized the adaptive and selectionist basis of evolutionary trends in higher plants as generally as zoologists have in animals. The fact that in green plants the modes of nutrition are so uniform means that the possible ways of becoming adapted to the environment are fewer, so that parallel evolutionary trends are expected to be more frequent. Stebbins points out ways in which trends affecting adjustment of both vegetative and floral parts may show adaptive reversals, though there are certain other trends which appear to be irreversible. He stresses the importance of studying developmental patterns and the nature of the meristem in relation to such questions as number of floral parts, vestigial structures, and trends from radial to bilateral symmetry.

The literature in the articles is covered up to 1965; there is an adequate index. There can be no doubt that the volume, in spite of its rather high price, is most valuable, and we look forward to the continuation of the series.

D. H. VALENTINE

Primer of Chromosome Practice. G. Haskell and A. B. Wills. Pp. xv+180. Oliver & Boyd, Edinburgh and London. 1968. Price £2 5s.

This book is intended to provide elementary practical instruction in chromosome cytology for those with limited resources, being aimed at students and teachers, but it also claims to be useful to research workers and technicians. According to the authors no concise practical book has previously been available but at this price the present volume is unlikely to appeal to those with limited means, as many will prefer to purchase Darlington & La Cour (1962) for practical instruction and refer to more advanced library sources for the theory.

Part I, approximately one-third of the book, is devoted to elementary theory covering mitosis and meiosis—unfortunately illustrated by a series of rather poor photomicrographs of *Vicia faba*—followed by informative accounts of chromosome form and number. The subject of polyploidy is dealt with at some length and followed up in the techniques and statistics sections by instructions for investigating some of the secondary effects of polyploidy in higher plants, e.g. the determination and significance of size distributions of stomata and pollen. This feature may well prove of interest to amateur botanists who have access to a microscope.

Part II (Techniques) covers the use of the microscope, simple staining, plant meristem squashes, anther smears, pollen culture, spermatocyte squashes and simple wax embedding for microtomy. A number of additional techniques are briefly described, including methods for meiosis in the locust testis, *Drosophila* salivary gland chromosomes and, perhaps rather ambitiously, the culture of human leucocytes for metaphase chromosome counts. A useful appendix lists sources of materials and describes the rearing of locusts and fruit fly larvae.

Although it is in general a readable little book, one's first impression is marred by a number of obvious printing errors and the poor quality of the plates; Plate XXXVI left, for example, is completely unintelligible. Several of these show incorrect adjustment of the microscope and wrong exposure, hardly a good advertisement for the section on photomicrography. Some of the practical techniques are treated too superficially for the beginner to succeed without much trial and error. This is a pity, because a book such as this should anticipate as many as possible of the likely pitfalls to enable the beginner working in isolation to diagnose his failures.

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K. J. ADAMS

Flora der Schweiz und angrenzender Gebiete. Hans Ernst Hess, Elias Landolt and Rosmarie Hirzel. Vol. I: Pteridophyta—Caryophyllaceae. Pp. 558 with 9 maps and numerous text illustrations. Birkhäuser Verlag, Basel. 1967. Price sFr. 118 (approx. £12).

The vital statistics of this *Flora* are awe-inspiring to say the least. As a solid brick, $11\frac{1}{2} \times 9\frac{1}{8} \times 2\frac{1}{2}$ in., weighing precisely 8 lb. $5\frac{1}{2}$ oz., it will stick out prominently from any library shelf. One is almost reminded of Cruikshank's vignette 'The Librarian's Nightmare'. Truly this is a fine monument to Helvetian non-conformism, and this not only in respect of its size. In their introduction the authors explain that they have chosen this unusual format on two grounds: firstly, to integrate text and illustrations in a convenient manner and, secondly, to keep the cost of production down. This may be true, but if one thumbs over the work an almost outrageous waste of space becomes immediately apparent. There is no reason whatsoever for covering only one half of a page with print when there is no illustration on that page. Roughly calculated, about 35 per cent of the book consists of empty space. For some curious aesthetic whim of a publisher, the buyer of this book is landed with both an unreasonably high price and an extremely unwieldy volume (there are two more to come, *nota bene!*). I just wonder whether or not the producers of this book have thought for how long the binding will stand up to the stress of everyday use? The reviewer's copy is already showing signs of fatigue.

The first volume consists of a preface, introductory notes and the systematic treatment of the Pteridophyta, Gymnospermae, Monocotyledones and Dicotyledones as far as and including the Caryophyllaceae in the system of Engler & Prantl. The introduction provides a brief but excellent survey of the geography, geology, orography, floristic history, soil and vegetation of the area. The text is accompanied by nine fine coloured maps and some extremely well executed black and white illustrations as well as diagrams.

The systematic section includes concise descriptions of the higher taxa followed by reasonably exhaustive family descriptions. The genera for each family are keyed out in clearly arranged and numbered dichotomous keys which seem to work rather well. Generic descriptions are adequate, and the printing of essential characters in italics is commendable. The same layout is used in the specific descriptions, which are supplemented by biological data such as times of flowering and fruiting. For each species a paragraph on habitat, cytology and distribution is provided. The critical notes on relationships and taxonomical status of each

plant will be of great value. Chromosome counts are given wherever available and are correlated with the relevant literature. The authors' taxonomic concept is in places rather out of date. One can only regret that more recent classifications of certain groups have not been taken into account, and it is disappointing to see that the writers of this monumental work are in many cases out of step with another great contemporary achievement, namely *Flora Europaea*. Why are genera such as *Asplenium*, *Athyrium*, *Woodsia*, *Polystichum* and even *Blechnum* still included in the *Polypodiaceae*, when most modern authors distribute them quite rightly over several independent families? Viewpoints differ and always will; but, whereas taxonomic concepts are debatable, any disregard for the established rules of botanical nomenclature, laid down by the Code and generally accepted by all sensible botanists, is intolerable. To one's dismay, names such as *Picea excelsa*, *Pinus montana*, *Sorghum vulgare*, *Phragmites communis*, *Muscari racemosum* and others have been used in favour of their legitimate substitutes. Also most regrettable is the use of *Lastrea* whereas other floras, notably *Flora Europaea*, have chosen *Thelypteris*. In view of the fact that this otherwise brilliant work will be the standard flora of Switzerland for the rest of the century, and possibly even the last one to be written, such blemishes are disturbing. And this becomes even more painful if one knows of Dr. Becherer's lifelong labours in Switzerland towards nomenclatural stability. The authors' statements 'auch änderten wir in der Regel keine Namen, die schon längere Zeit eindeutig verwendet worden sind' and '... waren die Argumente für Namensänderungen auf Grund der Priorität meistens nicht zwingend' express a defiance of the Code. The reviewer, although sympathetic toward non-conformism of many kinds, can only say that this sort of attitude is arrogant, if not irresponsible.

Rosmarie Hirzel's line drawings are exact as well as beautiful. The agrostologist is a little disappointed about the complete lack of spikelet details in many instances which would have been of great assistance to the less initiated student of this difficult family (e.g. *Heleochoa*, p. 271; *Cynodon*, p. 276; *Phragmites*, p. 228; *Gaudinia*, p. 290 and others). In a few cases the habit drawings are executed on far too small a scale, thus rendering the illustration almost useless (e.g. *Tragus*, p. 277; *Mibora*, p. 278; *Poa*, p. 332). Certainly there was no shortage of space for a more appropriate magnification!

Despite these shortcomings, which are no more than tiny pimples on an otherwise immaculate face, the authors are to be congratulated on their tremendous achievement, which is based on the labours and experience of generations of eminent Swiss botanists. The book can be thoroughly recommended to all students of European plants, provided that they can afford the price.

EDMUND LAUNERT

Critical Supplement to the Atlas of the British Flora. Edited by F. H. Perring. Pp. viii+159. Botanical Society of the British Isles and Thomas Nelson & Sons Ltd., London. 1968. Price £4 10s.

This Supplement contains all that was excluded from the *Atlas* proper (1962): *Hieracium*, *Euphrasia*, *Sorbus*, *Alchemilla*, *Rubus* and other critical genera, as well as diverse species-groups, hybrids and various infraspecific taxa; in all about 500 taxa. Consequently, most data are based on checked herbarium records, and the comments on the maps in the text form an essential part of the book. These are the main differences between the *Supplement* and the *Atlas* itself.

The editor's work must have been as varied as the taxa concerned. Some of the detail and much of the research and determination work was done by him, alone or in active collaboration with experts on different groups; some parts of the book, on the other hand, were written wholly by relevant specialists. The mere organizing and maintaining of this kind of work is a big task. In short, the book is an excellent example of well-planned team-work, involving the collaboration of numerous botanists.

The *Supplement* contains an astonishing amount of data that will be of interest to non-British botanists, even to those working in countries not immediately adjacent to the British Isles. As regards the *Atlas* itself, a good map is by far the best way to give distributional data. It eliminates the difficulties of language and place-names, too. The value of the maps will be increased when detailed plant maps come from other countries; but even now the text comments give abundant data on distribution outside the British Isles, thus considerably increasing the significance of the maps themselves. However, even if these islands are considered alone, they form a well-defined and reasonable phytogeographical area. It is useful to know that the two books now contain maps for all the British vascular plants that it is possible to map.

The *Atlas of the British Flora* occupies a nearly classic position among works on plant mapping and its methods. Much the same may be said of the *Supplement* too. It demonstrates very clearly that almost every kind of difficult taxon can be mapped, even in fair detail. In their layout the maps and the accompanying text gives a strong impression of providing a highly elastic pattern, easily adapted to various problematic plants. Every case is considered separately, and the best feasible possibility chosen. It does not matter that, when necessary, even very incomplete maps are given. Thus for an aggregate species (often already treated as such in the *Atlas* proper, to which clear page references are given), it has sometimes been possible to

determine infraspecific segregates for only some of the records; these, however, give the main trends in the distribution of the segregates. In fact, this is only a question of scale. In cases where exact determinations of segregates of a collective taxon are few in number, the use of larger squares for recording would, of course, give an impression of greater completeness. But the reader can very easily imagine for himself this generalization on the basis of the basic data for 10 km. squares. The situation in question is very clearly demonstrated in the text, and misunderstanding is hardly possible.

A positive feature of the book is the fact that complicated taxa and their records are accepted just as they are. Collective and uncertain records, intermediates, etc., are often omitted entirely. In several cases the text indicates which criteria are used in the limitation concerned, which expert is responsible for the maps, and whether records other than revised herbarium material are used. These are indicated by different map symbols. Throughout the book the relevant herbaria and other sources are listed. All this gives the reader a feeling of safety and allows him to judge the reliability of each case for himself. Literature references enable further records to be traced. Several maps and texts are based partly or wholly on recently published taxonomic studies. In fact, the *Supplement* is a good collection of references to and summaries of the British taxonomic literature concerned. Of course, it includes abundant unpublished material as well.

The text often gives short descriptions of the characteristics, habit, ecology and other biogeographical features of the taxa, and of known or assumed relationships with other taxa. This kind of information will certainly prove useful, particularly to foreigners whose knowledge of these plants is less intimate, and to whom the literature in question is not always readily available.

Although the local microspecies and other endemics will be quite unfamiliar to most non-British botanists (e.g. *Hieracium*, about two-fifths of the whole book), the numerous text comments on genera and species-groups will certainly be of universal interest. The book includes details of the distribution of a good representation of various exceptional categories of taxa (no matter, perhaps, what their names are for our present purpose), brilliantly depicting the genus as it occurs in Britain, and probably also elsewhere though it would be represented there mainly by different microspecies. In this book *Hieracia* (the *H. pilosella* group are treated as a separate genus, *Pilosella*) are living organisms with differing distributions and ecology, not dusty herbarium specimens, taxonomically and phytogeographically meaningless and remote and without interest for most botanists. These plants may prove to behave similarly elsewhere. The *Rubus fruticosus* group is represented by a selection of different types of distribution in the British Isles. However, the cover of mystery still prevails on *Taraxacum*; only three maps are given.

Some small, mainly technical, details catch a foreigner's eye as somewhat disturbing. Although even the isolated black solid dots in the maps are nearly always easy to find, the thin open circles and crosses are more often really difficult to see (e.g. pp. 19, 36, 152). Coastal localities cannot be seen at a glance, and complicated shorelines in several places form configurations of 'o' or 'x' which can hardly be solved without comparison with a neighbouring map. Fortunately the arrows show some of the most isolated localities, and the text may prevent serious misunderstandings. A map with vice-county names and numbers would have helped a foreigner when reading the text comments and in finding the thin symbols (although this information is given in the *Atlas* proper).

A considerable waste of space is caused by publishing all maps in their entirety, particularly those on pp. 77–88 (*Hieracium* Sections *Alpina* and *Subalpina*, 35 maps), which are almost all of taxa restricted to the Scottish Highlands. However, there are two splendid exceptions: a single large-scale ordinary map for the *Hieracium* species of the Section *Alpestris* in Shetland (p. 119) and a mere list of taxa and localities for 14 very rare *Potamogeton* hybrids (p. 139). On the other hand, the inclusion of two or even more taxa (often related) in one map with different symbols has spared much space. In considering layout the editor has clearly attempted very successfully to keep taxonomic entities together. If this attempt has sometimes succeeded at the expense of space the intention is nevertheless good.

As a rule the most necessary synonymy seems to be given. However, although a reader in northern Europe will immediately find that two of the three rare Teesdale *Alchemillas* expressly noted in the text (*A. subcrenata* and *A. acutiloba*) are very common in his country, he may need to ascertain that the third, *A. monticola*, is really *A. pastoralis*, the commonest of all.

Difficult groups and taxa ought not to be omitted from any mapping projects. Perhaps it is more practical to treat them separately, often consulting the appropriate experts and using exceptional methods in the checking and finishing phases. The resulting maps may not always be as complete as most others, but will still be of value. Mapping of critical taxa is not meaningless or impossible. The *Supplement* will no doubt give a fruitful impetus to the mapping of such plants in other countries too. It shows the main methods and principles to be followed in making such efforts elsewhere. These principles were in general by no means unknown earlier; but the *Supplement* contains a good collection of them, and constitutes a bold experiment in realizing them on a large scale. The editor and the other British botanists concerned deserve the very best congratulations for their beautiful work.

JUHA SUOMINEN

To obtain the 1½ million records used in the original *Atlas*, people of widely varying botanical ability—from national experts down to schoolchildren—had to be enrolled for field work, and it was inevitable that doubtful records would get through. This was not serious: it was the distribution patterns that were important.

The *Critical Supplement* was a different matter, for the very nature of critical groups made correct recording essential. But generally only the more competent observer will attempt to record criticals, much use was made of herbarium material and the knowledge of specialists, and it is clear that the compilers very thoroughly scrutinized the data. The result has surely justified the long time that this work was in production.

The book is uniform in format and presentation with the original volume. But here each map is accompanied by an explanatory text—a rather essential feature with critical groups and certainly one that adds to the interest of the maps. The value of maps of minor taxa in arguments about the origin and history of our flora will be obvious.

Undoubtedly the greatest single achievement in the work is Sell and West's mapping of all the British *Hieracium* microspecies that they recognize. One is filled with admiration for their industry in determining 50,000 specimens and processing the resulting information and for their making this available for the *Critical Supplement* when it could well have formed a separate work. The majority of us, mindful of the 223 names in Dandy's *List*, have despondently written '*Hieracium* sp.' too long. Sell and West's maps will surely encourage many to try at least to learn the commoner microspecies if not to master this difficult genus, for these maps show how few microspecies occur in most districts except the Scottish Highlands, which ones can be expected in any district, and the interesting distribution patterns of many of the microspecies (e.g. *H. shoobredii* in the Highlands, *H. strumosum* in the southern half and *H. vulgatum* in the northern half of Britain, *H. trichocaulon* in the south-east, *H. umbellatum* subsp. *bichlorophyllum* in the south-west).

Everyone will have a different idea of what taxa should have been included. Most of those one could reasonably expect are here, including—as well as *Hieracium*—*Alchemilla*, *Sorbus*, *Euphrasia* and *Rhinanthus* complete. We have to be content with a selection of the better-known *Rubi*. Evidently there is a problem in getting adequate data on common difficult-to-identify taxa. Consequently, as the compilers admit, the maps give only a rough idea of the distribution of the *Rubi* and the segregates of *Polypodium vulgare*, *Ranunculus ficaria*—and, oddly, *Nasturtium officinale* which one would have expected most people to be familiar with by now.

There are obviously good reasons for the absence of some taxa. It is difficult, if at all possible, to be sure of *Callitriche platycarpa* and the subspecies of *Asplenium trichomanes* without microscopic examination of pollen and spores; even cytological study has not solved the problem of the mountain *Cochleariae*; *Salix arenaria*, despite its specific rank in *Flora Europaea*, hopelessly grades into *S. repens* in Britain; and in my experience *Polygonum arenastrum* is by no means always satisfactorily distinguishable from *P. aviculare*. But I should have liked to see maps for *Symphytum officinale* with cream-coloured flowers, *Galeopsis bifida*, *Juncus kochii* and the segregates of *Tripleurospermum maritimum*.

It was an excellent idea to show records of the common intermediates as well as the main types in *Montia fontana*, *Malus sylvestris*, *Monotropa hypopitys* and *Centaurea nigra*. Mapping both the prostrate types in *Genista tinctoria* and *Sarothamnus scoparius* will do much to end a long-standing confusion—though in the case of the *Genista* the accompanying text is rather ambiguous.

The compilers have wisely limited *Asplenium adiantum-nigrum* subsp. *onopteris* to the south-west Irish plants. But they state that they accepted as *Erodium glutinosum* only densely glandular plants with flowers less than 7 mm. in diameter and 2–3-flowered peduncles—though it is known that this species can be eglandular with 12 mm. flowers and 5-flowered peduncles. Yet the map actually appears to show the distribution of *E. glutinosum* correctly.

What does one do when one meets with a marsh dandelion? The reasonable deduction from the maps is that one records *Taraxacum palustre* in Islay, *T. spectabile* in the Isle of Man, and both in Northumberland! But, seriously, as the compilers note, recorders have evidently had different concepts of *Palustria* and *Spectabilia*. Some have held the common view that *Palustria* cover the dandelions with appressed outer phyllaries, common in acid boggy meadows in the north and west. Others have followed Allen in restricting *Palustria* to local plants of rich fen and referring the rest of the marsh dandelions to *Spectabilia*. A composite map might have been a solution.

There are not the interesting climatic and ecological implications in the distribution of most hybrids that there are in the distribution of species and subspecies, because the occurrence of a hybrid normally depends on the chance of the parents growing together and crossing. Yet the maps of such hybrids as *Asplenium × alternifolium*, *Drosera × obovata*, *Scutellaria × hybrida* and *Juncus × diffusus* are welcome as the data were available. A few hybrids have distribution patterns in their own right through vegetative spread or introduction by man. *Equisetum × litorale*, *Nasturtium microphyllum × officinale*, various *Menth*

and Potamogetons, and *Glyceria* × *pedicellata* are examples included in the *Critical Supplement*. One wishes that *Veronica anagallis-aquatica* × *catenata*, *Juncus acutiflorus* × *articulatus* and *Carex demissa* × *hostiana* in the same category could have been added, but here again there is the problem of obtaining adequate information about common plants with poor distinguishing characters.

A book of this type inevitably raises interesting taxonomic questions. Those of us who have been perplexed by material of *Arenaria serpyllifolia*, *Monotropa hypopitys*, *Arctium minus* or *Centaurea nigra* will agree with the segregates being treated as subspecies in each case. Although it is reputed to have a different chromosome number, *Arenaria leptoclados* seems morphologically no more distinct from *A. serpyllifolia* than does var. *lloydii*, and the treatment here of all three as subspecies is reasonable. *Valerianella olitoria* var. *dunensis* and *Catabrosa aquatica* var. *minor* are probably more worthy of the subspecific rank accorded to them here than some other recent 'subspecies' that one can think of. But do *Poa angustifolia* and *P. subcaerulea* really deserve full specific rank?

The maps remind one of the unsatisfactory taxonomic situation in *Euphrasia*. It is now well known that there are two chromosome numbers in this genus in Britain, correlated with well-marked morphological characters, and that hybrids are abundant and fertile *within* each group but very rare *between* them. Is there not overwhelming justification here for treating the two groups (and possibly the rather different *E. salisburgensis*) as full species with the more distinct and widespread of the microspecies as geographical and/or ecological subspecies? The local Scottish endemics could be dropped, for taxonomists agree that not all material can be satisfactorily referred to one or another subspecies.

Much the same can be said of the annual *Salicornias*. Possibly leaving aside *S. pusilla*, the mass of unsound 'species' would be better reduced to two readily identifiable major ones based on the two levels of ploidy. If such a revision had already been done it might have been possible to map these major species for the *Critical Supplement*.

The compilers are to be congratulated on this fine book. It is indeed a worthy memorial to the great pioneers of 'critical' British botany to whom it is dedicated, and it has made worth while the efforts of all of us who contributed records.

P. M. BENOIT

Pflanzensoziologie und Palynologie. Bericht über das internationale Symposium in Stolzenau/Weser, 1962, der internationalen Vereinigung für Vegetationskunde. Reinhold Tüxen (editor). Pp. xvii + 275. Verlag Dr. W. Junk, Den Haag. 1967. Price f.50 (approx. £5 15s.)

The symposia organised by Prof. Tüxen at Stolzenau, and more recently at Rinteln, have become a well-known meeting place of those interested in phytosociology. Naturally, a large proportion of those attending the symposia come from Germany; in this respect the 1962 symposium is not untypical, with the second largest contingent (of 8 members) provided by that nation of admirable linguists the Dutch. Of the 28 papers in the present volume, 24 are in German, 3 in French and 1 in English.

Pollen-analytical investigations of vegetational history inevitably impinge intimately on phytosociological questions, and a number of contributions are concerned with the detailed interpretation of pollen diagrams in terms of the plant communities around the sampling site. G. Lang contributes a critical and more general consideration of the validity of comparing sub-fossil and modern assemblages; he concludes that some Late-glacial and early Post-glacial vegetation-types no longer exist, and that few present-day communities can be older than the Sub-Boreal. How far this is true perhaps depends on how narrowly one defines one's communities, and how far afield one is prepared to look for analogies to past communities. Other topics considered include the concepts of community and sociology in various branches of science (K. Friedrichs), the relation between present-day vegetation and pollen spectra (J. Heim), Quaternary vegetational history in Yugoslavia (A. Sercelj), a comparison between vegetational development in the Eemian and an earlier (?Cromerian) interglacial in Denmark (S. T. Andersen), vegetational history in Minnesota (W. van Zeist and H. E. Wright) and Japan (Tokio-Suzuki), the flora of Rumanian peat bogs (E. Pop), the interpretation of macrofossil assemblages in north-west German peats (G. Grosse-Brauckmann), pollen analyses of soils, and the relation of soil profile features to Weichselian climatic and vegetational change (A. Dücker) and to prehistoric human activity (H. Zoller).

Probably the papers of most general interest to B.S.B.I. readers will be Fr. J. J. Moore's phytosociological evaluation of Irish pollen diagrams and Dr. Franklyn Perring's 'The Irish Problem'. Fr. Moore points out that in the relatively young landscape of Ireland there are two completely different groups of soils—calcareous and base-poor respectively—with corresponding vegetation types, and that this difference is clearly reflected in Irish pollen diagrams. He cites evidence indicating that ash (unlike birch) is not seral to oak in Ireland, and suggests that on base-rich soils ash and elm form the climax forest. Dr. Perring's admirable paper on the Hiberno-American and Lusitanian elements in the Irish flora has already appeared in print in

this country, but may well be more accessible, even to English readers, in the present volume. Dr. Perring stresses the important point that similar distribution patterns do not necessarily imply that species have similar histories or ecological requirements.

Participants in the symposium will undoubtedly value this volume as a record of an enjoyable and intellectually stimulating occasion; the opening and closing remarks convey something of the friendly atmosphere in which these gatherings take place. To the non-participant, the volume offers some papers of considerable individual interest; it also offers a variety of entry points into the central European literature of the fields embraced by the title of the symposium. Unfortunately, its value on both counts is lessened by the five-year interval between the symposium and the publication of its proceedings.

Prof. Tüxen and his Dutch publishers have been largely successful in surmounting the hazards of trilingual publication, though some of the English summaries would have benefited from checking by someone familiar with the language and the subject concerned.

M. C. F. PROCTOR

The Principles of Pollination Ecology. K. Faegri and L. van der Pijl. Pp. ix+248. Pergamon Press, Ltd., Oxford. 1966. Price £3 3s.

It may be as well to begin by explaining what this book is about; no doubt *Blütenökologie* would convey a more immediate and accurate impression to a Continental botanist than 'Pollination Ecology' does to an English-speaking reader. In fact, this is an up-to-date introduction to 'classical' floral biology, written by two well known authorities on subjects related to pollination. As the authors emphasize, they have set out not to produce a comprehensive handbook, but to present the principles of the subject, which the reader may supplement and develop from his own wider reading and observation. Despite the expectations that may be aroused by the title, many obvious ecological relationships of the pollination process are touched on only briefly or omitted altogether. Nevertheless, within the limitations imposed by a rather short book, the authors have placed pollination firmly in the context of current thought in related branches of science, and have ably reviewed the more important developments of classical floral biology since the days of Knuth.

The book begins with a brief summary of the history of the subject, and a terse couple of pages on techniques, followed by two interesting short chapters on 'Pollination as spore dispersal' and 'Spore and pollen dispersal in lower plants and gymnosperms'. Chapter 5, on 'Pollination' runs to over 100 pages and forms the core of the book. It is followed by shorter chapters on 'Retrograde developments' (autogamy and apomixis), on the adaptations of three major groups of zygomorphic flowers, on 'Pollination ecology and speciation' and on 'Applied pollination ecology'. The book concludes with 65 pages of 'Case histories'—short accounts of the pollination of particular genera or species—a brief epilogue, and 12 invaluable pages of references. The 'Subject index' could with advantage have been more comprehensive.

Chapter 5 includes a short account of the structures of the angiosperm flower, and its general adaptations to pollination. The morphological 'flower' is distinguished from the 'blossom' or 'pollination unit', which may be a part of a flower (as in *Iris*), a flower or a group of flowers. There is a short but good account of wind pollination. The fidelity relationships of flowers and their visitors are discussed, and there is a rather detailed consideration of the various attractions to animal visitors that the flower provides. The authors give a simple division of blossom types into a number of broad categories, and the rest of the chapter is taken up with accounts of the main syndromes of adaptation to pollination by members of various animal groups. This includes good accounts of sapromyophily, and of bird and bat pollination.

Floral biology has suffered so much from uncritical repetition of 'facts' and assumptions from the older literature that the authors' fresh and critical approach comes often as a relief and sometimes as a revelation, even if one sometimes hesitates to agree with them. They point out that transfer of spores by insects is widespread in the lower plant groups (fungi, bryophytes, and possibly cycads and Gnetales. Their emphasis is (I believe rightly) on precision of transfer of pollen as the important factor in the evolution of pollination mechanisms, rather than 'cross fertilization' as such—though more could well have been said about breeding systems and the paramount part played by floral biology in their control. The authors eschew detailed classifications of flower types, and emphasize the importance of the adaptation syndrome, while at the same time pointing out that some looseness in the adaptation syndrome may assist in speciation and the build-up of adaptations. Adaptive radiation in relation to different pollinators is evident in so many families that this is a point which might have been further emphasized. The authors are certainly right in stressing that not all visitors are necessarily pollinators, and that many visitors may be irrelevant to the adaptation syndrome of a particular flower. Nevertheless, selection and adaptation take place in relation to the whole environment, and adaptation to a balance between several different pollinators or pollination mechanisms (of which the authors recognize some instances) must surely be common. By contrast with this tendency to diversification

there is an obvious tendency to convergence, remarked upon in various places in this book, but with little comment and no detailed discussion, though many examples lead one to feel that mimicry in relation to pollinators must be common among flowers.

The book is written in admirable and lucid (if sometimes idiosyncratic) English; a very little editing should have sufficed to deal with the remaining oddities—'Hymenopters' for 'Hymenoptera', 'respectively' (natural as *respektiv* or *beziehungsweise* in Scandinavian or German) for 'or', and so on. But these are trivial irritations. Errors and misprints seem to be few. One error is particularly unfortunate in that it is likely to be quoted and copied. The discovery of insect pollination is attributed to A. Dobbs (1750) (correctly) and 'H. Müller (1751)', apparently (apart from the intruding initial) on the authority of Sachs (1875, *Geschichte der Botanik* . . .), who himself was quoting at second-hand from Kölreuter. The reference, as correctly stated in Garnsey & Bayley-Balfour's English translation of Sachs's book, is to Philip Miller's *Gardener's Dictionary*, where the passage in question first appears in the article on 'Generation' in the 6th edition (1752).

However, these criticisms detract little from the book's very solid virtues. It is undoubtedly the best introduction to the subject available in English, and a book one warmly welcomes and can warmly recommend.

M. C. F. PROCTOR

ERRATA

Vol. 4 Part 5, p. 227 (1962), Table 2. Character 4 is not measured in mm. and the correct figures, reading from left to right, are 3·72, 6·35, 5·08, 7·70, 6·80, 7·13.

In the running-foot on each page of Vol. 7 part 1 (pp. 1-53), for 1968 read 1969 throughout.

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Journal of the Botanical Society
of the British Isles

Volume 7 Part 3 5 December 1969

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Price Twenty-five Shillings

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NATURAL HYBRIDIZATION IN BRITAIN BETWEEN *PRIMULA VULGARIS* HUDS. (THE PRIMROSE) AND *P. ELATIOR* (L.) HILL (THE OXLIP)

By S. R. J. WOODELL

Botany School, University of Oxford

ABSTRACT

In Britain *Primula vulgaris* and *P. elatior* meet in woodlands on the fringes of the restricted area of distribution of the latter species. Where they meet a limited amount of hybridization occurs, aided by frequent and regular disturbance. There is evidence that gene flow occurs in both directions. Despite high inter-fertility the extent of hybridization is limited, and it is suggested that ecological differentiation, probably partly the result of differential drought tolerance, is responsible. The hypothesis that *P. vulgaris* is 'hybridizing *P. elatior* out of existence' is examined, and is regarded as being without foundation. Indications are that these populations are changing little at the present time.

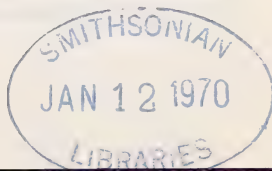
INTRODUCTION

It has been known for many years that *Primula vulgaris*, the primrose, and *P. elatior*, the oxlip, hybridize in Britain (Christy 1897, Valentine 1948). Christy (1922a) suggested that *P. elatior* was being 'hybridized out of existence' in Britain by the 'aggressive' *P. vulgaris*; this possibility will be discussed later, but it was based partly on the incorrect assumption that the F_1 hybrid was sterile. Valentine (1948) believed that most hybrids were of the F_1 generation, but he has more recently (1961) modified this view. Clifford (1958) on the basis of a brief visit to some of the localities where these species occur together, suggested that introgression was taking place. The present investigation was undertaken to determine whether introgression is occurring between these two species in Britain, and to assess Christy's hypothesis of replacement. Some preliminary ecological investigations have also been carried out, in relation to the mutual exclusiveness of the two species in Britain.

Artificial crossing between the species has yielded much information on their inter-fertility. Reciprocal crosses produce different results (Valentine 1947, 1956). The highest germination recorded from the cross using *P. vulgaris* as female parent is 64 per cent., and from the reciprocal cross 39 per cent. These are results produced under good greenhouse conditions; most crosses even under such conditions give much lower germination. The differences in seed germination are reflected in hybrid seed development (Woodell 1960a). When *P. vulgaris* is the female parent the seeds are small and well filled with endosperm and contain a well developed embryo. The reciprocal cross results in two types of seed, both large. One contains well developed endosperm and embryo, the other, more frequent, has aborted endosperm and embryo.

Valentine (1947) demonstrated that F_1 hybrids produce a high yield of viable seed, and have a pollen fertility of about 75 per cent. Using the hybrids as female parents he was able to obtain good seed set and vigorous and fertile backcross plants.

Primula elatior is distributed over western and central Europe, ranging from southern Russia in the east to England in the west, and from the Carpathians in the south to southern Sweden in the north. In Europe it occurs in meadows and open woodlands, with a preference for moist places. *P. vulgaris* is a species of 'Atlantic' distribution, having its northern limit in southern Sweden and extending from Spain to Syria in the south. It is generally a lowland species, and in Britain is a plant of woodland except in the far west, where in company with several other woodland herbs it emerges into less shaded habitats such as hedgebanks, meadows and cliff ledges.



