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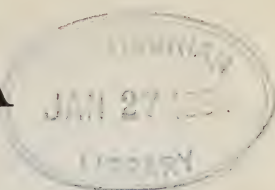
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MONTIA FONTANA L.

By S. M. WALTERS

Botany School, Cambridge University.

The Linnean species *Montia fontana* has long been recognised as very variable, and many attempts have been made to subdivide the aggregate into smaller taxonomic units. The earliest attempts were rather naturally based on the more obvious type of variation in habit which was closely correlated with differences of habitat; thus Gmelin (1805) recognised two species, *M. minor* and *M. rivularis*, the former a small terrestrial plant with erect stems, the latter a more or less submerged or floating aquatic plant with long trailing stems. The less striking variation shown by the ripe seed was first recorded by Chamisso (1831), whose *Montia lamprosperma* of N. Temperate and Arctic Eurasia was distinguished by the possession of a smooth, shining seed, in contrast to the dull, tuberculate seed type common in Central and Southern Europe. In most later work, the seed-coat differences have been used in attempts to define the species within the aggregate, usually in association with the habit characters. Thus Ascherson & Graebner (1919) give three species in the aggregate: *M. minor*, annual, with dull, tuberculate seed; *M. lamprosperma*, annual, but with looser growth, and shining seeds with very brittle coat; and *M. rivularis*, perennial, with shining, finely tuberculate seeds. Koch's *Synopsis* (1892) gives the same three species, but with slightly different diagnoses. The French and other W. European floras have generally adopted *M. minor*, the erect land form with dull tuberculate seeds, and *M. rivularis*, more or less aquatic, with more shining, finely punctate or tuberculate seeds. Lindberg (1901), in a general review of the problem, gave as his opinion that any attempt to use characters of habit or vegetative structure to define the taxonomic units within the aggregate was useless, and that the characters of the ripe seed provided the only satisfactory basis. He agreed fundamentally with Chamisso's division into two main types, for which he adopted the names *M. fontana* subsp. *lamprosperma* and subsp. *minor*; the *M. rivularis* of Continental authors he considered to be merely an aquatic form of *M. minor* and described, as var. *boreo-rivularis*, analogous aquatic forms of subsp. *lamprosperma*. Samuelsson (1922) considered the Scandinavian types within the aggregate, and gave a good review of previous treatments by Scandinavian workers; he agreed with Lindberg in distinguishing two forms on seed characters, and in rejecting any characters other than those of the ripe seed, though differing from him in his interpretation of *M. rivularis*.

In Britain, the division into two types – the northern shining-seeded and the southern dull, tuberculate-seeded types – had been generally accepted, until Beeby (1909) pointed out that British material was more satisfactorily divisible into three, not two, seed-types. These he called: subsp. *lamprosperma* (the northern type), subsp. *minor* var. *chondrosperma* Fenzl (the southern type), and his new subsp. *minor* var. *intermedia*. Each of these could exist in 'land and water states' which were 'merely temporary conditions directly induced by the environment, and not varieties.' Druce (1920) gave some details of the British distribution of var. *intermedia*, and stated that he had seen material referable to this from Belgium and Spain, and that it was 'doubtless elsewhere.' The existence of this third seed-type, intermediate between the other two, has undoubtedly contributed to the difficulties of British botanists attempting to apply continental work to the British material, and the distinctness of the three types has not generally been realised (cf. however Salmon (1931), who was obviously familiar with three types in the field).

A note by Hylander (1945) has done a great deal to clear the way to a solution of the taxonomic problem; in this the author points out that Beeby's var. *intermedia* is (as interpreted by Druce) at least in part identical with *M. lusitanica* Sampaio and refers material from Cork with certainty to this species.

Sampaio's *Montia lusitanica* is adequately described and discussed by the author (1912) who points out that the whole of the *Montia* material of Portugal is referable to this single species, and that previous references to *M. minor* and *M. rivularis* in Portugal were merely to habit-forms of extreme habitats (see below). He distinguishes his species from '*M. minor*, *rivularis* and *lamprosperma*' basically on seed size and characters of the seed-coat; and although the difference in size is certainly by no means so great or so constant as he suggests (see below), the seed-coat character '*dense et acute tuberculatis*' is clearly stated. Apparently no type material was quoted, but I have seen material determined by Sampaio (in Herb. Inst. G. Sampaio, Porto, by courtesy of the Director), and there is no doubt as to the identity of this plant with var. *intermedia* Beeby.

Decker (1927) described as a new species, *M. limosa*, a plant which he collected in Brandenburg, Germany and was unable to refer either to *M. minor* or to '*M. rivularis*.' There can be no doubt from his description that this new species is *M. lusitanica*; thus he recognised it as distinct from the common *M. minor* of the district by the appearance of its seeds under a lens – '*ihre scharf gekörnelt, wenig glänzenden Samen.*' Decker suggests that Ascherson and Graebner's '*M. rivularis*,' particularly records from the N. German plain, is in large part his *M. limosa*. Compare also Lindberg's comments (1901) on material determined as *M. rivularis* from C. Europe, from which it is clear that he was aware of the somewhat intermediate nature of the seed type of Continental '*M. rivularis*,' although he considered the differences – a rather shiny seed with smaller tubercles – not sufficient to justify its separation from *M. minor*, and seemed to think that even these seed differences are attributable to environmental modification.

Comparison of herbarium material with ripe seeds soon confirms the view that throughout N., W. and C. Europe the aggregate *M. fontana* is largely divisible into three plants distinguished on seed type, and that over a considerable area, including parts of England and much of N.W. Europe, two or all three types may occur together, yet remain distinct. In total range, moreover, the three types show striking differences; one (*M. lamprosperma* Cham.) is N. Temperate-Arctic and Alpine; one (*M. minor* auct.) is Temperate European; and the third, *M. lusitanica*, is W. European.

If the morphological separation on seed type were more or less complete, it might be taxonomically justifiable to treat the three as separate species. In fact, however, in parts of northern England, and elsewhere in N.W. Europe, there occur plants whose ripe seeds have small and somewhat variably developed tubercles, intermediate between *M. lusitanica* and *M. lamprosperma*. Between *M. verna* and the other two, there are in Britain and N.W. Europe as a whole apparently very few intermediate types, but such seed types undoubtedly occur more frequently in the Mediterranean region. It would seem best therefore to treat the aggregate as a single species, *M. fontana* L., with geographical subspecies, viz.:—

- (1) subsp. *fontana* (*M. lamprosperma* Cham., the plant of the Linnean Herbarium).
- * (2) subsp. *chondrosperma* (Fenzl) comb. nov. (*M. fontana* var. *chondrosperma* Fenzl (1843) in Ledebour, *Fl. Ross.*, 2, 152).
- (3) subsp. *intermedia* (Beeby) comb. nov. (*M. fontana* var. *intermedia* Beeby, *M. lusitanica* Samp. *M. limosa* Decker).

Plants with seed type between that of (1) and (2) could be treated as the expected

* I have followed Mr. J. E. Dandy's advice in the matter of nomenclature of this subspecies. Neither *M. verna* Neck. nor *M. minor* Gmel. is legitimate, both being renamings of *M. fontana* L.

intermediates between geographical subspecies if they were only very local or rare; but the occurrence of this type over a considerable area where, locally, the other subspecies may be almost absent (as seems to be the case, for example, in the Isle of Man), suggests that, whether the plant is of hybrid origin or not, it requires recognition as a widespread population type of similar status to the others. It is moreover fairly clear that many European records for '*M. rivularis*,' based on seed type, refer to such plants with seeds with small low tubercles near to ssp. *fontana* (cf. remarks by Hylander, 1945, 143-5). The most reasonable taxonomic treatment would here seem to be to treat such types as constituting a fourth subspecies (see below for description). It is interesting that Mansfeld (1940), following Decker, gives four species under the aggregate *M. fontana* in Germany, which seem to correspond with the four subspecies here proposed.

It is impossible to determine what Gmelin's *M. rivularis* was – the Gmelin Herbarium was destroyed in Karlsruhe during the last war – and a great deal of confusion surrounds the use of the name. This is partly due to the fact that there is a general habitat and correlated habit difference between ssp. *chondrosperma* and the other subspecies, by virtue of which it is often possible to distinguish roughly in the field between two types of plant. For example, in areas such as the Channel Isles, N.W. France and N. Italy where subsp. *chondrosperma* and subsp. *intermedia* are almost the only subspecies present, a classification on habit into '*M. minor*' and '*M. rivularis*' will very largely separate these two subspecies. Material distributed as *M. rivularis* from N. Italy in Fiori, Béguinot & Pampanini, *Flora Italiana Exsiccata* (no. 789) – which is typical subsp. *intermedia* – has the following note on the label: – 'species rather similar to the preceding (i.e. *M. minor*) . . . characterized by its submerged, not erect, habit, by the position of the flowering branches, and by the structure of the seed surface . . . Grows only in water poor in minerals . . .'. Decker (1927) makes similar remarks on his *M. limosa*. In areas where all four subspecies may be found, as in England and parts of Germany, '*M. minor*' will generally be subsp. *chondrosperma*, whilst '*M. rivularis*' will include aquatic or sub-aquatic forms of all four subspecies – though such forms of subsp. *chondrosperma* are not common. Lastly, in areas where there is apparently only one subspecies, as in Portugal, the attempt to apply the habit characters will give '*M. minor*' and '*M. rivularis*' which are, as Sampaio rightly recognized, merely modifications of the one type – here subsp. *intermedia* – to terrestrial or aquatic habitats.

It is not possible to decide how valid is the ecological separation of the subspecies (particularly of ssp. *chondrosperma* from the others) and to what extent the correlated habit characters are purely phenotypic, without extensive study of the plants in the field and in cultivation; but there is little doubt that differences in ecological preference do exist, and that it is therefore possible to use a variety of habit and habitat characters with some degree of success. If we consider the characters, other than those of the seed, which have been used in attempts to define the different types, this will be clearer.

1. The habitat of subsp. *chondrosperma* is generally described as wet, or at least seasonally wet, sandy places. In such a habitat the habit of the plant is more or less tufted, with short erect flowering branches. The aquatic or semi-aquatic habitats favoured by the other subspecies would naturally call for a loose submerged or floating habit.

2. Annual or perennial habit may be expected to show a similar correlation. The typical subsp. *chondrosperma* of sandy soil is, as Necker's name *M. verna* suggests, a spring-flowering annual, whilst aquatic plants would naturally flower later and may normally remain green throughout the winter. This is presumably the basis of the colour differences referred to by some authors – '*M. minor*' is described as yellow-green, whilst '*M. rivularis*' is pure green.