Primula elatior in Britain is almost confined to oak-ash woodland on the chalky boulder clay of East Anglia, where it grows in great abundance to the almost total exclusion of *P. vulgaris*, except on the margins of its range. In one or two outlying localities it can be found outside woodland (Woodell 1965b). On the fringes of the area of *P. elatior* hybridization is frequent.

MATERIALS AND METHODS

A number of woodlands, containing either 'characteristic' species populations or hybrid populations, were sampled. In the 'characteristic' populations a random sample of thirty long-styled (pin) and thirty short-styled (thrum) plants were collected; from each the largest flower and leaf was taken. In hybrid populations a small area was selected and every plant within it sampled.

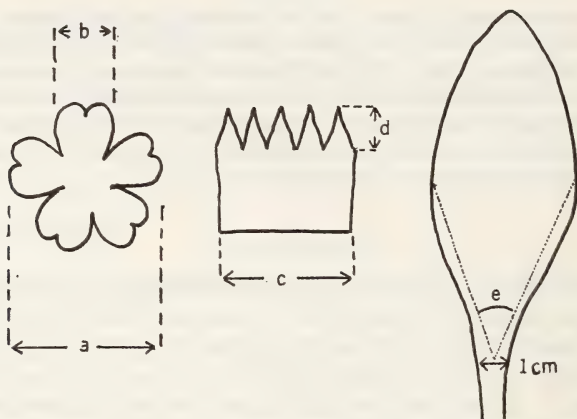


Fig. 1. Measurements made on flowers and leaves of sample plants. *a*, Corolla diameter. *b*, Petal width. *c*, calyx circumference. *d*, Calyx tooth length. *e*, leaf angle.

On each plant the following measurements were made (Fig. 1)

1. Corolla diameter (mm)
2. Petal width (mm)
3. Circumference of calyx (mm)
4. Length of calyx teeth (mm)
5. Leaf angle.
6. Throat pattern, scored in three classes:
 - O. Flower pale yellow with diffuse orange marks in throat, not distinguishable from 'characteristic' *P. elatior*.
 - OP. Intermediate between O and P.
 - P. Flower sulphur yellow, with greenish stellate throat markings; not distinguishable from 'characteristic' *P. vulgaris*.

After measurement each flower was kept in 80 per cent. alcohol, and pollen fertility was estimated later by teasing out anthers in acetocarmine and counting the proportion of round, stainable pollen grains. In order to minimize seasonal differences in dimensions of floral parts (Woodell 1965a) all populations were sampled within a few days.

One character that has been shown by Valentine (*in litt.*) to be important is the pedunculate nature of the inflorescence. In cultivation F_1 hybrids can show both non-pedunculate and pedunculate inflorescences, and backcrosses to primrose likewise. However I regard this as an unreliable *field* character since I have collected plants in the field which have only pedunculate inflorescences, and in cultivation they have produced non-pedunculate flowers.

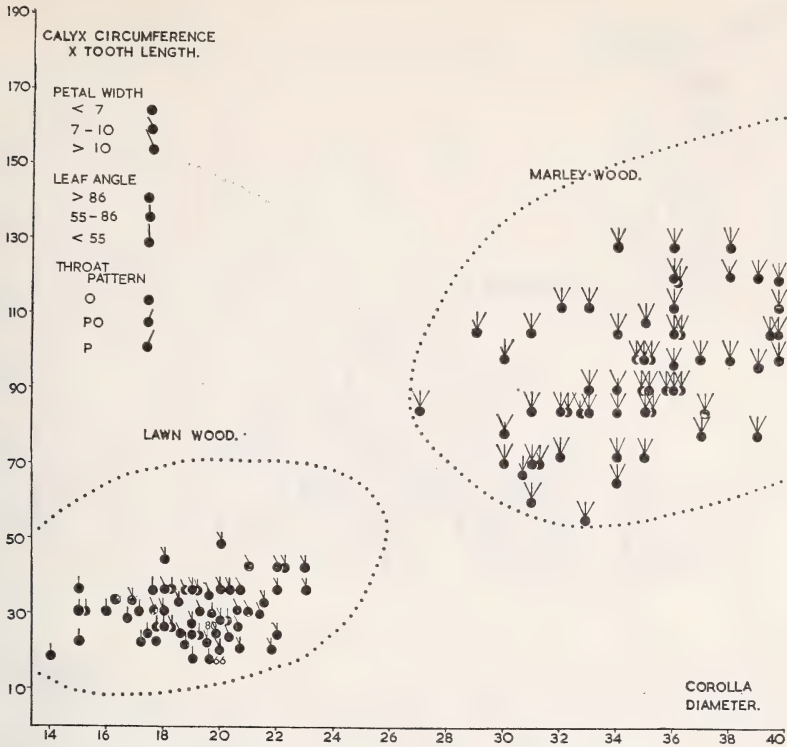


Fig. 2. Pictorialized scatter diagram of populations of 'characteristic' *P. elatior* from Lawn Wood, Suffolk, and *P. vulgaris* from Marley Wood, Berkshire.

While some characters, *e.g.* corolla diameter, clearly distinguish these two species, others *e.g.* petal width and leaf angle, show some overlap. However they show sufficient differences to make them valuable in displaying the overall variation within and between the species. Other characters which have been assessed, *e.g.* flower colour, show environmental fluctuation or change with age, and so cannot be used.

RESULTS

Before presenting the results of this investigation it should be pointed out that these are species that show considerable plasticity in response to environmental changes (Woodell 1965a) and that some of the measurements may therefore show these effects. For instance, individuals in some mixed populations fall outside the range of either species in 'characteristic' populations. This may be a plastic response. However, although such responses will be involved, they are unlikely to be large enough to invalidate the conclusions, and they have been avoided as far as possible by confining sampling to a short period.

The scatter diagrams in Figs. 2-7 depict samples from several populations, representative of the whole range of populations studied. Two 'characteristic' populations are shown in Fig. 2, one of *Primula vulgaris* from Marley Wood, Berks. about 85 Km from the nearest population of *P. elatior*, and one of *P. elatior* from Lawn Wood, Suffolk. Lawn Wood is well within the larger of the two areas of distribution of *P. elatior* in Britain and 4 Km from the nearest known populations of *P. vulgaris*. Other populations of both species were sampled, and they fell within the ranges indicated by the dotted lines on the diagrams. These lines, showing the total range of variation found in the pure species populations, are on all the scatter diagrams. In addition all the individuals with pollen fertilities of less than 90 per cent. are indicated on the diagrams by numbers giving the percentage fertility.

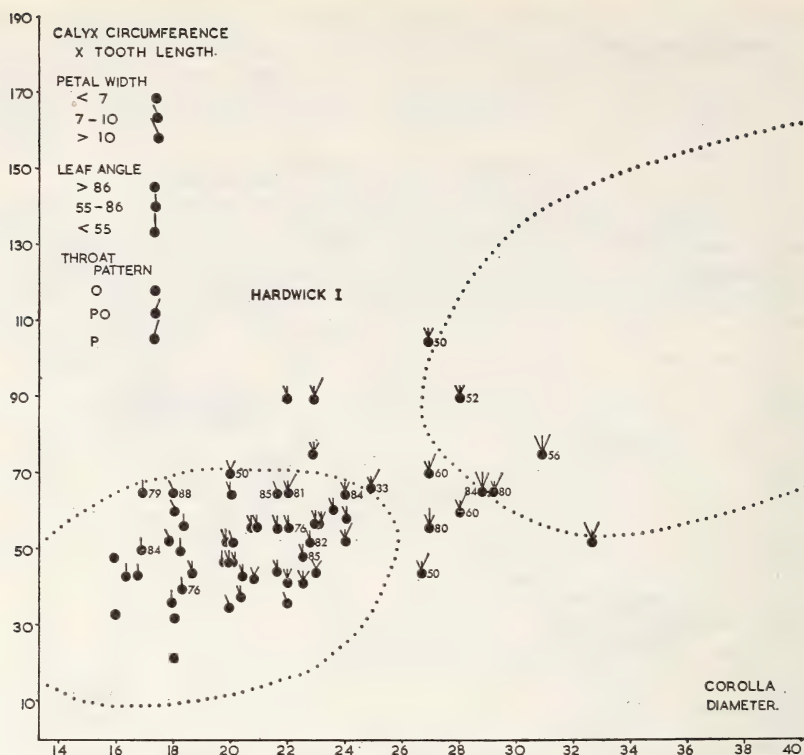


Fig. 3. Scatter diagram of population from Hardwick Wood, Cambridgeshire.

The population from Hardwick Wood, Cambridgeshire (Fig. 3) can be seen to consist mainly of *P. elatior*. There are a few individuals within the range of *P. vulgaris*, and several falling between the two species. The pollen fertility figures indicate that almost all the plants that appear to be *P. vulgaris* have low fertilities, as do most of the putative hybrids. Further, many individuals falling within the range of *P. elatior* have low fertilities. These facts indicate that hybridization has taken place, followed by considerable backcrossing to *P. elatior*. In comparison with this population, those in Gransden Wood, Cambridgeshire (Fig. 4) are interesting. Gransden II (open circles) resembles the Hardwick Wood population, but Gransden I (closed circles) from a site only a few hundred metres away represents almost the opposite situation. There are many primroses, a few plants within the range of variation of *P. elatior*, and many hybrids. Some of the plants falling within the range of *P. vulgaris* have low pollen fertilities. Further, a few plants fall well beyond the normal range of *P. vulgaris*, and this may be the result of the release of variation by hybridization, similar to that in, for example, *Geum* (Marsden Jones 1930) and *Viola* (Clausen 1926), or it may be the sort of environmental effect discussed above. Apparently hybridization is taking place in this wood on a fairly large scale.

Figs. 5 and 6 show two populations from Potton Wood, Bedfordshire, on the extreme southwest edge of the range of the oxlip in Britain. The wood is occupied almost entirely by primroses, but its northeast corner contains a number of oxlips and many hybrids. The population depicted in Fig. 5, Potton Wood II, includes the bulk of the plants in this area, and it can be inferred from these data that there are many hybrids and a good deal of backcrossing to both parents. The population depicted in Fig. 6, Potton Wood I, was sampled as 'characteristic' primrose. It is clear that there is some variation toward *P. elatior*, and the pollen fertility figures suggest some backcrossing to *P. vulgaris*.

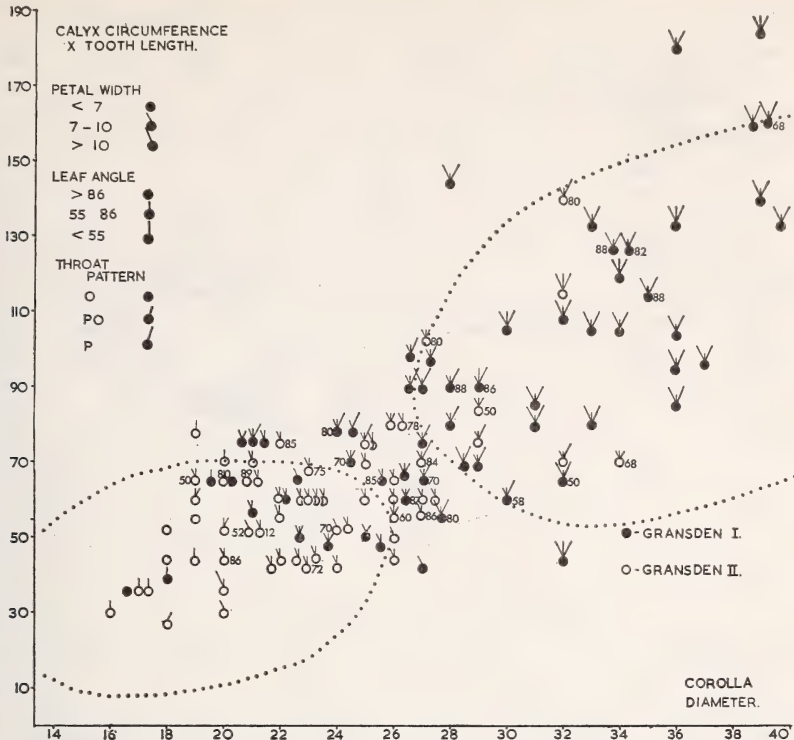


Fig. 4. Scatter diagram depicting two populations from Gransden Wood, Cambridgeshire.

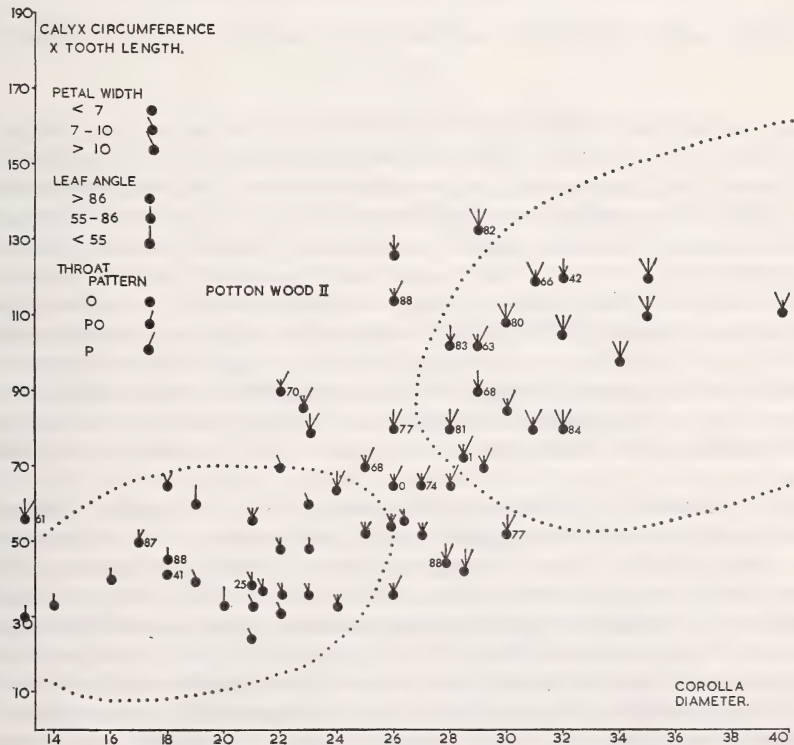


Fig. 5. Scatter diagram of mixed population from Potton Wood, Bedfordshire.

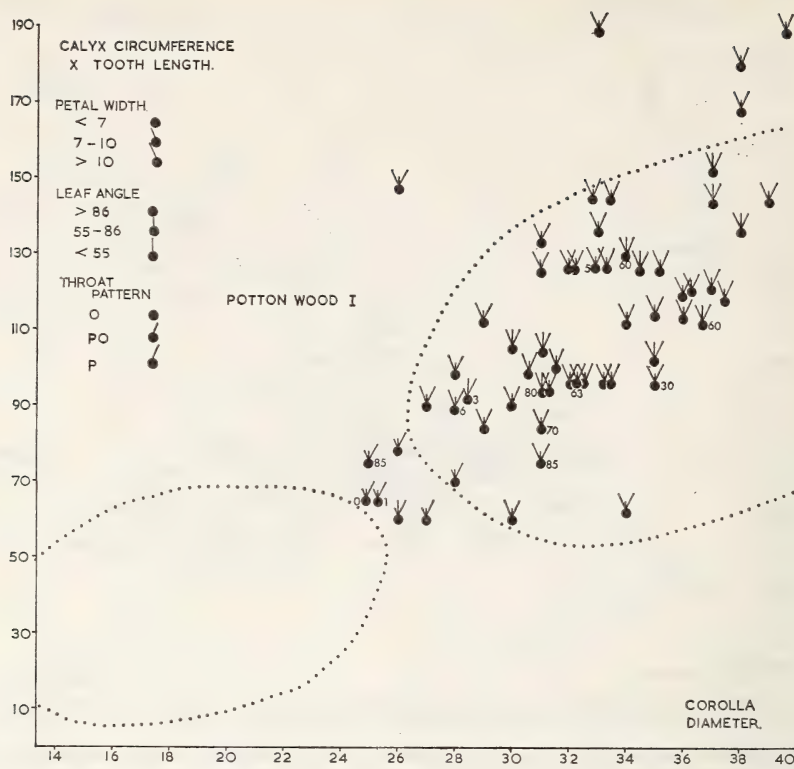


Fig. 6. Scatter diagram of apparently 'characteristic' *P. vulgaris* from Potton Wood, Bedfordshire.

The population from Dickleburgh, Norfolk (Fig. 7) is an outlier from the main area of *P. elatior*, about 21 Km from the nearest known population and 27 Km from the border of the main area. It is in reedswamp, and possibly represents a relic of a once more continuous range, split up by extensive drainage (Woodell 1965b). In the vicinity the nearest plant of *P. vulgaris* is about 150 metres distant, and that of *P. veris* is about 200 metres away. Christy reported hybrids here between *P. elatior* and *P. veris*, but they cannot be found now, and there is reason to believe that they have been destroyed by conversion of part of the area to arable land (Woodell, 1965b). Fig. 7 indicates that of the ten plants that make up the total population, at least three are hybrids. It might be suggested that the aberrant plants are not hybrids but have been influenced by the uncharacteristic environment. In view of the intermediate throat pattern of these three plants and the low pollen fertility of one of them I think this unlikely. The throat pattern is more or less independent of environmental fluctuation.

The data presented in these scatter diagrams and in the table of pollen fertilities (Table 1) indicate that in Britain a good deal of gene exchange has taken place between these two species. Marley Wood is representative of several populations of *P. vulgaris* sampled, and they have, characteristically, a high pollen fertility. On the other hand *P. elatior* was found by Valentine (1948) to have a moderate proportion of infertile pollen, and this is indicated in the Lawn and Ditton Wood populations. The hybrid populations have higher frequencies of infertile pollen, and contain many plants with fertilities below 60 per cent. Especially notable is the population from the apparently 'characteristic' *P. vulgaris* area in Potton Wood (Potton I) which has a wide range of fertilities and a relatively low mean fertility.

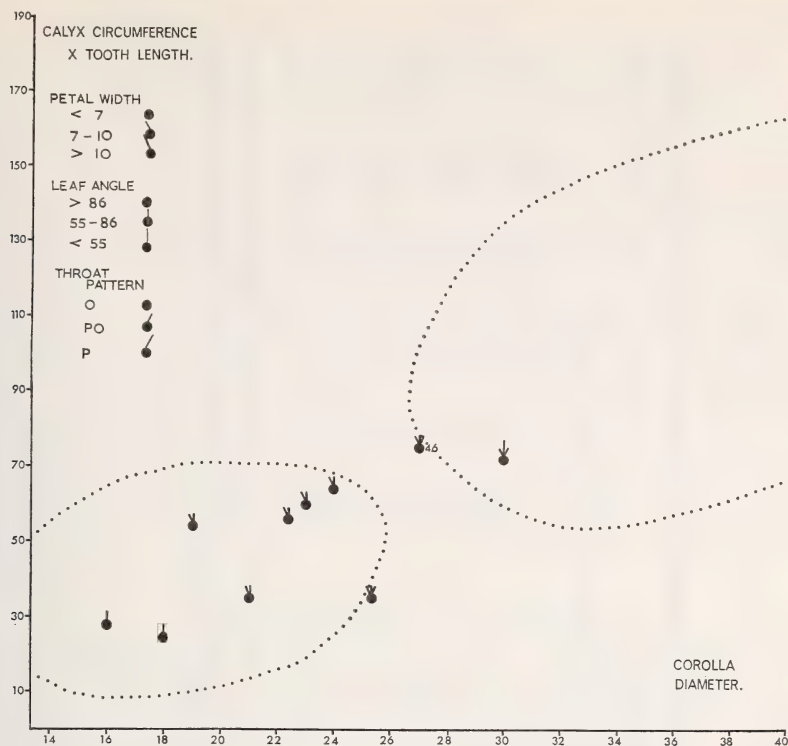


Fig. 7. Scatter diagram of population from Dickleburgh, Norfolk.

DISCUSSION

1. The background to hybridization

Primula elatior and *P. vulgaris* are largely allopatric, and this fact alone is responsible for maintaining them as separate species over most of their ranges. They meet often on the western fringes of the range of *P. elatior*, where they hybridize frequently. Hybrids occur in Austria, and further east in Europe populations of the species are close to each other. In Britain *P. elatior* is a woodland species and in woodland is in direct contact with *P. vulgaris*. In the woods on the margins of its British range it occurs together with *P. vulgaris*, often occupying the damper portions of the woods. However the habitat requirements of the species are so similar that they overlap considerably in many woods.

It is agreed (e.g. Anderson 1953, Baker 1951) that hybridization is often a consequence of human-disturbance of the habitat. These woodlands are subject to disturbance that is both sustained and regular. In many examples of introgression that have been described, the causal disturbance has ceased, and the return to more 'normal' conditions has resulted in the elimination of most hybrids and the establishment of a variable parent population; the only evidence of past introgression. Dansereau (1941) cites *Cistus ladaniferus* and *C. laurifolius* as an example of this. Disturbance maintained over a long period in the same place is uncommon. One natural situation in which this occurs, so that hybridization between *Aquilegia formosa* and *A. pubescens* is aided by a permanent intermediate natural habitat, is discussed by Grant (1952).

The British woodlands containing *P. elatior* are often managed as reserves for pheasant raising, or as fox coverts. The timber has frequently been exploited by the declining practice of coppicing. Under this régime there are widely spaced 'standard' trees, usually oaks, giving an open canopy. Beneath them is a luxuriant growth of understory shrubs, the most

Site	Pollen Fertility (per cent.)											N	Mean	S.E.M.
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-95	96-100			
Marley Lawn						1	1	1		1	60	60	99.9	0.01
Ditton						1	3	3	4	5	57	60	98.9	0.66
Dickleburgh											43	59	93.9	1.35
Gransden II				1					1	1	7	10	91.9	1.64
Potton I				1	1	1	2	2	11	17	25	59	91.5	1.32
Hardwick II	2			1	2	2	2	1	3	3	42	56	90.1	3.68
Rockells	1	1			2	2	2	1	11	1	38	59	88.8	2.62
Hardwick I			1	2	1	1	3	5	7	9	30	58	88.0	2.45
Gransden I				1	3	4		5	8	6	31	58	87.7	2.21
Potton II		1			1	2	2	6	12	10	24	58	87.6	2.13
			1	2			6	4	12	4	27	56	87.5	5.56

TABLE 1. Pollen fertility: Numbers in different percentage classes from samples of 'characteristic' and hybrid populations. (Marley Wood: *P. vulgaris*. Lawn and Ditton Woods: *P. elatior*. Remaining sites: Hybrid).

commonly used being hazel (*Corylus avellana*). The shrubs are allowed to grow for some years (usually between eight and fourteen) and then cut, leaving the stumps or 'stools' to regenerate. The timber is used for such purposes as fencing. Regeneration is rapid and the cycle is regularly repeated. Every century or so the standard trees are felled and replaced. This régime results in moderate disturbance every decade and major disturbance every century. When the canopy is opened up, encouraging profuse growth and flowering of the herbaceous vegetation, the soil is churned up by the foresters. In these circumstances it is hardly surprising that where partly inter-fertile species grow together hybridization occurs. Hybrids produced by one coppicing disturbance can live through at least one cycle, and probably through more. There is unpublished evidence that individual plants of both species may live for several decades, and I know of one hybrid between *Primula veris* and *P. elatior* that has almost certainly survived in the wild for over sixty years. Each coppicing provides the opportunity for new F_1 hybrids to be produced and for existing hybrids to interbreed and to backcross with the parent species. A very similar situation in a Buckinghamshire wood has led to limited introgression between two species (*Primula veris* and *P. vulgaris*) which normally remain distinct throughout Britain (Woodell 1965a).

Thus conditions in these woods would seem to be ideal for almost unrestricted hybridization. Yet the amount of hybridization is restricted. The possible reasons for this must now be considered.

2. The restriction of hybridization

The area occupied by *P. elatior* in Britain is one of cold winters and warm summers; a relatively 'continental' climate. Little is known of the vegetational history of the region, or of the history of the *Primula* species there. Though the area was poorly drained, and may have had large areas of swamp before drainage, it seems unlikely that it was distinct from the rest of southern Britain in being unforested. Similarly it seems likely that *P. elatior* has been here for a long time, and is not a recent immigrant. If the trends of recent decades, with the increase in land drainage, are any indication, then *P. elatior* was probably more continuous throughout this part of Britain, not split into a number of relatively small isolated populations as it is now. Valentine (1948) has suggested that the surrounding areas were completely forested prior to clearance and that *P. vulgaris* has been similarly split into discrete populations by man's activities. He pointed out that there is no evidence that *P. vulgaris* has ever migrated in any quantity across the intervening open land since clearance. If *P. elatior* was restricted to the chalky boulder clay before clearance and *P. vulgaris* was excluded from it then the conditions controlling their distributions were presumably maintained until forest clearance. It is not possible to say whether conditions have altered in favour of either species, but *P. vulgaris* cannot now successfully invade the area of *P. elatior*.

It is probable that in the wild germination is much lower than that obtained under greenhouse conditions by Valentine (1947) in the absence of competition. A significant establishment of hybrids is probably restricted to each coppicing disturbance. The quantity of hybrid offspring must be measured in terms of viability, opportunity (which includes flowering overlap and common insect pollen vectors) and competition, and also in terms of the ecological differentiation between the species.

Viability is high, as we have seen, and none of the other factors classed as internal restrictive factors by Baker (1951) is known to operate. Flowering overlap is complete; *P. elatior* flowers almost exclusively in April, within the longer flowering period (February to May) of *P. vulgaris*. What is known of the pollen vectors indicates that the two species share at least some of them (Christy 1922b, Woodell 1960b). We have seen that disturbance is frequent and regular, yet relatively few hybrids become established, and their rate of spread is such that in the few thousand years since forest clearance began they do not appear to have materially altered the balance between the two species.

Valentine (1948) presented arguments for the view that these mixed populations have remained stable for a very long time, and that if any change in the balance occurs it will be

as a result of a shift in climatic or edaphic conditions. He states: 'hybridization is symptomatic of the mixture of the species, but it is not fundamentally concerned with the replacement of one species by the other.' This statement was made in the belief that most of the hybrids were F_1 plants, and in spite of the fact that my data show that there are many backcrosses there is no reason to disagree with it.

Since coppicing is now declining, many of these woods may revert to a more 'natural' condition, and I would expect that in the long term the number of hybrids will decrease and the boundaries between parent species become sharper. The factors restricting hybridization under the present régime are still not clear, but in the light of the evidence discussed above internal restrictive factors are unlikely to be involved. Ecological differentiation may be very important, however, and this will be discussed later. Before this is done it is necessary to examine briefly the hypothesis, put forward by Christy (1922a) that *Primula elatior* is being 'hybridized out of existence' in Britain.

3. Christy's hypothesis

Christy's argument, briefly, is as follows: Woodlands containing *P. elatior* are frequently cleared. Such clearance results in profuse flowering, and at the same time pollen vectors have freer access to the flowers and pollen transfer is likely to take place from the *P. vulgaris* plants outside (*sic*) the woods to *P. elatior* within them. A good deal of hybridization takes place, and then when the wood grows up again both the plants of *P. elatior* and the hybrids cease to flower. The next time the wood is cleared, both hybrids and *P. elatior* will flower, but many of the latter will have died, and hybridization will again occur between the remaining plants of *P. elatior* and *P. vulgaris*. Frequent repetition of this process will result in complete elimination of *P. elatior* and the possession of the ground by hybrids. These in turn will die because they are likely to be shorter lived. This would mean that when the hybrids had died the ground would be unoccupied by any species of *Primula*. Christy had never seen *P. elatior* extending its boundaries, and he considered *P. vulgaris* to be an 'aggressive' species which would ultimately occupy the ground vacated by *P. elatior*.

There is much evidence which indicates that this hypothesis is unlikely to be correct, but it is unnecessary to detail all of it. The points enumerated here are sufficient to indicate the unsoundness of Christy's view:

- (i) Christy was of the opinion that F_1 hybrids between these species are sterile. This is incorrect.
- (ii) Christy stated that hybrids are shorter-lived than parents. Present indications are that they are longer-lived.
- (iii) He transplanted several plants of *P. vulgaris* to a pure *P. elatior* wood in Essex. After seventeen years they had declined in numbers, and there were a few hybrids. This wood was carefully searched in 1967 but no primroses or hybrids could be found. Similarly, attempts to establish *P. vulgaris* in woods containing *P. elatior* in continental Europe were unsuccessful.
- (iv) Valentine (1948) found that the numbers of *P. vulgaris* plants on the margins of the predominantly *P. elatior* Knapwell Wood, Cambs., declined markedly during the period 1937-1947.
- (v) *P. elatior* has been isolated and has survived at Dickleburgh, Norfolk, possibly for centuries, surrounded by *P. vulgaris*.
- (vi) Buff Wood, Cambs., has been under observation by Valentine for thirty years, and Gransden and Hardwick Woods have been visited for ten years. In none of these is there any obvious change in the proportions of hybrids and parents.*

None of this evidence supports Christy, and I have no evidence that does support his hypothesis. In the present state of our knowledge it must be regarded as unproven.

* Dr. S. M. Walters and Mr. D. J. Ockenden conducted a field class in Buff Wood in April 1968, in which they resurveyed Valentine's transect of 30 years ago. Their results suggest that there has been no major change in this population in the last 30 years.

One fact that may have influenced Christy's interpretation of the situation is that in several woods more hybrids occur in association with *P. elatior* than with *P. vulgaris*. Hardwick Wood (Fig. 3) and Gransden Wood (Fig. 4) illustrate this. In woods which have both species *P. elatior* often occupies areas with more bare soil than *P. vulgaris*, and it is possible that reduced competition may favour the establishment of hybrids in these areas.

4. Ecological differentiation of the two species

Baker (1951) has mentioned several examples of the fact that, where two species hybridize, knowledge of the ecological factors distinguishing the species' ranges often help to indicate factors restricting gene flow. In the case of *Primula vulgaris* and *P. elatior*, the ecological differentiation of their areas of occurrence is not immediately apparent. In the British Isles *P. elatior* is almost exclusively confined to the chalky boulder-clay, and *P. vulgaris* is found on the margins of this soil type. Valentine (1948) investigated associated species and soil moisture in Buff Wood. The areas occupied by the two species are floristically similar, but *P. vulgaris* is abundant in areas dominated by *Mercurialis perennis* and *Endymion non-scriptus* whereas *P. elatior* is found in association with *Anemone nemorosa*, *Ranunculus ficaria* and *Filipendula ulmaria*, the last being a common species of moist places. Valentine concluded that soil moisture was a controlling factor. However, his measurements of soil moisture were inconclusive.

If soil moisture *per se* was responsible for the distribution of these species the extensive drainage of recent years would favour *P. vulgaris*, and we have seen that this is apparently not so. Furthermore, Good (1944) showed that in Dorset *P. vulgaris* is limited, on light soils, to areas of high precipitation, indicating a high water requirement. This clearly needs further investigation.

A number of woods has been sampled in the study area, 20 with populations of *P. elatior*, 9 with *P. vulgaris* and the remainder with both species and hybrids. Using thrown quadrats, percentage frequencies of associated species were determined. Most of the species showed little differences in frequency between *P. elatior* and *P. vulgaris* woods. Five species merit comment, and the results for these are in Table 2.

TABLE 2. Mean percentage frequencies of five species in 20 woods containing *P. elatior* and 9 with *P. vulgaris*.

Species	Mean per cent. frequency in woods containing:	
	<i>P. elatior</i>	<i>P. vulgaris</i>
<i>Filipendula ulmaria</i>	30	9
<i>Endymion non-scriptus</i>	15	41
<i>Poa trivialis</i>	44	19
<i>Ranunculus ficaria</i>	24	47
<i>Mercurialis perennis</i>	40	43

These data agree with Valentine's in showing the association of *Filipendula ulmaria* with *P. elatior*. Of the other species, *Endymion non-scriptus* has a preference for well drained soils, and little is known of *Ranunculus ficaria* and *Poa trivialis* with respect to soil preferences. The apparent indifference of *Mercurialis* is interesting in view of Valentine's data. However, in woods where the two *Primula* species occur together the differences in associated species are accentuated; for instance in Rockell's Wood, Essex, in populations about 100 metres apart, *P. vulgaris* is associated with *Brachypodium sylvaticum*, *Deschampsia cespitosa*, *Endymion non-scriptus* and *Mercurialis perennis*, the last named being dominant. With *P. elatior*, *Filipendula ulmaria* is abundant, *Poa trivialis* and *Arum maculatum* are frequent, and *Mercurialis* is rare. This is comparable with Valentine's account of Buff

Wood, and would suggest that where the two species grow together competition forces them into more distinct habitats than those they occupy when apart.

Martin (1965) investigated soil waterlogging and aeration in relation to nutrient availability in Cambridgeshire boulder clay woods, with special reference to *Mercurialis perennis*, which is excluded from the more waterlogged soils. He found that soil acidity and the distribution of major plant nutrients could not account for the distribution of this species. Low oxygen concentration, and especially the presence of toxic quantities of ferrous iron exclude *Mercurialis* from the wetter soils. *Deschampsia cespitosa* is tolerant of wet soils, possibly because it has an effective intercellular air space system and can protect itself by a zone of oxidation round the roots. *Primula elatior* can tolerate these waterlogged soils but as yet the mechanism of tolerance is unknown.

In these woods the association of *Primula vulgaris* with *Mercurialis* suggests that it is unable to tolerate waterlogging as well as *P. elatior*. Some experiments have been carried out to test this view.

Seeds and young plants were planted in John Innes potting compost under three different water régimes; free drained, water table 4 cm below soil surface and waterlogged. Germination was so poor that no conclusions could be drawn from this part of the experiment. (Abeywickrama (1949) stated that seeds of both species will germinate under water.) The young plants of both species performed best in the soil with a 4 cm water table. In waterlogged soils both species performed very poorly, and in free drained soils *P. vulgaris* was superior. Table 3 summarises the results. I have included the results for *P. veris*, a plant of much drier habitats in Britain, and it will be seen that it performed very well in free-drained pots, and disliked waterlogging.

TABLE 3. The mean number of leaves, and mean dry weights of plants of *Primula vulgaris*, *P. elatior* and *P. veris* after 25 weeks under three different drainage régimes. Six plants used for each treatment.

Species	Free drained		Water table at 4 cm		Waterlogged	
	Mean no. leaves	Mean dry wt.	Mean no. leaves	Mean dry wt.	Mean no. leaves	Mean dry wt.
<i>P. vulgaris</i>	11 $\pm$ 3.3	2.86 $\pm$ 0.77	12 $\pm$ 2.6	6.44 $\pm$ 1.4	6 $\pm$ 2.4	0.64 $\pm$ 0.23
<i>P. elatior</i>	2 $\pm$ 0.6	0.87 $\pm$ 0.02	4 $\pm$ 0.9	2.5 $\pm$ 0.62	0.5 $\pm$ 0.3	0.45 $\pm$ 0.01
<i>P. veris</i>	26 $\pm$ 5.21	6.76 $\pm$ 0.78	13 $\pm$ 3.03	3.76 $\pm$ 0.59	All dead	

Clearly neither species is tolerant of waterlogging, and this result agrees with those of Abeywickrama (1949) who found little difference in their tolerance to drowning. He suggested that *P. elatior* is less tolerant of low soil moisture than *P. vulgaris* and my results agree with this. I think it very likely that the controlling factor of these species' distribution in these woods is drought tolerance; *P. vulgaris* may resist dry spells more successfully. One indication of this is the poor flowering of *P. elatior* in the spring following a dry summer.

5. Conclusion

Despite a high interfertility, and the provision by regular disturbance of ample opportunity for hybridization, the amount of hybridization between these species is restricted. Internal restricting factors are probably less important than external ones, especially ecological differentiation, the nature of which is not yet clear, but which probably involves drought tolerance. In woods where the species co-exist they are more clearly differentiated ecologically than when they grow apart, and the hybrids occupy mainly the intermediate zone between them. There is little evidence of extensive infiltration of the genes of either of these species into the other, or of replacement of one by the other.

ACKNOWLEDGMENTS

My thanks are due to Professors D. H. Valentine and Harlan Lewis and to Dr. D. M. Moore, all of whom have made valuable suggestions and kindly criticised the manuscript. I am indebted to Miss J. Bell and Miss C. Cox for technical assistance. This work was carried out while I was in receipt of a grant from the Nature Conservancy, which I gratefully acknowledge. I wish to thank all the landowners who gave me access to their woods.

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STUDIES ON BRITISH POPPIES

III. A NOTE ON STERILITY IN *PAPAVER RHOEAS* L.

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ABSTRACT

Varying degrees of sterility are encountered in populations of *Papaver rhoeas* and are shown to be due to structural heterozygosity. Complete sterility may be associated with vegetative abnormalities and it is suggested that plants showing these features are sometimes confused in the field with interspecific hybrids between *P. rhoeas* and *P. dubium*.

HISTORICAL

Some previous evidence of sterility in *Papaver rhoeas* resulting from cytological aberrations has been reported by Newton (1929) and Philp (1933). The former worker observed frequent irregularities in reduction division in this species and the production of non-viable gametes with aberrant chromosome complements. Philp observed that the condition of partial or complete male-sterility may vary even in one plant, and noted that inbreeding for a few generations is usually accompanied by general sterility.

OBSERVATIONS

The examination of pollen samples of *Papaver rhoeas* for use in breeding experiments and the observation of male-sterility in natural populations supports the previous reports that partial or complete sterility is quite common in this species. Thus among 290 plants grown in field trials from seed collected from wild populations, four were completely male-sterile, and the examination of pollen from 16 pot-grown plants showed only five to have completely well filled and presumably viable pollen. Of the rest, seven had shrivelled sterile grains accounting for up to 5 per cent. of the total, three had 5–20 per cent. non-viable grains and one was male-sterile. Preparations of pollen mother cells from plants in the two latter groups showed the sterility to be associated with the presence of anaphase bridges at both the first and second meiotic divisions. In addition to the complete or ruptured bridges, acentric fragments were present in some of the cells (Fig. 1). These formations are most likely to arise from cross-overs within a paracentric inversion and so it seems possible that the affected plants are inversion heterozygotes. None of these plants showed any obvious vegetative abnormalities.

Numerous meiotic irregularities were also seen in two plants whose vegetative growth was visibly abnormal and which proved to be completely sterile. Both plants were appreciably smaller than normal plants of the same age. One had thickened dark green and rather distorted leaves; the foliage of the other was bluish-green with acute leaf serrations, each one terminated by a strongly developed hair. In both plants many of the buds failed to open properly. These malformations are strikingly similar to those observed in artificially-raised hybrids between *P. rhoeas* and *P. dubium* (McNaughton & Harper 1960). The assumption of hybridity in the field is usually based on failure to set seed, on a capsule form superficially intermediate between that of the putative parents, or on abnormality in leaf form. It can be seen from the foregoing account that failure to set seed and foliage abnormalities may be shown by plants of *P. rhoeas* which are structural heterozygotes. The apparently intermediate capsule form in such plants would result from the shrivelling of the capsule consequent upon the failure to set seed, this shrivelling being more apparent at the base of the capsule than at the top where the shape is maintained by the stigmatic disc.

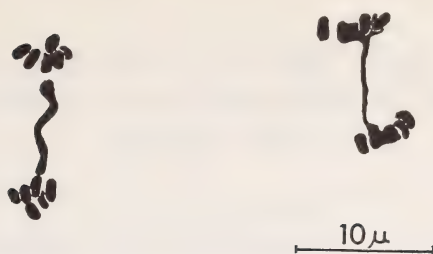


Fig. 1. Anaphase bridges at the first meiotic division in pollen mother cells.

The presence of chromosomal aberrations in *Papaver rhoeas* combined with its rigorous outbreeding results in the occurrence of sterility to the extent of 1–2 per cent. in many populations. While similar structural variations may occur between homologous chromosomes in the other British species, the self-compatibility and consequent degree of inbreeding of these species will result in structural heterozygosity and meiotic irregularity appearing less frequently.

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THE ORIGIN AND DISTRIBUTION OF DIPLOID AND TETRAPLOID *TRIPLEUROSPERMUM INODORUM* (L.) SCHULTZ BIP.

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ABSTRACT

The diploid cytotype of *Tripleurospermum inodorum* (Compositae-Anthemideae), previously known only from the Baltic region and eastern Canada, has an Atlantic distribution in Europe and is common in the British Isles and northern France. The tetraploid cytotype, previously known from Scandinavia and western Canada, occurs at a number of sites in central and eastern Europe and probably has a Continental distribution in Europe. Diploid and tetraploid may have mutually exclusive distributions. Diploid *T. inodorum*, now restricted to man-made habitats, may have diverged from the closely related *T. maritimum* before the Weichsel glaciation and tetraploid *T. inodorum* may have arisen from diploid *T. inodorum* by chromosome doubling and catastrophic selection. Chromosome counts for *Tripleurospermum tenuifolium* ($2n = 18$), *T. disciforme* ($2n = 18$) and *T. tchichatchevii* ($2n = 36$) are reported for the first time.

INTRODUCTION

The genus *Tripleurospermum* (Compositae-Anthemideae) consists of some 25 to 35 herbaceous species. The genus is centred in the Caucasus and Western Asia, and although a wide range of taxa occur in this area, from desert annuals to alpine perennials, they are taxonomically little-known and poorly understood. Herbarium material is scanty and often unsatisfactory, lacking the ripe achenes that are essential for the determination of many species. Pobedimova (1961), in the introduction to her treatment of the genus in *Flora URSS.*, pointed out that the delimitation of species is often very difficult, and Fedorov (1949) wrote 'One can often see completely unsuccessful determinations made not only by novices but also by prominent specialists, who obviously make the same fundamental mistakes in the identification of species of this genus (*Tripleurospermum*).'

However, *T. inodorum* (L.) Schultz Bip., a widespread and often abundant annual weed of arable land and waste places in Europe and most other temperate areas of the world, and the related *T. maritimum* (L.) Koch, a perennial or biennial maritime species found on the coasts of western and northern Europe, are well-known to European botanists and have been the subjects of a number of biosystematic and cytotaxonomic studies. These studies have usually been restricted to a relatively small area; for instance, Turesson (1922) restricted his investigations to the province of Skåne in Sweden, Vaarama (1953) worked mainly within Fennoscandia, Nehou (1954) in Brittany, Rottgardt (1956) in Schleswig-Holstein, and Hämet-Ahti (1967) in Northern Fennoscandia. The ecology of the two species and their morphological differences are now reasonably well understood, but their nomenclature is confused and varies from author to author. Nehou (1954), Lövkqvist (1963), Kay (1965) and Hämet-Ahti (1967) concluded from biosystematic studies of the two taxa that they merited separation as distinct species, and this is the view taken in the present paper. *T. inodorum* and *T. maritimum* are mutually interfertile at the diploid level, as are several other morphologically well-differentiated species of *Tripleurospermum*, and extensive hybridization may occasionally take place when the ecological isolation which normally separates the two species breaks down.

PREVIOUS CYTOTAXONOMIC WORK ON *T. INODORUM*

The earliest published chromosome count for a plant which may have belonged to this species was made by Tahara (1921); $n = 9$ for a *Tripleurospermum* from northern

Japan. Hüser (1930) determined haploid chromosome numbers of $n = 9$ for three 'forms of *Matricaria inodora*' found in the southern Baltic region; a cliff-form from Bornholm and a beach-form from near Rostock (both probably *T. maritimum*), and an arable-field form also from near Rostock (probably *T. inodorum*). Vaarama (1953) investigated the cytology of *Tripleurospermum* in Fennoscandia. He regarded the Fennoscandian taxa as three subspecies of the species *T. maritimum*: subsp. *inodorum* (L.) Hyl. ($2n = 36$), subsp. *salinum* ($2n = 18$) and subsp. *ambiguum* ($2n = 18$). The chromosome morphology of the tetraploid subsp. *inodorum* indicated that it was of amphiploid origin. Vaarama (personal communication) has told me that the count of $2n = 54$ that he reported in this paper for var. *villosum* of subsp. *ambiguum* was an error, and that this variety is probably also diploid ($2n = 18$). Subsp. *salinum* is a seashore plant occurring only occasionally in ruderal habitats in Fennoscandia, and subsp. *ambiguum* is a highly variable circumpolar group including among a number of maritime and weedy types the ruderal variety *boreale* which has been displaced as a weed in most of Fennoscandia by the aggressive tetraploid subsp. *inodorum* in the past century. Unfortunately Vaarama's work has not been published in detail. Vaarama's subsp. *salinum* probably corresponds to *T. maritimum* in the restricted sense of the present paper, and his subsp. *inodorum* and subsp. *ambiguum* var. *boreale* to tetraploid and northern diploid *T. inodorum* respectively. In Britain, I have found that northern Scottish forms of *T. inodorum* morphologically resembling the northern 'ambiguum' (or, more correctly, 'phaeocephalum' (Pobedimova 1961, Hämet-Ahti 1967)) type are connected by a continuous cline of variation to southern English diploids of the typical *inodorum* type, the latter being morphologically very similar to tetraploid *T. inodorum* (Kay 1965).

Rottgardt (1956) studied *T. inodorum* and *T. maritimum* in Schleswig-Holstein, regarding them as *Matricaria maritima* subsp. *inodora* and subsp. *maritima*. She investigated two populations of diploid and two populations of tetraploid *T. inodorum*, as well as one population of *T. maritimum*, and she found that the cytotypes of *T. inodorum* are morphologically similar to one another but physiologically and ecologically slightly different. Mulligan (1958) reported that there are two similar forms of the introduced weed '*Matricaria maritima* var. *agrestis*' (presumably *T. inodorum*) with separate distributions in Canada—one in the Prairie Provinces, a tetraploid ($2n = 36$) cornfield weed (four sites in Saskatchewan), and the other in the eastern Maritime Provinces, a ruderal rather than a cornfield weed, diploid ($2n = 18$), with pollen grains half the volume of those of the prairie tetraploids. He recorded diploids from seven sites, in Quebec, New Brunswick, Nova Scotia and Prince Edward Island. All plants from both sites in Prince Edward Island had supernumerary chromosomes; one plant had two ($2n = 18 + 2B$) and the rest one ($2n = 18 + 1B$). This is the first record of supernumerary chromosomes in *Tripleurospermum*. I have found that supernumerary chromosomes are widespread both in diploid *T. inodorum* and in *T. maritimum*, occurring in about 10 per cent. of all plants counted.

Lövkvist (1963), in a preliminary account of a re-investigation of Turesson's work on '*Matricaria maritima*' (Turesson 1922), concluded that *T. inodorum* and *T. maritimum* should be regarded as separate species 'at least as far as the situation in Scandinavia is considered'. Unfortunately Lövkvist's chromosome counts, some of which should clearly be assigned to *T. inodorum*, are all allocated to *T. maritimum*: $2n = 18$ from West Skåne, Lancashire (near sea), Cheshire (Wirral), Ireland (coast, near Dublin) and Brittany, and $2n = 36$ from Prague, Skåne (two ruderal sites) and Stockholm (one ruderal site).

THE DISTRIBUTION OF THE CYTOTYPES IN EUROPE

The chromosome counts made by previous workers that are well documented and clearly apply to *T. inodorum* are those of $2n = 18$ for plants from northern Germany (Hüser, Rottgardt), $2n = 18$, $18 + 1B$, $18 + 2B$ for plants from eastern Canada (Mulligan) and $2n = 36$ for plants from Fennoscandia (Vaarama), northern Germany (Rottgardt) and western Canada (Mulligan). When the work described in the present paper began, the cytological status of British and western European *T. inodorum* was unknown, and it seemed possible that the situation in Britain and western Europe might be similar to that

described for Fennoscandia by Vaarama, with aggressive tetraploids invading and displacing the diploids.

Plants and achenes were collected from wild populations of *T. inodorum*, by the author and by friends and colleagues, from as many sites in the British Isles as possible, and also from a few sites in western Europe. The central and eastern European material was collected in the field by local botanic gardens and research stations. The identity of all material of *T. inodorum* was checked by examination of the morphology of the achenes. *T. maritimum*, the species most likely to be confused with *T. inodorum*, has achenes with broad, inflated, often contiguous ribs and elongated oil-glands, contrasting with the well-separated, dense ribs and rounded oil-glands of *T. inodorum* (Nehou 1954).

Chromosome counts were made from root-tip Feulgen squash preparations in most cases; a few counts were made from pollen mother cell squashes. The most effective technique for root-tip squashes was found to be pre-treatment in colchicine solution for three hours (0.1 per cent. for seedlings, 0.2 per cent. for root-tips from established plants) followed by overnight fixation in acetic alcohol (1:3) at room temperature, maceration in 1N HCl for eight minutes at 60° C, staining in Feulgen's solution for $\frac{1}{2}$ to 2 hours, and squashing in acetocarmine.

The chromosome numbers of 287 plants from 119 naturally occurring British and European populations of *T. inodorum* were counted. The results are summarized in Figs. 1 and 2 and Table 1. A number of plants originating from populations cultivated in Botanic Gardens were also counted but are not shown in the maps and table; those from Lyons, Nancy, Turin, Hamburg, Kassel, Leipzig, Munich, Aarhus, Lund, Cluj (Rumania), Riga, Athens, Ashkhabad and Vladivostok were tetraploid ($2n = 36$) and only the plants grown in Rouen Botanic Garden 'de la flore Normande' were diploid ($2n = 18$).

Although no material could be obtained from most of western Germany and the Low Countries, the general picture of the distribution of the cytotypes is clear, taking into account the counts made previously by German and Scandinavian workers. Tetraploid *T. inodorum* has a continental distribution, occurring mainly in eastern, north-eastern and central Europe; diploid *T. inodorum* has an Atlantic distribution, occurring in northern and western Europe. British *T. inodorum* is nearly all diploid, with a single isolated record of a tetraploid. Tetraploids and diploids meet in northern and eastern Germany, and tetraploids extend to northern and eastern France (Nancy and Strasbourg districts). The tetraploid plant found in Paris was collected in Montparnasse Cemetery, an unusual habitat for *T. inodorum*, and may, like the single British record of a tetraploid discussed below, have been a sporadic and temporary introduction.

The single record of tetraploid *T. inodorum* in Britain is extremely interesting. $2n = 36$ was found for the two plants that were counted in a morphologically uniform group of ten plants grown from achenes collected from a single isolated plant of *T. inodorum* found in barley stubble near Ardley in northern Oxfordshire in August 1962. The achenes of this plant resembled those of typical continental European plants in their rapid germination, and its offspring also resembled typical tetraploid plants in their habit and leaf-morphology. The self-fertility of the isolated Ardley plant was unusual, because strong self-incompatibility is normal in *T. inodorum*, a species which normally grows in populations, not as isolated individuals. The occurrence of a plant of *T. inodorum* in the Ardley area was also unusual in itself, because *Anthemis cotula* is the normal mayweed in the Ardley area; *Anthemis cotula* and *Tripleurospermum inodorum* have mutually exclusive distributions in the whole Oxford area (Kay 1965). The area in which the Ardley plant was found in 1962 was searched thoroughly two years later, in 1964, but no plants of *T. inodorum* were found, although *Anthemis cotula* was still abundant. It therefore seems likely that the tetraploid plant of *T. inodorum* found at Ardley was a temporary and isolated introduction, perhaps originating from grass-seed imported from Scandinavia; *T. inodorum* achenes are a common and abundant contaminant of Scandinavian grass-seed (Kolk 1962) and Scandinavian *T. inodorum* is normally tetraploid (Vaarama 1953). It is probable that tetraploid *T. inodorum* has been repeatedly introduced into Britain as a contaminant of crop-seed, and



Fig. 1. Distribution of the cytotypes of *T. inodorum* in the British Isles. ○— $2n=18$; ●— $2n=36$.

its failure to establish itself here may have been due partly to poor adaptation to local ecological conditions and partly to inbreeding depression in small isolated pioneer populations (as perhaps at Ardley), but the major factor involved in its exclusion has possibly been reproductive interaction with the well-established and numerically superior diploids (see below).

Diploid and tetraploid *T. inodorum* are morphologically and ecologically very similar to one another. Several populations of each cytotype have been compared by Rottgardt (1956) and Kay (1965) with similar results. When grown side by side under identical conditions, tetraploid plants usually grow faster, to a larger size, and have a more erect habit than diploid plants; but some populations of diploids are indistinguishable from tetraploids in these characters even in comparative cultivation, and diploids are usually indistinguishable from tetraploids in the field. Tetraploids nearly, but not quite, always have pollen

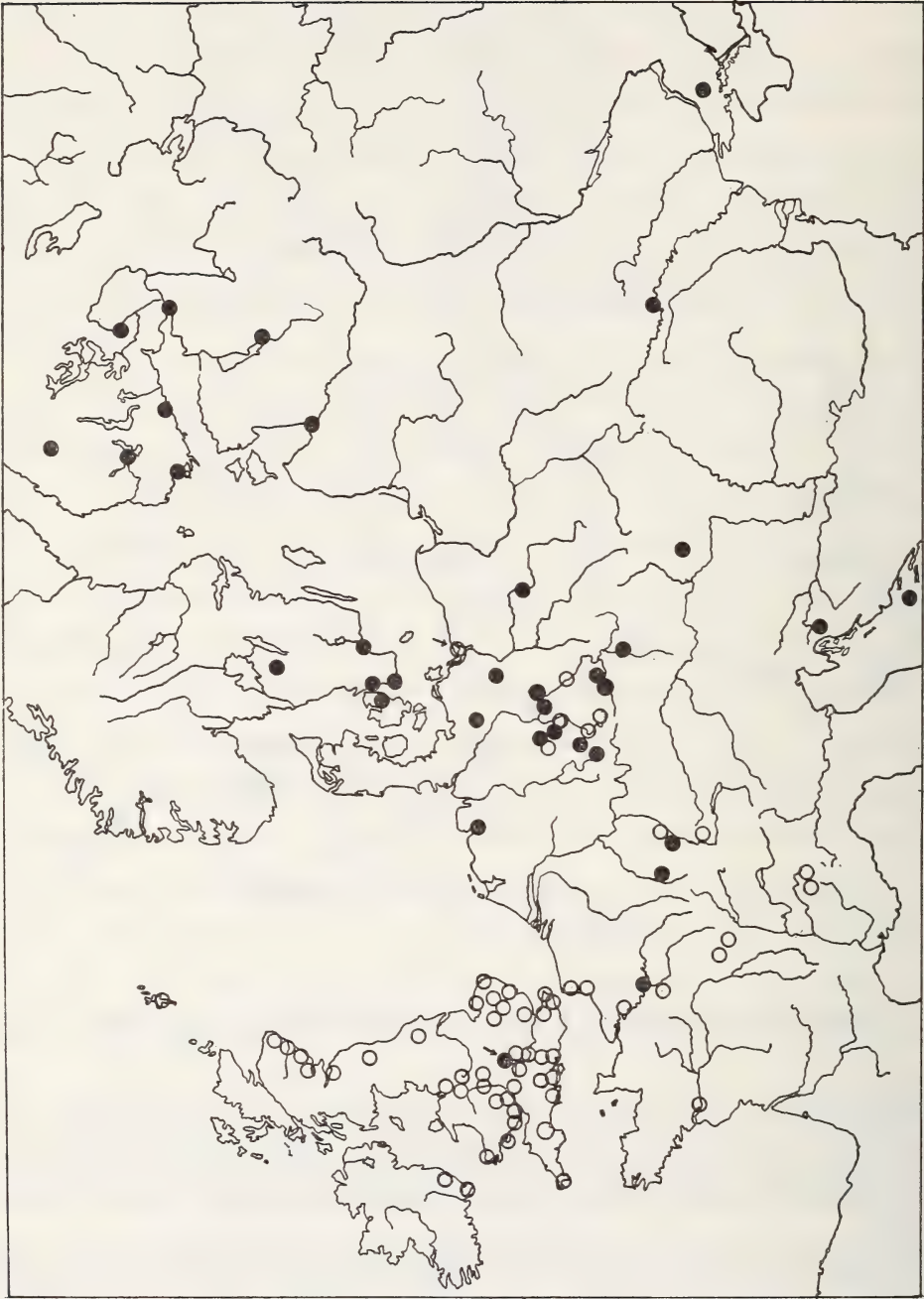


Fig. 2. Distribution of the cytotypes of *T. inodorum* in Europe. O— $2n=18$; ●— $2n=36$.

TABLE 1. Location, habitat, year of collection, number of individuals counted and chromosome numbers found for sampled populations of *T. inodorum*.

Abbreviations used: Ar, cultivated land; Rs, roadside; R, waste place; W, spontaneous but precise habitat not known; a, achene; pl, plant.

Location		Habitat	Year of collection	Number of individuals counted	Chromosome numbers (2n)
<i>British Isles</i>					
Perranuthno.	SW 541 293	Ar	1963	3a	18
Polzeath	SW 957 753	Rs	1962	1a	18
Exeter	SX 976 930	Ar	1963	3a	18
Dorchester	SY 680 904	Rs	1963	3a	18
Salisbury	SU 046 209	Ar	1963	2a	18
Bransgore	SZ 190 970	Ar	1963	3a	18
Fareham	SU 591 061	Ar	1962	3a	18
Harting	SU 774 200	Ar	1962	2a	18
Odiham	SU 728 484	Ar	1962	2a	18
Reading	SU 714 688	Ar	1962	3a	18
Cuxton	TR 717 673	Ar	1963	4a	18
M2	TQ 903 593	Rs	1963	2a	18
Dover	TR 336 442	Ar	1963	3a	18
Manston	TR 340 654	Ar	1963	2a	18
Ross-on-Wye	SO 644 260	Rs	1966	2a	18
Stow-on-the-Wold	SP 154 274	R	1966	3a	18
13 sites in Oxfordshire and Berkshire		Rs, Ar	1962	15pl, 3a	18
Ardley, Oxon.	SP 549 287	Ar	1962	2a	36
Heyford	SP 497 266	Ar	1962	2pl	18, 18 + 1B
Ipsden	SU 634 840	Rs	1962	2pl	18, 18 + 1B
Brentwood	TQ 634 897	Rs	1963	1a	18
Aldeburgh	TM 463 558	R	1963	2a	18, 18 + 1B
Bury St. Edmunds	TL 797 639	Ar	1962	3a	18
Eltisley	TL 267 588	Ar	1962	2pl	18
Wymondham	TM 091 993	Ar	1963	3a	18
Happisburgh	TG 379 314	Ar	1963	4a	18
Brancaster	TF 795 443	W	1962	2pl	18, 18 + 1B
Cleobury Mortimer	SO 659 766	Ar	1967	2a	18
Kidderminster	SO 893 791	Rs	1967	3a	18
Birmingham	SP 047 838	R	1967	2a	18
Burton-on-Trent	SK 149 257	Ar	1962	2a	18
Whitchurch	SJ 562 368	Ar	1967	3a	18
Dunhamtown	SJ 734 882	Ar	1962	2a	18, 18 + 1B
Dunhamtown	SJ 713 905	Ar	1962	3a	18
Stillington	SE 577 664	Ar	1962	2a	18
Stillington	SE 582 673	Rs	1962	2a	18
Piercebridge	NZ 208 217	Ar	1962	3a	18
Llanrhian	SM 814 308	Ar	1967	3a	18
Fishguard	SM 969 358	Ar	1963	3a	18
Cardigan	SN 125 382	Ar	1963	2a	18
Aberaeron	SN 459 623	R	1964	3a	18
Llangennydd	SS 437 916	Ar	1964	3a	18, 18 + 1B (once)
Paviland	SS 447 867	Ar	1967	2a	18
St. Brides Major	SS 909 727	Ar	1967	1a	18
Coedkernew	ST 262 841	Rs	1966	2a	18
Hay-on-Wye	SO 194 399	Ar	1967	3a	18, 18 + 1B, 18 + 2B
Queensferry	NT 155 770	Ar	1962	3a	18
Coupar Angus	NO 213 391	Ar	1962	2a	18
Tannadice	NO 505 577	Ar	1962	1a	18

<i>Location</i>		<i>Habitat</i>	<i>Year of collection</i>	<i>Number of individuals counted</i>	<i>Chromosome numbers (2n)</i>
<i>British Isles—(cont.)</i>					
Stonehaven	NO 894 900	Ar	1962	2pl	18
Reinchall	NO 853 935	Ar	1962	3a	18, 18 + 1B (once)
Bucksburn	NJ 884 106	Ar	1962	2a	18
Newburgh	NJ 937 269	Ar	1962	2a	18
Scalloway, Shetland		W	1962	1a	18
Lady's Island, Wexford		Ar	1966	3pl	18
Kilbride, Wicklow		Ar	1964	2pl	18
<i>France</i>					
Nantes		W	1965	3a	18
Grand-Quevilly (Rouen)		W	1964	1a	18
Palaiseau 48°43'N, 2°14'E		Ar	1963	3a	18
Paris—Montparnasse		R	1963	2a	36
24 km N of Abbeville		Rs	1963	3a	18
9 km S of Le Touquet		Rs	1963	3a	18 + 1B (twice), 18 + 2B
Marigny l'Eglise 47°21'N, 3°56'E		W	1967	4a	18
Dompierre-en-Morvan 47°15'N, 4°15'E		Ar	1966	2a	18
Bonneval-sur-Arc 45°22'N, 7°03'E		Ar	1966	2a	18
Lanslevillard (Savoie)		W	1966?	2a	18
Nancy		W	1967	3a	36
Strasbourg		Ar	1962?	2a	36
Bas-Rhin		Ar	1962?	1a	18
<i>Germany</i>					
Freiburg im Breisgau		Ar	1967	4a	18
Ems estuary		W	1966?	3a	36
Rohrsen (Weser)		W	1967	3a	36
Rudolstadt 50°44'N, 11°20'E		W	1967	2a	18
Ballenstedt (Harz)		W	1966	3a	18
Roblingen-See (22 km W of Halle)		W	1966	3a	18
Hornburg 52°02'N, 10°38'E		W	1965	3a	36
Grabsleben, Gotha		W	1965	3a	36
Halberstadt 51°54'N, 11°04'E		W	1966	3a	36, 37 (once)
Lengenfeld (Vorgtland)		W	1965	3a	18
Lommatsch 51°12'N, 13°19'E		W	1967	3a	18
Dessau 51°51'N, 12°15'E		W	1967	3a	36
Elster 51°50'N, 12°49'E		W	1966	3a	36
Parchim 53°26'N, 11°51'E		W	1966	3a	36
Gransee 53°00'N, 13°10'E		W	1963	2a	36
<i>Poland</i>					
Wolin 53°51'N, 14°38'E		W	1960	3a	18
Szczepankowo (Poznan)		W	1962	3a	36
Pokrzywno, nr. Poznan		W	1967?	2a	36
<i>Czechoslovakia</i>					
Kadaň 50°23'N, 13°15'E		Rs	1961	2a	36
Most 50°31'N, 13°39'E		W	1961	1a	36
Prague (3 sites)		Ar	1961	5a	36
Ivanka 48°14'N, 18°07'E		W	1967?	3a	36
<i>Yugoslavia</i>					
Viš 43°03'N, 16°11'E		W	1965	3a	36, 37 (once)
Ogulin 45°16'N, 15°14'E		W	1967?	3a	36

<i>Location</i>	<i>Habitat</i>	<i>Year of collection</i>	<i>Number of individuals counted</i>	<i>Chromosome numbers (2n)</i>
<i>Denmark</i>				
Tastrup 55°29'N, 10°19'E	Ar	1962	3a	36
<i>Sweden</i>				
Landskrona 55°53'N, 12°50'E	W	1964	2a	36
Bunkeflo 55°34'N, 12°59'E	W	1967	3a	36
Bäckaskog 56°05'N, 14°20'E	W	1967	3a	36
Vartofta-Åsak 58°06'N, 13°40'E	W	1967	3a	36
<i>Finland</i>				
Sauvo 60°22'N, 22°44'E	W	1967?	3a	36
Porvoo 60°24'N, 25°40'E	W	1966?	3a	36
Nokia 61°29'N, 23°31'E	W	1967?	3a	36
Kinnula 63°24'N, 25°00'E	W	1966?	3a	36
<i>U.S.S.R.</i>				
Salaspils (Riga)	W	1962?	4a	36, 35 (once)
Pskov	W	1962?	3a	36
Leningrad	W	1962?	2a	36
Priorsersk 61°01'N, 30°08'E	W	1962?	3a	36
Kamenets-Podolski	W	1962	3a	36
Askaniya Nova 46°27'N, 33°53'E	W	1966	3a	36

grains twice the volume of those from diploids. Tetraploid achenes usually germinate more rapidly and completely than diploid achenes; high dormancy is especially marked in British diploids, but achenes from north German diploids closely resemble achenes from tetraploids growing in the same area in their germination behaviour. Only one morphological character has been found to differentiate diploids from tetraploid consistently in comparative cultivation—the shape of the terminal lobes of the first true leaves of the seedling, which are relatively broad and blunt in tetraploids but narrow and acute in diploids (Kay 1965).