3. The difference between 'terminal' and 'lateral' inflorescences is often mentioned. The short, erect branches of typical ssp. *chondrosperma* terminate in cymes of flowers. The so-called 'lateral' cymes of '*M. rivularis*' arise by the continued vegetative growth of a lateral bud below the inflorescence; this is clearly a reflection of the general vegetative vigour of an aquatic or semi-aquatic plant, and is in no way a fundamental difference.

4. Connate leaf-bases, it is sometimes claimed (? following Gmelin's original description of *M. minor*), distinguish subsp. *chondrosperma*. Again this character seems to be merely an expression of difference in vegetative vigour – the comparatively short, slender stems normally show the opposite leaf-bases in contact, as opposed to the separated leaf-bases of the more vigorous aquatic shoots of '*M. rivularis*.' Quite apart from the difficulty of using such a character, it is very doubtful whether it has any basis other than the obvious modificatory one.

Given this different habitat preference, these vegetative characters, even if shown to be purely phenotypic, would normally serve to distinguish subsp. *chondrosperma* from the other subspecies. Yet herbarium identification relying on habit characters alone may be completely unreliable – aquatic forms of subsp. *chondrosperma*, for example, undoubtedly occur, in Britain and elsewhere.

The comparative descriptions of the subspecies which follow are based on personal observations, and on the descriptions of the seeds given by Lindberg (1901) and Beeby (1909). The details of the cellular structure of the seed-coat, and the shape, size and distribution of the tubercles on it, can be seen either directly under the binocular microscope or, as Lindberg stated, by removing a portion of the coat (easily detachable in subsp. *fontana*, less easily in the others) and studying under low power of the microscope. The vice-comital distribution is given for Britain and is based only on material personally examined. It is clearly very far from complete, but is useful as indicating the difference in British distribution. Records from Ireland are as yet too inadequate to justify publication, and Irish material needs much further study.

(1) subsp. **FONTANA**

M. fontana L. (1753), *Sp. Pl.*, 87, *sensu stricto*.

M. lamprosperma Chamisso (1831), *Linnaea*, 6, 564.

M. rivularis auct., ? C. C. Gmelin.

Ripe seed 1.1 to 1.35 mm., smooth and shining seen under lens; under higher magnification, individual cells of seed-coat easily seen as a reticulate pattern, rather elongated, irregular in size and shape, with slightly convex outer walls; those in rows by keel elongated along row; seed-coat thin, brittle, often, in dried material, broken open. Plant variable in habit, usually looser than subsp. *chondrosperma*, often submerged (var. *boreo-rivularis* Lindb. f.), green or yellow-green. *Habitat*: trickles of water or very wet places, on acid soil or rock only.

Distribution: Circumpolar Arctic and N. Temperate; also in the S. Hemisphere into the Antarctic. Common in Scotland and N. England. V.c.'s: 45, 46, 49, 50, 58, 61, 64, 65, 68, 69, 70, 72, 73, 77, 78, 80, 83, 85-90, 92, 93, 96-98, 100, 104, 105, 107-112.

(2) subsp. **chondrosperma** (Fenzl) comb. nov.

M. fontana var. *chondrosperma* Fenzl (1843), in Ledebour, *Fl. Ross.*, 2, 152.

M. verna Necker (1768), *Delic. Fl. Gallo-Belg.*, 1, 78, nomen illeg., quoad descr.

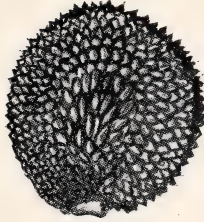
M. minor C. C. Gmelin (1805), *Fl. Bad.*, 1, 301, nomen illeg., quoad descr.

Ripe seed 1.0 to 1.2 mm., dull and entirely covered with rather coarse tubercles as

PLATE 1.



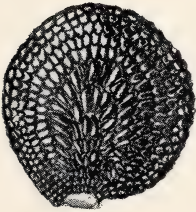
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Seeds of *Montia fontana* (x 25).

1. subsp. *chondrosperma*, Odiham Common, N. Hants., v.c. 12, C. E. Palmer, 1902, Herb. Univ. Oxon.
2. subsp. *intermedia*, rill below County Gate, N. Devon, v.c. 4, W. C. Barton, 1917 (Wats. B. E. C. Distr.) Herb. Univ. Cantab.
3. subsp. *variabilis* (with obvious tubercles by keel), Umberley Brook, Brampton East Moor, Chatsworth, Derby, v.c. 57, P. S. Green, 1950, Herb. Univ. Cantab.
4. subsp. *variabilis* (with very low tubercles by keel), stream, Yewdale, Coniston, N. Lancs., v.c. 69, J. Comber, 1911, Herb. Univ. Cantab.
5. subsp. *fontana*, Loch Tay, Mid Perth, v.c. 88, G. C. Druce, Herb. Univ. Oxon.

seen under lens; under high magnification cells of surface more or less hexagonal, each with a broad, blunt tubercle occupying most of the outer wall of cell (cells in centre of plano-convex surfaces of seed rather larger and somewhat elongated); tubercles finely papillose under microscope (high power). Plant usually tufted, yellowish-green, not submerged, with short erect branches terminating in cymes. *Habitat*: light acid soils, usually sandy or gravelly, with high water table at least in spring; only rarely more or less submerged in water, and then much modified in habit.

Distribution: Central and southern Europe; also Australia (see p. 6). The common, and in some areas the only, subsp. in southern England; rarer in N. England and Scotland. V.c.'s: S, 1-3, 7, 9-12, 14-21, 26-30, 33, 34, 36-38, 40-43, 45, 46, 49, 52, 58, 61-63, 66, 69, 71, 77, 83-85, 95, 105.

(3) subsp. **intermedia** (Beeby) comb. nov.

M. fontana subsp. *minor* var. *intermedia* Beeby (1909), *Ann. Scot. Nat. Hist.*, 104.

M. lusitanica Sampaio (1912), *Ann. Sc. Acad. Polyt. Porto*, 7, (1) 52.

M. limosa Decker (1927), *Verh. Bot. Vereins. Brandenburg*, 69, 57.

M. rivularis, auct. mult., ? C.C. Gmelin.

Ripe seed rather smaller than in the preceding spp., 0.85 to 1.1 mm., finely tuberculate at edge and rather shiny under lens, under higher magnification seen to have (2-) 3-4 (-5) rows of cells on each side of keel bearing small but relatively narrow and high tubercles, one in centre of each cell; tubercles finely papillose under high power of microscope; cell-walls quite obvious, cells rather elongated. Plant usually loose in habit, often more or less aquatic, with long bright green trailing branches bearing apparently axillary cymes only. *Habitat*: as for subsp. *fontana*.

Distribution: W., C. and S. Europe; also Australia (see p. 6). Common in W. England and Wales; rare in Scotland. V.c.'s: S, 1-6, 8-11, 13, 14, 16-22, 24, 27, 30, 35-37, 39-49, 52, 54, 55, 57, 58, 60, 62-64, 66, 69-71, 88, 100.

(4) subsp. **variabilis** subsp. nov.

M. rivularis auct. mult., ? C. C. Gmel.

A subsp. *fontana* differt: semine maturo 0.9—1.1 mm. magis minusve plano minus nitido quam in subsp. *fontana*, oculo valde armato tuberculis minimis varie evolutis saepe humillimis circa carinam praedito, seminibus maturis plantarum simul lectarum saepe conspicue inter se dissimilibus.

Typus in Herb. Univ. Cantab.: v.c. 45, Pembrokeshire; just north of Tedion Mt., at edge of outlet from shallow pool, Martletwy, 22 June 1952, *E. Milne-Redhead*.

Ripe seed 0.9 to 1.1 mm., more or less smooth (under lens) but not so shining as subsp. *fontana*; under higher magnification showing variable development of small usually very low tubercles around keel, the variation often obvious between different ripe seeds of same gathering. Plant usually loose in habit, resembling commonest forms of subsp. *intermedia*, and found in similar habitats.

Distribution: West and Central Europe; elsewhere? Locally common in N. England and Wales, and occurring throughout the area where both subsp. *fontana* and subsp. *intermedia* occur, but in certain districts (e.g. Isle of Man) the common and perhaps the only subspecies. V.c.'s: 1-6, 9, 17, 30, 32, 35, 38-52, 55, 57, 59, 62, 64-66, 69-73, 75-77, 79, 83, 86, 88, 90, 91, 98-100, 108, 110.

The seed sizes given in these descriptions are in each case the range of measurements of 'largest diameter' made on three ripe seeds from each of four British gatherings. The

size differences shown, though insufficient to use as a taxonomic character, are nevertheless consistently, in my experience, to be found; and, so far as subsp. *intermedia* is concerned, support Sampaio's description of the seeds of his *M. lusitanica* as smaller than those of the other species of *Montia* he knew. It would, however, seem that Sampaio's material was somewhat atypical; for it can hardly be claimed, as he did, that the other subspecies have seeds $1\frac{1}{2}$ to 2 times as large as subsp. *intermedia*. Measurements made on seeds in material determined by Sampaio as *M. lusitanica* gave a size range virtually identical with that found for the British material.

NOTE ON AUSTRALIAN MATERIAL

Whilst the common *M. fontana* of the S. Hemisphere is undoubtedly subsp. *fontana*, it is interesting that in Australia both subsp. *chondrosperma* and subsp. *intermedia* seed-types also occur. Of 11 sheets with ripe seed, lent by the National Herbarium, Botanic Gardens, Sydney, no fewer than seven were referable to subsp. *chondrosperma*, and three to subsp. *intermedia*. The remaining gathering, a Tasmanian one, was the expected subsp. *fontana*. This situation is very interesting, and would repay further investigation. Several possibilities suggest themselves; for example, the seed-coat character, so clearly correlated with distributional differences in Europe, may occur more or less sporadically in the Australian populations; or both subsp. *chondrosperma* and *intermedia* may be aliens in the Australian flora.

I am indebted to Mr. D. E. Allen and Mr. J. E. Dandy for help with nomenclature, to Dr. N. Hylander of the University of Uppsala, who originally suggested the investigation to me and has contributed much to it, to Mr. R. Anderson, Curator of the National Herbarium, Sydney and Mr. E. J. McBarron for information and the loan of Australian material, and to Miss C. Lambert for the seed drawings.

SUMMARY

The Linnean species *Montia fontana* is divisible in north-west Europe into four taxa which it is suggested should be given subspecific rank, viz. :—

- (1) subsp. *fontana*, northern in European distribution;
- (2) subsp. *chondrosperma* (Fenzl) comb. nov., southern in European distribution;
- (3) subsp. *intermedia* (Beeby) comb. nov., western in European distribution;
- (4) subsp. *variabilis* subsp. nov., intermediate in seed-coat marking and distribution type between 1 and 3.