Ecologically, the cytotypes are phytosociologically indistinguishable; diploid and tetraploid fill the same niche in the weed community. The overall distributions of the cytotypes suggest differing climatic adaptations, with the diploids adapted to wetter and more maritime climates, and the few observations that have been made of their ecological preferences in the zone of overlap tend to confirm this. Rottgardt (1956) noted that, in Schleswig-Holstein, the diploids occurred on the uplands and on poorer sandy soils, the tetraploids in the lowlands; in East Germany, diploids are found in upland areas and near the Baltic coast, tetraploids elsewhere.

Neither mixed populations of diploid and tetraploid *T. inodorum* nor naturally occurring triploids have yet been reported. It is interesting to consider the possible course of events in a natural mixed population, such as may often be formed when crop-seed containing achenes of one cytotype as a contaminant is sown in a field already containing the other cytotype. *T. inodorum* is a strongly self-incompatible annual plant, cross-pollinated mainly by flies, and triploid seed can readily be formed in high yield by crossing diploids and tetraploids (Kay 1965). The triploid plants resulting from crossing are, although vigorous, of extremely low fertility, and triploid seed is, from the reproductive point of view, wasted. The cytotype producing the smaller number of flowers in a mixed population will lose a higher proportion of its progeny in the production of triploids, and should be eliminated in a few generations. Thus mixed populations of diploids and tetraploids are likely to be unstable and transitory and, in the absence of marked ecological differences between the cytotypes, the first cytotype to establish a sufficiently large population in a

hitherto unoccupied area (a frequent event for an aggressive weed of arable land) is likely to quickly eliminate pioneer plants of the other cytotype and to remain in possession. The boundary between an area occupied by diploids and an area occupied by tetraploids is likely to be sharp and may coincide with a field border; the areas could be inter-digitated with enclaves of one cytotype lying well within the area of the other. This kind of situation, 'obligate allopatry', hypothetical for the cytotypes of *T. inodorum*, has been shown to exist between *Clarkia biloba* and *C. lingulata* (Lewis 1962).

THE ORIGIN OF DIPLOID AND TETRAPLOID *T. INODORUM*

T. inodorum is a weed of man-made habitats, arable land and waste places, and appears to have no natural habitat in the greater part of its range. It is most abundant and widespread in western, northern, central and eastern Europe; it is absent from the Mediterranean region and it is local in south-central Europe (the Alps), south-eastern Europe, Asia Minor, the Caucasus and central Asia. The only natural habitats in which apparently native populations of *T. inodorum* maintain themselves at the present day are *solonchak* regions on the Lower Volga and mountain slopes in the Caucasus. These populations are morphologically rather different from typical *T. inodorum*, with the ray-florets often short or absent, but fall within the extreme limits of variation found in other populations of the species (Pobedimova 1961).

(a) *Diploid T. inodorum*

Diploid *T. inodorum*, which appears to have no natural habitat at present (if, as seems probable, the Volga and Caucasus populations are tetraploid), has three likely modes of origin:

1. From *T. maritimum*
2. From the common ancestor of *T. maritimum* and *T. inodorum*
3. From a Caucasian or central Asian species unrelated to *T. maritimum*.

T. maritimum is diploid and almost completely inter-fertile with diploid *T. inodorum* (Kay 1965), with which it is sympatric in a large part of the native range of *T. maritimum* on the coasts of western and northern Europe. It is easy to suppose that *T. inodorum* might have originated from *T. maritimum* since the spread of agriculture to the Atlantic coasts in about 3,000 B.C. There are, however, considerable ecological, morphological and physiological differences between *T. maritimum* and *T. inodorum*, and the discovery of achenes which appear to belong to *T. inodorum* in a Late Pleistocene deposit at Upton Warren in Worcestershire (Coope, Shotton & Strachan 1961) dating from the beginning of the Gottweig Interstadial, about 42,000 years ago, suggests that a recent origin from *T. maritimum* is unlikely. The third possible mode of origin of diploid *T. inodorum*, from a Caucasian or central Asian species unrelated to *T. maritimum*, seems ecologically, geographically, and genetically unlikely. The second possible mode of origin, divergence from a common ancestor, is supported by the interfertility and similarity in geographical range but sharp ecological separation of diploid *T. inodorum* and *T. maritimum*. The initial separation of the two species may have taken place in the early Pleistocene. Diploid *T. inodorum* may have originally occupied a natural habitat that no longer exists as such. One possible habitat is in the vicinity of drinking-places used seasonally by wild herbivores, especially in lowland areas, where the soil may have been heavily trampled in winter and spring but relatively undisturbed in summer. This kind of habitat may have been rather similar to the farmyards in which *T. inodorum* now flourishes, and the Upton Warren site, where *T. inodorum* was associated with a number of other weeds including *Polygonum aviculare* and *Potentilla anserina*, may have been of this type. *T. inodorum* achenes survive burial in soil well (Kay 1965), and retain 30 per cent. of their initial germinating capacity after passage through the bovine digestive tract (Dorph-Petersen 1925).

(b) *Tetraploid T. inodorum*

Although tetraploid *T. inodorum* is morphologically very close to diploid *T. inodorum*, it is not necessarily an autotetraploid derived from diploid *T. inodorum* by chromosome doubling. Vaarama (1953) considered it to be an allotetraploid derived from '*T. maritimum* ssp. *maritimum*' (*T. maritimum*) and '*T. maritimum* ssp. *ambiguum* var. *boreale*' (northern diploid *T. inodorum*), but this apparent allotetraploidy could be secondary, the consequence of chromosomal rearrangements in an autotetraploid. Allotetraploidy resulting from doubling of the chromosome number in a sterile diploid interspecific hybrid is most unlikely in this case; all the F_1 hybrids between species of *Tripleurospermum* that I have obtained (*T. inodorum* $\times$ *T. maritimum*, *T. inodorum* $\times$ *T. tchichatchevii*, *T. inodorum* $\times$ *T. disciforme*, *T. inodorum* $\times$ *T. decipiens*, *T. disciforme* $\times$ *T. decipiens*, *T. inodorum* $\times$ *T. tenuifolium*) have proved to be fertile (see below) and even if a sterile interspecific hybrid were formed it would be unlikely to persist vegetatively until chromosome doubling took place, because *T. inodorum* and many other species of *Tripleurospermum* are annual or biennial. Rottgardt (1956) observed that the chromosomes of tetraploid *T. inodorum* are half the size of those of diploid *T. inodorum*, indicating that the doubling of the chromosome number took place some time ago.

Triploid hybrids between diploid and tetraploid *T. inodorum* can be produced very easily by ordinary cross-pollination. The triploid plants are vigorous. Trivalents predominate in pollen mother cell meiosis, averaging 4.85 per cell in 20 cells analysed; the plants are pollen sterile but, under favourable conditions, will set about 10 per cent. of the normal number of achenes when used as the female parent in crosses with diploids or tetraploids. The functional female gametes produced by the triploids can be either 'reduced' ($n = 12$ or 13) or unreduced (in the one example observed, $n = 26$). The aneuploid offspring of the triploids are less vigorous than their parents, but also, in some cases, have some degree of fertility (3–5 per cent.) on the female side; in principle, the diploid or tetraploid level might eventually be regained and gene-flow in both directions between diploid and tetraploid is theoretically possible (Kay 1965). Chromosome homology and hybrid fertility does not necessarily indicate an especially close relationship between taxa in *Tripleurospermum*. I have found that diploid F_1 hybrids between diploid *T. inodorum* and *T. disciforme* (C. A. Mey.) Schultz Bip. ($2n = 18$) and between diploid *T. inodorum* and *T. tenuifolium* (Kit.) Freyn ($2n = 18$) and tetraploid F_1 hybrids between tetraploid *T. inodorum* and *T. tchichatchevii* (Boiss.) Bornm. ($2n = 36$) are more than 50 per cent. seed fertile, with regular pollen mother cell meiosis, although *T. disciforme*, *T. tenuifolium* and *T. tchichatchevii* are morphologically and ecologically very different from one another and from *T. inodorum*.

Artificial autotetraploids have not yet been synthesized from diploid *T. inodorum* but I have synthesized artificial autotetraploid *T. maritimum* and it is moderately fertile (c. 25 per cent. as ovule parent, 50 per cent. as pollen parent) with relatively normal pollen mother cell meiosis (63 per cent. bivalent formation) producing a majority of normally reduced diploid ($n = 18$) gametes (Kay 1965). Thus low fertility resulting from meiotic irregularities is unlikely to have been a barrier to the establishment of newly-formed autotetraploid *T. inodorum*. However, *T. inodorum* is normally strongly self-incompatible; the self-incompatibility is sporophytic and tetraploids are as self-incompatible as diploids (Kay 1965), so a single autotetraploid plant would normally be unable to set seed by self-fertilization. Even if a small group of self-incompatible autotetraploids were to establish themselves in a numerically superior diploid population, they would eventually be eliminated because they would produce a greater proportion of triploid seed than the diploids. The best prospects for the establishment of autotetraploids appear to exist in small marginal and pioneer populations, growing in habitats where individual plants are often isolated from one another and the number of plants in the population may vary greatly from year to year. Roadside and botanic garden populations meet some of these criteria. One would expect self-fertility to be advantageous in this type of habitat, and self-fertility has in fact been found in a number of such populations of *T. inodorum* (Table 2). In the one case that I have analysed, self-incompatibility was recessive to self-fertility (Kay 1965). A single

original autotetraploid plant arising in a marginal habitat of this type in nature might be both self-fertile and isolated from other (diploid) *T. inodorum* plants, and could then establish a new tetraploid population; self-fertility in itself would, of course, confer a degree of isolation at first, but would presumably be selected against as the density of the tetraploid population increased. The whole process would resemble the mechanism of 'catastrophic selection' involved in the origin of new species of *Clarkia*, as described by Lewis (1962).

TABLE 2. Self-incompatibility and self-fertility in *T. inodorum* plants isolated in a greenhouse.

Origin	Total number tested		Self-fertile (at least 3 per cent. achene-set)		Self-incompatible	
	Plants	Popns.	Plants	Popns.	Plants	Popns.
British Isles $2n = 18$	75	24	9	2	66 (37)	24 (19)
$2n = 36$	3	1	2	1	1	1
Europe $2n = 18$	9	4	2	1	7 (2)	4 (2)
$2n = 36$	37	10	12	6	25 (10)	8 (5)

The figures in brackets show the number of cases in which unsuccessful selfings were checked by simultaneous successful crosses on the same plant.

The populations in which self-fertility was found were as follows: small roadside populations at Ipsden, Oxfordshire and Stillington, Yorkshire; a single isolated tetraploid plant at Ardley, Oxfordshire; Botanic Garden populations at Kassel (Germany), Turin (Italy), Cluj (Rumania) and Ashkhabad (Turkmenistan); cornfield populations (self-fertility low) at Tastrup, Denmark and Prague, Czechoslovakia; and a population of unknown status in Wolin Island, Poland. Some self-incompatible plants were also found in most of these populations.

The most likely mode of origin of tetraploid *T. inodorum* therefore appears to be by chromosome doubling from diploid *T. inodorum*, probably in marginal populations on the eastern boundary of the range of the species, preceded or followed by some hybridization with Caucasian or central Asian species of *Tripleurospermum*. Climatic changes may then have separated the diploids and tetraploids, with the diploids surviving in refugia in northern and western Europe (trampled places near water?) and the tetraploids surviving in refugia in south-eastern Europe or the Caucasus (solonchak areas?). Both tetraploids and diploids may have started their association with man as habitation-weeds, spreading into cultivated crops as agriculture developed and extending their ranges until they met again in central and northern Europe. Obligate allopatry may then have stabilized their ranges. The distribution of the cytotypes in Canada resembles their distribution in Europe, with diploids in the eastern Maritime Provinces and tetraploids in the more continental climate of the Prairies; this could be due in part to the differing climatic adaptations of the cytotypes, but an alternative and perhaps more likely explanation is that most of the *T. inodorum* introduced to eastern Canada came with French, Scottish and English settlers from western Europe, where diploids predominate, whereas most of the *T. inodorum* introduced to the Prairies came with crop-seed from northern and eastern Europe, where tetraploids predominate.

Much work remains to be done on the problem of the origin and inter-relationships of diploid and tetraploid *T. inodorum*, especially in the field in central Europe, on the status of the Volga solonchak populations, and on the relationships between *Tripleurospermum* spp. and *T. inodorum* in the Caucasus and the Middle East.

ACKNOWLEDGMENTS

I would like to express my thanks to Dr. S. R. J. Woodell for his interest and advice, and to Dr. L. A. Boorman, Miss Alison Davies, Dr. T. T. Elkington, Dr. R. A. Finch, Dr. C. J. Grant, Dr. R. M. Harley, Dr. J. Květ, Dr. E. G. Pobedimova, Mr. W. Scott, Professor O. Wilmanns, and many botanic gardens and research institutions for their help in collecting material of *T. inodorum*. I am also grateful to Professor C. D. Darlington for providing laboratory facilities in the Botany School, Oxford.

Part of the investigation was carried out while I held a Nature Conservancy post-graduate research studentship.

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STUDIES IN THE POLLINATION ECOLOGY OF *VIOLA*. I. THE POLLEN-CONTENT OF STIGMATIC CAVITIES

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ABSTRACT

Samples of chasmogamous flowers of three species of *Viola* from seven different habitats were examined for the contents of their stigmatic cavities. Flower and pollen morphology are described. Insect exclusion experiments suggest that self-pollination is rare and emasculations have established that intraspecific and interspecific pollen transfer is frequent. The quantity of pollen introduced into the stigmatic cavity is affected by several factors. Rain reduces pollination in exposed habitats and similar decreases are detected in sheltered or north- or east-facing habitats due to the smaller amount of sunlight incident upon them. Percentage pollination remains high in habitats with no blossoms of other genera; anthophilous insects visit *Viola* for food. Habitats with a variety of blossoms besides *Viola* may lure sufficient insects to ensure the pollination of all species, including the inconspicuous ones. However, large stands of showy blossoms may monopolize the insect visitors in a habitat also occupied by less attractive species. It is argued that gene flow in disturbed or marginal habitats may be increased by the greater availability of potential pollinators.

INTRODUCTION

The three species chosen for the present study, *Viola riviniana* Rchb., *V. reichenbachiana* Jord., and *V. hirta* L., produce chasmogamous flowers in spring and cleistogamous flowers in summer. The chasmogamous flowers are morphologically complex and are manifestly entomophilous (see page 143). They are self-compatible (Valentine 1962), although experiments on *V. riviniana* described below suggest that self-pollination is rare, a point reported also by Sprengel for *V. odorata* L., by Darwin for *V. canina* L. (both in Knuth 1908), and for *V. mirabilis* L. (Kerner & Oliver, 1902). Further experiments on *V. riviniana*, also reported below, suggest that the pollination mechanism is highly functional, and personal observations confirm that the chasmogamous flowers of all three species are capable of producing viable seed. Several authors, notably Schmiedeknecht (1878, 1930), Müller (1883) and Knuth (1908), have reported that the flowers are visited by a variety of insects. Despite these conditions, however, they frequently fail to set seed, a fact recorded for *V. mirabilis* (Kerner & Oliver 1902), *V. odorata* and *V. riviniana* (West 1930), *V. hirta* (Knuth 1908) and subsection *Rostratae* Kupffer (Gregory 1912).

It seems reasonable to suppose that the failure to set seed in the chasmogamous flowers of *Viola* may be due mainly to the breakdown in the transference of pollen. This process depends upon the distribution and availability of suitable vectors, and these in turn are affected by a large number of ecological factors. Four such factors are considered in this paper, namely weather, amount of shade in the habitat, direction of slope of the habitat and the proximity of other blossoms of the same, or of different species.

MATERIALS AND METHODS

Material was gathered from seven different habitats in the chalk countryside of southern England. Six of these habitats occurred within an area of approximately 30 hectares (80 acres) of woodland and parkland near Winterslow, Wiltshire, and the seventh was an exposed hillside, known as Juniper Top, near Dorking in Surrey. A small sample of white-flowered *V. odorata* was collected from an eighth habitat in the Winterslow locality, but will not be considered with the main bulk of data.

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Fifty flowers from one colony within each habitat were picked and preserved in a 9 : 1 mixture of 70 per cent. ethanol and glycerol. This viscous fluid minimized movement of loose pollen amongst the specimens. Care was taken to choose flowers in mid-anthesis, a condition recognized by the presence of unwrinkled corollas of fresh appearance and glistening at the mouth of the corolla-tube, borne by pedicels sharply hooked at the distal end.

In the laboratory specimens were dissected, and the style removed and transferred to glycerine jelly stained to the colour of claret by the addition of basic fuchsin. This mountant left the styler tissue greenish-yellow in colour, but stained pollen grains red.

The chief topographical and floral features of each habitat are summarized in Table 1.

FLOWER AND POLLEN MORPHOLOGY

Flowers

The accounts of visitors to the chasmogamous flowers of *Viola* referred to in the introduction reveal that hover-flies (Diptera: Syrphidae), bee-flies (Diptera: Bombyliidae) and bees (Hymenoptera: Apoidea) are most frequently attracted to them. The flowers may thus be termed myophilous (fly-loving) and melittophilous (bee-loving). Pollination syndromes of flowers of this type include characters such as zygomorphy, pale blue to violet colouring, moderately deep corolla-tubes, distinct nectar-guides, diurnal pollen and nectar presentation, nectar and pollen open or fairly effectively concealed, and a sweet odour, (Baker & Hurd 1968, Faegri & van der Pijl 1966). These characters are present to a greater or lesser degree in the three species under discussion.

Fig. 1. shows that the size and arrangement of organs differ slightly between the species, particularly the styles, which are illustrated by Fig. 2. During anthesis the ovary is completely enclosed by the ring of stamens and much of the style is similarly hidden by the cone of connective appendages. The tip of the style is the only part of the gynoecium visible in the open flower, and bears short papillae, except in *V. hirta*. The number and size of these papillae are greater in *V. reichenbachiana* than in *V. riviniana* although much variation is found in both species.

The style is tubular with a lumen which is continuous with the cavity of the ovary but for a constriction near the base. Its interior walls stain deeply with PAS (periodic-acid Schiff), and secrete mucilage which so fills the lumen that the stigma-opening can be seen to be moist. The stigmas are absent as external receptive surfaces so pollen germinates only with the lumen of the style. The style pivots upon the distinct area of flexure near its base. The tissues in this region are elastic hence the style may be strongly deflected by a visiting insect, but immediately regains its normal position once the visit has ended.

Observations with fresh flowers in the laboratory show that during early anthesis movement of the style causes no visible changes at the opening of the stigmatic cavity. At full anthesis, however, disturbance of the style causes the exudation of a drop of mucilage at the stigma-opening. In an attempt to determine the possible function of this phenomenon, a small camel-hair brush loaded with violet pollen was repeatedly drawn over the stigma-opening at the same time as the style was raised with a mounted needle. In newly-opened flowers the majority of the pollen merely fell on to the anterior petal. However, in flowers two to three days old, a high proportion of grains adhered to the stigma-opening, presumably as a result of the sticky nature of the mucilage.

McLean & Ivimey-Cook (1956) suggest that disturbance of the style closes the lumen in the area of flexure hence increasing the pressure of mucilage within. As a consequence of this a drop is exuded from the stigma-opening and any pollen in the vicinity adheres to it. Then, when the style springs back into place, the basal lumen resumes its normal shape and capacity, the mucilage drop is withdrawn into the stigmatic cavity and pollination is effected. MacLeod, in Knuth (1908), suggested that the mucilage was deposited upon visiting insects to form a moist and viscous area suitable for the reception of the dry, powdery pollen. The results of my own observations rather favour the former explanation

TABLE 1. Chief topographical and floral features of habitats. Shelter denotes the shade afforded by the dominant plants, the symbols indicate: + much shade, - shade only when sun low in arc, 0 none. Distribution of blossoms (N.B. not plants) within a 20 square-yard area indicated: (a) large clumps; (b) small clumps; (c) singly; (d) evenly.

Site No.	Height Above Sea Level (feet)	Direction of Slope	General Description and Grid Reference	Type	Soil Drainage	Cover	Dominant Plants	Shelter	Blossoms	Distribution
A	350-370	NE	Edge of wood SU 251 338	15 cm clay with flints on chalk	Good excepting after wet weather	15 cm leaf mould	<i>Quercus robur</i> <i>Crataegus monogyna</i> <i>Rubus fruticosus</i>	+ + 0	<i>Viola reichenbachiana</i> <i>Mercurialis perennis</i>	a, b, c.
B	345-355	NE	Edge of wood SU 253 337	As site A	As site A	15 cm leaf mould			<i>Viola riviniana</i> <i>Endymion non-scriptus</i> <i>Anemone nemorosa</i> <i>Primula vulgaris</i> <i>Taraxacum officinale</i>	b, c, a c b c
C	440-410	NE	Glade in wood SU 255 335	As site A	As site A	100 per cent. grass and tussocks	Graminae	0	<i>Viola hirta</i> <i>Viola riviniana</i> <i>Ajuga reptans</i> <i>Taraxacum officinale</i>	b, c c c c
D	350-370	W	Slope between wood and field SU 254 339	5-10 cm clay on chalk	Good	100 per cent. grass and tussocks, some <i>Mercurialis</i> stands	Graminae <i>Fagus sylvatica</i> at edge	0	<i>Viola reichenbachiana</i> <i>Viola hirta</i> <i>Glechoma hederacea</i> <i>Primula vulgaris</i> <i>Mercurialis perennis</i> <i>Fragaria vesca</i>	b b, c b, c a, b a c

E	390	—	In wood near a ride SU 254 339	30 cm clay on chalk	Poor	10 cm leaf mould	<i>Quercus robur</i> <i>Corylus avellana</i> <i>Rubus fruticosus</i>	+	<i>Viola reichenbachiana</i> <i>Endymion non-scriptus</i> <i>Primula vulgaris</i> <i>Adoxa moschatellina</i> <i>Lathraea squamaria</i>	b b b b b
F	350	S	Coppiced wood SU 254 339	As site E	Fair	Patchy leaf mould, much bare soil	<i>Corylus avellana</i> cut 2 years previously. Occasional: <i>Quercus robur</i> <i>Betula pendula</i>	—	<i>Viola reichenbachiana</i> <i>Viola riviniana</i> <i>Endymion non-scriptus</i> <i>Primula vulgaris</i> <i>Glechoma hederacea</i> <i>Anemone nemorosa</i> <i>Orchis mascula</i> <i>Fragaria vesca</i> <i>Bellis perennis</i> <i>Ranunculus ficaria</i>	a, b a, b b a, b b b, c b b b c
G	300	—	Tree stand in horse paddock SU 254 342	As site E	Fair	Bare soil	<i>Fagus sylvatica</i>	+	<i>Viola odorata</i>	a
H	440-460	W	Exposed chalk hill TQ 182 527	Thin clay on chalk	Good	Very scant leaf-mould many bare patches	Graminae	0	<i>Viola hirta</i> subsp. <i>hirta</i> <i>Viola hirta</i> subsp. <i>calcareo</i> <i>Viola riviniana</i> subsp. <i>riviniana</i> <i>Viola riviniana</i> subsp. <i>minor</i> <i>Taraxacum officinale</i> just outside habitat	b, c c b, c c c c

although I believe both to be valid. The drop of mucilage seems to increase the area to which pollen grains may adhere. The opening of the stigmatic cavity is very small and any mechanism that increases the chance of pollen passing through it would increase the efficiency of the pollination mechanism.

Pollen

It is impossible to distinguish between the pollen grains of the three species of *Viola* under study on the basis on morphology alone. The following description is therefore valid for all three species, with some additions for *V. riviniana*.

The pollen is powdery, and when examined fresh the grains are ellipsoidal to spheroidal with the colpi appearing as narrow grooves. When moistened for more critical examination they frequently become entirely spheroidal and the colpi may gape widely. There are three colpi arranged equidistantly from one another around the equator, with their longitudinal axes meridionally directed. They are very slightly biased towards one pole, hence in microscopical preparations a number of differing shapes can be seen. In surface view the exine lacks any distinguishing morphological features; it is smooth and very finely granular in appearance, without a trace of a reticulum.

V. riviniana has tricolpate and tetracolpate grains. A further distinction can be made according to size and exine thickness, there being small, thick-walled and large, thin-walled grains, a feature first reported by West (1930).

A character which helped to distinguish *Viola* pollen from that of other genera encountered in this study was its tendency to take up basic fuchsin stain more slowly. In a fresh preparation they would invariably appear paler than all other grains, with the colouring concentrated in the walls but absent at the colpi. The only character that appeared to vary significantly between *Viola* species was size, a feature manifest in the diameter of the polar view. Samples were measured in an attempt to demonstrate differences sufficient to separate the species.

The first series of samples were from the habitats under study and four species were investigated: *V. riviniana*, *V. reichenbachiana*, *V. hirta* and *V. odorata*. Eight preparations were made, two per species, each from a single flower and a separate plant. The dimension measured was the diameter of the polar view. An analysis of variance on the data, followed by the calculation of the least significant difference, showed significant differences in pollen diameter between species, except *V. hirta* and *V. odorata*. However, the difference between *V. riviniana* and *V. reichenbachiana* was so small as to suggest that the pollen of these species found in the stigmatic cavities would in practice be indistinguishable. In order to settle the matter a second series of samples were measured, and this time three flowers of each species from widely separated localities in Europe were used. Significant differences in diameter now appeared only between the two pairs of species, i.e. between *V. riviniana* + *V. reichenbachiana* and *V. hirta* + *V. odorata*. Pollen grains at either size extreme could be named with some confidence, but generally the character was not used because of its unreliability. Actual figures for the polar view diameter were $30\cdot5\mu$ – $44\cdot2\mu$ for *V. riviniana* and *V. reichenbachiana*, and $25\cdot5\mu$ – $34\cdot5\mu$ for *V. hirta* and *V. odorata*.

INSECT EXCLUSION EXPERIMENTS AND EMASCULATIONS

The experiments described here were carried out at habitats B (edge of wood) and C (glade in wood) in Wiltshire in the spring of 1966 on *V. riviniana*.

Insect exclusion experiments

Small polythene bags were placed over thirty individual plants from which all open flowers had been removed. Each bag, 19×21 cm, had a sealing mechanism at one end and this allowed the plant within to bloom freely while excluding airborne insects.

Eight days later the flowers were picked and preserved. In the laboratory the styles were mounted and examined for pollen. Twenty five out of thirty specimens bore no traces

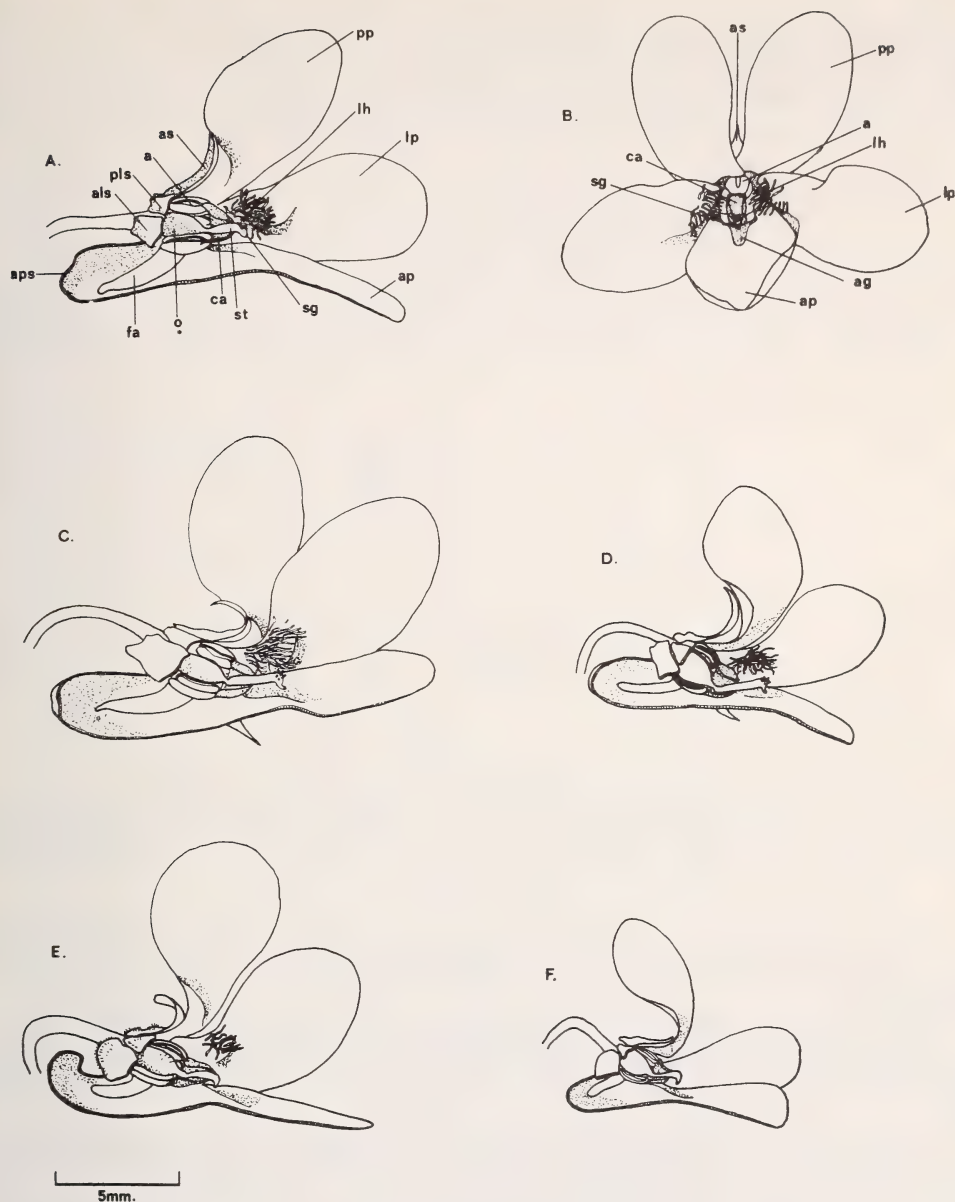


Fig. 1. Half-flower diagrams of A. *Viola reichenbachiana*, C. *V. riviniana* subsp. *riviniana*, D. *V. riviniana* subsp. *minor*, E. *V. hirta* subsp. *hirta*, F. *V. hirta* subsp. *calcarea* and B. a ventral or 'insect's eye view' of *V. reichenbachiana*.

Symbols: a = anther
 ag = anterior groove
 als = anterio-lateral sepal
 ap = anterior petal
 aps = anterior petal spur
 as = posterior sepal
 ca = connective appendage
 fa = filament appendage

lh = lateral hairs
 lp = lateral petal
 o = ovary
 pls = postero-lateral sepal
 pp = posterior petal
 sg = stigma-opening
 st = style.

of pollen either on the stylar papillae or within the stigmatic cavity. Of the five that did, two had been ravaged by snails, one was in a bag into which a pair of March flies (*Bibio ferruginatus* L.) had found their way, and another had been damaged by a deer. Signs of ovule development were present in two of these disturbed flowers. No foreign pollen was observed at all. These results strongly suggest that self-pollination is uncommon.

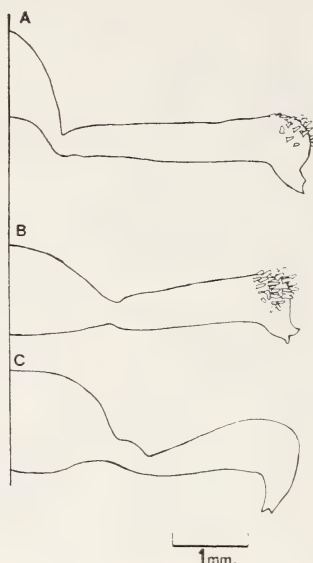


Fig. 2. Styles of A. *Viola riviniana*, B. *V. reichenbachiana*, C. *V. hirta*.

Emasculations

Thirty flowers were emasculated whilst still in bud and then allowed to bloom normally. After four days of warm, sunny weather they were gathered and placed immediately in preservative.

In the laboratory each flower was dissected and examined for the effectiveness of emasculation; only two specimens bore traces of anther tissue. The styles were mounted in the usual way and examined for pollen. The ovules were checked for signs of development.

Twenty-seven out of thirty styles contained *Viola* pollen, and thirteen ovaries contained developing ovules. In most specimens the pollen was deeply inserted into the stigmatic cavity but frequently there was sufficient to form a bunch of grains adhering to the stigma-opening. Little pollen was found in the papillary region of the style. The average number of violet pollen grains per stigmatic cavity was fifteen, and the average number of foreign grains (mostly of *Endymion non-scriptus*) was six (see Fig. 3). This is positive evidence that transference of pollen is frequent under suitable conditions.

CONTENTS OF STIGMATIC CAVITIES

A total of 525 stigmatic cavities were examined. The pollen grains were clearly visible when stained with basic fuchsin but it was usually impossible to tell whether or not they were viable. Wrinkled and empty grains appeared in the samples very occasionally. Detection of pollen transfer between the species of *Viola* was not possible because of the difficulties in identifying the pollen grains. Occasionally very large numbers of pollen grains were

found in a cluster at the stigma-opening. The capacity of the stigmatic cavity varied from specimen to specimen and so the number of grains they could contain also varied considerably. It is difficult to estimate how many grains filled a stigmatic cavity, but the figures from the present study suggest that the number must be about thirty for *V. riviniana* and *V. reichenbachiana*, and somewhat less for *V. hirta*.

The data are summarized in Table 2. The term 'blossom' is used here in the sense of Faegri & van der Pijl (1966), that is, as an ecological term as opposed to a morphological one. 'Shelter' denotes the shade afforded by the dominant trees or shrubs.

The occurrence of large numbers of foreign pollen grains in some stigmatic cavities was most striking. In view of the limited capacity of the stigmatic cavity it would be expected that homogeneity of pollen loads would be at a premium. The presence of foreign grains suggests the strong competition for pollen vectors amongst the spring-flowering plants.

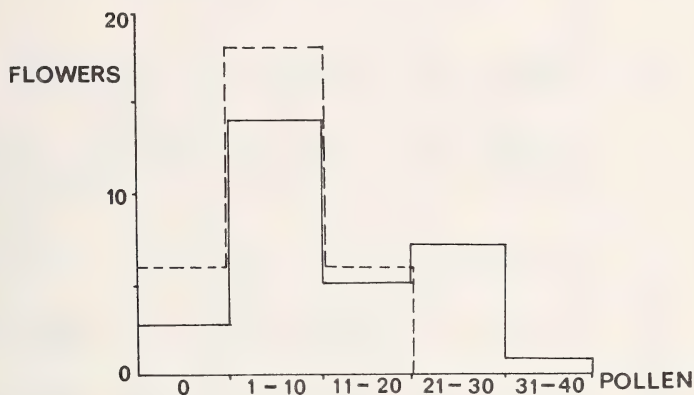


Fig. 3. Histogram of the number of pollen grains per stigmatic cavity in emasculated flowers. Ordinate: number of emasculated flowers, abscissa: absolute counts of pollen in stigmatic cavity. Solid line indicates *Viola* pollen; broken line indicates *Endymion* pollen.

EFFECTS OF WEATHER AND SHELTER

The influence of the weather preceding the collection of flowers of *V. hirta* is illustrated by Fig. 4. Comparative data for *V. reichenbachiana* show a large decrease in the number of pollen grains in the stigmatic cavities after rain, although the percentage of specimens containing them remains remarkably constant in all weathers (samples 6, 7, 8). The effect on *V. hirta* is very striking, and as all samples of this species were taken from exposed habitats the combined influence of weather and absence of shelter may be inferred from these results. Rain is detrimental and sometimes disastrous to insects trapped in the open whilst visiting flowers (Perkins 1919, Rau 1935), and Rayment (1935) has described how rain can occasionally lead to the decapitation of solitary bees. It is to be expected that wind and rain will eliminate insect visitors more rapidly in exposed places than in sheltered ones. My own observations confirm that some visitors to *Viola* (e.g. the syrphid *Platychirus albimanus* Fabr. and the bumblebee *Bombus agrorum* Fabr.) will remain active even in very light rain when sheltered by a canopy of tree branches, but not in exposed places. Also they recommence activity sooner after bad weather in sheltered habitats. Again Frison (1923) pointed out that the first bees out in spring are essentially bees which nest in the woods where the blossom at the time of their emergence is located. It is interesting thus to note that the percentage of *Viola* pollen per sample in *V. reichenbachiana* differs only marginally between sheltered and exposed habitats.

Viola riviniana samples reveal a different situation. The percentage of *Viola* pollen drops markedly at habitat B (edge of wood), which was sheltered, and remains consistently

TABLE 2. Data on contents of stigmatic cavities. Symbols for habitat as in Table 1. Symbols for preceding weather show type of weather followed by number of days of this type. Symbols for shelter: + presence or - absence. Symbols for foreign pollen: E = *Endymion non-scriptus*, A = *Anemone nemorosa*, P = *Primula vulgaris*, T = *Taraxacum officinale*, Gl = *Glechoma hederacea*.

Species	Sample	Percentage of sample containing			Total number of pollen grains per sample		Percentage of pollen total		Habitat	Corolla	Preceding weather	Shelter	Other Blossoms	Foreign pollen		
		No.	Size	<i>Viola</i> only	<i>Viola</i> & Foreign	No pollen	<i>Viola</i>	Foreign							<i>Viola</i>	Foreign
<i>V. riviniana</i>	11	30	76.6	3.4	20.0	414	2	99.8	0.2	F	large	sun 5	—	many	+	+
	12	30	66.7	20.0	13.3	358	16	95.7	4.3	F	typical	sun 5	—	many	+	+
	13	15	40.0	13.3	46.7	61	4	93.8	6.2	B	typical	sun 5	+	few	+	+
	14	30	17.0	46.6	36.4	—	—	—	—	B	typical	sun 1	+	many	+	+
	16	30	83.3	0	16.7	510	0	100	0	H	small	mixed	—	(1966) none	—	—
	17	30	93.3	0	6.7	470	0	100	0	H	typical	mixed	—	none	—	—
subsp. <i>minor</i>	6	18	72.2	11.0	16.8	226	9	96.2	3.8	E	typical	rain 2	+	few	+	+
	7	30	60.0	30.0	10.0	462	21	95.7	4.3	E	typical	sun 5	+	few	+	+
	8	30	70.0	23.3	6.7	382	28	93.2	6.8	F	typical	sun 5	—	many	+	+
	9	30	90.0	0	10.0	585	0	100	0	A	typical	sun 5	+	none	+	+
	10	30	66.7	23.3	10.0	419	24	94.6	5.4	D	typical	sun 5	—	many	+	+
<i>V. hirta</i>	1	15	13.3	0	86.7	3	0	100	0	C	mixed colours	rain 2	—	few	—	—
	2	30	50.0	3.3	46.7	119	1	99.2	0.8	C	mixed colours	sun 5	—	few	—	+
	3	30	38.5	3.9	57.6	93	1	99.4	0.6	D	pale	sun 2	—	many	—	Gl
	4	30	63.3	0	36.7	162	0	100	0	D	dark	sun 3	—	many	—	
	5	30	73.3	3.3	23.4	167	4	97.7	2.3	D	mixed	sun 5	—	many	—	
subsp. <i>calcareo</i>	18	30	42.9	0	57.1	128	0	100	0	H	pale	mixed	—	none	—	Gl
	19	7	65.0	0	35.0	22	0	100	0	H	small	mixed	—	none	—	
<i>V. odorata</i>	20	30	85.0	0	15.0	154	0	100	0	H	pale	mixed	—	none	—	Gl
	15	20	65.0	0	35.0	125	0	100	0	G	white	sun	+	none	+	+

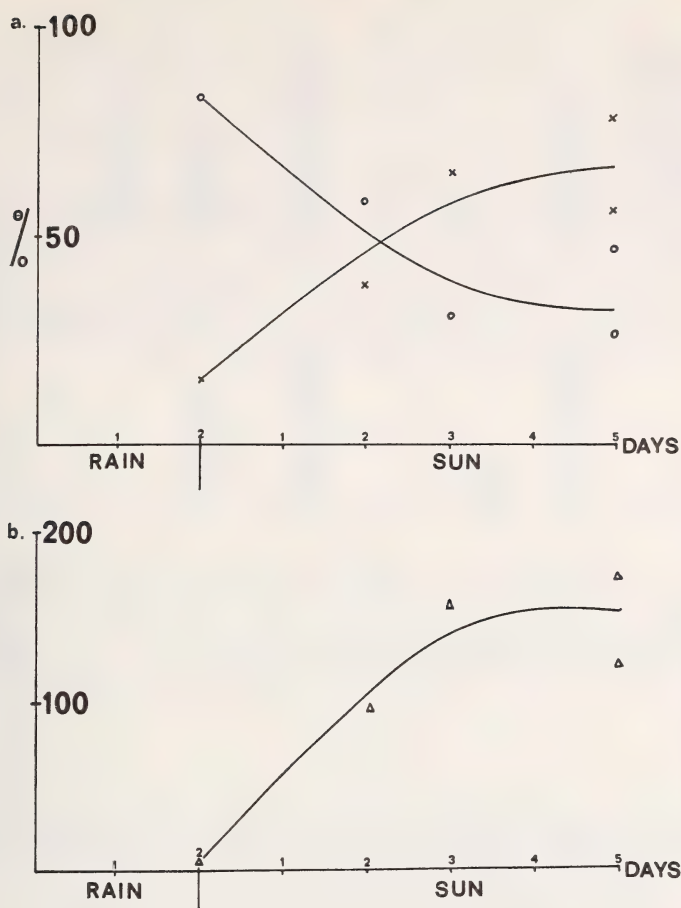


Fig. 4(a). Percentage pollination of samples of *Viola hirta* plotted against the number of days of rain or sun preceding the collection of the samples, x = percentage of sample containing *Viola* pollen only, o = percentage of sample containing no pollen.

(b) Actual counts of *Viola* pollen grains in samples of *V. hirta* plotted against the number of days of rain or sun preceding the collection of samples.

higher in the open habitats. This point will be met subsequently when the presence of other blossoms is discussed, but it is worth mentioning here that this habitat was more deeply shaded than the others, being further into the wood. This may well have discouraged some insect visitors; Kerner & Oliver (1902) reported that deep shade of this nature excludes many insects.

Pollination varies widely after unsettled weather and this may be expected from the differential responses of insect groups to changes in weather. Linsley (1958) notes that bumble bees (*Bombus* spp.), will remain active in cloudy weather while many solitary bees (e.g. *Andrena* spp.), will cease activity directly cloud obscures the sun; females return to the nest and males seek some sheltered spot. Again Perkins (1919) noted that solitary bees never leave their nests unless the sun is shining, and that they appear to be aware of imminent changes in the weather, ceasing activity as soon as the sun disappears behind cloud.

EFFECTS OF DIRECTION OF SLOPE AND TEMPERATURE

Fig. 5 presents data which strongly suggests that the direction of slope affects pollination. Slope and shelter together control the amount of sunlight incident upon the actual habitat occupied by the violets. As indicated above a large variety of insect visitors to *Viola* are strongly affected by the presence or absence of sunlight and many require a minimum temperature before commencing activity. The behaviour of many of the dipteran visitors is strongly influenced by the temperature, which must rise above a flight-threshold (Knight 1967). The emergence of many solitary bees is associated with the temperature of the ground in which they are overwintering. Shading of the burrow entrances, for example by vegetation obscuring the sun as it moves in its arc, may inhibit activity entirely (Linsley 1958). It is to be expected, therefore, that west and south-facing slopes will foster more potential visitors than north and east-facing slopes, and flight into sheltered habitats will be less common until temperatures there remain at a higher level.

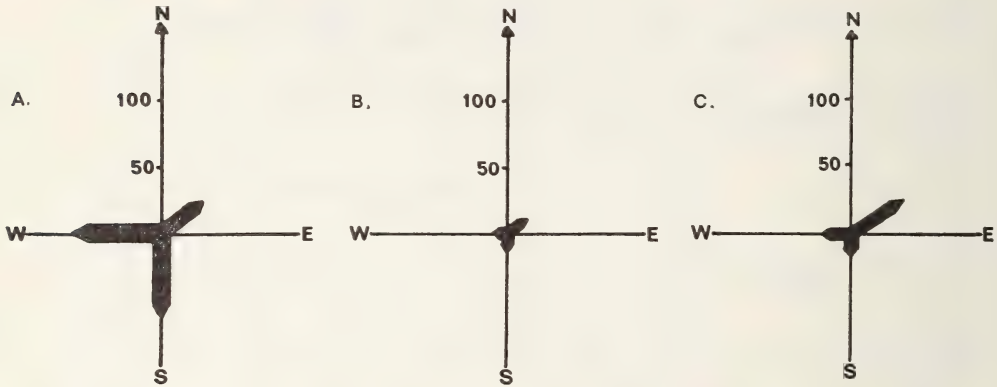


Fig. 5. Diagrams to show the relationship between percentage pollination and the direction of slope of the habitat. Habitat types are north, east, south or west facing slope.

- A. Average percentage with *Viola* pollen only, per habitat type.
- B. Average percentage with *Viola* + foreign pollen, per habitat type.
- C. Average percentage with no pollen, per habitat type.

EFFECTS OF PROXIMITY OF BLOSSOMS OF OTHER GENERA

Table 2 shows that pollen of four species, besides *Viola*, was found in the stigmatic cavities: *Endymion non-scriptus*, *Primula vulgaris*, *Anemone nemorosa* and *Taraxacum officinale*. Although the actual numbers per sample are extremely small when compared to the numbers of *Viola* grains, it is clear that the more blossoms of other species there are in a habitat, the more foreign pollen is deposited in the stigmatic cavities of violets, see Fig. 6b; also, the percentage containing *Viola* and foreign pollen together remains highest in these habitats, see Fig. 6c. The *Viola* pollen counts were very similar from habitats in which there were no blossoms of other genera and those with many; for example all four species of foreign pollen were recorded from habitat F (coppiced wood), yet the count remained high. However, in habitat B (edge of wood), the *Viola* pollen count dropped markedly and in 1967 the number of blossoms of other species was scant. It seems, therefore, that the samples can be categorized according to the frequency of other blossoms in the habitat from which they were collected, namely: none, few and many (see Fig. 6a, b, c).

In the first category, anthophilous insects (those feeding on flowers) seeking food must visit *Viola*, consequently the incidence of pollen in the stigmatic cavities is high. In the third category violets may actually benefit from the presence of other blossoms: data from

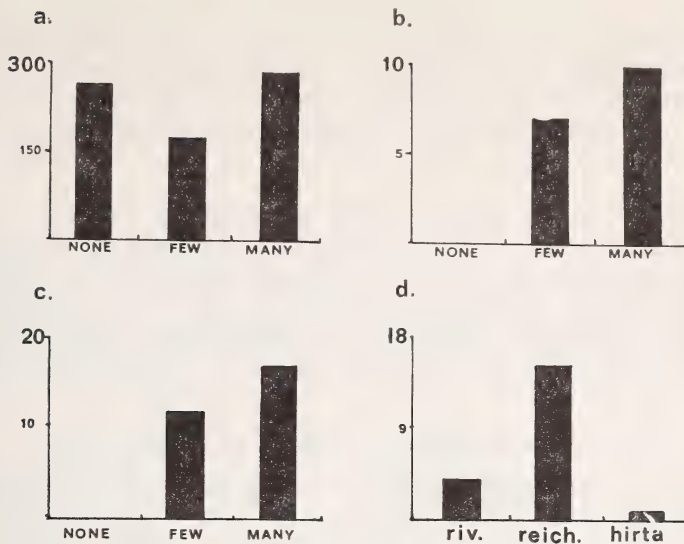


Fig. 6a, b, c. Diagrams to show the relationships between pollen counts and habitat type; habitat types are: None = no blossoms of other genera, Few = few blossoms of other genera, Many = many blossoms of other genera. (a) Average *Viola* pollen counts, (b) average foreign pollen counts, and (c) average percentage with both *Viola* and foreign pollen.

d. Average foreign pollen count for each species of *Viola*; riv. = *V. riviniana*, reich. = *V. reichenbachiana*, hirta = *V. hirta*.

visitor collections in these three habitat types show that those with a variety and abundance of conspicuous blossoms enjoy the greatest number and variety of insect-visitors. By examining the pollen carried by these insects it has been possible to show that a proportion of them visit *Viola* although probably initially attracted to the spot by more conspicuous blossoms. Also, while the number of foreign pollen grains in the stigmatic cavities is increased, pollination is maintained at a high level. That insect visits are increased by other blossoms is suggested also by the peak for *V. reichenbachiana* in Fig. 6d. This species had more visits from Diptera, less constant to one blossom, than the other two violet species. It may be prudent to point out here that there is no evidence from my own studies to suggest that the presence of foreign pollen in a stigmatic cavity interferes with the growth of *Viola* pollin-tubes.

In the second category (few other blossoms), percentage pollination fell, particularly in habitat B in 1966. Data from analyses of pollen on insect visitors to *Viola* show *Endymion* to be the most frequent foreign pollen found mixed with *Viola*, also *Endymion* is the most commonly occurring contaminant in the present study. In habitat B there were large stands of *Endymion* in 1966. The figures suggest, firstly, that some visitors to *Viola* also frequently visit *Endymion*, and secondly, that the flowers of the latter may be the most attractive to these visitors hence tending to monopolize their attentions and bringing about a fall in the pollination of *Viola*.

Another blossom present in great abundance in some habitats was *Primula vulgaris*, but very little pollen of this species was found in the samples. Detailed observations in the field established that the most frequent, and almost sole diurnal visitors to *Primula* in these habitats were the bee-fly *Bombylius major* L. and the Brimstone butterfly *Gonepteryx rhamni* L. and they were constant to this blossom. There were, therefore, no vectors evident that carried *Primula* pollen to *Viola* during daylight. However, although in the course of a week of observations all three *Viola* species were seen to receive visits from *Bombylius major*,

Primula pollen was found in *V. reichenbachiana* alone. Detailed analyses of insect visitors to *Primula vulgaris* and to the three species of *Viola* (to be published elsewhere) show that in some habitats *Primula vulgaris* and *V. reichenbachiana* are visited chiefly by Diptera whilst the remaining species of *Viola* receive visits from a wider variety of insects, especially Hymenoptera. The present work suggests that *Primula vulgaris* and *V. reichenbachiana* have the most visitors in common and reveals the activity of individual specimens that visited them both.

V. hirta differs from the other two *Viola* species in that it flowers earlier than both *Endymion* and *Primula*. The only foreign pollen found in samples of this species was that of *Taraxacum*, and then in very small quantities (Fig. 6d). The proportion of stigmatic cavities of this species containing no pollen at all (Table 2) suggests that while attraction from more conspicuous blossoms is less of a problem than a month later, the flowering period is so early as to be in the critical period of fluctuating temperatures governing the emergence and flight of its visitors.

EFFECTS OF PROXIMITY OF BLOSSOMS OF THE SAME GENUS

Evidence on the effect of the proximity of other violets is very scant, but inspection of Table 2, samples 3, 18, 4 and 20, shows that pollination in pale and dark specimens of *V. hirta* does differ markedly; this point is illustrated by Fig. 7. Sample 15, from an isolated clump of white-flowered *V. odorata* gives a high figure for percentage pollination. This contrasts with those for pale corollas and suggests that in the company of dark violets pollination of pale ones falls off, but when growing in isolation (sample 15) pollination is maintained at a high level.

V. riviniana subsp. *minor* and *V. hirta* subsp. *calcareae* are both small-flowered violets and both maintained a high percentage pollination although subsp. *minor* contained more pollen per stigmatic cavity. There is very little evidence from these figures that corolla-size influences pollination in *Viola*. However, bumblebees attempting to enter them and evidently not succeeding in obtaining any food frequently fly off, or crawl over the petals, pierce the petal spur and suck the nectar through the hole. Brian (1957) has described how certain

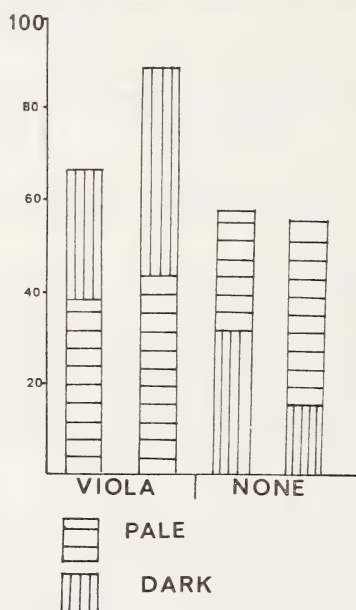


Fig. 7. Percentage pollination of pale blue and dark blue flowers of *Viola hirta*. Ordinate: percentage pollination, abscissa: left, samples containing *Viola* pollen only; right, samples containing no pollen.

species of bumblebees are prone to this 'thieving' behaviour, and it is possible that some flowers are not pollinated because of it.

Tetracolpate grains, at present thought to be confined to *V. riviniana*, were occasionally found in the stigmatic cavities of *V. reichenbachiana* and *V. hirta*. This is evidence that interspecific pollen transfer within the genus does occur, but quantitative estimates were not possible in this study.

DISCUSSION AND CONCLUSIONS

The question of the distinction between insect visitors and pollinators, and data on their pollen loads and behaviour, are being prepared for a subsequent paper. The present work is concerned only with the results of insect activity and the effects of weather, shading and other blossoms upon it. Rain can be harmful to insects caught visiting flowers and can reduce pollination in exposed places. Shaded or north or east facing habitats may experience similar reductions in pollination as a result of the diminution of sunlight incident upon the insects and their homes. Pollination is frequent in habitats in which *Viola* is the only available source of food for anthophilous insects. Habitats with a variety of blossoms may lure sufficient insects to ensure the pollination of all species including the inconspicuous ones. Large stands of showy blossoms may monopolize the insect visitors in habitats also occupied by less attractive plant species.

Stebbins (1959) in his review on the role of hybridization in evolution concludes that, in general, hybridization is increased in marginal and changing environments. More specifically Anderson (1954), working on populations of *Viola*, reported an increased degree of introgression in disturbed sites. Again Camp (1961) describes the rapid changes in gene frequency in violet populations growing in disturbed and marginal habitats, and points out that the genus *Viola* is at present going through an explosive phase in its evolution. This must be attributed partially to the character of the breeding system which in *Viola* combines regular in-breeding, chiefly by means of summer cleistogamous flowers, with occasional out-breeding followed the fertilization of chasmogamous flowers in spring (Valentine 1962). It has been evident in the course of my own work that disturbed and marginal habitats attract a greater number and variety of insects (see pp. 152–153) and it is these habitats that yielded samples containing the highest numbers of foreign pollen grains (Table 1, habitats, B, D, E, F). Deposition of foreign pollen in the stigmatic cavities of the chasmogamous flowers may be taken as proof of the transference of pollen between species and we have seen that this process was most frequent in the types of habitat under discussion. It seems reasonable to suppose that in these situations the out-breeding capability of *Viola* most nearly fulfills its potential.

Current theory on natural hybridization as outlined by Stebbins (1959) and substantiated by the work of a number of other authors (e.g. Anderson 1954) maintains that establishment of hybrids is more common in disturbed or marginal habitats than in stable or uniform ones. The results of the present work on *Viola* suggest that, in some entomophilous species at least, one of the reasons for this is that prior to establishment there exists a greater variety of genotypes available for selection as a result of a (temporary) shift to out-breeding. There is a marked increase in the pollination of the chasmogamous flowers, and in the production of seed from them. The overall effect is the release of a greater than normal variety of recombinants, some of which may increase the chances of exploiting these kinds of environment. That disturbed and marginal habitats may lead to a greater abundance and variety of pollinators, and that this factor strongly influences the frequency of hybridization, has not been fully appreciated in evolutionary studies.

ACKNOWLEDGMENTS

I wish to thank Professor C. D. K. Cook for his help and encouragement during the preparation of this paper. My thanks also to Professor H. G. Baker for scrutinizing the manuscript and for commenting upon it. I thank Mr. Sankey of the Juniper Hall Field

Centre for making available facilities for fieldwork and Sir Geoffrey and Lady Codrington for their most generous and prolonged hospitality whilst fieldwork was in progress. My thanks are due also to the University of Liverpool for the provision of a grant for this research.

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NOMENCLATURAL CHANGES IN THE *LIST OF BRITISH VASCULAR PLANTS*

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ABSTRACT

This paper lists some changes considered necessary or advisable in the nomenclature of the *List of British Vascular Plants* (1958) prepared by J. E. Dandy for the British Museum (Natural History) and the Botanical Society of the British Isles. Explanations of the changes are given. One new name in *Erica* is proposed, in a contribution by R. Ross.

The ten years which have elapsed since the publication of the *List of British Vascular Plants* have seen exceptional activity in taxonomic research on species of vascular plants occurring in the British Isles, much of it inspired by the preparation of *Flora Europaea*, a major undertaking which has already, within this period, produced two published volumes. With botanists all over Europe working on this project, as well as carrying out their usual researches, it is not surprising that numerous changes affecting the taxonomy and nomenclature of British plants have been proposed, some of which have already been adopted in the second editions of A. R. Clapham, T. G. Tutin & E. F. Warburg's *Flora of the British Isles* (1962) and *Excursion Flora of the British Isles* (1968). Certainly some of the name changes are necessary under the International Code, being nomenclatural changes in the strict sense, *i.e.* the results of bibliographical investigation or the examination of types. The great majority of the proposed name changes, however, are simply the consequences of taxonomic re-arrangement. Whenever a specific or infra-specific taxon is transferred from one genus to another its name changes; and the same thing happens whenever a species is reduced to subspecific rank, or a subspecies raised to specific level. Many taxonomic re-arrangements of course result from discoveries made in the course of research (as when supposed taxa are united or divided); others, however, may merely reflect idiosyncratic views about the rank or position of taxa whose limits are not changed at all. It would therefore be unwise to accept all the proposed changes willy-nilly. A full assessment of the number of these changes to be adopted in any future edition of the *List of British Vascular Plants* must await the completion of *Flora Europaea*, especially as further changes will no doubt be proposed in the later volumes of that work.

Nevertheless it is important to indicate to British botanists the changes in nomenclature which are necessary or advisable at the present time, and these are accordingly listed below. The list is restricted to those changes which are necessary on purely nomenclatural grounds, together with some which, though due to taxonomic re-arrangement, are likely to be non-controversial. Only taxa already in the *List of British Vascular Plants* are included; proposed additions and segregates do not come within the scope of this paper.

All the changes listed are explained by synonymy, discussion or reference to literature. Some of them have already been adopted in Clapham, Tutin & Warburg's *Flora of the British Isles* ed. 2 (1962) and *Excursion Flora of the British Isles* ed. 2 (1968); in such cases references to these two works are given by the abbreviations *CTW* ed. 2 and *CTW Exc* ed. 2 respectively.

The numbering of the entries follows that of the *List of British Vascular Plants*.

- 15/2 ASPLENIUM BILLOTII F. W. Schultz, *Flora* (Regensb.) **28**, 738 (1845). *CTW Exc* ed. 2, 13.
[*A. rotundatum* Kaulf. ex Holl, *Flora* (Regensb.) **13**, 374 (1830), nom. nud.]

A. cuneatum F. W. Schultz, op. cit. **27**, 807 (1844), non *A. cuneatum* Lam. (1786).

[*A. obovatum* auct., non Viv.]

Cf. I. Manton & T. Reichstein, *Bauhinia* **2**, 79 (1962); A. C. Jermy, *Brit. Fern Gaz.* **9**, 119 (1963); J. A. Crabbe, A. C. Jermy & J. D. Lovis, *Fl. Eur.* **1**, 16 (1964). British plants of this species were included under *A. lanceolatum* Huds., *Fl. Angl.* ed. 2. 454 (1778), but this name is not applicable, being a superfluous substitute for *A. trichomanes-ramosum* L. (1753) as well as a later homonym of *A. lanceolatum* Forsk. (1775).

18/2 *ATHYRIUM DISTENTIFOLIUM* Tausch ex Opiz, *Kratos (Zeitschr. Gymnas.)* **1819(4)**, 14 (1820). *CTW Exc* ed. 2, 15.

Polypodium molle All., *Fl. Pedemont.* **2**, 287 (1785), non *P. molle* Schreb. (1771).

Aspidium alpestre Hoppe, *Neu. Bot. Taschenb.* **1805**, 216 (1805).

Athyrium alpestre (Hoppe) Rylands in T. Moore, *Ferns Gr. Brit. Irel.*, sub t. 7 (1857), non *A. alpestre* Clairv. (1811).

Cf. A. C. Jermy, *Brit. Fern Gaz.* **9**, 119 (1963), *Fl. Eur.* **1**, 18 (1964).

21/2 *DRYOPTERIS PSEUDOMAS* (Wollaston) Holub & Pouzar, *Fol. Geobot. Phytotax. (Praha)* **2**, 332 (1967).

D. filix-mas var. *borreri* Newm., *Hist. Brit. Ferns* [ed. 3], 189 (1854).

Lastrea pseudomas Wollaston in Irvine, *The Phytologist* **1**, 172 (1855) ('pseudo-mas').

[*Dryopteris borreri* T. Moore, *Index Fil.*, 349 (1862), nom. syn.]

D. borreri (Newm.) Tavel, *Verhandl. Schweiz. Naturf. Ges.* **118**, 153 (1937).

21/6 *DRYOPTERIS CARTHUSIANA* (Vill.) H. P. Fuchs, *Bull. Soc. Bot. France* **105**, 339 (1959). *CTW* ed. 2, 32. *CTW Exc* ed. 2, 18.

Polypodium spinulosum O. F. Muell., *Fl. Dan.* **4(12)**, 5 (1777), non *P. spinulosum* Burm. f. (1768).

P. carthusianum Vill., *Hist. Pl. Dauph.* **1**, 292 (1786).

P. lanceolatocristatum Hoffm. in Roem. & Usteri, *Bot. Mag.* **3(9)**, 9 (1790).

Dryopteris spinulosa Watt, *Can. Naturalist New Ser.* **3**, 159 (1866), nom. illegit.

D. lanceolatocristata (Hoffm.) Alston, *Watsonia* **4**, 41 (1957).

Cf. A. C. Jermy, *Brit. Fern Gaz.* **9**, 119 (1963); V. H. Heywood, *Fl. Eur.* **1**, 21 (1964).

24/1 *THELYPTERIS LIMBOSPERMA* (All.) H. P. Fuchs, *Amer. Fern J.* **48**, 144 (1958). *CTW* ed. 2, 36. *CTW Exc* ed. 2, 11.

Polypodium montanum Vogler, *Diss. Polypod.*, 1 (1781), non *P. montanum* Lam. (1779).

[*P. oreopteris* Ehrh. ex Willd., *Fl. Berol. Prodr.*, 292 (1787), nom. syn.]

P. limbospermum All., *Auct. Fl. Pedemont.*, 49 (1789, Jan.-Mar.).

P. oreopteris Ehrh., *Beitr. Naturk.* **4**, 44 (1789, ?Apr.).

Thelypteris oreopteris (Ehrh.) Slosson in Rydb., *Fl. Rocky Mount.*, 1043, 1069 (1918).

Cf. A. C. Jermy, *Fl. Eur.* **1**, 13 (1964).

24A *GYMNOCARPIUM* Newm., *The Phytologist* **4**, 371 (1851).

Thelypteris sect. *Carpogymnia* H. P. Fuchs in Janchen, *Cat. Fl. Austriae* **1**, 898 (1959).

Carpogymnia (H. P. Fuchs) Á. & D. Löve, *Univ. Colorado Stud. Ser. Biol.* **24**, 8 (1966).

Though *Gymnocarpium* was formerly united with *Thelypteris* the two genera are so distinct that they are placed in different families by some modern authors: cf. A. C. Jermy, *Fl. Eur.* **1**, 13, 22 (1964); Á. & D. Löve, *Taxon* **16**, 191 (1967). The latter authors have proposed a

new generic name, *Carpogymnia*, to replace *Gymnocarpium*, on the ground that this is to be regarded as a later homonym of '*Gymnocarpum* Steud.' (1821); and in support of their action they cite an opinion given by the General Committee in *Taxon* **15**, 287 (1966). In fact Steudel (*Nomencl. Bot.*, 385; 1821) did not publish '*Gymnocarpum* Steud.' but actually printed '*Gymnocarpum*. Forsk.', meaning *Gymnocarpus* Forsk. (1775); and De Candolle (*Prodr.* **3**, 369; 1828), who adopted the spelling '*Gymnocarpum*', also attributed the name to 'Forsk.' With due respect to the opinion of the General Committee, it is difficult to see how a mere error or 'correction' of spelling can be accepted as valid publication of a new name, and until this matter has been given further consideration the name *Gymnocarpium* is to be retained. Cf. F. S. Crosswhite, *Taxon* **16**, 109-112 (1967); R. E. Holttum, *Taxon* **17**, 529 (1968).