The value of characters other than those of the seed-coat is discussed. Vice-comital distribution of the four subspecies in Britain is given, and also some indication of the distribution in Europe, and a note on their occurrence in Australia.

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NUPHAR INTERMEDIA LEDEB., A PRESUMED RELICT HYBRID, IN BRITAIN

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INTRODUCTION

Nuphar intermedia was originally described by Ledebour (1832) from plants obtained from Heiligenzee and Zee von Camby in North Germany. As was implied by the name given it, the species was intended to embrace plants which lay between the generally accepted variation ranges of *N. lutea* (L.) Sm. and *N. pumila* (Timm) DC. Subsequently, Caspary (1870) and other students of the Nymphaeaceae pointed out the similarity between wild plants which had been referred to Ledebour's *N. intermedia* and artificial hybrids



Fig. 1. Scottish and northern English ranges of *N. intermedia* and its presumed parents *N. pumila* and *N. lutea*. *N. intermedia* occurs at open circles, *N. pumila* at black circles and *N. lutea* in shaded vic-counties.

between *N. lutea* and *N. pumila*, and it has since been customary to assume that *N. intermedia* does not in fact represent a pure breeding species but simply an assemblage of natural hybrids. Particular interest attaches to this ascription of a hybrid origin to *N. intermedia* because, in many localities from which this taxon has been reported, one or other, and sometimes both, of the presumed parents are 'missing'. That this is so for certain British stations of *N. intermedia* is apparent from Fig. 1, which shows the Scottish and northern English ranges of the two parents and the presumed hybrid. The distribution of *N. lutea* is shown by vice-counties, those of *N. pumila* and *N. intermedia* by spot marking, the localities indicated being those from which specimens exist in the herbaria of the British Museum (Natural History), the Royal Botanic Gardens of Kew and Edinburgh, and Cambridge University. *N. lutea* is, of course, mainly a lowland plant of lakes, slow rivers and canals, while *N. pumila* today is, for the most part, confined to high-level lakes in mountainous regions, an exception being the remarkable colony which exists in one of the Shropshire meres, a locality first reported by Cox (1855). While many of the colonies of *N. intermedia* occur within the area of overlap of the two presumed parents, one, in Ardnamurchan, is in a vice-county (v.c. 97, Westernness) from which neither has been recorded; and others, in southern Scotland and in Northumberland, are remote from areas where *N. pumila* is known today.

If *N. intermedia* is indeed a hybrid, this persistence outside of the range of its presumed parents is of considerable historic as well as taxonomic interest. The present paper contains a review of the evidence for accepting it as such, as well as some speculation relating to its possible origin in the British stations. Particular attention is paid to the colony in Chartners Lough, Northumberland, where *N. intermedia* exists in a station very distant from the nearest "pure" *N. pumila*. The important work of Caspary in connection with the problem of *N. intermedia* in Continental Europe is also reviewed.

N. intermedia IN CHARTNERS LOUGH, NORTHUMBERLAND

This station for *N. intermedia* was first discovered by Sir John Trevelyan, and placed on record by Winch (1832), in his remarkable flora of Northumberland and Durham, as *N. lutea* var. β *pumila*. From this date Chartners became a classical locality for the plant, featuring in practically all local and national floras in which the genus was treated in any detail. The taxonomic treatments given it differed according to the nomenclature currently in favour :

- N. J. Winch (1832),* "*N. lutea* var. β *pumila*" (collector Sir J. Trevelyan).
- H. C. Watson (1835), "*N. pumila*" (collector Sir W. C. Trevelyan).
- W. J. Hooker (1835), "*N. pumila* (= *N. kalmiana*)" (collector Sir J. Trevelyan).
- H. C. Watson (1847), "*N. pumila* De C." (collector Sir W. C. Trevelyan)
- W. J. Hooker & G. A. W. Arnott (1855), "*N. pumila* De C."
- J. T. Syme (1863), "*N. lutea* Sm. var. β *minor*."
- J. G. Baker & G. R. Tate (1868), "*N. intermedium* Ledeb."
- J. D. Hooker (1884), "*N. luteum* Sm. var. *N. intermedium* Ledeb."
- W. R. Hayward (1892), "*N. luteum* β *N. intermedia* Ledeb."
- J. L. Luckley (1893), "*N. lutea* var. β ."
- C. E. Moss (1920), "*N. pumila* var. *intermedia* Moss."

Winch himself (1832) reported the results of what must be one of the earliest examples of British experimental taxonomy – a transplant experiment on the Chartners plant – in the following words : "Some years since, the least yellow water lily was transplanted from the subalpine moors into the ponds at Wallington, where it now scarcely differs

* Referred to as *N. minima* in a letter dated 26.4.24 from Winch to J. E. Smith (Smith 1832).

from the common water lily; in both varieties, at least I consider them as such, the stigma is entire when young, but becomes toothed as it grows older." H. C. Watson (1847) commented upon this report as follows: "A specimen in my herbarium, from Sir W. C. Trevelyan, appears to confirm this transformation, but Mr. Borrer has lately explained that the Northumberland plant is not *pumila*, but a rather small variety of *N. lutea*. In size of flower and leaf the specimen corresponds more closely with the Highland *N. pumila*; while in the repand margin, the specimen is certainly more like *N. lutea*."

Baker and Tate (1868), whose flora of Northumberland and Durham superseded that of Winch, were also familiar with the Chartners Lough plant and the Wallington transplants. They considered that the plant agreed with the *N. intermedia* of Ledebour, but were led by the absence of *N. pumila* from the vicinity to dismiss the possibility that it could have arisen from the hybridisation of *N. lutea* and *N. pumila*.

Luckley (1893) gave a final report on Sir J. Trevelyan's transplant experiment, contradicting Winch in declaring that the Chartners plant "discovered about 100 years ago by Sir J. Trevelyan, was introduced into a pond at Wallington, where I saw it growing during the lifetime of the late Sir W. C. Trevelyan Bart., without the plant having undergone any change."

The Chartners plant has been assiduously collected by generations of British botanists, and herbarium sheets of it exist in most of the larger herbaria. Three sheets of particular interest are those of material collected by W. C. Trevelyan, the two incorporated in the herbaria of Winch and H. C. Watson, whose comments are quoted above, and another bearing Caspary's signature, dated 1856, declaring the specimen to be *N. kalmiana* of Hooker's "Flora Scotica," or *N. minima* of Syme's "English Botany" (1825). Other interesting sheets are those of material collected by Fraser Robinson in 1905. On one of these, in the British Museum, there is a note which states that *N. intermedia* was the only water lily present in Chartners Lough, where it was "still very abundant," and that the lough itself appeared to show signs of drying out, being about half an acre in extent.

Chartners Lough lies on the Wallington Moors at a height of c. 1,050 ft., about a quarter of a mile from the isolated farm of Chartners. The appearance of the lough today clearly differs little from that when Fraser Robinson's note was written, and the area of open water is still about half an acre. The east bank is overhung by peat hags and evidently erosion is actively in progress here, since the peat is severely undercut. It seems that Chartners, like other small loughs in the neighbourhood, may actually be migrating slowly eastwards (Smythe, 1930). On the west lies a small area of bog containing *Sphagnum recurvum* P. Beauv., *Oxycoccus palustris* Pers., *Polytrichum commune* Hedw., *Carex rostrata* Stokes and *Eriophorum vaginatum* L. At the margin of the lough there is a narrow zone of reedswamp with *Carex rostrata* and *Juncus effusus* L., and *Sphagnum cuspidatum* Hoffm. grows in the water. The greater part of the water surface is covered by *Nuphar* plants. The lough and the neighbouring bog are enclosed by a bank of thick peat, and at a slightly lower level, between the farm and the lough itself, there is a large area of drier bog, much burnt over.

The nearest other locality for a *Nuphar* species to Chartners is at Kimmer near Eglingham, some 15 miles to the north-east, a locality mentioned by Winch for *N. lutea*. In Winch's time there were several other localities for *N. lutea* within 20 miles of Chartners, e.g. Wide Haugh near Dilston (18 miles S.S.W.), Prestwick Carr (18 miles S.S.E.) and Sewing Shields (18 miles S.W.). *N. lutea* is now extinct in many of these localities due to water pollution or drainage.

The nearest stations for *N. pumila* today are in Stirlingshire and W. Perthshire, some 85-90 miles to the north-west. *N. intermedia* is recorded in Dumfriesshire and Lanarkshire, some 65 miles to the west.

MORPHOLOGICAL COMPARISONS BETWEEN *N. intermedia*, *N. lutea* AND *N. pumila*

For the purpose of a morphological comparison of *N. intermedia* with its presumed parents a random collection of 30 flowers has been taken from the Chartners colony. This has been compared with samples of *N. lutea* from the following twelve localities (L. 1-12):

1. Royal Canal, nr. Ballycormack, Co. Longford, v.c. H 24.
2. Loch Bannow, Lanesborough, Co. Longford, v.c. H 24.
3. Lough Craiggamore, W. Galway, v.c. H 16.
4. R. Thames at Cookham, Berkshire, v.c. 22.
5. Lode near Wicken Fen, Cambridgeshire, v.c. 29.
6. Lode near R. Ant, Sutton Broad, E. Norfolk, v.c. 27.
7. Ellesmere, Shropshire, v.c. 40.
8. Small lake in Tregaron Bog, Cardiganshire, v.c. 46.
9. Esthwaite Water, N. Lancashire, v.c. 69.
10. Loughrigg Tarn, Westmorland, v.c. 69.
11. Grasmere, Westmorland, v.c. 69.
12. Monkhill Lough, near Carlisle, Cumberland, v.c. 70.

and of *N. pumila* from Lochanovie, Easterness, v.c. 96 (P 1), and Shropshire, v.c. 40 (P 2).

In Table 1, in which the biometrical data for the three taxa are compared, the *N. lutea* samples are aggregated so that the information given may be taken to be representative of a general lowland sample of this species. The data for the *N. pumila* samples are given separately for the floral characters (except for petal length) so that comparison may be made between the population from Lochanovie and the interesting isolated Shropshire colony, both of which are regarded as being typical *N. pumila*. The Avinlochan colony (N. of Aviemore, Inverness, v.c. 95—P 3), discussed further below, is possibly itself affected by hybridisation, and the data for it have not been included in the *N. pumila* aggregate.

TABLE 1

Meristic and size data for floral characters in British *Nuphar* taxa. For localities see text. (All size measurements in mm.)