- 24/4 GYMNOCARPIUM DRYOPTERIS (L.) Newm., *The Phytologist* **4**, 371 (1851).
 CTW Exc ed. 2, 20.
Polypodium dryopteris L., *Sp. Pl.*, 1093 (1753).
Thelypteris dryopteris (L.) Slosson in Rydb., *Fl. Rocky Mount.*, 1044, 1069 (1918).
Carpogymnia dryopteris (L.) Á. & D. Löve, *Univ. Colorado Stud. Ser. Biol.* **24**, 8 (1966).

Cf. A. C. Jermy, *Brit. Fern Gaz.* **9**, 119 (1963), *Fl. Eur.* **1**, 22 (1964).

- 24/5 GYMNOCARPIUM ROBERTIANUM (Hoffm.) Newm., *The Phytologist* **4**, 371 (1851). CTW Exc ed. 2, 20.
Polypodium robertianum Hoffm., *Deutsch. Fl.* 1796, Add. Emend. (1796).
Thelypteris robertiana (Hoffm.) Slosson in Rydb., *Fl. Rocky Mount.*, 1044, 1069 (1918).
Carpogymnia robertiana (Hoffm.) Á. & D. Löve, *Taxon* **16**, 191 (1967).

Cf. A. C. Jermy, *Brit. Fern Gaz.* **9**, 119 (1963), *Fl. Eur.* **1**, 22 (1964).

- 46/17 RANUNCULUS OMIOPHYLLUS Ten., *Fl. Nap.* **4**, 338 (1830). CTW ed. 2, 78.
 CTW Exc ed. 2, 36.
R. lenormandii F. W. Schultz, *Flora (Regensb.)* **20**, 726 (1837) ('*Lenormandi*').
 Cf. C. D. K. Cook, *Fl. Eur.* **1**, 237 (1964), *Watsonia* **6**, 258 (1966), *Mitt. Bot. Staatssamml. München* **6**, 90 (1966).

- 46/22b RANUNCULUS PELTATUS Schrank, *Baier. Fl.* **2**, 103 (1789). CTW ed. 2, 81 (excl. subsp. *pseudofluitans*). CTW Exc ed. 2, 37.
R. aquatilis subsp. *peltatus* (Schrank) Syme in Sowerby, *Engl. Bot.* ed. 3, **1**, 19 (1863).

Cf. C. D. K. Cook, *Fl. Eur.* **1**, 237 (1964), *Mitt. Bot. Staatssamml. München* **6**, 113 (1966).

- 46/22c RANUNCULUS PENICILLATUS (Dumort.) Bab., *Man. Brit. Bot.* ed. 7, 7 (1874).
Batrachium penicillatum Dumort., *Bull. Soc. Bot. Belg.* **2**, 216 (1863).
Ranunculus aquatilis var. *pseudofluitans* Syme in Sowerby, *Engl. Bot.* ed. 3, **1**, 20 (1863) ('*pseudo-fluitans*').
 [*R. pseudo-fluitans* Newbould ex Syme, loc. cit. (1863), nom. syn.]
R. pseudofluitans (Syme) Newbould ex Baker & Foggitt, *Thirsk Nat. Hist. Soc. Bot. Exch. Club, Cur. Rep.* **1864**, 5 (1865).
R. heterophyllum subsp. *pseudofluitans* (Syme) Moore & More, *Contrib. Cyb. Hibern.*, 5 (1866).
R. aquatilis subsp. *pseudofluitans* (Syme) Clapham in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 99 (1952).
 [*R. aquatilis* subsp. *sphaerospermus* Clapham, op. cit., 100 (1952) pro parte, non *R. sphaerospermus* Boiss. & Blanche.]
R. calcareus Butcher, *Naturalist* **1960**, 125 (1960).
 [*R. peltatus* subsp. *pseudofluitans* (Syme) C. D. K. Cook in Clapham,

Tutin & Warb., *Fl. Brit. Is.* ed. 2, 81 (1962), comb. invalid., basion. non cit.]

Cf. C. D. K. Cook, *Mitt. Bot. Staatssamml. München* 6, 155 (1966).

66/7 FUMARIA DENSIFLORA DC., *Cat. Pl. Hort. Bot. Monspel.*, 113 (1813). *CTW Exc* ed. 2, 50.

F. micrantha Lag., *Gen. Sp. Pl.*, 21 (1816).

Cf. P. D. Sell, *Fl. Eur.* 1, 257 (1964).

97/7 *CARDAMINE RAPHANIFOLIA Pourr., *Hist. Mém. Acad. Sci. Toulouse* 3, 310 (1788). *CTW* ed. 2, 163.

C. latifolia Vahl, *Symb. Bot.* 2, 77 (1791).

Cf. B. M. G. Jones, *Fl. Eur.* 1, 287 (1964).

100/6 ARABIS SCABRA All., *Auct. Synops. Meth. Stirp. Horti Taurin.*, 22 (1773); reimpr. in *Mél. Phil.-mat. Soc. Turin* 5, 74 (1774). *CTW Exc* ed. 2, 73.
A. stricta Huds., *Fl. Angl.* ed. 2, 292 (1778).

The name *A. stricta* has been used for this species, with *A. scabra* All. cited as a synonym; cf. B. M. G. Jones, *Fl. Eur.* 1, 293 (1964). Evidently there has been misunderstanding about dates, due to the fact that Allioni at different times gave the name *A. scabra* to two quite independent species based on different types. *A. scabra* All. (1773), based on species n. 453 of Haller's *Hist. Stirp. Indig. Helvet.* (1768), is the correct name for the species which has recently been called *A. stricta* but was in fact formerly known to British botanists as *A. scabra*; cf. G. C. Druce, *Brit. Pl. List* ed. 2, 7 (1928), *Comit. Fl. Brit. Is.*, 20 (1932). The later *A. scabra* All., *Fl. Pedemont.* 1, 268 (1785), based on Haller's species n. 447, is a synonym of *A. pumila* Jacq., which is not a British species.

113/8 VIOLA PERSICIFOLIA Schreb., *Spicil. Fl. Lips.*, 163 (1771). *CTW Exc* ed. 2, 83.
V. stagnina Kit. in Schult., *Österr. Fl.* ed. 2, 1, 426 (1814).

Cf. D. H. Valentine, H. Merxmüller & A. Schmidt, *Fl. Eur.* 2, 275 (1968).

115/2 *HYPERICUM INODORUM Mill., *Gard. Dict.* ed. 8, n. 6 (1768). *CTW Exc* ed. 2, 88.

H. elatum Aiton, *Hort. Kew.* 3, 104 (1789).

Cf. N. K. B. Robson, *Not. R. Bot. Gard. Edin.* 27, 185 (1967), *Fl. Eur.* 2, 263 (1968).

130 PETRORRHAGIA (Ser.) Link, *Handb. Erkenn. Gewächse* 2, 235 (1831).
Gypsophila sect. *Petrorhagia* Ser. in DC., *Prodr.* 1, 354 (1824).
Kohlrauschia Kunth, *Fl. Berol. Fam. Nat. Dispos.* 1, 108 (1838).

Cf. P. W. Ball & V. H. Heywood, *Bull. Brit. Mus. (Nat. Hist.) Bot.* 3, 119–172 (1964).

130/1 PETRORRHAGIA NANTEUILII (Burnat) Ball & Heywood, *Bull. Brit. Mus. (Nat. Hist.) Bot.* 3, 164 (1964).

Dianthus nanteuilii Burnat, *Fl. Alp. Marit.* 1, 221 (1892).

Kohlrauschia nanteuilii (Burnat) Ball & Heywood, *Watsonia* 5, 115 (1962).

[*K. prolifera* auct., non (L.) Kunth.]

[*Petrorhagia prolifera* auct., non (L.) Ball & Heywood.] *CTW Exc* ed. 2, 93.

Cf. P. W. Ball, *Fl. Eur.* 1, 188 (1964).

130/2 *PETRORRHAGIA SAXIFRAGA (L.) Link, *Handb. Erkenn. Gewächse* 2, 235 (1831).
Dianthus saxifragus L., *Sp. Pl.*, 413 (1753).

Kohlrauschia saxifraga (L.) Dandy, *Watsonia* 4, 42 (1957).

Cf. P. W. Ball, *Fl. Eur.* 1, 187 (1964).

131/10 CERASTIUM DIFFUSUM Pers., *Synops. Pl.* 1, 520 (1805). *CTW Exc* ed. 2, 103.
Sagina cerastoides Smith, *Trans. Linn. Soc.* 2, 343 (1794), non *Cerastium cerastoides* (L.) Britton (1894).

Cerastium tetrandrum Curt., *Fl. Lond.* 2(6), t. 31 (1798), nom. superfl. illegit. $\equiv$ *Sagina cerastoides* Smith.

C. atrovirens Bab., *Mag. Zool. Bot.* 2, 317 (1838).

Cf. P. D. Sell & F. H. Whitehead, *Fl. Eur.* 1, 145 (1964).

141/5 ARENARIA NORVEGICA subsp. ANGLICA Halliday, *Watsonia* 4, 209 (1960).
CTW ed. 2, 256. CTW Exc ed. 2, 112.

[*A. gothica* auct., non Fries.]

Cf. A. O. Chater & G. Halliday, *Fl. Eur.* 1, 120 (1964).

149/1c MONTIA FONTANA subsp. AMPORITANA Sennen, *Bull. Géogr. Bot. Le Mans* 21, 110 (1911).

M. fontana var. *intermedia* Beeby, *Ann. Scot. Nat. Hist.* 1909, 104 (1909).

M. lusitanica Samp., *Ann. Sci. Acad. Polytechn. Porto* 7(1), 52 (1912).

M. fontana subsp. *intermedia* (Beeby) Walters, *Watsonia* 3, 5 (1953).

Cf. S. M. Walters, *Fl. Eur.* 1, 115 (1964).

158/2 SUAEDA VERA J. F. Gmel., *Syst. Nat.* 2, 503 (1791). CTW Exc ed. 2, 124.
Chenopodium fruticosum L., *Sp. Pl.*, 221 (1753), non *Suaeda fruticosa* Forsk. (1791).

[*Suaeda fruticosa* auct., non Forsk.]

Cf. P. W. Ball, *Fl. Eur.* 1, 103 (1964).

162/2 $\times$ 1 *TILIA CORDATA $\times$ PLATYPHYLLOS = T. $\times$ VULGARIS Hayne, *Getr. Darstell. Beschr. Gewächse* 3, t. 47 (1813) (pro sp.). CTW Exc ed. 2, 127.

[*T. $\times$ europaea* auct., non L.]

Cf. K. Browicz, *Fl. Eur.* 2, 248 (1968).

195/4 LOTUS SUBBIFLORUS Lag., *Var. Ci. Lit. Art. Madrid* 2(4), 213 (1805). CTW Exc ed. 2, 161.

[*L. hispidus* Desf., *Tab. Éc. Bot.*, 190 (1804), nom. nud.]

[*L. hispidus* sensu DC. in Lam. & DC., *Fl. Franç.* ed. 3, 5, 572 (1815), non Desf. ex DC. (1805).]

Cf. P. W. Ball, *Feddes Repert.* 79, 41 (1968), *Fl. Eur.* 2, 175 (1968).

211/11/212 RUBUS ECHINATUS Lindl., *Synops. Brit. Fl.*, 94 (1829).

R. discerptus P. J. Muell., *Pollichia* 16-17, 146 (1859).

Cf. B. A. Miles, *Watsonia* 6, 295 (1967); Y. Heslop-Harrison, *Fl. Eur.* 2, 19 (1968).

211/11/371 RUBUS CALICULATUS Kalt., *Fl. Aach. Beck.* 2, 283 (1844).

R. viridis Kalt., tom. cit., 284 (1844), non *R. viridis* Presl ex Ortm. (1835).

Cf. Y. Heslop-Harrison, *Fl. Eur.* 2, 24 (1968).

211/11/375 RUBUS GLANDULOSUS Bellardi, *Mém. Acad. Sci. Turin* 5, 230 (1793).

R. bellardi Weihe & Nees in Bluff & Fingerh., *Compend. Fl. Germ.* 1, 688 (1825), nom. superfl. illegit. $\equiv$ *R. glandulosus* Bellardi.

Cf. Y. Heslop-Harrison, *Fl. Eur.* 2, 24 (1968).

218/2 AGRIMONIA PROCERA Wallr., *Erst. Beitr. Fl. Hercyn.*, 203 (1840). CTW Exc ed. 2, 180.

[*A. odorata* auct., non Mill.]

Cf. V. Skalický, *Fl. Eur.* 2, 32 (1968).

220/3/1 ALCHEMILLA GLAUCESCENS Wallr., *Linnaea* 14, 134 (1840). CTW ed. 2, 397.

[*A. minor* auct., non Huds.]

Cf. M. E. Bradshaw, P. D. Sell & S. M. Walters, *Watsonia* 5, 260 (1963); S. M. Walters, *Fl. Eur.* 2, 54 (1968).

- 229/1 CRATAEGUS LAEVIGATA (Poir.) DC., *Prodr.* **2**, 630 (1825). *CTW Exc* ed. 2, 190.
Mespilus laevigata Poir., *Encycl. Méth. Bot.* **4**, 439 (1798).
Crataegus oxyacanthoides Thuill., *Fl. Env. Par.* ed. 2, 245 (1799).
Cf. J. do Amaral Franco, *Feddes Rept.* **74**, 25 (1967), *Fl. Eur.* **2**, 74 (1968).
- 229/3 *CRATAEGUS LACINIATA Ucria, *Nuov. Racc. Opusc. Aut. Sicil.* **6**, 251 (1793).
C. orientalis Pall. ex Bieb., *Fl. Taur.-cauc.* **1**, 387 (1808).
Cf. J. do Amaral Franco, *Fl. Eur.* **2**, 77 (1968).
- 246/1 RIBES RUBRUM L., *Sp. Pl.*, 200 (1753). *CTW Exc* ed. 2, 203.
R. vulgare var. *sylvestre* Lam., *Encycl. Méth. Bot.* **3**, 47 (1789).
R. sylvestre (Lam.) Mert. & Koch, *Röhl. Deutsch. Fl.* **2**, 249 (1826).
Cf. D. A. Webb, *Fl. Eur.* **1**, 383 (1964).
- 254/7 EPILOBIUM TETRAGONUM L., *Sp. Pl.*, 348 (1753) subsp. TETRAGONUM. *CTW*
ed. 2, 475.
E. adnatum Griseb., *Bot. Zeit.* **10**, 854 (1852).
- 254/8 EPILOBIUM TETRAGONUM subsp. LAMYI (F. W. Schultz) Nyman, *Consp. Fl.*
Eur., 247 (1879). *CTW* ed. 2, 475.
E. lamyi F. W. Schultz, *Flora (Regensb.)* **27**, 806 (1844).
Cf. P. H. Raven, *Fl. Eur.* **2**, 310 (1968).
- 254/14 *EPILOBIUM PEDUNCULARE Cunn., *Ann. Nat. Hist.* **3**, 31 (1839).
E. linnaeoides Hook. f., *Bot. Antarct. Voy.* **1**(1), 10 (1844).
Cf. R. Melville, *Kew Bull.* **14**, 296 (1960), **15**, 477 (1962); P. H. Raven, *Fl. Eur.* **2**, 311 (1968).
- 255/1 EPILOBIUM ANGUSTIFOLIUM L., *Sp. Pl.*, 347 (1753).
Chamaenerion angustifolium (L.) Scop., *Fl. Carniol.* ed. 2, **1**, 271 (1772).
Cf. P. H. Raven, *Bull. Brit. Mus. (Nat. Hist.) Bot.* **2**, 331–332 (1962), *Fl. Eur.* **2**, 309 (1968),
 who retains this species and its allies in *Epilobium*. Even if treated as a separate genus these
 species cannot take the name *Chamaenerion*, which is an illegitimate substitute for *Epilobium*.
Chamaenerion was the original name used by Tournefort for *Epilobium* (*sensu lato*) and
 was adopted in the same sense by Séguier, Scopoli and some other authors after 1753;
cf. J. E. Dandy, *Reg. Veg.* **51**, 18, 39 (1967).
- 265 SWIDA Opiz, *Oek.-techn. Fl. Böhm.* **2**, 174 (1838) ('Swjda').
Cornus sect. *Thelycrania* Dumort., *Florula Belg.*, 83 (1827).
 [Swjda Opiz, *Oek. Neuigk. Verh.* **1835**, 624 (1835), nom. nud.]
Thelycrania (Dumort.) Fourr., *Ann. Soc. Linn. Lyon Nouv. Sér.* **16**, 394
 (1868).
Cf. Z. Pouzar, *Preslia* **36**, 341 (1964).
- 265/1 SWIDA SANGUINEA (L.) Opiz, *Oek.-techn. Fl. Böhm.* **2**, 174 (1838).
Cornus sanguinea L., *Sp. Pl.*, 117 (1753).
Thelycrania sanguinea (L.) Fourr., *Ann. Soc. Linn. Lyon Nouv. Sér.* **16**,
 394 (1868).
- 265/2 *SWIDA SERICEA (L.) Holub, *Fol. Geobot. Phytotax. (Praha)* **2**, 427 (1967).
Cornus sericea L., *Mant. Pl. Alt.*, 199 (1771).
C. stolonifera Michaux, *Fl. Bor.-amer.* **1**, 92 (1803).
Thelycrania sericea (L.) Dandy, *Watsonia* **4**, 47 (1957).
- 319/3 †EUPHORBIA VILLOSA Waldst. & Kit. ex Willd., *Sp. Pl.* **2**, 909 (1800). *CTW*
Exc ed. 2, 244.
 [*E. pilosa* auct., non L.]
Cf. A. R. Smith & T. G. Tutin, *Fl. Eur.* **2**, 217 (1968).

- 319/8 EUPHORBIA SERRULATA Thuill., *Fl. Env. Par.* ed. 2, 237 (1799). *CTW Exc* ed. 2, 245.
E. verrucosa L., *Sp. Pl.*, 459 (1753), nom. ambig. rejic.
E. stricta L., *Syst. Nat.* ed. 10, 2, 1049 (1759), nom. superfl. illegit. ≡
E. verrucosa L.
 Cf. A. R. Smith & T. G. Tutin, *Fl. Eur.* 2, 219, 220 (1968). The earliest name for this species is *E. verrucosa* L. (1753), which Linnaeus unnecessarily changed to *E. stricta* in 1759: the species was numbered '42' with the same definition in both his 1753 and 1759 works. *E. verrucosa* L., *Syst. Nat.* ed. 10, 2, 1049 (1759), was published as a new species (numbered 'D') which is a different entity from *E. verrucosa* L. (1753) and is referable to *E. brittingeri* Opiz ex Samp. As the name *E. verrucosa* has been in general use for the latter species it is to be rejected as ambiguous.
- 320/1/4(5,6) POLYGONUM ARENASTRUM Bor., *Fl. C. France* ed. 3, 2, 559 (1857). *CTW* ed. 2, 545. *CTW Exc* ed. 2, 250.
P. microspermum Jord. ex Bor., tom. cit., 560 (1857).
P. calcatum Lindm., *Bot. Notis.* 1904, 139 (1904).
P. aequale Lindm., *Svensk Bot. Tidskr.* 6, 692 (1912).
 Cf. B. T. Styles, *Watsonia* 5, 204 (1962); D. A. Webb & A. O. Chater, *Fl. Eur.* 1, 79 (1964).
- 320/18 *POLYGONUM AUBERTII L. Henry, *Rev. Hort.* 79, 82 (1907).
Bilderdykia aubertii (L. Henry) Moldenke, *Rev. Sudamer. Bot.* 6, 29 (1939).
 [*Polygonum baldschuanicum* auct., non Regel.]
 Cf. D. A. Webb, *Fl. Eur.* 1, 81 (1964) (as *Bilderdykia aubertii*). Webb segregates the genus *Bilderdykia* Dumort., *Florula Belg.*, 18 (1827); but if this were accepted its correct name would apparently be *Fallopia* Adans., *Fam. Pl.* 2, 277, 557 (1763).
- 326/1 PARIETARIA JUDAICA L., *Fl. Palaest.*, 32 (1756). *CTW Exc* ed. 2, 257.
P. diffusa Mert. & Koch, *Röhl. Deutsch. Fl.* 1, 827 (1823).
 Cf. C. C. Townsend, *Watsonia* 6, 368 (1968).
- 327 *SOLEIROLIA Gaudich. in Freycinet, *Voy. Monde*, Bot., 504 (1830).
Helxine Req., *Ann. Sci. Nat.* 5, 384 (1825), non *Helxine* L. (1758).
- 327/1 *SOLEIROLIA SOLEIROLII (Req.) Dandy, *Feddes Repert.* 70, 4 (1965). *CTW Exc* ed. 2, 256.
Helxine soleirolii Req., *Ann. Sci. Nat.* 5, 384 (1825).
 [*Soleirolia soleirolii* (Req.) Dandy ex P. W. Ball, *Fl. Eur.* 1, 69 (1964), comb. invalid., basion. non rite cit.]
- 343/12b SALIX CINEREA subsp. OLEIFOLIA Macreight, *Man. Brit. Bot.*, 212 (1837).
S. acuminata Mill., *Gard. Dict.* ed. 8, n. 14 (1768).
S. atrocineria Brot., *Fl. Lusit.* 1, 31 (1804).
S. oleifolia Smith, *Fl. Brit.* 3, 1065 (1804), non *S. oleifolia* Vill. (1789).
S. cinerea subsp. *atrocineria* (Brot.) Silva & Sobrinho, *Agron. Lusit.* 12, 248 (1950).
- 357/2 × 1 ERICA MACKAIANA × TETRALIX = E. × PRAEGERI Ostenf., *New Phytol.* 11, 120 (1912).
 [*E. × stuartii* auct., ?an E. F. Linton.]
 Cf. D. A. Webb, *Watsonia* 6, 296 (1967).

357/7

Erica erigena* R. Ross, nom. nov.E. mediterranea* var. *hibernica* Hook. & Arn., *Brit. Fl.* ed. 7, 266 (1855).*E. hibernica* (Hook. & Arn.) Syme in Sowerby, *Engl. Bot.* ed. 3, 6, 42 (1866), non *E. hibernica* Utinet (1839).[*E. mediterranea* auct., non L.]

Cf. R. Ross, *J. Linn. Soc. (Bot.)* **60**, 71 (1967) (as *E. hibernica*): this paper on some Linnaean species of *Erica* was on the point of appearing when my attention was drawn by Mr. D. McClintock to the existence of the name *E. hibernica* Utinet, *Ann. Fl. Pomone* **1839-40**, 94 (1839), which is validly published and thus makes *E. hibernica* (Hook. & Arn.) Syme an illegitimate later homonym. Utinet's name, which is not so far listed in *Index Kewensis*, was based on a cultivated South African winter-flowering heath, and its epithet indicates its time of flowering, not its place of origin. Hooker & Arnott's epithet *hibernica*, referring to the Irish origin of their plant, is now replaced by *erigena*, which has the same significance. [Contributed by R. Ross.]

379/3

VINCA MAJOR subsp. HIRSUTA (Boiss.) Stearn, *J. Bot., Lond.* **70**, Suppl., 27 (1932).V. major* var. *hirsuta* Boiss. in Tchihatcheff, *As. Mineure* **3(2)**, 67 (1866).[*V. herbacea* auct., non Waldst. & Kit.]*Cf.* W. T. Stearn, *Proc. Bot. Soc. Brit. Is.* **5**, 341 (1964).

400/3

MYOSOTIS STOLONIFERA (DC.) Gay ex Leresche & Levier, *Deux Excurs. Bot.*, 83 (1880). *CTW Exc* ed. 2, 307.[*M. stolonifera* Gay, *Ann. Sci. Nat. Sér. 2 (Bot.)* **6**, 351 (1836), nom. nud.]*M. caespitosa* var. *stolonifera* DC., *Prodr.* **10**, 106 (1846).*M. lingulata* var. *stolonifera* (DC.) Willk. in Willk. & Lange, *Prodr. Fl. Hisp.* **2**, 503 (1870).*M. brevifolia* C. E. Salmon, *J. Bot., Lond.* **64**, 294 (1926).*Cf.* D. Welch, *Watsonia* **6**, 276-279 (1967).

406/2

***CALYSTEGIA PULCHRA Brummitt & Heywood, *Proc. Bot. Soc. Brit. Is.* **3**, 385 (1960).**[*C. sepium* subsp. *dahurica* Webb & Walters in Clapham, Tutin & Warb., *Excurs. Fl. Brit. Is.*, 302 (1959), comb. invalid., basion. non cit., pro parte, non *Convolvulus dahuricus* Herbert.][*C. sepium* subsp. *pulchra* (Brummitt & Heywood) Tutin in Clapham, Tutin & Warb., *Fl. Brit. Is.* ed. 2, 666 (1962), comb. invalid., basion. non cit.]*Convolvulus dubius* J. L. Gilbert, *J. Northampt. Nat. Hist. Soc. Field Club* **34**, 149 (1963).[*Calystegia dahurica* auct., non (Herbert) G. Don.]

409/1

LYCIUM BARBARUM L., *Sp. Pl.*, 192 (1753). *CTW Exc* ed. 2, 313.L. halimifolium* Mill., *Gard. Dict.* ed. 8, n. 6 (1768).*Cf.* N. Feinbrun & W. T. Stearn, *Israel J. Bot.* **12**, 120 (1963).

424/2

SCROPHULARIA AURICULATA L., *Sp. Pl.*, 620 (1753). *CTW Exc* ed. 2, 321.[*S. aquatica* auct., non L.]

Cf. A. Vaarama & H. Hiirsalmi, *Hereditas* **58**, 335 (1967). This species has usually been known as *S. aquatica*, but the original definition of *S. aquatica* L. (loc. cit.) refers to *S. umbrosa* Dumort., as also does the specimen in the Linnaean Herbarium (773/3, named '3 aquatica') which is to be taken as lectotype. Owing to its misapplication the name *S. aquatica* has become a long-persistent source of error and is to be rejected as an ambiguous name, leaving the correctness of the name *S. umbrosa* unaffected.

Watsonia **7** (3), 1969.

Linnaeus's definition of *S. auriculata* refers to the species which has commonly been called *S. aquatica*; it is represented in the Linnaean Herbarium by a specimen (773/4, named 'auriculata') which is to be taken as lectotype.

- 426/2 LIMOSELLA AUSTRALIS R.Br., *Prodr. Fl. Nov. Holl.*, 443 (1810).
L. subulata Ives, *Trans. Phys.-med. Soc. New-York* **1**, 441 (1817).
 Cf. A. Lourteig, *C.N.F.R.A. Biol.* **1**, 166 (1964).
- 435/1/12 EUPHRASIA TETRAQUETRA (Bréb.) Arrond., *Bull. Soc. Polymath. Morbihan* **1862**, 96 (1863).
E. officinalis subvar. *tetraquetra* Bréb., *Fl. Normand.* ed. 2, 183 (1849).
E. occidentalis Wettst., *Monogr. Gatt. Euphrasia*, 135 (1896).
 Cf. P. D. Sell & P. F. Yeo, *Watsonia* **6**, 301 (1967).
- 461 LAMIASTRUM Heist. ex Fabr., *Enum. Meth. Pl.*, 51 (1759).
Galeobdolon Adans., *Fam. Pl.* **2**, 190, 560 (1763), nom. superfl. illegit.
 ≡ *Lamiastrum* Heist. ex Fabr.
- 461/1 LAMIASTRUM GALEOBDOLON (L.) Ehrend. & Polatsch., *Österr. Bot. Zeitschr.* **113**, 108 (1966). *CTW Exc* ed. 2, 349.
Galeopsis galeobdolon L., *Sp. Pl.*, 580 (1753).
Galeobdolon luteum Huds., *Fl. Angl.* ed. 2, 258 (1778).
- 484/1 CRUCIATA LAEVIPES Opiz, *Seznam Rostl. Kvet. Ceské*, 34 (1852).
Valantia cruciata L., *Sp. Pl.*, 1052 (1753).
Galium cruciata (L.) Scop., *Fl. Carniol.* ed. 2, **1**, 100 (1772).
Aparine latifolia Moench, *Meth. Pl.*, 640 (1794), nom. superfl. illegit.
 ≡ *Valantia cruciata* L.
Galium valantia Gaertn., Meyer & Scherb., *Oek.-techn. Fl. Wetter.* **1**, 188 (1799), non *G. valantia* Weber (1780).
Valantia ciliata Opiz ex J. & C. Presl, *Fl. Čech.*, 34 (1819), non *V. ciliata* Banks & Soland. (1794).
 [Cruciata chersonensis Ehrend., *Not. R. Bot. Gard. Edin.* **22**, 396 (1958) pro parte, non *Valantia chersonensis* Willd.]
 Cf. F. Ehrendorfer, *Ann. naturhist. Mus. Wien* **65**, 16 (1962).
- 514/1 FILAGO VULGARIS Lam., *Fl. Franç.* **2**, 61 (1778). *CTW Exc* ed. 2, 393.
 [Gnaphalium germanicum L., *Sp. Pl.*, 857, 1230 (1753), nom. syn.]
Filago germanica L., op. cit. ed. 2, 1311 (1763), non *F. germanica* Huds. (1762).
 Cf. G. Wagenitz, *Willdenowia* **4**, 51 (1965).

Nomenclatural complications in *Filago* have been discussed by a number of authors in recent years. J. Holub & J. Chrtek, *Taxon* **11**, 195–201 (1962), pointed out that the generic name *Filago* L. should be typified by *F. pygmaea* L., which is also the type species of *Evax* Gaertn. (1791). These authors considered, but rejected, the idea of conserving the name *Filago* in its present sense; instead, they replaced *Evax* Gaertn. by *Filago* L., and adopted the name *Gifola* Cass. (1819) for the genus currently known as *Filago*. Later, however, the name *Filago* L. was proposed for conservation in its present sense (i.e. with *F. pyramidata* L. as type) by G. Buchheim & G. Wagenitz, *Reg. Veg.* **34**, 61–62 (1964), and so may continue in use pending an official decision on the proposal.

As to the species, there has been especial confusion in the nomenclature of *F. vulgaris* and *F. pyramidata* (see 514/3 below), springing from emendations made by Linnaeus on the penultimate page of his *Species plantarum* (1753). In his text he had treated *Gnaphalium germanicum* (i.e. *F. vulgaris*) and *F. pyramidata* as separate species in different genera, but in the Addenda he united the two under the name *F. pyramidata* as the third species of *Filago*, so that the name *Gnaphalium germanicum* (1753) was published only as a synonym.

In the second edition of the *Species plantarum* (1763) Linnaeus separated the two species under the names *F. pyramidata* and *F. germanica*, but by now the latter name was invalidated by *F. germanica* Huds. (1762). Wagenitz (1965) has admirably elucidated the complications involved, and has shown that the correct name for *F. germanica* L. (non Huds.) is *F. vulgaris* Lam.

W. Greuter, *Boissiera* **13**, 136 (1967), *pace* Wagenitz, has continued to use the name *F. germanica* on the ground that *Gnaphalium germanicum* and *Filago pyramidata* of the *Species plantarum* (1753) are to be treated as alternative names within the meaning of the International Code, so that *G. germanicum* is validly published from 1753. This argument has no real foundation: Linnaeus did not publish the names as alternatives. It is clear that he changed his mind during the production of the volume and that the opinion which he gave in his Addenda was his final and decisive view at that time; this is confirmed by his treatment in the second edition of *Flora Suecica*, published two years later (1755), where on p. 302 the Swedish plant (*i.e.* *F. vulgaris*) was referred to *F. pyramidata* with *G. germanicum* included ('*Spec. plant.* 1199. & 857, n. 35').

- 514/2 *FILAGO LUTESCENS* Jord., *Obs. Pl. Nouv.* **3**, 201 (1846). *CTW Exc* ed. 2, 393.
 [*F. apiculata* G. E. Smith, *The Phytologist* **2**, 575 (1846), nom. provis.]
 F. apiculata G. E. Smith ex Bab., *Man. Brit. Bot.* ed. 3, 174 (1851), nom.
 superfl. illegit. $\equiv$ *F. lutescens* Jord.
Cf. G. Wagenitz, *Willdenowia* **4**, 51 (1965).

- 514/3 *FILAGO PYRAMIDATA* L., *Sp. Pl.*, 1199, 1230 (1753). *CTW Exc* ed. 2, 393.
 F. spathulata C. Presl in J. & C. Presl, *Delic. Prag.*, 99 (1822).
Cf. G. Wagenitz, *Willdenowia* **4**, 52 (1965).

- 533A *LEUCANTHEMUM* Mill., *Gard. Dict. Abridg.* ed. 4, **2** (1754).
Cf. V. H. Heywood, *Proc. Bot. Soc. Brit. Is.* **3**, 177–179 (1959), who recognizes *Leucanthemum* and *Tanacetum* as genera distinct from *Chrysanthemum* and gives cogent reasons for doing so. His treatment will be followed in *Flora Europaea* and is accepted here; for otherwise it will be necessary to find another name in *Chrysanthemum* for *C. (Tanacetum) vulgare* (see below), and in the circumstances there seems to be no point in doing this.

- 533/2 *LEUCANTHEMUM VULGARE* Lam., *Fl. Franç.* **2**, 137 (1778).
 Chrysanthemum leucanthemum L., *Sp. Pl.*, 888 (1753).

- 533/3 **LEUCANTHEMUM MAXIMUM* (Ramond) DC., *Prodr.* **6**, 46 (1838).
 Chrysanthemum maximum Ramond, *Bull. Sci. Soc. Philom. Paris* **2**, 140
 (1800).

- 533B *TANACETUM* L., *Sp. Pl.*, 843 (1753); *Gen. Pl.* ed. 5, 366 (1754).

- 533/4 *TANACETUM PARTHENIUM* (L.) Schultz Bip., *Ueber Tanacet.*, 55 (1844).
 Matricaria parthenium L., *Sp. Pl.*, 890 (1753).
 Chrysanthemum parthenium (L.) Bernh., *Syst. Verz. Pfl. Erfurt*, 145 (1800).

- 533/5 *TANACETUM VULGARE* L., *Sp. Pl.*, 844 (1753).
 T. officinarum Crantz, *Inst. Rei Herb.* **1**, 273 (1766), nom. superfl. illegit.
 $\equiv$ *T. vulgare* L. (*T. foliis bipinnatis incisiss serratis* L.).
 Chrysanthemum vulgare (L.) Bernh., *Syst. Verz. Pfl. Erfurt*, 144 (1800),
 non *C. vulgare* (Lam.) Gaterau (1789).
 C. tanacetum Karsch, *Phan.-Fl. Prov. Westfalen*, 294 (1853), non *C.*
 tanacetum Vis. (1847).

Cf. J. Raynal, *Taxon* **17**, 516 (1968). If retained in *Chrysanthemum* this species would require a new combination; for both the existing combinations in *Chrysanthemum* are later homonyms, and the name *Tanacetum officinarum* Crantz, despite Raynal's statement, is a superfluous substitute for *T. vulgare* L., Linnaeus's full phrase-name (*nomen specificum legitimum*) being cited by Crantz as a synonym. The oldest legitimate specific name after *T. vulgare* appears to be *T. crispum* (L.) Kerner, *Abbild. Oek. Pfl.* **3**, 126 (1789), based on *T. vulgare* var. *crispum* L., *Sp. Pl.*, 845 (1753).

540/6 *CIRSIIUM ACAULE* Scop., *Ann. Hist.-nat.* **2**, 62 (1769). *CTW Exc* ed. 2, 412. *Carduus acaulos* L., *Sp. Pl.*, 1199 (1753).

Cirsium acaulon (L.) Scop., *Fl. Carniol.* ed. 2, **2**, 131 (1772) ('*Acaulos*'), non *C. acaule* Scop. (1769).

Cirsium acaule Scop. (1769) was described from the neighbourhood of Cavalese, in the Italian Tyrol, apparently as a new species, there being no reference, direct or indirect, to the earlier *Carduus acaulos* L. Subsequently Scopoli, dealing with the flora of Carniola, transferred *Carduus acaulos* to *Cirsium* as *C. acaulon* (L.) Scop. without any mention of his earlier *C. acaule*. The two entities are now placed in the same species, for which the correct name under *Cirsium* is *C. acaule* Scop. The existence of this name prevents the acceptance of Linnaeus's epithet *acaulos* in the genus *Cirsium*.

558/1/11 *HIERACIUM TENUIFRONS* Sell & West, *Watsonia* **6**, 303 (1967).

[*H. gracilentum* Backh., *The Phytologist* **4**, 806 (1853) pro parte, non *H. alpinum* var. *gracilentum* Fries.]

Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 78 (1968).

558/1/22 *HIERACIUM SINUANS* F. J. Hanb., *J. Bot., Lond.* **30**, 167 (1892).

[*H. pulmonarium* Smith in Sowerby, *Engl. Bot.* **33**, t. 2307 (1811), nom. superfl. illegit., pro parte, non *H. pulmonarioides* Vill.]

Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 82 (1968).

558/1/80 *HIERACIUM DECOLOR* (W. R. Linton) A. Ley, *J. Bot., Lond.* **47**, 10 (1909).

H. silvaticum var. *subcyaneum* W. R. Linton, *Acc. Brit. Hierac.*, 39 (1905).

H. caesium var. *decolor* W. R. Linton, op. cit., 59 (1905).

H. subcyaneum (W. R. Linton) Pugsl., *J. Bot., Lond.* **79**, 182 (1942).

Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 96 (1968). The name *H. decolor* was misapplied by Pugsley to the species now called *H. pseudoleyi* (see 558/1/140 below).

558/1/103 *HIERACIUM STENSTROEMII* (Dahlst.) Johanss., *Bih. Svenska Vet.-akad. Handl.* **28**(3, 7), 27 (1902).

H. serratifrons subsp. *stenstroemii* Dahlst., *Svenska Vet.-akad. Handl.* Ny Följd **25**(3), 86 (1893).

H. exotericum var. *glevense* Pugsl., *J. Linn. Soc. (Bot.)* **54**, 144 (1948).

H. glevense (Pugsl.) Sell & West, *Watsonia* **3**, 234 (1955).

Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 105 (1968).

558/1/116 *HIERACIUM PILIGERUM* (Pugsl.) Sell & West, *Watsonia* **6**, 310 (1967).

H. variicolor var. *piligerum* Pugsl., *J. Linn. Soc. (Bot.)* **54**, 156 (1948).

Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 107 (1968).

558/1/140 *HIERACIUM PSEUDOLEYI* (Zahn) Roffey, *Lond. Cat. Brit. Pl.* ed. 11, 26 (1925).

H. saxifragum subsp. *pseudoleyi* Zahn in Engler, *Pflanzenr.* **IV.280** (Heft 75), 251 (1921) ('*pseudo-Leyi*').

[*H. decolor* sensu Pugsl., *J. Linn. Soc. (Bot.)* **54**, 184 (1948).]

Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 96 (1968).

- 558/1/153 HIERACIUM POLLICHAIE Schultz Bip., *Pollichia* **13**, 23 (1855).
 [H. *pollichiae* Schultz Bip. ex G. F. Koch, *Oesterr. Bot. Wochenbl.* **3**, 247 (1853), nom. nud.]
 H. *roffeyanum* Pugsl., *J. Bot., Lond.* **79**, 197 (1942).
 Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 116 (1968).
- 558/1/179 HIERACIUM CARPATHICUM Bess., *Primit. Fl. Galic.* **2**, 154 (1809).
 H. *perthense* F. N. Williams, *Prodr. Fl. Brit.* **1**, 163 (1902).
 Cf. P. D. Sell & C. West, *Watsonia* **6**, 103 (1965).
- 558/1/194 HIERACIUM SPARSIFRONS Sell & West, *Watsonia* **6**, 312 (1967).
 H. *sparsifolium* var. *oligodon* E. F. Linton in W. R. Linton, *Acc. Brit. Hierac.*, 78 (1905).
 H. *oligodon* (E. F. Linton) Pugsl., *J. Ecol.* **33**, 346 (1946), non H. *oligodon* Naeg. & Peter (1886).
- 558/1/212 HIERACIUM SUBUMBELLATIFORME (Zahn) Roffey, *Lond. Cat. Brit. Pl.* ed. 11, 29 (1925).
 H. *aestivum* subsp. *subumbellatiforme* Zahn in Engler, *Pflanzenr.* **IV.280** (Heft 79), 919 (1922).
 H. *pseudamplidentatum* Pugsl., *J. Linn. Soc. (Bot.)* **54**, 284 (1948).
 Cf. P. D. Sell & C. West in F. H. Perring, *Crit. Suppl. Atl. Brit. Fl.*, 128 (1968).
- 570/2 *ELODEA ERNSTIAE St. John, *Darwiniana* **12**, 644 (1963) ('*Ernstiae*').
 [E. *callitrichoides* auct., non (Rich.) Casp.]
 Cf. D. H. Kent, *Proc. Bot. Soc. Brit. Is.* **5**, 232 (1964).
- 577/13 × 16 POTAMOGETON PUSILLUS × TRICHOIDES = P. × GROVESII Dandy & Taylor, *Watsonia* **6**, 316 (1967).
 [P. × *trinervius* auct., non G. Fisch.]
- 579/1 RUPPIA CIRRHOSA (Petagna) Grande, *Bull. Orto Bot. Univ. Napoli* **5**, 58 (1918).
Buccaferrea cirrhosa Petagna, *Inst. Bot.* **5**, 1826 (1787).
Ruppia spiralis L. ex Dumort., *Florula Belg.*, 164 (1827).
 Cf. J. C. Gamero, *Darwiniana* **14**, 578 (1968).
- 582/1 ERIOCAULON AQUATICUM (Hill) Druce, *Pharm. J.* **83**, 700 (1909). *CTW Exc* ed. 2, xxiv.
Cespa aquatica Hill, *Herb. Brit.* **1**, 96* (1769).
Eriocaulon septangulare With., *Bot. Arrang. Veg.* **2**, 784 (1776).

In 1909 G. C. Druce drew attention to the existence in his copy of Hill's *Herbarium Britannicum* (vol. 1; 1769) of an additional plate 66 illustrating, with dissections, a genus *Cespa* with the single species *C. aquatica* ('Water Turffwort'). The species depicted was *Eriocaulon septangulare*, described under that name by Withering in 1776, and so Druce on grounds of priority published the new combination *E. aquaticum* (Hill) Druce. For some reason Druce in his later works did not persist in the use of the name *E. aquaticum*; thus in his *British plant list* ed. 2, 118 (1928), he retained the name *E. septangulare* (with *E. aquaticum* cited as a synonym), and in his *Comital Flora*, 320 (1932), he used the name *E. septangulare* without mention of *E. aquaticum*. Possibly he now thought his combination *E. aquaticum* to be invalidated by *E. aquaticum* Sagot ['Mss. in Herb. Sagot.'] ex Koern. in Mart., *Fl. Brasil.* **3(1)**, 489 (1863); but this name was published only as a synonym of *E. melanocephalum* Kunth and so cannot invalidate *E. aquaticum* (Hill) Druce.

The additional plate 66 present in Druce's copy of the *Herbarium Britannicum* does not appear in all copies of the work; but at the British Museum, Bloomsbury, and at the Linnean Society of London there are copies which contain not only this additional plate

but also four additional pages of text (numbered 96*–99*) in which *Cespa aquatica* is described at length. These extra pages and plate (reproduced here as Figs. 1–5 (pp. 170–174) were presumably not issued soon enough for inclusion in all copies of the *Herbarium Britannicum*. According to Hill's statement on p. 96* the plant concerned had been collected in the previous year ('mense Septemb. anni elapsi') on the island of Skye by James Robertson, and had been communicated to Hill, with an illustration and description, by John Hope of Edinburgh. Hope himself published an account of it in *Phil. Trans. Lond.* **59**, 241–246, t. 12 (1770), in which he stated that it had been found by Robertson in September 1768. Thus Hill's 'anni elapsi' was 1768, so that his additional pages and plate were issued, or at least printed, in 1769. Hill in any case died in 1775, before Withering's publication of *E. septangulare* in 1776.

Hope correctly placed the plant in *Eriocaulon*, but misidentified it with *E. decangulare* L., a species confined to North America. Hill, on the other hand, treated it as forming a new genus, *Cespa*, which, according to his footnote on p. 98*, he considered to differ from *Eriocaulon* in having the corolla 'dipetala', *Eriocaulon* being 'tripetalum'. Hope mentioned the plant's vegetative resemblance to '*Calamaria* Dill. *Musc. Tab.* 80' (*Isoetes* L.) in which, however, a flowering stem was unknown; Hill's footnote on p. 96* makes the same point.

605/10 JUNCUS SUBULIFLORUS Drejer, *Fl. Excurs. Hafn.*, 127 (1838). CTW Exc ed. 2, 463.

J. leersii Marsson, *Fl. Neu-Vorpommern*, 451 (1869).

[*J. conglomeratus* auct., non L.]

The definition of *J. conglomeratus* L., *Sp. Pl.*, 326 (1753), is taken unchanged from Royen, *Fl. Leyd. Prodr.*, 44 (1740), with a secondary reference to Linnaeus's *Flora Suecica*, 99, n. 278 (1745). Royen's plant, which is preserved at Leiden and is the obligate lectotype, has been examined and found to be the conglomerate form of *J. effusus* L., as also is the specimen in the Linnaean Herbarium (449/2) named by Linnaeus '2 conglomeratus' and marked 'Fl. suec.' Thus the name *J. conglomeratus* L. belongs to the synonymy of *J. effusus* L., and the species which has commonly been known as *J. conglomeratus* must take another name. The earliest name available is apparently *J. subuliflorus*.

614/7 *NARCISSUS POETICUS × TAZETTA = N. × MEDIOLUTEUS Mill., *Gard. Dict.* ed. 8, n. 4 (1768) ('*Medio-luteus*') (pro sp.).

N. biflorus Curt., *Bot. Mag.* **6**, sub t. 193 (1792) (pro sp.).

Cf. A. Fernandes, *R. Hort. Soc. Daff. Tulip Year Book* **1968**, 48 (1968), who gives the parentage of this hybrid as *N. poeticus* L. × *N. tazetta* L.

637 PSEUDORCHIS Séguier, *Pl. Veron.* **3**, 254 (1754).

Leucorchis E. Meyer, *Preuss. Pflanzengatt.*, 50 (1839).

Cf. J. E. Dandy, *Reg. Veg.* **51**, 18, 75 (1967).

637/1 PSEUDORCHIS ALBIDA (L.) Á. & D. Löve, *Taxon* **18**, 312 (1969).

Satyrium albidum L., *Sp. Pl.*, 944 (1753).

Orchis albida (L.) Scop., *Fl. Carniol.* ed. 2, **2**, 201 (1772).

Habenaria albida (L.) R.Br. in Aiton, *Hort. Kew.* ed. 2, **5**, 193 (1813).

Gymnadenia albida (L.) Rich., *Orch. Eur. Annot.*, 35 (1817); reimpr. in *Mém. Mus. Hist. Nat. Paris* **4**, 57 (1818).

Entaticus albidus (L.) Gray, *Nat. Arrang. Brit. Pl.* **2**, 205 (1821).

Platanthera albida (L.) Lindl., *Synops. Brit. Fl.*, 261 (1829).

Peristylus albidus (L.) Lindl., op. cit. ed. 2, 261 (1835).

Leucorchis albida (L.) E. Meyer in Patze, Meyer & Elkan, *Fl. Prov. Preuss.*, 91 (1848).

Bicchia albida (L.) Parl., *Fl. Ital.* **3**, 397 (1860).

All the synonyms cited above, in addition to the basionym, have been applied at one time or another to the British plant.



Fig. 1. Hill, *Herbarium Britannicum*, vol. 1, additional plate 66.

A G G R E G A T Æ. 96*

AGGREGATIS ADDITAMENTUM.

O R D O Q U I N T U S.

Calyce proprio diphyлло.

G E N U S I.

C E S P A *.

T U R F W O R T.

Plate 66.

Caput rotundatum : flores masculi et feminei
aggregati.

I. C E S P A A Q U A T I C A.

W A T E R T U R F W O R T.

Caulis contortus ; folia subtus convexa.

Tab. 66.

CAULIS triuncialis, contortus.

FOLIA dissepimentis divisa.

FLORES albi.

PERENNIS. Sub aquis. Rarior. Septembri florens.

Planta hæc rara & singularis mense Septemb.
anni elapsi, in lacu parvo insulæ Skye dictæ ad Sco-
tiæ parten occidentalem a Jacobo Robertson, Bot.
studioso inventa fuit, et a Domino Jo. Hope, Bot.
Prof. Edinburg. nobilissimo Johanni Comiti de
BUTE, cum icone et descriptione missa, ad charac-
teras Eriocauli, adhuc obscuras, elucidandas.

* Calamaria Dillenii, Isoetes Linnæi, fructificatione ignota,

[G]

Plurimæ

Fig. 2. Hill, *Herbarium Britannicum*, vol. 1, page 96*.

*97

A G G R E G A T Æ.

Plurimæ crescunt simul: sub aqua, præter capitulum & scapi summitem penitus demersæ, radicibus ita intertextis ut fundum lacus lutosum tegant, & quibusdam in locis lacus superficies ejusdem plantæ matta vi aquæ suspensa obtegatur: facile tamen hæ plantæ separantur.

Radix: Perennis, solida, interne alba, ex cujus parte inferiore oriuntur plurimæ radiculæ teretes simplicissimæ pennæ passerinæ crassitudinis, albæ, fere pellucidæ, per totam longitudinem dissepimentis opacis transversis, sive articulationibus interceptæ: in centro harum per totam longitudinem est linea quædam opaca. Extremities describere non audeo, quia in singulis speciminibus mihi oblatis omnes radiculæ ruptæ fuerunt. Sapor radicularum primo insipidus, levi postea cum acrimoniâ.

Folia radicalia: Ex parte superiore radice oriuntur plurima folia radicalia, suberecta, similia quoad figuram externam, & simili modo disposita ac in *Agave Americanâ*; sesquiunciam longa, latâ basi, margine integerrimâ: sensim attenuantur in apicem acutum, pagina inferiore convexa, superiore concava, nervosa & spatia his nervis longitudinalibus definita iterum dividuntur dissepimentis transversis, singulis singulis propriis.

Truncus: scapus erectus; e centro foliorum oritur, vagina tenui membranacea, apice bifido, duas uncias longa, respectu nervorum & dissepimentorum foliis simili, inclusus; teres, supra vaginam nudus, contortus.

Fructificatio androgyna terminalis imbricata in capitulo globoso.

Calyx communis, squamis plurimis, nigris, subrotundis,

Fig. 3. Hill, *Herbarium Britannicum*, vol. 1, page 97*.

A G G R E G A T Æ. 98*

tundis, concavis, membranaceis, parte inferiore ciliatis.

Duæ sunt series florum fœmineorum in radio.

FLOS FŒMINEUS in radio.

Squama ovata, nigra, superne ciliata, sensim definens in unguem brevem, externe adstat singulis flosculis.

Cal. prop. Perianthium diphyllum, foliolis ovatis, concavis, nigris, superne ciliatis, in unguem angustum sensim definientibus. Not. ciliæ squamarum sunt albæ.

Corolla dipetala*, petalis albis oblongis, concavis, sensim definientibus in ungues angustos, apice & dorso ciliatis, macula nigra in medio fere laminæ notatis.

Pistillum germen compresso-subrotundum. Stylus brevis. Stygmata duo, longa, filiformia.

Pericarpium capsula compresso-subrotunda, nigra, bilocularis.

Semen in singulis loculis unicum læve, dissepimento affixum, citrini coloris ad apicem umbilicatum.

FLORES MASCULI in disco plures.

Squama adstat flosculis ut in fœmineo flore.

Calyx perianthium diphyllum, foliolis cuneiformibus, concavis, ciliatis.

Corolla monopetala, infundibuliformis, ore bilabiato fimbriato.

Stamina filamenta (quatuor? †) filiformia, corollæ longitudine vel longiora. Antheræ nigræ, oblongæ.

* Eriocaulon tripetalum.

† Staminum numerum definire vix audeo.

EXPLI-

Fig. 4. Hill, *Herbarium Britannicum*, vol. 1, page 98*.

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A G G R E G A T Æ.

EXPLICATIO TABULARUM.

PARTES FRUCTIFICATIONIS.

Flos Fœmineus.	{	A	Squama calycis communis.
		B	Squama quæ singulis flosculis fœmineis adstat.
		C	Foliola duo perianthii proprii flosculum fœmineum tegentia.
		D D	Eadem foliola perianthii proprii e situ naturali remota.
		E	Pars germinis.
		F	Petala.
		G G	Eadem petala e situ naturali remota.
		H	Pericarpium.
		I	Stylus.
		K	Stigmata.
		L	Pericarpium transverse sectum.
		M	Semina duo.
Flos Masculus.	{	N	Squama quæ singulis flosculis masculis adstat.
		O	Foliola duo perianthii proprii.
		P	Petalum.
		R	Petalum apertum ut insertio staminum appareat.
		S	Petalum staminibus remotis.
		T	Stamen.

O R D O S E X T U S.

Calyce polyphyllo.

HER-

Fig. 5. Hill, *Herbarium Britannicum*, vol. 1, page 99*.

- 643 DACTYLORHIZA Nevski, *Acta Inst. Bot. Acad. Sci. URSS Ser. 1*, **4**, 332 (1937).
Orchis subgen. *Dactylorchis* Klinge, *Acta Horti Petrop.* **17**, 148 (1898).
O. subgen. *Dactylorhiza* Nevski in Komarov, *Fl. URSS* **4**, 696 (1935),
 nom. superfl. illegit. $\equiv$ *O.* subgen. *Dactylorchis* Klinge.
Dactylorchis (Klinge) Vermeul., *Stud. Dactylorch.*, 64 (1947).
 Cf. P. F. Hunt & V. S. Summerhayes, *Watsonia* **6**, 128–132 (1965). These authors list name changes made necessary in this genus by the adoption of the older name *Dactylorhiza* in place of *Dactylorchis*. Their views on the taxonomy of the British species and subspecies are accepted here.
- 643/1 DACTYLORHIZA FUCHSII (Druce) Soó, *Nom. Nova Gen. Dactylorch.*, 8 (1962).
 CTW Exc ed. 2, 488.
Orchis fuchsii Druce, *Bot. Soc. Exch. Club Brit. Is.* **4**, 105 (1915).
Dactylorchis fuchsii (Druce) Vermeul., *Stud. Dactylorch.*, 69, 142 (1947).
 [*Dactylorhiza fuchsii* (Druce) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 350 (1960), comb. invalid., basion. non rite cit.]
- 643/1a DACTYLORHIZA FUCHSII subsp. FUCHSII.
- 643/1b DACTYLORHIZA FUCHSII subsp. OKELLYI (Druce) Soó, *Nom. Nova Gen. Dactylorch.*, 8 (1962).
Orchis maculata var. *okellyi* Druce, *Irish Naturalist* **18**, 211 (1909) ('O'Kelly').
O. maculata subsp. *okellyi* (Druce) Druce in Hayward, *Bot. Pocket-book* ed. 15, 277 (1917).
Dactylorchis fuchsii subsp. *okellyi* (Druce) Vermeul., *Stud. Dactylorch.*, 69 (1947).
 [*Dactylorhiza fuchsii* subsp. *okellyi* (Druce) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 351 (1960), comb. invalid., basion. non rite cit.]
- 643/1c DACTYLORHIZA FUCHSII subsp. HEBRIDENSIS (Wilmott) Soó, *Nom. Nova Gen. Dactylorch.*, 8 (1962).
Orchis hebridensis Wilmott, *J. Bot., Lond.* **77**, 192 (1939).
Dactylorchis maculata subsp. *hebridensis* (Wilmott) Vermeul., *Stud. Dactylorch.*, 69 (1947).
Orchis fuchsii subsp. *hebridensis* (Wilmott) Clapham in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 1317 (1952).
Dactylorchis fuchsii subsp. *hebridensis* (Wilmott) H.-Harrison f., *Ber. Geobot. Forsch. Inst. Rübel* **1953**, 55 (1954).
 [*Dactylorhiza fuchsii* subsp. *hebridensis* (Wilmott) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 351 (1960), comb. invalid., basion. non rite cit.]
- 643/2 DACTYLORHIZA MACULATA (L.) Soó, *Nom. Nova Gen. Dactylorch.*, 7 (1962).
Orchis maculata L., *Sp. Pl.*, 942 (1753).
Dactylorchis maculata (L.) Vermeul., *Stud. Dactylorch.*, 68, 125 (1947).
 [*Dactylorhiza maculata* (L.) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 348 (1960), comb. invalid., basion. non rite cit.]
- 643/2a DACTYLORHIZA MACULATA subsp. RHOUMENSIS (H.-Harrison f.) Soó, *Nom. Nova Gen. Dactylorch.*, 7 (1962).
Orchis fuchsii subsp. *rhoulensis* H.-Harrison f., *Trans. Proc. Bot. Soc. Edin.* **35**, 53 (1949).
Dactylorchis maculata subsp. *rhoulensis* (H.-Harrison f.) H.-Harrison f., *Watsonia* **4**, 48 (1957).

- [*Dactylorhiza maculata* subsp. *rhoumensis* (H.-Harrison f.) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 349 (1960), comb. invalid., basion. non rite cit.]
- [*Dactylorchis fuchsii* subsp. *rhoumensis* (H.-Harrison f.) Clapham in Clapham, Tutin & Warb., *Fl. Brit. Is.* ed. 2, 1046 (1962), comb. invalid., basion. non cit.]
- 643/2b DACTYLORHIZA MACULATA subsp. ERICETORUM (E. F. Linton) Hunt & Summerh., *Watsonia* **6**, 132 (1965). *CTW Exc* ed. 2, 488.
Orchis maculata subsp. *ericetorum* E. F. Linton, *Fl. Bournemouth*, 208 (1900).
O. ericetorum (E. F. Linton) A. Benn., *Ann. Scot. Nat. Hist.* **1905**, 39 (1905).
Dactylorchis maculata subsp. *ericetorum* (E. F. Linton) Vermeul., *Stud. Dactylorch.*, 69 (1947).
- 643/3 DACTYLORHIZA INCARNATA (L.) Soó, *Nom. Nova Gen. Dactylorch.*, 3 (1962). *CTW Exc* ed. 2, 489.
Orchis incarnata L., *Fl. Suec.* ed. 2, 312 (1755).
Dactylorchis incarnata (L.) Vermeul., *Stud. Dactylorch.*, 65, 101 (1947).
 [*Dactylorhiza incarnata* (L.) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 337 (1960), comb. invalid., basion. non rite cit.]
- 643/3a(e) DACTYLORHIZA INCARNATA subsp. INCARNATA.
Orchis strictifolia Opiz, *Naturalientausch* **1-10**, 217 (1825).
O. latifolia var. *gemmana* Pugsl., *J. Linn. Soc. (Bot.)* **49**, 578 (1935).
Dactylorchis incarnata subsp. *gemmana* (Pugsl.) H.-Harrison f., *Ber. Geo bot. Forsch. Inst. Rübel* **1953**, 55 (1954).
Dactylorhiza incarnata subsp. *gemmana* (Pugsl.) Sell, *Watsonia* **6**, 317 (1967).
- 643/3b DACTYLORHIZA INCARNATA subsp. PULCHELLA (Druce) Soó, *Nom. Nova Gen. Dactylorch.*, 4 (1962).
Orchis incarnata var. *pulchella* Druce, *Bot. Soc. Exch. Club Brit. Is.* **5**, 167 (1918).
Dactylorchis incarnata subsp. *pulchella* (Druce) H.-Harrison f., *Ber. Geobot. Forsch. Inst. Rübel* **1953**, 55 (1954).
 [*Dactylorhiza incarnata* subsp. *pulchella* (Druce) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 339 (1960), comb. invalid., basion. non rite cit.]
- 643/3c DACTYLORHIZA INCARNATA subsp. COCCINEA (Pugsl.) Soó, *Nom. Nova Gen. Dactylorch.*, 4 (1962). *CTW Exc* ed. 2, 489.
Orchis latifolia var. *coccinea* Pugsl., *J. Linn. Soc. (Bot.)* **49**, 579 (1935).
O. strictifolia subsp. *coccinea* (Pugsl.) Clapham in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 1319 (1952).
Dactylorchis incarnata subsp. *coccinea* (Pugsl.) H.-Harrison f., *Ber. Geobot. Forsch. Inst. Rübel* **1953**, 54 (1954).
 [*Dactylorhiza incarnata* subsp. *coccinea* (Pugsl.) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 339 (1960), comb. invalid., basion. non rite cit.]
- 643/3d DACTYLORHIZA CRUENTA (O. F. Muell.) Soó, *Nom. Nova Gen. Dactylorch.*, 4 (1962). *CTW Exc* ed. 2, 487.
Orchis cruenta O. F. Muell., *Fl. Dan.* **5(15)**, 4 (1782).
O. incarnata subsp. *cruenta* (O. F. Muell.) Aschers. & Graebn., *Synops. Mitteleur. Fl.* **3**, 720 (1907).

Dactylorchis incarnata subsp. *cruenta* (O. F. Muell.) Vermeul., *Stud. Dactylorch.*, 124 (1947).

[*Dactylorhiza cruenta* (O. F. Muell.) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 340 (1960), comb. invalid., basion. non rite cit.]

D. incarnata subsp. *cruenta* (O. F. Muell.) Sell, *Watsonia* **6**, 317 (1967).

643/3f DACTYLORHIZA INCARNATA subsp. OCHROLEUCA (Boll) Hunt & Summerh., *Watsonia* **6**, 130 (1965).

Orchis incarnata var. *ochroleuca* Boll, *Arch. Ver. Freunde Naturgesch. Meklenb.* **14**, 307 (1860).

O. incarnata subsp. *ochroleuca* (Boll) Schwarz, *Mitt. Thüring. Bot. Ges.* **1(1)**, 94 (1949).

Dactylorchis incarnata subsp. *ochroleuca* (Boll) H.-Harrison f., *Ber. Geobot. Forsch. Inst. Rübel* **1953**, 55 (1954).

643/4 DACTYLORHIZA PRAETERMISSA (Druce) Soó, *Nom. Nova Gen. Dactylorch.*, 5 (1962). *CTW Exc* ed. 2, 489.

Orchis praetermissa Druce, *Bot. Exch. Club Soc. Brit. Is.* **3**, 340 (1914).

Dactylorchis praetermissa (Druce) Vermeul., *Stud. Dactylorch.*, 67 (1947).

[*Dactylorhiza praetermissa* (Druce) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 343 (1960), comb. invalid., basion. non rite cit.]

643/5 DACTYLORHIZA PURPURELLA (T. & T. A. Stephenson) Soó, *Nom. Nova Gen. Dactylorch.*, 5 (1962). *CTW Exc* ed. 2, 489.

Orchis purpurella T. & T. A. Stephenson, *J. Bot., Lond.* **58**, 164 (1920).

Dactylorchis purpurella (T. & T. A. Stephenson) Vermeul., *Stud. Dactylorch.*, 67 (1947).

[*Dactylorhiza purpurella* (T. & T. A. Stephenson) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 344 (1960), comb. invalid., basion. non rite cit.]

[*Dactylorchis majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. A. Webb, *Irish Fl.* ed. 4, 169 (1963), comb. invalid., basion. non cit.]

[*Dactylorhiza majalis* subsp. *purpurella* (T. & T. A. Stephenson) D. A. Webb, *op. cit.* ed. 5, 167 (1967), comb. invalid., basion. non cit.]

643/6 DACTYLORHIZA KERRYENSIS (Wilmott) Hunt & Summerh., *Watsonia* **6**, 131 (1965). *CTW Exc* ed. 2, 488.

Orchis majalis var. *occidentalis* Pugsl., *J. Linn. Soc. (Bot.)* **49**, 586 (1935).

O. majalis subsp. *occidentalis* (Pugsl.) Pugsl., *Proc. Linn. Soc.* **148**, 124 (1936).

O. kerryensis Wilmott, *Proc. Linn. Soc.* **148**, 126 (1936).

O. occidentalis (Pugsl.) Wilmott, *Bot. Soc. Exch. Club Brit. Is.* **11**, 551 (1938).

O. occidentalis subsp. *kerryensis* (Wilmott) Clapham in Clapham, Tutin & Warb., *Fl. Brit. Is.*, 1321 (1952).

[*O. majalis* subsp. *kerryensis* (Wilmott) D. A. Webb, *Irish Fl.* ed. 2, 163 (1953), comb. invalid., basion. non cit.]