Taxon sample	Sepal		Petal		Carpel	
	length	width	number	length	number	diameter
<i>N. pumila</i> agg. (P1 + P2)	20.13 $\pm$ 0.24	12.54 $\pm$ 0.20	11.42 $\pm$ 0.17	4.74 $\pm$ 0.11	9.42 $\pm$ 0.11	7.96 $\pm$ 0.14
P1	20.77 $\pm$ 0.36	13.20 $\pm$ 0.22	11.63 $\pm$ 0.21		9.26 $\pm$ 0.15	7.88 $\pm$ 0.19
P2	19.56 $\pm$ 0.31	12.14 $\pm$ 0.33	10.86 $\pm$ 0.13		9.54 $\pm$ 0.16	8.36 $\pm$ 0.15
P3(Avinlochan)	23.54 $\pm$ 0.44	13.45 $\pm$ 0.43	10.56 $\pm$ 0.41	5.00 $\pm$ 0.13	10.90 $\pm$ 0.20	10.11 $\pm$ 0.23
<i>N. intermedia</i>	25.23 $\pm$ 0.59	19.80 $\pm$ 0.46	9.82 $\pm$ 0.25	8.22 $\pm$ 0.34	11.58 $\pm$ 0.18	9.20 $\pm$ 0.18
<i>N. lutea</i> agg. (L1 — 12)	33.76 $\pm$ 0.77	31.70 $\pm$ 1.14	15.11 $\pm$ 0.22	15.12 $\pm$ 0.25	15.78 $\pm$ 0.19	12.40 $\pm$ 0.22

FLORAL CHARACTERS

Both meristic and size characters have been compared, the dimensions selected in the latter case being those which are most readily and consistently assessable, viz. maximum length and width of largest sepal, length of largest petal and diameter of stigmatic disc. The meristic characters are petal and carpel number.

(1) *Sepals*. The sample data of Table 1 for dimensions of largest sepal show that the two *N. pumila* samples hardly differ significantly for this character ($p \approx .04$). The Avinlochan population evidently has somewhat longer sepals, while in the Chartners population of *N. intermedia*, the average sepal length is some 25 per cent greater and the average sepal width about 50 per cent greater than in *N. pumila*. Clearly these figures also indicate a shape difference, which is illustrated in Fig. 2. The sepals of *N. lutea* are rounded (Fig. 2a), those of *N. pumila* obovate (Fig. 2d) and those of *N. intermedia* intermediate in shape as well as in size (Fig. 2b). Characteristically all three possess five sepals. There is, however, some variation in this feature, as can be seen from Table 2.

TABLE 2

Distribution of sepal number in British *Nuphar* taxa. Percentage representation in each class.

Taxon	No. of sepals			
	4	5	6	7
<i>N. pumila</i> (P1 + P2)	3.46	93.10	1.72	1.72
<i>N. intermedia</i> (Chartners)	—	89.18	—	10.82
<i>N. lutea</i> (L1 — 12)	—	95.73	4.27	—

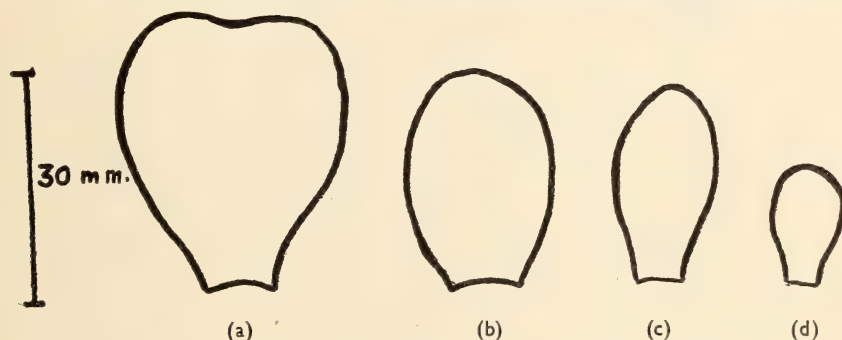


Fig. 2. Characteristic sepal shapes in British *Nuphar* taxa. (a) *N. lutea* from Ellesmere; (b) *N. intermedia* from Chartners Lough; (c) "introgressed" *N. pumila* from Avinlochan and (d) *N. pumila* from Lochanovie.

(2) *Petals*. The size relationship apparent between the three taxa in sepal length holds also in petal length, as may be seen from the data for this character given in Table 1, except that proportionately the petals of *N. intermedia* exceed those of *N. pumila* to a greater extent. Characteristic shapes are illustrated in Fig. 3.



Fig. 3. Characteristic petal shapes in British *Nuphar* taxa. Circles mark the position of the nectaries. (a) *N. lutea*; (b) *N. intermedia*; (c) "introgressed" *N. pumila*; and (d) *N. pumila*. Sources of material as in Fig. 2.

The sample data of Table 1 for petal number would seem to suggest that the three taxa stand in a different relationship, since the mean number of petals for *N. intermedia* is, statistically speaking, significantly less than in the *N. pumila* aggregate. However, as will be seen from the data of Caspary given in Table 6, in certain populations of continental *N. intermedia* the average petal number may actually exceed the average number found in British *N. lutea*, a matter discussed further below.

(3) *Stamens*. The variation in stamen shape has been observed by several authors, e.g. Syme (1863) and Moss (1920). Thus, according to Syme, in *N. pumila* the anthers are not more than one and a half times as long as broad. Koch (1843) stated that this feature, among others, differentiates *N. pumila* from *N. spenneriana* Gaudin, in which the anthers are said to be four times as long as broad. Planchon (1853), however, believed

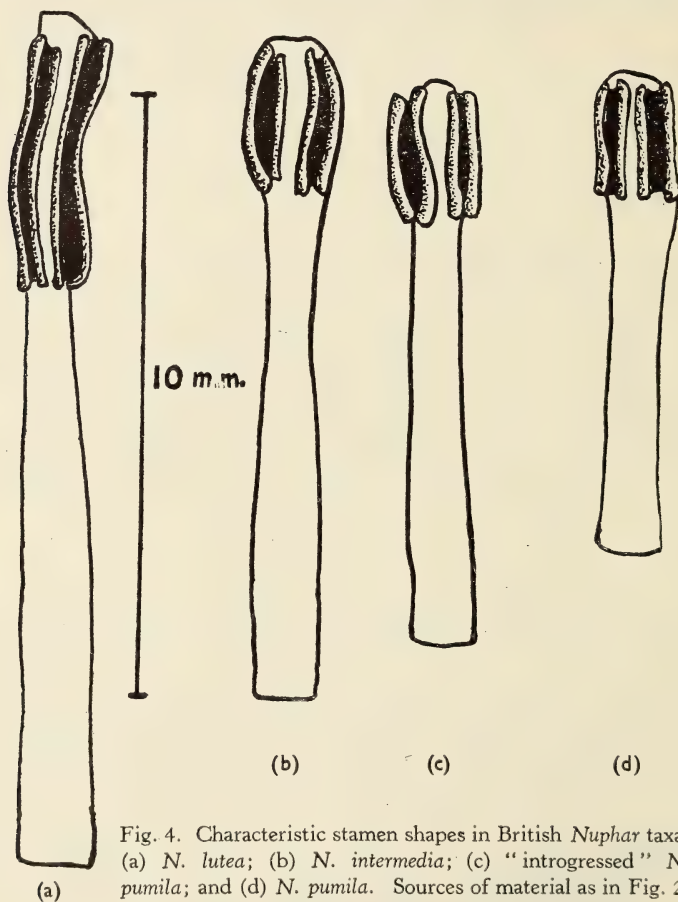


Fig. 4. Characteristic stamen shapes in British *Nuphar* taxa. (a) *N. lutea*; (b) *N. intermedia*; (c) "introgressed" *N. pumila*; and (d) *N. pumila*. Sources of material as in Fig. 2.

the character of anther length to be variable in *N. pumila*, ranging from oblong (four times as long as broad) to almost square. Planchon noted that he had seen specimens described as *N. pumila* from Scotland and America with elongated anthers. Moss (1920) used anther shape as a discriminating character in dealing with *N. lutea* and *N. pumila*, stating that the anthers in the former were usually four times as long as broad, and in the latter about twice as long as broad.

In the *N. pumila* from Lochanovie and Shropshire the anthers have a squarish form (Fig. 4d) whereas those of *N. lutea* in all the British populations examined are considerably elongated (Fig. 4a). Again *N. intermedia* is intermediate in this character (Fig. 4b). The

anther shape in the Avinlochan colony (Fig. 4c) is somewhat elongated compared with normal *N. pumila*, approaching *N. intermedia* in this character. It is possible that the Scottish plants with elongated anthers seen by Planchon came from this locality.

Statistical data for stamen number have not been obtained from all the *Nuphar* colonies investigated, but the counts that have been made suggest a mean stamen number for *N. lutea* of c. 105, for *N. intermedia* of c. 66 and for *N. pumila* of c. 52.

(4) *Pistils*. In the dimensions of the stigmatic disc the size relationships of the three taxa parallel those in sepal and petal length, with *N. intermedia* again intermediate between *N. lutea* and *N. pumila*. The Avinlochan colony is quite anomalous in this character; the mean value given in Table 1 refers to maximum diameter and this is high, owing to a certain amount of ovary fasciation found in many individuals of this colony (Fig. 6e).

Carpel number is an important diagnostic in *Nuphar*. The two *N. pumila* samples, P 1 and P 2, are in close agreement in this character, and the *N. intermedia* is again intermediate between these and the *N. lutea* aggregate sample. The relationships of the three are shown graphically in Fig. 5. As a result of fasciation in individuals of the Avinlochan sample (see Fig. 6e), the mean carpel number is greater here than in the other two *N. pumila* samples. The frequency distribution of carpel number in this sample is compared with that in the *N. intermedia* and *N. pumila* samples in Fig. 7.

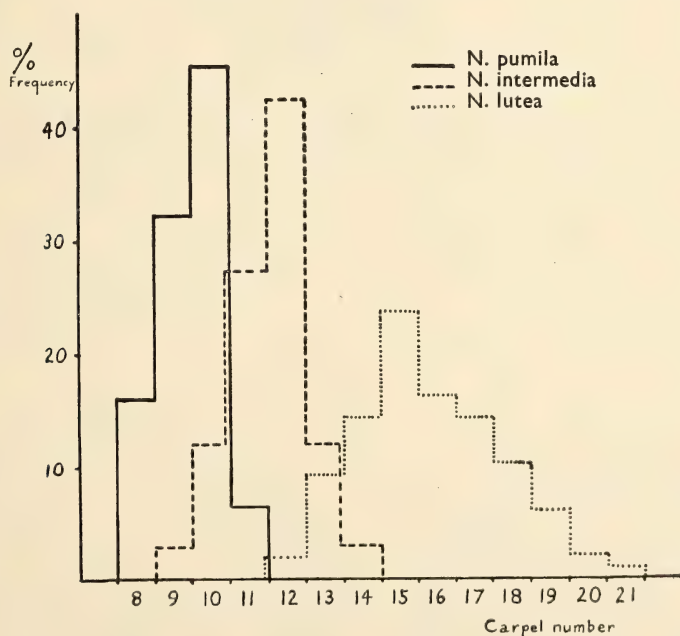


Fig. 5. Frequency histograms of carpel number in British *Nuphar* taxa.

Particularly in *N. lutea*, the stigmatic rays are singularly variable in form. This feature seems to have been overlooked previously by European taxonomists, although in N. America, where the genus is highly polymorphic, Miller and Standley (1912) have emphasized its importance in the diagnoses of some seventeen species. The stigmatic discs illustrated in Fig. 6a-c give some indication of the variability in this character in *N. lutea*; the individuals from which drawings were made were derived from Tregaron and Ellesmere. The rays may be linear and widely spaced, ovate, or so broad as to

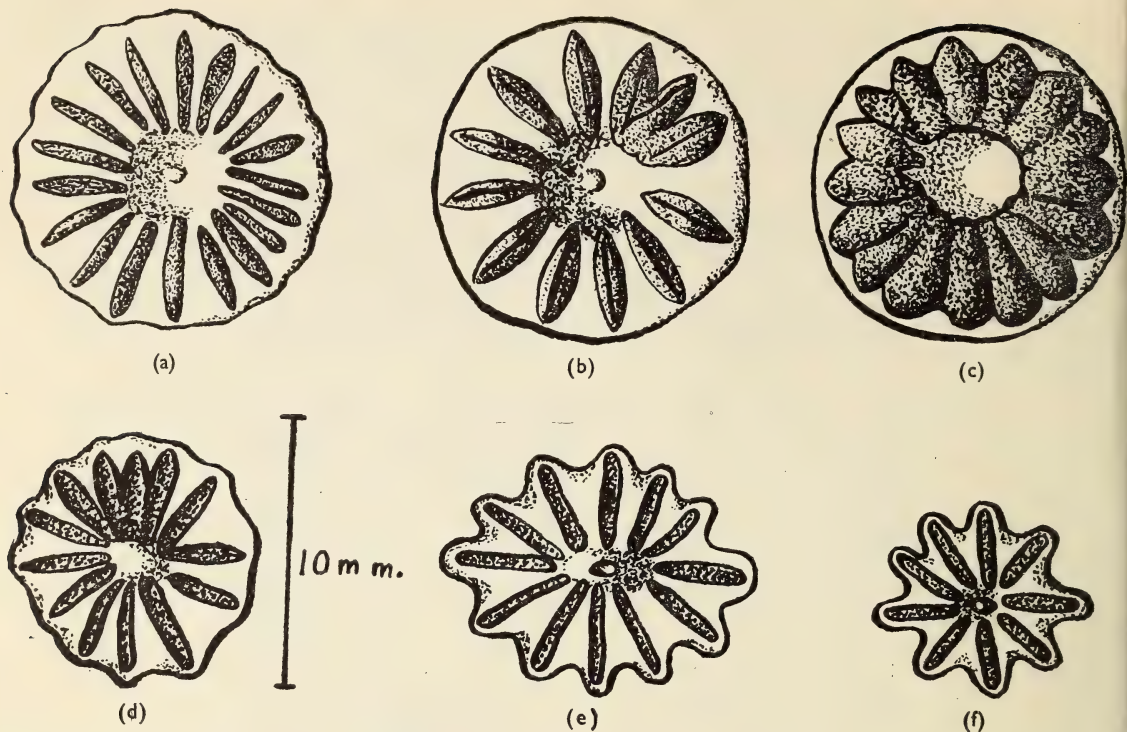


Fig. 6. Characteristic forms of stigmatic disc in British *Nuphar* taxa. (a)-(c) *N. lutea*; (d) *N. intermedia*; (e) "introgressed" *N. pumila*; and (f) *N. pumila*. *N. lutea* from Ellesmere and Tregaron, other sources of material as in Fig. 2.

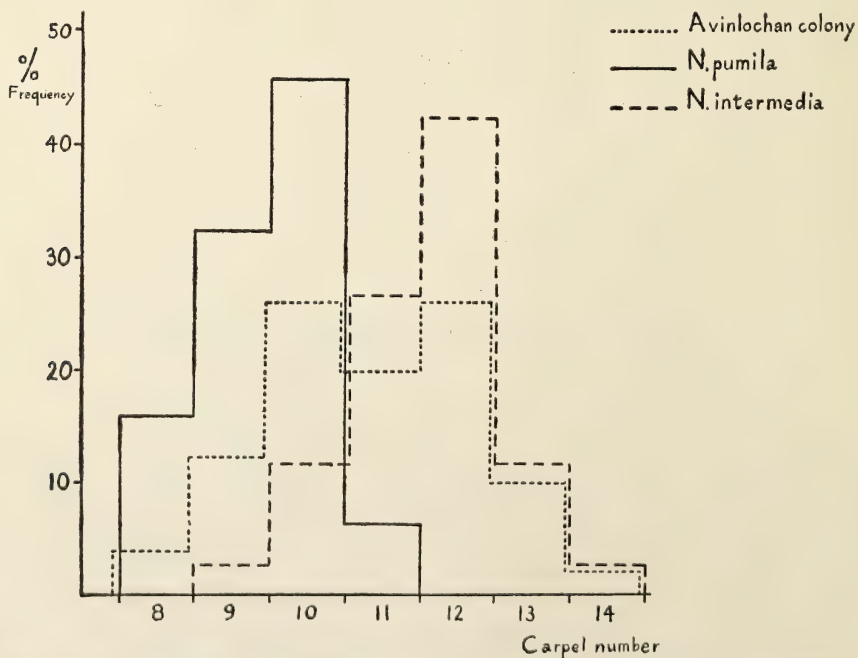


Fig. 7. Frequency histograms of "introgressed" *N. pumila*, *N. pumila* and *N. intermedia*.

coalesce and present a continuous ring of stigmatic surface on the disc. The rays themselves may be smooth or more or less furrowed, and their prominence above the surface of the stigmatic disc is likewise variable. The central depression of the disc may be shallow or deep, and with or without an umbo. The margin of the disc is characteristically entire, a key "qualitative" feature distinguishing *N. lutea* and *N. pumila*; occasionally, however, it is somewhat sinuous in *N. lutea*, as is found, for example, in some plants in the population in Sutton Broad. In Britain, at least, *N. pumila* appears to be not nearly so variable in the character of the stigmatic disc; the margin is uniformly deeply scalloped and the stigmatic rays are linear. The axile process, however, may or may not be developed.

In *N. intermedia* the disc has a distinctly undulate margin (Fig. 6d) and so is intermediate in this character between *N. lutea* and *N. pumila*. In the Chartners Lough colony the stigmatic rays, although greater in number than in *N. pumila*, are similar in

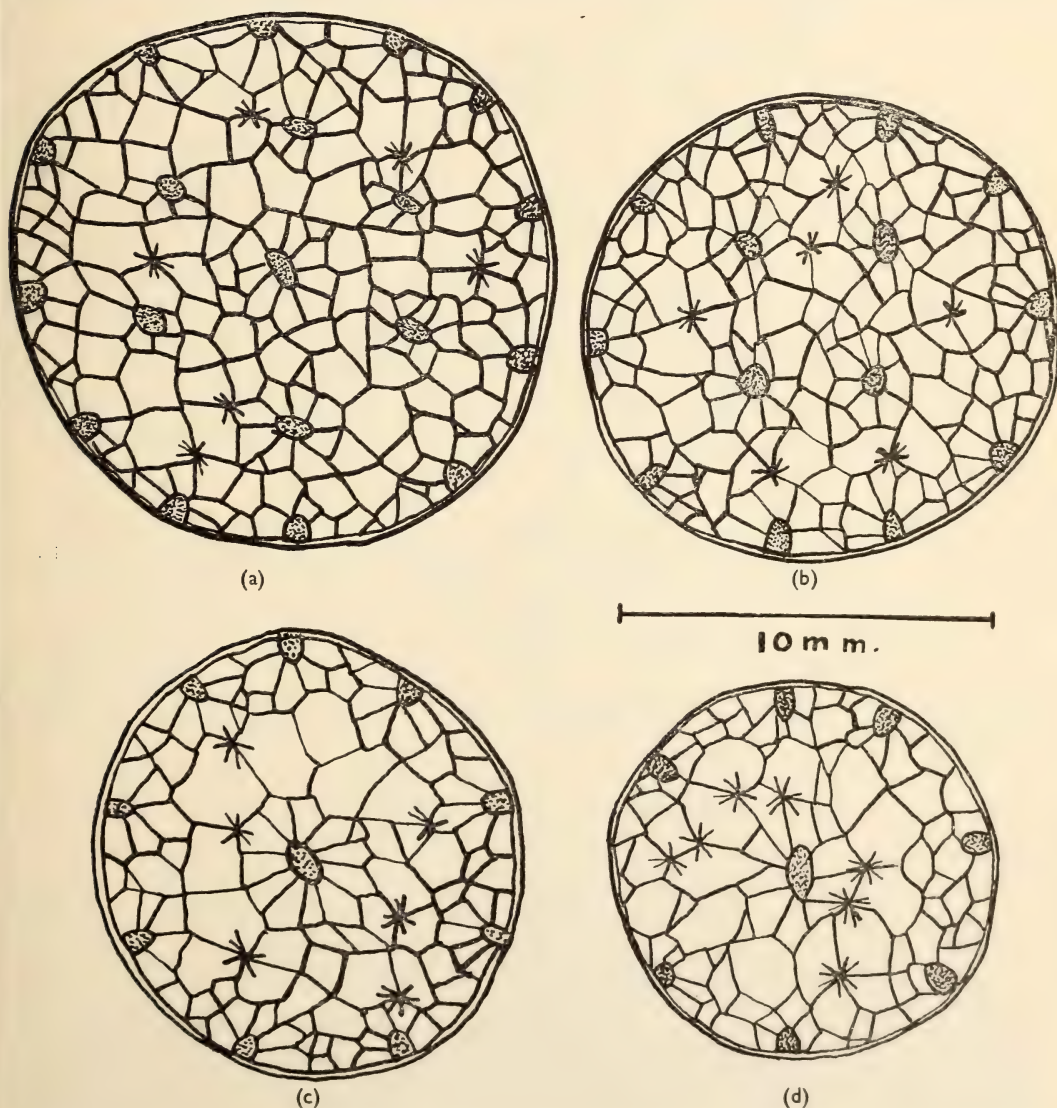


Fig. 8. Characteristic forms of peduncle anatomy in British *Nuphar* taxa. (a) *N. lutea*; (b) *N. intermedia*; (c) "introgressed" *N. pumila*; and (d) *N. pumila*. Sources of material as in Fig. 2.

form; but in some individuals there is a tendency for the rays to coalesce, as in some forms of *N. lutea*.