Dactylorchis majalis subsp. *occidentalis* (Pugsl.) H.-Harrison f., *Ber. Geobot. Forsch. Inst. Rübel* **1953**, 55 (1954).

[*Dactylorhiza latifolia* subsp. *occidentalis* (Pugsl.) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 342 (1960), comb. invalid., basion. non rite cit.]

D. latifolia subsp. *occidentalis* (Pugsl.) Soó, *Nom. Nova Gen. Dactylorch.*, 4 (1962).

[*D. majalis* subsp. *occidentalis* (Pugs.) D. A. Webb, op. cit. ed. 5, 167 (1967), comb. invalid., basion. non cit.]

D. majalis subsp. *occidentalis* (Pugs.) Sell, Acta F. R. N. Univ. Comen. Bot. **14**, 19 (1968).

643/7

DACTYLORHIZA TRAUNSTEINERI (Sauter) Soó, *Nom. Nova Gen. Dactylorh.*, 5 (1962). *CTW Exc* ed. 2, 487.

Orchis traunsteineri Sauter in Reichenb., *Fl. Germ. Excurs.*, 140¹⁸ (1830).

O. majalis subsp. *traunsteinerioides* Pugs., *Proc. Linn. Soc.* **148**, 124 (1936).

O. traunsteinerioides (Pugs.) Pugs., *J. Bot., Lond.* **78**, 179 (1940).

Dactylorchis traunsteineri (Sauter) Vermeul., *Stud. Dactylorch.*, 66 (1947).

[*Orchis majalis* subsp. *traunsteineri* (Sauter) D. A. Webb, *Irish Fl.* ed. 2, 163 (1953), comb. invalid., basion. non cit.]

[*Dactylorhiza traunsteineri* (Sauter) Soó, *Ann. Univ. Sci. Budapest. Sect. Biol.* **3**, 344 (1960), comb. invalid., basion. non rite cit.]

[*D. traunsteineri* subsp. *traunsteinerioides* (Pugs.) Soó, tom. cit., 345 (1960), comb. invalid., basion. non rite cit.]

D. traunsteineri subsp. *traunsteinerioides* (Pugs.) Soó, *Nom. Nova Gen. Dactylorh.*, 6 (1962).

[*Dactylorchis majalis* subsp. *traunsteineri* (Sauter) D. A. Webb, op. cit. ed. 4, 169 (1963), comb. invalid., basion. non cit.]

[*Dactylorhiza majalis* subsp. *traunsteineri* (Sauter) D. A. Webb, op. cit. ed. 5, 168 (1967), comb. invalid., basion. non cit.]

663/18

CAREX SAXATILIS × VESICARIA = C. × GRAHAMII Boott, *Trans. Linn. Soc.* **19**, 215 (1844) ('*Grahami*') (pro sp.).

C. × *ewingii* E. S. Marshall, *J. Bot., Lond.* **49**, 197 (1911).

[*C. stenolepis* auct., non Less.]

Cf. A. C. Jermy & T. G. Tutin, *Brit. Sedges*, 94 (1968).

663/66

CAREX MURICATA subsp. LEERSII Aschers. & Graebn., *Synops. Mitteleur. Fl.* **2(2)**, 40 (1902).

C. leersii F. W. Schultz, *Flora (Regensb.)* **53**, 459 (1870), non *C. leersii* Willd. (1787).

[*C. polyphylla* auct., non Kar. & Kir.]

Cf. A. C. Jermy & T. G. Tutin, *Brit. Sedges*, 176 (1968).

665/1

PHRAGMITES AUSTRALIS (Cav.) Trin. ex Steud., *Nomencl. Bot.* ed. 2, **2**, 324 (1841). *CTW Exc* ed. 2, 522.

Arundo phragmites L., *Sp. Pl.*, 81 (1753).

A. vulgaris Lam., *Fl. Franç.* **3**, 615 (1778), nom. superfl. illegit. ≡ *A. phragmites* L.

A. palustris Salisb., *Prodr. Stirp.*, 24 (1796), nom. superfl. illegit. ≡ *A. phragmites* L.

A. australis Cav., *An. Hist. Nat.* **1**, 100 (1799).

Calamagrostis nigricans Mérat, *Nouv. Fl. Env. Par.*, 29 (1812).

Phragmites communis Trin., *Fundam. Agrost.*, 134 (1820).

Cf. W. Greuter, *Boissiera* **13**, 174 (1967); W. D. Clayton, *Taxon* **17**, 168 (1968).

683/20

*BROMUS WILLDENOWII Kunth, *Révis. Gram.*, 134 (1829).

Festuca unioides Willd., *Hort. Berol.*, t. 3 (1803), non *Bromus unioides* Kunth (1816).

Ceratochloa unioides (Willd.) Beauv., *Ess. Nouv. Agrost.*, Expl. Planch., 11 (1812).

[*Bromus unioides* auct., non Kunth.]

Cf. P. H. Raven, *Brittonia* **12**, 221 (1960); A. Melderis, *Proc. Bot. Soc. Brit. Is.* **7**, 392 (1968).

BOOK REVIEWS

The Diversity of Green Plants. P. R. Bell and C. L. F. Woodcock. Pp. ix + 374. Edward Arnold. London. 1968. Price £4 (board), £2 (paper).

This is a new morphology text-book intended for undergraduates. It aims by means of a selected series of examples to cover the range of organization shown by autotrophs: algae, bryophytes and trachaeophytes. This it does in some 340 pages of which over half carry an illustration. There is also a 17 page glossary and a brief bibliography of 86 references. The text-figures (there are some 230) are a special feature. They are mostly clear simplified outline diagrams and about two-thirds are original. To the undergraduate picking up the book for the first time this feature will give it an instant appeal. The selection of examples, which is probably similar to those cited in most undergraduate courses in British Universities, is an additional selling point.

The usefulness of this book is difficult to assess: it is in no sense a work of reference for in so short a text it can go no further than, if as far as, many lectures would on any part of the field covered. It could be useful in an introductory first year course which includes a broad survey of systematics and morphology. The diagrams include much that is seen in practical classes and it is perhaps in the laboratory that the book may be of most value. It will be useful to teachers in sixth forms and to their students who may require a concise one-volume guide to plant form.

This is not a work for more advanced students. The authors give a too condensed and often oversimplified account of the subject matter. There is no morphological theorizing, names like Lam, Meeuse, Melville and Zimmermann never crop up and Eames, *Morphology of Angiosperms* (1961) does not occur among the references. The authors are uncommitted to the extent of using neutral terms like micro- and mega-sporangiophores for stamens and carpels but without any explanation or discussion of homology. There are some brief passages on evolution and two interesting ideas were introduced here. One (p. 7) concerns the rate of production of carbohydrate and the role this may have had in the evolution of cell walls in early land plants. The other (p. 341) speculates on the ecological effect induced by differential rates of decay of angiosperm and gymnosperm leaves (surely only those of some conifers). The evolution of Osmundaceous ferns and of the female cone in conifers, for which there is ample palaeobotanical evidence, are passed over so summarily that the student is unlikely to be even awakened to their existence, although Florin (1951) is at least mentioned.

There are a number of minor errors in both the text and figures which will irritate the specialist teacher though they are probably not very dangerous to the student: the size of the capsule and involucre in *Lophocolea* (fig. 4.9) in proportion to the rest of the leaves; the shape of the antheridial branch in *Sphagnum* (4.17) and the somewhat irregular arrangement of leaves, not in clear vertical ranks as is typical. The perspective in the drawing of the dehiscent capsule of *Andreaea* (4.19b) makes interpretation difficult. The leaf-bases of *Lepidodendron* (5.23) lack an outline delimiting the leaf scar. There is no primary xylem in the transverse section of *Lyginopteris* (7.1). The fibrous layer (endothecium) has been separated from the epidermis in the *Lilium* anther (8.22). The diagram (8.43b) showing a transverse section of a host stem with a haustorium of *Cuscuta* does not very satisfactorily define the limit of penetration achieved by the parasite. In the text Cycads (p. 239) are said to have trilete pollen. It is, in fact, sulcate or anacolpate; however, as these terms are not used, it might possibly have been described as monolete. The statement (pp. 250, 258 and fig. 7.26) that the 'air bladder' in the Cordaitales and *Pinus* is developed between the exine and the intine is an oversimplification (cf. Erdtman 1957): but the exine is defined in the singular (p. 348) 'as the outer layer [not layers] of the wall of a spore or pollen grain'. *Ligustrum* pollen as figured (8.24) is colpate (it is, strictly, colporate) but not porate as labelled.

The authors have missed the opportunity to present an exciting account of the diversification of autotrophic plants and instead have produced another pedestrian and somewhat superficial text-book.

P. D. W. BARNARD

Flora of Iraq, Volume 9. N. L. Bor, with economic and distributional notes by Evan Guest. Edited by C. C. Townsend, Evan Guest and Ali Al-Rawi. Pp. vi + 588, with 216 plates (1 in colour). Ministry of Agriculture, Baghdad, Iraq. 1968. Obtainable from R. Maclehose & Co., Glasgow. Price £3 10s.

This volume of the *Flora of Iraq* is a most remarkable achievement for a man who has long passed the age of retirement, and this is especially noteworthy in an era of youth-worship. Norman Loftus Bor hardly needs any introduction: as one of our leading agrostologists he has gained renown with his work on the Gramineae of India, Pakistan and Ceylon as well as with his participation in Rechinger's *Flora of the*

Lowlands of Iraq, not to mention his numerous contributions towards our knowledge of this family in various scientific journals all over the world.

The first two volumes of the *Flora of Iraq* (all that had previously appeared) have already been thoroughly reviewed in *Watsonia* 6, 390–391. Either the importance of the Gramineae or Dr. Bor's immense drive may be the reason for the appearance of this volume (No. 9) many years ahead of schedule.

The systematic treatment of the volume is preceded by an introduction to the morphology of the Gramineae, which is a welcome help to those less experienced who try to find their way through the keys. This part is followed by a key to the Tribes, which may pose some problems to the non-specialist since it is based on the proverbially tedious spikelet characters. Within each Tribe a key to the genera is provided. More important than this, however, and of greater value as far as practical use is concerned, is the artificial key to the genera (pp. 21–40), where basically more conspicuous characters such as type of inflorescence, arrangement and shape of spikelets etc. are used to break down the large number of genera into recognizable groups. The inflorescence types are magnificently illustrated on eleven interleaved plates. A random trial proved the workability of this key; but the reviewer alas, was, irritated very much by its inconvenient lay-out (this criticism applies to all the keys in the book). For this, of course, the author cannot be blamed. One really wonders why in A.D. 1968 planners of taxonomic works can still advocate the use of un-numbered indented keys which can sometimes only properly be used with the help of a measuring device. Within the key to the Tribes (stretching over several pages), for example, there are not less than 15 lines beginning with 'spikelets'! How will the inexperienced user ever find his way through such a maze when even the trained taxonomist finds it difficult? I should point out that most modern taxonomic works have introduced numbered keys, most notably *Flora Europaea*, *Flore du Gabon*, *Flora of the British Isles*, *Flora Iranica*, etc. etc.

The descriptions both generic and specific are adequate. Bibliographic references are confined to the Middle East, and only the most important synonymy is given. Most praiseworthy are the notes dealing with economic aspects of species as well as the fact that most of the local plant names have been translated from the Arabic. Nomenclaturally the work is up-to-date. Not without sadness does one note that the Common Reed now bears the name *Phragmites australis*, but this is not the place to lament either the absence of a list of 'nomina specifica conservanda' from the *International Code of Botanical Nomenclature*, or the eagerness of some colleagues who just cannot let sleeping dogs lie.

The most outstanding feature of this volume is its almost luxurious amount of illustration. Besides the really attractive coloured frontispiece of *Bromus danthoniae* by Mary Grierson, there are 215 (not 212 as stated on p. vi) plates of line drawings, mainly executed by Derrick Erasmus. Most of these plates are excellent, and indeed a few of these, e.g. Plate 215 (*Zea mays* L.), show that he is not just another plant illustrator but an artist at work.

Both the author and the authorities of the Royal Botanic Gardens, Kew, are to be congratulated on this volume.

EDMUND LAUNERT

The Natural Geography of Plants. H. A. Gleason and A. Cronquist. Pp. viii + 208 illustrations (mostly photographs). Columbia University Press, New York & London. 1964. Price £4 10s.

Although this book has been available for over 4 years, no review has yet appeared in these pages. As it is a remarkable book, in several ways, I feel that no apology is required for bringing it to the notice of readers of *Watsonia* after this time. A word of explanation is necessary, however, on account of the somewhat misleading title. A more informative one would be 'The Natural Geography of Plants of North America'; even this would not be a strictly accurate summary of the contents. It is true that the North American flora figures largely in this work and that the authors have addressed their remarks principally to those inhabitants of the United States and Puerto Rico who are anxious to look with an intelligent eye on the natural vegetation around them; but the plants of these regions are used to illustrate principles of plant geography that are applicable to all parts of the world, particularly, of course, to the North Temperate region, in which the British Isles are situated.

The main part of the work, as Cronquist explains in the preface, was written by Gleason. This comprises 21 out of 22 chapters and deals with various aspects of the theory of plant geography such as distribution, migration and dispersal at the present day and in past time (both historical and geological), joint migration and floristic groups and provinces. Cronquist's main contribution is the last and largest chapter in the book (pp. 275–414), which gives a very full analysis of the vegetation of North America, north of Mexico.

One of the most valuable and interesting features of *The Natural Geography of Plants* is the way that the authors appeal to the reader to go out and look around him, point out aspects of plant distribution that he will observe, and then provide reasoned answers to the questions raised by the consideration of these aspects. The very large number of black-and-white photographs, of a uniformly high quality although obtained from various sources, must also be noted.

One of the factors governing plant distribution that is given great emphasis is *time*. The authors return continually to this topic, stressing that: 'Plants have had, not decades or centuries, but thousands or even tens of thousands of years to carry on their migrations, and even short steps become wonderfully effective if continued long enough' (p. 44); '... we must never forget the importance of time in phytogeography' (p. 49); 'time is the important factor' (p. 264); and that one should 'never forget the importance of past vegetational history in explaining the present distribution of plants' (p. 269). Indeed they seem to imply that migration over long periods, either by short stages with extinction in the middle of the range or by long-distance dispersal, can be invoked as a cause of most of the widely discontinuous distributions that exist today; but they admit that there are some for which they can give not even the vaguest explanation. The possibility of causes such as continental drift (for which more and more favourable evidence seems to be accumulating) is not even mentioned. It is pointed out that almost all distributions are discontinuous to the extent that a species does not occupy all suitable ecological niches (owing to incomplete migration, migratory barriers or competition), so that the more obvious discontinuities often differ only in degrees from those that are familiar in the small-scale plant community.

After dealing with these mainly autecological topics, the authors turn to consider species in relation to one another. The concepts of 'joint migration' and 'joint ranges' are used to introduce the plant community, and a large section of the book treats this subject in a fair amount of detail, first in general ('Floristic groups and Provinces') and then with reference to North America.

Although this book is addressed to the 'interested layman', it contains an abundance of information and ideas that will prove useful and stimulating to anyone, professional or amateur, who wishes to consider questions involving the distribution of plants, in both space and time.

The format is pleasing and the price not excessive for today. I should, however, have liked the index to include the Latin names in their alphabetical sequence, not merely in parenthesis after the common 'English' (*i.e.* American) name. For that matter, the practice of using 'English' names in the text, with the Latin one in parenthesis only when first mentioned, is rather confusing to an English-speaking non-American, let alone a reader whose native tongue is not English.

N. K. B. ROBSON

Mountain Flowers in Colour. A. Huxley. Pp. 428 incl. 112 colour and 36 black and white full-page plates. Blandford, London. 1967. Price £1 10s.

This attractive volume is designed to cater for the English-speaking visitor to any of the main European mountain areas who has a little knowledge of botany and a strong desire to identify what he can of the rich mountain flora of Europe. The market for such a book is greatly stimulated by the spread of tourism in recent years, and it is remarkable that, as the author says, there was, in English, no single volume that could be said to give any moderately comprehensive selection of the mountain plants of Europe since H. S. Thompson's *Alpine Plants of Europe*, published in 1911 and long out of print.

The book 'is based unashamedly on its illustrations', which are generally of a high quality, and would certainly enable any user with no technical knowledge of plants to identify such distinctive species as the Lady's Slipper Orchid, *Cypripedium calceolus* or the Mountain Avens, *Dryas octopetala*. It would also be true that the illustrations on the whole distinguish well between the rather numerous species of the famous mountain genera like *Saxifraga* and *Gentiana*. Nevertheless one feels some doubt about the complete absence of *any* keys for identification; there is no method of using the book at all to arrive, for example, at the fact that the small white-flowered cushion alpine is a *Saxifraga* and not, perhaps, a *Draba* or an *Arenaria*. Some compromise between the arid dichotomous keys of a technical Flora and a complete reliance on illustrations would surely have been preferable?

The selection of species to include is, of course, easy to criticise—no selection can satisfy everyone, and it would be unreasonable to condemn the exclusion of, for example, most alpine grasses and sedges, because, clearly, these are not what the layman calls 'mountain flowers'. It would, however, be less easy to defend the somewhat cavalier treatment of the *Cruciferae*; familiar alpine species such as *Kernera saxatilis* or *Cochlearia* spp. surely deserved inclusion? The treatment of critical genera is unsatisfactorily variable; for example, a more rigorous policy of including only the two aggregate Linnaean species *Alchemilla alpina* and *Alchemilla vulgaris* would have prevented the error of including twice (once as *A. hybrida* and once—correctly—as *A. glaucescens*) what is in fact the same plant!

A final, more serious criticism. Nowhere in the otherwise excellent, lucid introductory material can I find any reference to the urgent problems of protection of the mountain flora of Europe. It is emphatically not good enough, in the modern age, to provide people with a stimulus to admire the rare and the beautiful without administering a warning. Tourism can so easily destroy what it thrives on. Surely all authors of popular works on natural history must at the very least face their readers with the challenge of the conservation of nature. To mention, for example, that *Eritrichium nanum* is 'rare' in the Alps without saying it is

legally protected seems like a betrayal of trust. A paragraph on conservation could so easily have been included on p. 11 of the Introduction where rarity is discussed. May I commend the idea to the author if, as he deserves, his otherwise admirable book quickly reaches a second edition?

S. M. WALTERS

B-P-H: Botanico-Periodicum-Huntianum. Edited by George H. M. Lawrence, A. F. Gunther Büchheim, Gilbert S. Daniels and Helmut Dolezal. Pp. 1063. Hunt Botanical Library, Pittsburgh, Pa., U.S.A. 1968. Price \$30.00.

Abbreviations of botanical periodicals have long posed a problem both for authors and for editors, and while the data given in the *World List of Scientific Periodicals* have been accepted as a standard by some they have been rejected by others. A major difficulty in using that work is that one must know the full title of a periodical in order to trace its relevant abbreviation, and a further complication is that details of periodicals which ceased publication prior to 1900 are omitted.

Prior to the appearance of *Botanico-Periodicum-Huntianum* no adequate reference book devoted entirely to botanical periodical literature existed. This work, the compilation of which was undoubtedly a herculean task involving much international cooperation, is a vast compendium of some 12,000 titles comprising much of the world's periodical literature relating to all branches of botany. Under the title of each periodical cited, the editors have attempted to provide the following information: (a) an internationally acceptable unambiguous abbreviation; (b) title, as given on the title-page of the first volume; (c) place of publication of first volume; (d) volumation and pertinent publication dates; (e) index reference for the title in the Union List of Periodicals.

The selection of periodicals covers a very wide field indeed, and is particularly comprehensive on central European literature, providing references to many important early, but obscure or overlooked, series. There are, however, some surprising omissions, and among those which readily come to mind, so far as current periodicals are concerned, are the botanical series of the Finnish journal *Aquilo*, and of the *Revue Roumaine de Biologie*. *The Annals of the Natal Museum*, Pietermaritzburg, which has been in existence since 1906, and which contains several important revisions of genera of South African Gramineae, is omitted, and the *Israel Journey of Botany* is excluded, although it may be found under its pre-1963 title as *Bulletin of the Research Council of Israel. Section D Botany*.

The abbreviations adopted are not always entirely satisfactory—could they ever be so? Our own publication, *Proceedings of the Botanical Society of the British Isles*, is provided with the abbreviation *Bot. Soc. Brit. Isles Proc.*, though cross references, a most valuable feature of the book, show that it has also been cited as *Proc. bot. Soc. Br. Isl.* and *Proc. Bot. Soc. Brit. Isles*, the latter being the abbreviation in most common use in European literature, and which, I suspect, is likely to be retained as standard.

The volumation and pertinent publication dates are of considerable interest, and it is possible to trace many of the great historical periodicals such as *Acta physico-medica academiae caesareae leopoldino-carolinae naturae curiosorum exhibitia ephemerides sive observationes historicas et experimentia . . .*, first published in Nuremberg in 1727, through their many changes of titles and numerous series. The accumulation of such data is, I know from personal experience, time-consuming and needs much careful checking and rechecking. Despite the excellence of this section of the book there are a number of incomplete or inadequate references which I feel could have been improved upon, e.g. the reference to *Contributions du laboratoire de botanique de l'université de Montréal* gives vols. 1–?, 1922–38. An examination of the run of the periodical at the Library of the Royal Botanic Gardens, Kew, revealed that the entry should read nos. 1–30, 1922–38, and that the superseding periodical, *Contributions de l'institut botanique de l'université de Montréal* commenced at no. 31, 1938, and not as vol. 1 as given in B-P-H. The East German periodical *Drudea: Mitteilungen des Geobotanischen Arbeitskreises Sachsen-Thüringen*. Jena, is cited as Vols. 1–4. 1961–64, whereas, so far as I am aware the publication is still current. *Deutsche botanisch Monatsschrift*. Sonderhausen, Germany. Vols. 1–23, 1883–1912, appears as a bare statement, whereas the serial had at least four different subtitles during the course of its existence.

The blemishes referred to are, however, of minor importance in a work of such vast proportions and the editors are more than justified in closing with Alexander Pope's words:

*Whoever thinks a faultless piece to see
Thinks that ne'er was, nor is, nor ne'er will be.*

Professor Lawrence and his colleagues are to be congratulated on the production of a volume of a very high standard, reasonably priced in view of its bulk and content, which will serve as an invaluable reference book for many years to come.

D. H. KENT

Essays on Form in Plants. C. W. Wardlaw. Pp. xiv + 399. Manchester University Press. 1968. Price £2 15s.

The essays in this book have been selected by Professor Wardlaw from his published work on aspects of form in plants. They are presented in chronological order, the earliest being dated 1944 and the latest 1966. The kernel of the book is provided by the development of the author's thoughts on plant morphogenesis but at each stage he has made a wider application of his point of view. Thus the complementary aspects of the various botanical disciplines, of phylogeny and ontogeny, and of levels of organization within the organism are all examined. Indeed, their immanence can be sensed throughout the book. Wardlaw's treatment of these issues is an important contribution to theoretical botany and anyone who is struggling for a comprehensive view of plants must be grateful for the groundwork accomplished by him. In his earlier books, the amount of factual information is immense; for students of morphogenesis, therefore, his recent *Morphogenesis in Plants* will continue to be the most useful work to have at hand. The present volume, which gives access to the ideas without a heavy load of fact, may be preferred by the non-specialist wishing to extend or clarify his thinking. It also makes available to the individual and small library a number of articles which otherwise are difficult to obtain.

Wardlaw's studies of the shoot apex of ferns are represented mainly by summary papers reprinted from *Nature*. From these early studies came the elaboration of the concept of the growth centre as a site of special metabolism that induces a physiological field within which no new growth centre can originate. The nature of the organ to be formed by a growth centre becomes fixed after a (sometimes) perceptible interval, the factors which evoke development along a particular path being a subject for further investigation.

The anatomist looks for signs of differentiation in the immediate derivatives of the apical meristem; but still the visible pattern appears 'out of the blue'. Wardlaw, while stressing that this pattern must earlier be present at the invisible, chemical level, was intrigued by the problem of how chemical pattern could arise: how heterogeneity can come from homogeneity. By a coincidence, this problem was also exciting interest at Manchester in the neighbouring Mathematics Department where the late A. M. Turing was providing an answer in his 'Chemical Basis of Morphogenesis'. The two papers in which Wardlaw comments on and applies Turing's theory of diffusion-reaction systems are included in this volume. In his later work, Wardlaw, taking into account the interactions between different levels of organization, between the whole and its parts, formulates his hypothesis of the *organismal reaction system*.

Of especial interest to readers of this journal is the entertaining article 'A surfeit of species'. Wardlaw is concerned not so much with the documenting of species as with knowing the host that have been documented. He commends an effort to find out whether morphological parallelism is matched by morphogenetic parallelism. If the same means have been used in different taxa to reach similar structural ends, the comprehension of the labyrinth of speciation is made easier.

A remarkable feature of Wardlaw's gift is his capacity to cherish the past whilst looking forward irrepressibly to the future. In the introductory and concluding chapters there can also be detected a hint of his warm and chivalrous approach to science and life.

F. CUSICK

British Mosses and Liverworts. E. Vernon Watson. Pp. xvi + 495, 18 plates, 8 + 242 text figures. 2nd Edition. Cambridge University Press, London. 1968. Price £4.

During the last twenty-five years there has been a greater interest taken in British bryology, especially in the field, than ever before. The stimulus has come mainly from the staff of the Universities, often members of our Society, and the British Bryological Society. As the standard works by H. N. Dixon and S. M. Macvicar were becoming scarce and out of date, a pressing need was felt for a work that would cover at least the commoner species likely to be encountered by the student. This need was most ably filled by Dr. Watson's work, which by his method of description, illustration, and remarks on habitat and ecology, has brought many students on to a more comprehensive study of the subject.

Those of our members who have an interest in plant communities will need to be able to name, and recognize again, the bryophytes found in the various habitats that they may be studying or mapping for conservation or other purposes. The illustrated introduction and glossary, followed by keys to all the species mentioned in the book—over 300, will guide the novice along the right methods of approach. Well over 200 taxa are illustrated and described, with valuable helpful remarks on their habitats and associates. Less common species receive adequate mention including aids to recognition.

At the end of the descriptive part is a series of habitat lists, 24 in all, with the species commonly or constantly found in each enumerated. The taxonomy and nomenclature is, of course, in accordance with the latest research. There really is far more pertinent information about the taxa which are illustrated than is to be found in any other work currently available. This book is an essential aid to the ecologist as well as a beginner at bryology and is strongly recommended as good value for the price.

E. C. WALLACE

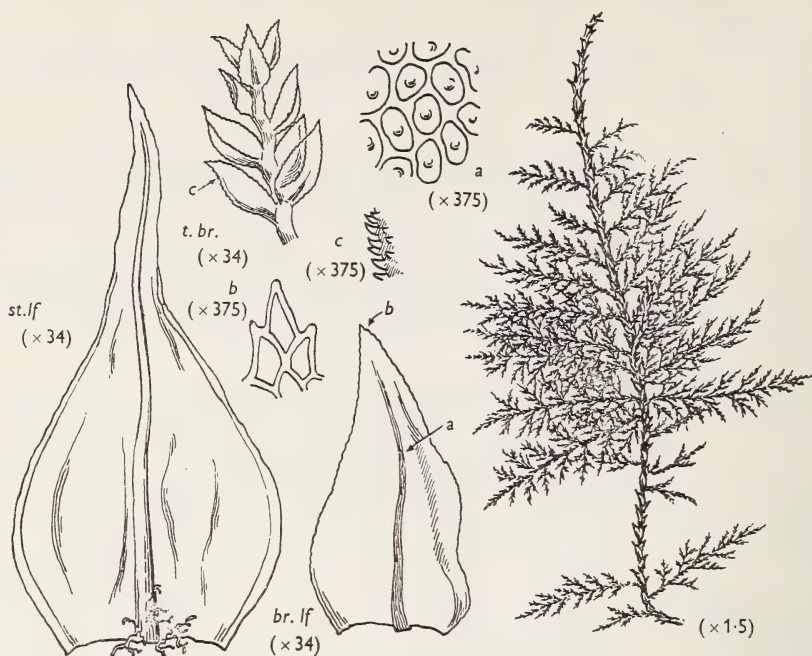


Fig. 136. *Thuidium tamariscinum*: st.lf, stem leaf; br.lf, leaf of primary branch; t.br. tip of fine branchlet.

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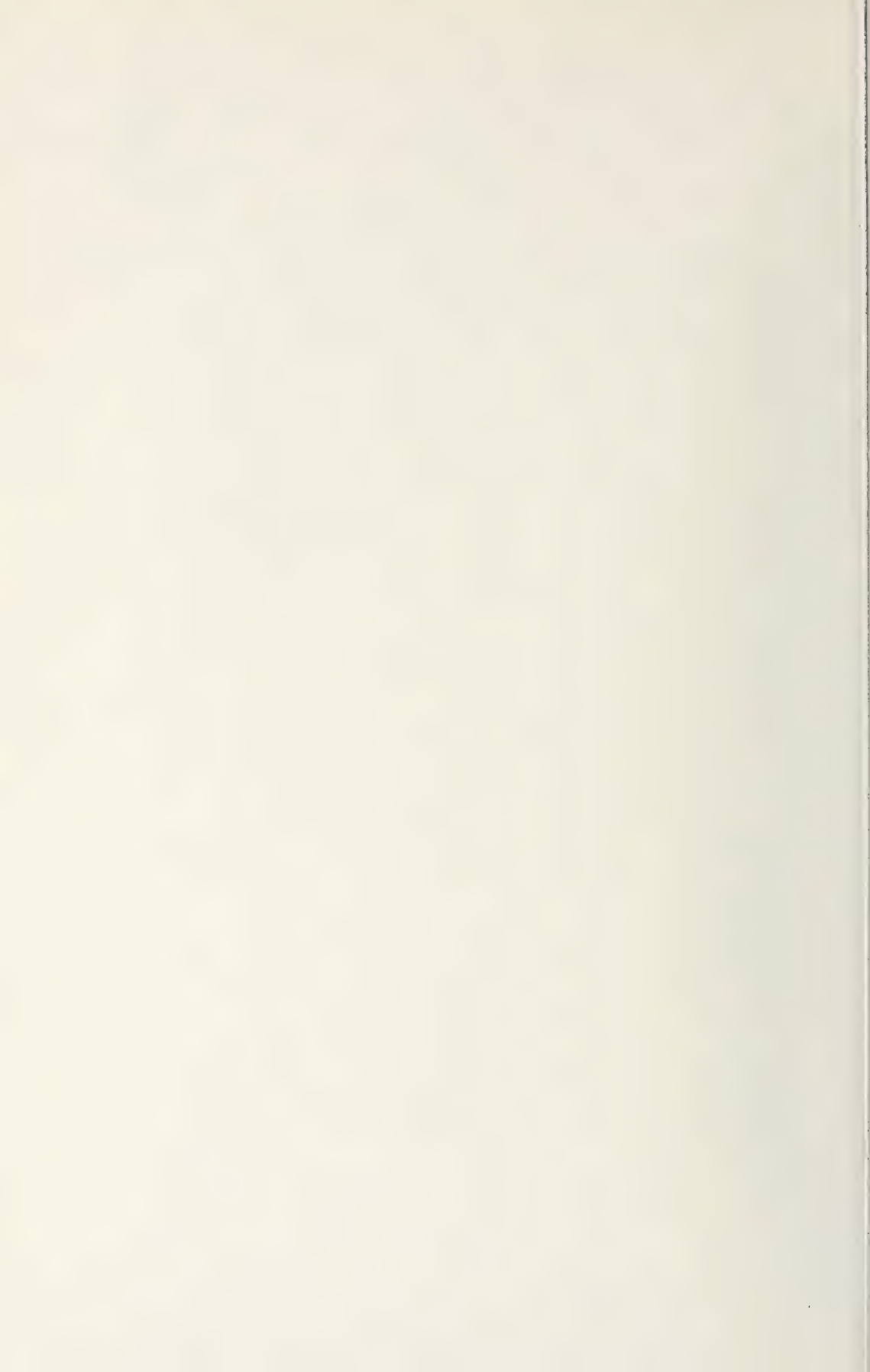
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