(5) *Peduncles*. The flower stalk in *N. lutea* is usually 50-70 per cent thicker than in *N. pumila*, and this difference in thickness is correlated with a difference in number of vascular bundles. In *N. lutea* these are usually distributed in an outer ring and an inner ring with a solitary central bundle (Fig. 8a). In *N. pumila* the central bundle and the outer ring are present, but the inner ring is missing (Fig. 8d). In the peduncles of *N. intermedia* the distribution of the bundles is much more variable, a common arrangement being an outer ring and a central group of four (Fig. 8b), so, in this character again, the condition is intermediate. In the Avinlochan colony the central bundle is retained, but there are a greater number of vascular bundles in the outer ring, compared with *N. pumila* (Fig. 8c).

VEGETATIVE CHARACTERS

Sample data for leaf size are tabulated in Table 3, the dimensions given being maximum length and width of leaf. Again *N. intermedia* lies between *N. lutea* and *N. pumila*, approaching more closely the latter. This relationship is present also in thickness of petiole and, as with the peduncle, this is reflected in the ratio of the number of vascular bundles present in the petioles, the ranges in the plants examined being from 17-23 in *N. lutea* ($M = 19.81 \pm 0.41$), 8-13 in *N. intermedia*, 7-12 in the Avinlochan colony and 6-10 in *N. pumila*. The number of vascular bundles is constant from petiole base to petiole apex. There is also some difference in the shape of the petiole in cross-section, a feature mentioned in most descriptions of the species. That of *N. pumila* is elliptical or lens-shaped (Fig. 9d) and that of *N. lutea* is trigonous (Fig. 9a); again *N. intermedia* lies in between the two in this feature (Fig. 9b). The number of lateral veins in the leaf ranges from 23-28 ($M = 25.33 \pm 0.35$) in *N. lutea* and 11-18 in *N. pumila* (for the aggregate sample, $P1 + P2$, $M = 14.50 \pm 0.39$). In the *N. intermedia* samples studied the range was 15-22 ($M = 18.08 \pm 0.53$).

TABLE 3
Leaf characters of European *Nuphar* taxa (all size measurements in cm.).

Taxon	No. of lateral veins	Leaf	
		Length	Width
<i>N. pumila</i>			
P. a	14.50 ± 0.39	12.60 ± 0.44	9.60 ± 0.36
P. b	13.86 ± 0.65	9.87 ± 0.22	7.38 ± 0.16
P. c	12.00 ± 0.36	9.89 ± 0.15	7.24 ± 0.15
<i>N. intermedia</i>			
I. a	18.08 ± 0.53	14.80 ± 0.72	10.90 ± 0.50
I. b	16.91 ± 0.73	11.63 ± 0.56	9.28 ± 0.34
I. c	14.33 ± 0.69	11.10 ± 0.21	10.09 ± 0.44
<i>N. lutea</i>			
L. a	25.33 ± 0.35	29.50 ± 0.93	26.16 ± 1.02
L. b	22.86 ± 0.64	23.70 ± 1.46	18.60 ± 1.23

Sources of material : a - living British (for localities see text); b - herbarium British (vice-county sources for *N. pumila* : 40, 86-88, 92, 96-98, 109; for *N. intermedia* 68, 72, 77, 83, 85, 88, 89, 97, 109; and for *N. lutea* 6-9, 11-23, 25-39, 33, 37, 40, 41, 43, 48, 59, 70-72, 81, 86, 89, 98); c - herbarium continental European (sources of *N. pumila* and *N. intermedia* include Scandinavia, the Alps and neighbouring mountain systems; *N. lutea* from Scandinavia, central and western Europe, N.W. Russia and the Balkans).

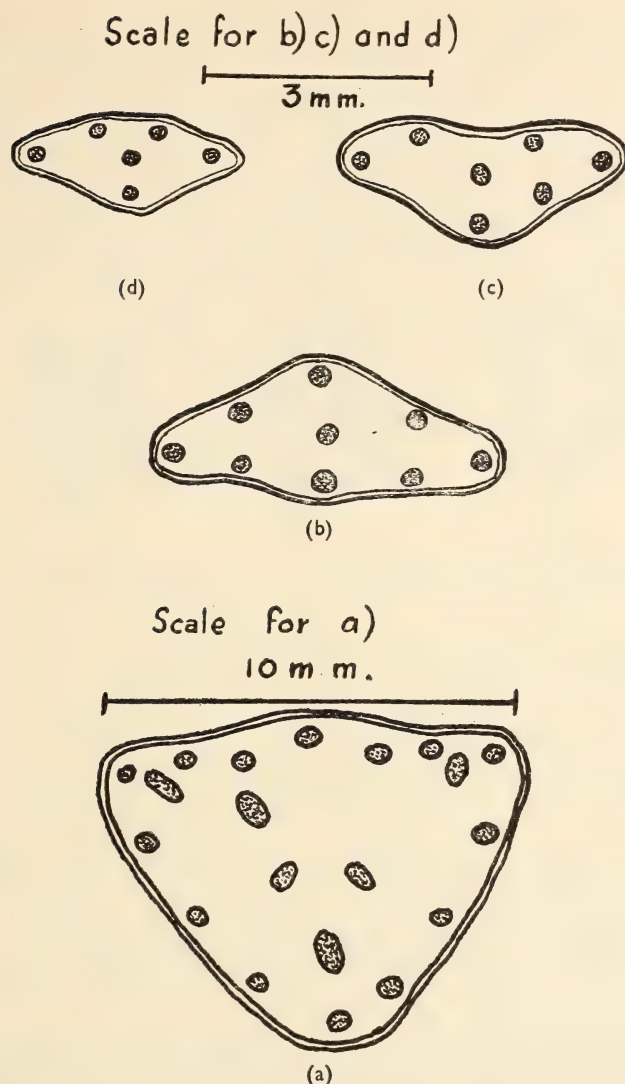


Fig. 9. Characteristic forms of petiole anatomy in British *Nuphar* taxa. (a) *N. lutea*; (b) *N. intermedia*; (c) "introgressed" *N. pumila*; and (d) *N. pumila*. Sources of material as in Fig. 2.

CHROMOSOME NUMBER AND FERTILITY OF THE CHARTNERS LOUGH PLANTS

The somatic chromosome number of *N. intermedia* was determined from root-tip material of plants from Chartners Lough collected in July and fixed in Nawashin's modification of Langlet's fluid. In all of the plants examined $2n = 34$. This is the first count reported for *N. intermedia*. The number $2n = 34$ is the same as that determined for both *N. lutea* and *N. pumila* from continental material (Langlet and Söderberg, 1927) and is the same as that observed in British plants of *N. lutea* from Ellesmere, Esthwaite Water and Monkhill Lough, and of *N. pumila* from Shropshire, examined cytologically during the present studies. A mitotic metaphase plate from *N. intermedia* is illustrated in Fig. 10b, together with ones from *N. lutea* (Fig. 10a) and *N. pumila* (Fig. 10c), all from British sources. There appear to be no characteristics of chromosome size or morphology which would serve in any way to discriminate the three.

It has unfortunately not yet been possible to observe the course of meiosis in *N. intermedia*. That this is irregular is suggested by the low pollen fertility of the Chartners Lough plants, c. 15 per cent. This contrasts with a pollen fertility of c. 97 per cent in *N. lutea* (plants from Ellesmere), c. 85 per cent in the Avinlochan colony and c. 95 per cent in *N. pumila* (plants from Lochanovie). The average diameter of the fraction of perfect grains produced by the Chartners Lough *N. intermedia* was $45.57 \mu \pm 0.41$ and this is not significantly different from the pollen diameter of *N. lutea* ($44.9 \mu \pm 0.30$) although significantly greater than that of the pollen of *N. pumila* ($42.87 \mu \pm 0.34$).

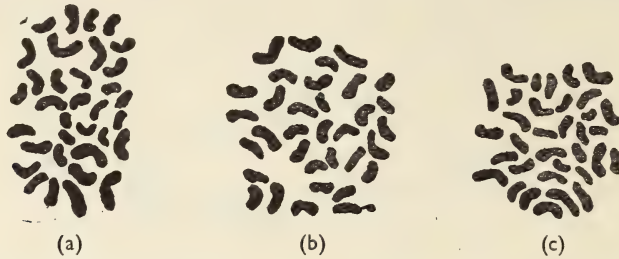


Fig. 10. Somatic chromosomes in British *Nuphar* taxa. (a) *N. lutea* from Esthwaite Water; (b) *N. intermedia* from Chartners Lough; and (c) *N. pumila* from Shropshire ($\times$ c. 3,000).

Infertility is equally well marked on the female side in *N. intermedia*. Whereas ripening of the fruit proceeds quite normally, a high percentage (c. 80 per cent) of ovules aborts, so that the loculi of the ripe fruit are very irregularly filled. Among the seeds which do set there is considerable variability in size (range in maximum length : 2.00-5.00 mm., $M = 4.06 \pm 0.08$). The range of variation is smaller in both *N. lutea* (range 3.50-5.00 mm., $M = 4.96 \pm 0.05$) and in *N. pumila* (range 2.00-4.00 mm., $M = 3.32 \pm 0.05$).

Attempts to germinate *N. intermedia* seed were made during 1952. Fruits from Chartners Lough were allowed to rot in water and the seeds collected immediately they were released. Germination actually began in these *N. intermedia* seeds more rapidly than those of *N. lutea* or *N. pumila* collected and ripened in the same season. Of a total of 102 seeds, 7 germinated within two months of release and initial growth was vigorous.

N. intermedia ELSEWHERE IN THE BRITISH ISLES : THE EVIDENCE OF HERBARIUM MATERIAL

To supplement the study of *N. intermedia* in Chartners Lough twenty specimens of British plants referred to *N. intermedia* preserved in various herbaria have been examined. The localities from which these were collected are those indicated in Fig. 1. These herbarium specimens may be taken to represent a fairly random sample from the taxonomic unit "*N. intermedia*" as it has been interpreted by British botanists. In Table 4 the

TABLE 4

Meristic and size data for floral characters in British *Nuphar* taxa (ex herbariis; localities as in Table 3).

Taxon	Sepal		Carpel		Peduncle
	length	width	number	diameter	diameter
<i>N. pumila</i>	16.77 ± 0.28	10.52 ± 0.18	9.53 ± 0.29	5.62 ± 0.26	3.86 ± 0.09
<i>N. intermedia</i>	19.09 ± 0.22	15.11 ± 0.71	10.53 ± 0.36	6.29 ± 0.19	4.67 ± 0.27
<i>N. lutea</i>	29.16 ± 0.57	23.69 ± 0.70	15.58 ± 0.30	10.31 ± 0.25	6.33 ± 0.21

(All size measurements in mm.)

data obtained from them are compared with equivalent data derived from 105 specimens of British *N. lutea* and 58 specimens of British *N. pumila*. Naturally not all of the herbarium specimens have been equally favourable for the assessment of the selected attributes, but in no case do the means of Table 4 refer to less than 15 individuals for *N. intermedia*, 16 for *N. pumila* and 51 for *N. lutea*.

Direct comparison between the data for Table 4 and those of Table 1 is not permissible except in the case of carpel number, because of the considerable shrinkage resultant from drying in herbarium specimens, which ranges from 20-30 per cent. However, it is evident that the size relationships revealed by the herbarium samples of the three taxa are closely similar to those indicated by the fresh samples, the proportional differences in sepal size being almost identical (see Fig. 12). The same is true also of peduncle and carpel diameter. The correspondence of carpel number (a feature not, of course, affected by drying) between the herbarium samples and the fresh ones is quite remarkably close for *N. lutea* and *N. pumila* (Fig. 11). The difference between the means for carpel number of the herbarium and fresh samples of *N. intermedia* (1.16) is quite small, although just significant statistically ($p = .04$).

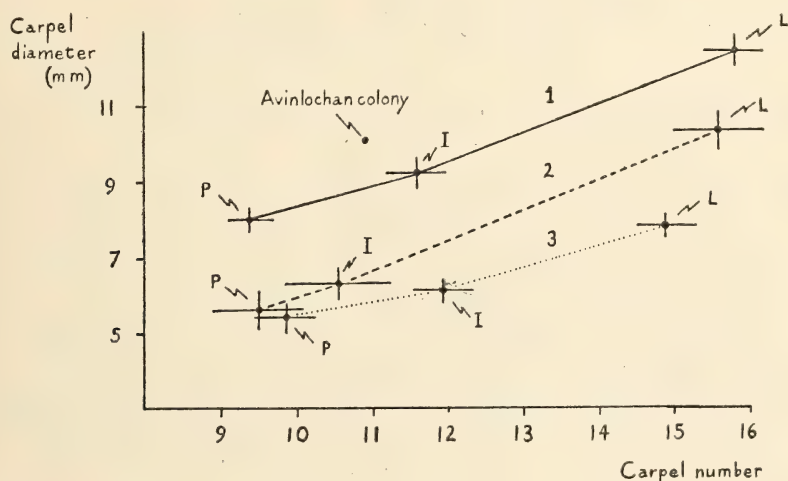


Fig. 11. The relation of carpel number to carpel diameter in European *Nuphar* taxa. Series 1 from living British plants; Series 2 from British plants *ex herbariis*; and Series 3 from continental plants *ex herbariis*. P = *N. pumila*; I = *N. intermedia*; and L = *N. lutea*. The means of each sample are inserted, and distances corresponding to twice the standard error are indicated either side of the mean. The Avinlochan colony ("introgressed" *N. pumila*) is indicated separately.

N. intermedia IN CONTINENTAL EUROPE

As with material from British sources, the specimens of the three *Nuphar* taxa from continental localities in the British Museum and Kew herbaria have been employed as samples for the purpose of a biometrical study. The numbers of plants examined were 99 for *N. lutea*, 92 for *N. pumila* and 87 for *N. intermedia*. Data from these samples comparable with those of Table 4 for British samples are given in Table 5. The same size relationship prevails between the three taxa as in the British fresh and British herbarium material (Figs. 11 and 12). The continental and British herbarium samples of *N. pumila* and *N. intermedia* are closely similar in size, carpel number, ovary diameter and peduncle diameter, none of the differences being statistically significant. In *N. lutea*, the mean values of sepal length and width for the continental herbarium sample are slightly smaller than for the British herbarium sample. The carpel numbers are

not significantly different, although the difference in the diameter of the stigmatic disc is certainly so.

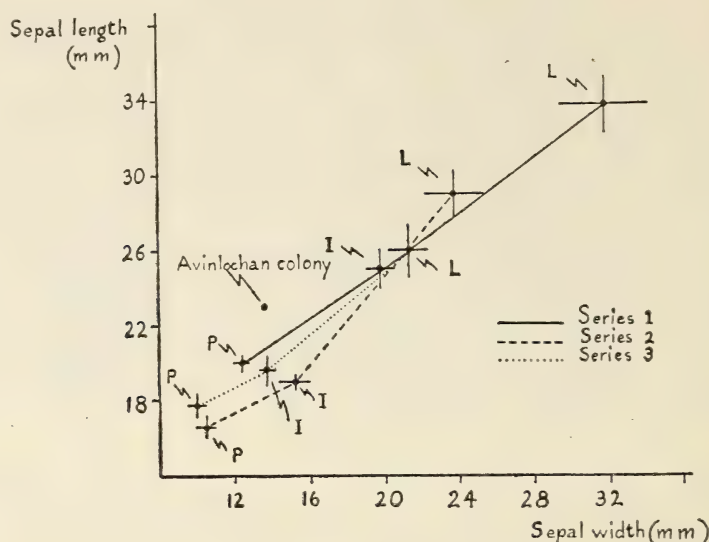


Fig. 12. The relation of sepal length to sepal width in European *Nuphar* taxa. Code as in Fig. 11.

TABLE 5

Meristic and size data for floral characters in Continental European *Nuphar* taxa (*ex herbariis*; localities as in Table 3).

Taxon	Sepal		Petal	Carpel		Peduncle
	length	width	length	number	diameter	diameter
<i>N. pumila</i>	17.93 $\pm$ 0.31	10.02 $\pm$ 0.21	5.85 $\pm$ 0.39	9.85 $\pm$ 0.22	5.43 $\pm$ 0.21	3.48 $\pm$ 0.08
<i>N. intermedia</i>	19.63 $\pm$ 0.37	13.74 $\pm$ 0.27	7.27 $\pm$ 0.22	11.96 $\pm$ 0.20	6.07 $\pm$ 0.13	3.84 $\pm$ 0.09
<i>N. lutea</i>	25.91 $\pm$ 0.63	21.50 $\pm$ 0.50	14.30 $\pm$ 0.39	14.93 $\pm$ 0.20	7.85 $\pm$ 0.17	6.05 $\pm$ 0.23

(All size measurements in mm.).

Robert Caspary, who conducted extensive researches on the Nymphaeaceae in the period 1855 to 1891, accumulated a very large amount of statistical data on both *Nuphar* and *Nymphaea* in Europe, and must be considered to be the first botanist to recognise the importance of population studies in investigating the variability of these genera. The counts of petal number, stamen number and carpel number which he published (1870) for plants of *N. pumila* and *N. intermedia* have been condensed in the data given in Table 6. The "*N. pumila* aggregate" in Table 6 refers to collections of the species from six stations in the Vosges and Black Forest. The *N. intermedia* sample was also derived from localities in these areas. For *N. lutea* Caspary reports only observed ranges and these are given (together with their mid-points) in Table 6 for comparison. Caspary's *N. pumila* aggregate differs little in carpel and petal number from the British *N. pumila* aggregate, for which data are given in Table 1. While his data suggest a reasonable correspondence in carpel number between the *N. intermedia* samples he examined and that of the Chartners Lough sample, there is clearly a considerable difference in petal number, the mean in Caspary's sample being almost twice that of the Chartners sample, and actually greater than that for the aggregate British *N. lutea* sample, for which data are

given in Table 1. It is also notable that in *N. lutea* the range quoted by Caspary for continental plants (13-26) differs in the same direction from the British range of 11-20 in the aggregate sample (83 plants).

TABLE 6

Meristic data for floral parts from Continental European *Nuphar* taxa (data after Caspary 1870).

Taxon	Petal number	Stamen number	Carpel number	Total number floral parts
<i>N. pumila</i>	10.71 $\pm$ 0.16	46.38 $\pm$ 1.03	10.03 $\pm$ 0.05	69.08 $\pm$ 1.42
<i>N. intermedia</i>	18.16 $\pm$ 0.85	94.51 $\pm$ 2.20	13.18 $\pm$ 0.31	130.60 $\pm$ 2.87
<i>N. lutea</i>				
(a) midpoint	19.50	146.50	17.00	190.00
(b) range	13-26	86-207	10-24	130-250

In addition to his data on meristic variation in *Nuphar*, Caspary (1869, 1879) provided much information on seed and pollen fertility. For plants referred to *N. intermedia* he reported a range of pollen fertilities from 14 to 71 per cent, these being in contrast with *N. lutea* and *N. pumila*, in neither of which did he obtain plants with pollen fertility lower than 95 per cent. Seed set was correspondingly lower in the *N. intermedia* examined by Caspary, but was surprisingly variable, the mean number in colonies observed by him ranging from 5.6 to 41.7. This compares with a range of 32.7-135.1 mean numbers per fruit for *N. pumila* colonies and 93.8-418.1 for *N. lutea* colonies.

One of Caspary's (1869, 1870) most important contributions to the understanding of *N. intermedia* was to cross *N. lutea* and *N. pumila* reciprocally and bring the F_1 hybrids to flower in cultivation. Morphological comparisons of these hybrids with wild *N. intermedia* convinced him that the latter had originated in the same manner in nature. Pollen counts in the artificial hybrids showed 86.3 per cent malformed pollen (*N. lutea* female parent) and 85.6 per cent (*N. pumila* female parent). The corresponding average numbers of seeds per fruit were 14.9 and 18.4.

DISCUSSION

The status of the presumed parents

The evidence presented above suggests that while both *N. lutea* and *N. pumila* may show considerable local variability, they form reasonably homogeneous units throughout their European areas and do not intergrade to any appreciable extent. The geographical distributions of the two are at present not completely mutually exclusive, but, generally speaking, *N. pumila* has a more northerly range than *N. lutea*, and also tends to replace *N. lutea* in mountainous regions (Meusel, 1943). However, geographical and ecological isolation cannot be looked upon as the only, or even the main, factors holding the two species apart today, since, as we have seen, the experiments of Caspary, in which he crossed reciprocally typical representatives of the two, showed that, while they are inter-fertile enough to produce a vigorous F_1 , the F_1 itself is of relatively low fertility. There is thus a partial inherent barrier to gene exchange in spite of their possession of the same chromosome number, and *N. lutea* and *N. pumila* must be looked upon as ecospecies in Turesson's terminology. It remains probable, however, that the original differentiation of the two species from their common ancestor took place under conditions of spatial isolation, and that the present distributional trends - *N. pumila* towards the north and *N. lutea* more southerly - in Europe reflect former complete vicariousness. There is no

evidence from which we can deduce the period when this geographical isolation was last complete, but there is little reason to believe that it could have been so during the post-glacial period. Differentiation of the two ecospecies may have actually been completed by late Tertiary, or it may perhaps have taken place during an interglacial. In any case, it is likely that during one or more of the Pleistocene glacial maxima the areas of both were severely compressed in southern or eastern refugia, possibly with some commingling of the populations. The subsequent immigration in the post-glacial into the formerly glaciated area would then see a "sorting out" of the ecospecies, *N. pumila* penetrating further north and becoming extinct in the south except where local microclimates favoured its persistence. The much-studied *N. pumila* populations of the Vosges and other central European mountains are no doubt relics of this nature. A similar history may be postulated for the remarkable southern colonies in the British Isles, those in Merioneth and Shropshire, if indeed the latter has not resulted from a relatively recent human introduction.

The status of N. intermedia

On the basis of the morphological evidence given above, *N. intermedia* might appear to be as homogeneous a unit in Europe as *N. lutea* or *N. pumila*. Two interpretations of this situation are possible, namely, (a) that it forms a separate third pure-breeding species, or, (b) that the plants placed under it are all hybrids of the same parentage presumably having arisen in several different localities independently. The first of these possibilities would seem to be ruled out decisively by the impaired fertility of the plants placed under *N. intermedia*. No populations are known which would fit the diagnosis of *N. intermedia* and which possess at the same time a fertility comparable with that in *N. lutea* or *N. pumila*.

This leaves the second interpretation, long accepted by systematists, that *N. intermedia* is the assemblage of hybrids from the cross *N. lutea* $\times$ *N. pumila*. Caspary's demonstration that the artificial F_1 hybrid of this parentage resembles closely plants placed under *N. intermedia* would seem to put this interpretation beyond doubt.

This ascription of a hybrid origin to *N. intermedia* does not, however, solve all the problems connected with it. The remarkable apparent homogeneity of *N. intermedia*, considered simply as a taxonomic unit, requires some explanation. The data of Tables 1, 3, 4 and 5 show that the intrinsic variability of the three aggregates of the taxon considered here, the Chartners sample, and those of British and Continental European herbarium material, is not appreciably greater than that found in comparable samples of *N. lutea* and *N. pumila*. Had the herbarium samples alone been involved, this would hardly have been a matter for surprise; "*N. intermedia*" was, after all, a taxon created to cover plants falling between *N. lutea* and *N. pumila*, and it is only to be expected that plants preserved in herbaria under this name should have been selected to be as "intermediate" as possible in character. The case of the Chartners Lough colony is somewhat different, since the sample analysed covered the full range of variation observed, there being no question of selection for plants of intermediate character.

The presumed parents of *N. intermedia* differ from each other mostly in "quantitative" characters, and this fact, and the extremely intermediate nature of Caspary's artificial hybrids, would seem to suggest a polygenic control of the characters involved. In a hybrid colony containing generations later than the F_1 , one might expect some degree of segregation, and certainly a wider range of variation than in "pure" colonies of either parent. The relatively narrow variation range of the Chartners colony, and others like it, indicates either that subsequent generations to the F_1 are not present, or that some form of selection is acting to ensure the survival only of plants near the F_1 mode (Fig. 5).

The possibility that colonies like that in Chartners Lough are in fact ancient clones derived from a single original F_1 plant cannot be dismissed from consideration. The

capacity of *Nuphar* to reproduce vegetatively is well known. The bottom of Chartners Lough in the area of the *Nuphar* is entirely covered with entangled rhizomes, and although verification would appear now to be impossible, it does not seem inconceivable that all are ramifications of a single huge plant. If so, the age of this plant must be enormous, far exceeding the century or so for which individual *Nuphar* plants have been observed to persist in cultivation.

No seedlings were noted in the Chartners Lough colony, and it is quite obvious that, under the existing conditions, seedlings would find considerable difficulty in establishing themselves against the competition of the mature plants, particularly for light. Nevertheless the successful germination of seeds from the fruits of the season of 1952 shows that propagation by this means is at least feasible. The low pollen and ovule fertility points to the probability that severe meiotic irregularities are present, arising possibly from structural differences between the parental chromosomes. If so, it is possible that genetical recombination is severely limited, and that only those spores survive and function which approach a particularly favourable genetical balance.

It may be that the uniformity of such colonies as the Chartners one is maintained by a combination of several factors – by the extensive occurrence of vegetative propagation of successful plants, by the fact that only a limited amount of genetical recombination is possible, and by the stringent elimination, through competition, of ill-adapted seedlings.

Anomalous populations

A comment on the Avinlochan colony seems appropriate at this point. This colony has usually been accepted by systematists as falling within the range of *N. pumila*, and was so in the course of the present study until it was realised that it combined a relatively low pollen fertility with certain anomalous features not encountered in other populations of *N. pumila*. Accordingly, the biometrical data relating to this colony have been kept separate in the tables and not incorporated in the *N. pumila* aggregate. Considering all of these data, it will be seen that the Avinlochan colony does, in fact, in its morphological features depart somewhat from the other colonies of *N. pumila* in the direction of *N. lutea*. This and the depressed fertility would seem to indicate that it has in the past suffered genetical contamination from *N. lutea*. The ovary fasciation illustrated in Fig. 6 is present to a greater or lesser degree in the bulk of individuals of the colony, and must be looked upon as sub-pathological. A similar, but even more extreme, example of the incidence of ovary fasciation of this type was encountered by Caspary (1870) in a colony, referred to *N. pumila*, in Titisee. Caspary's data suggest that there is a considerable amount of variation within and amongst the *Nuphar* populations of the lakes of the Vosges and the Black Forest, and here again the possibility of different degrees of introgression of *N. pumila* and *N. lutea* is present. The great variation in pollen fertility observed by Caspary in these colonies points in the same direction.

The distributional problem of N. intermedia

The final problem concerns the existence of *N. intermedia* in localities like Chartners in isolation from one or both parents – a circumstance, in the case of the Chartners colony, once considered to rule out the possibility of its being of hybrid origin (Baker and Tate, 1868). Once again there is more than one possible explanation. The simplest would be that colonisation has arisen relatively recently from a chance hybrid seed carried by some agency – presumably water-fowl – from a locality where the two parents exist today in close proximity. While this explanation cannot altogether be rejected, it would seem improbable. With the Chartners colony the minimum distance of transport would have to be of the order of 80-90 miles and it would seem to be pressing the idea of chance

long-range dispersal rather far to assume that all of the hybrid colonies marked in Fig. 1 have arisen in this manner.

The alternative explanation, that the isolated southern *N. intermedia* colonies originated in their present stations at the time when the two parental species occurred together in the neighbourhood, would seem to be more probable. It is likely that *N. pumila*, like other boreal and montane species, has been in the process of area-contraction for some considerable time. It can hardly be doubted that *N. pumila* did exist in N. England at one time during the early post-glacial period, but without fossil evidence it is difficult to say how long it is likely to have persisted in the Cheviot area. Two factors probably led to its extinction: the climatic amelioration and the gradual elimination of suitable habitats through the growth of peat bogs. Smythe (1930) has suggested that Chartners and the other remaining lakelets on the Northumberland Fells may have arisen as moraine-dammed lakes in the closing stages of the last glaciation; how many others in the area once open to colonisation by *N. pumila* have now entirely disappeared we have no means of knowing.

N. lutea, although no doubt a later immigrant into the British Isles than *N. pumila*, is known to have been present in early boreal times; reproductive contacts with *N. pumila* may have taken place repeatedly during the replacement of one by the other in southern and lowland districts. Where in the neighbourhood of expanding populations of *N. lutea*, the hybrids probably became eliminated by competition and genetical "swamping." In a few more isolated localities, particularly in relatively upland stations where their "intermediate" genotype may have been of adaptative value, they appear to have been able to persist.

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REGIONAL VARIATION OF *ALNUS GLUTINOSA* (L.) GAERTN. IN BRITAIN

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MORPHOLOGICAL VARIATION

In its external morphology *Alnus glutinosa* is a rather variable species and it is possible that a similar physiological variability exists. The most obvious differences are in habit, leaf size and shape, and catkin size.

Generally, the alders in the north and west of Britain are shorter and more gnarled than those to the south and east, but this may well be a habitat modification, brought about by exposure to strong winds and growth in less suitable soils, and not genotypic. The multiple-stemmed bush habit is most frequent on waterlogged soils but may be induced by damage to the sapling.

Leaf outline varies from orbicular through cuneate to ovate or obovate. The apex may be strongly emarginate, rounded or even acutely pointed as in *Alnus incana*. The leaf outline is fairly constant for each tree, although the shape of the apex may vary. The margin may be undulate with one or two pronounced sets of teeth, or smoothly curving and with only tiny serrations.

The hairiness of lamina surface, vein angles and petioles is also variable.

Asymmetric leaves are frequent, and differences between long and short shoot leaves do not appear to be as pronounced as in *Betula*.

Pistillate catkins may be globular or elongated, and the free points of the fused scales may or may not be visible.

Size of seeds (fruits) also varies considerably, and roughly proportionately with catkin size. The range of variation illustrated by Kujala (1924) for Scandinavia is less than that now recognized in Britain (Plate 2).

Catkins less than 10 mm. long have very tiny seeds (1.5×1.0 mm.) which in turn give rise to small, weak seedlings.

Leaf and catkin sizes were selected for statistical examination in 1949. Leaves were collected at random from spur shoots and from near the apex of long shoots, avoiding immature or obviously deformed specimens. Length was measured from the insertion of the petiole to the distal end of the mid-vein, and breadth at the broadest point at right angles to this line.

Pistillate catkins could not always be measured at the green-ripe stage, but it was found possible to utilise old catkins provided length was measured from the insertion of the stalk to the tip of the centre scale, ignoring the extra length given by any reflexed basal scales.

Twenty leaves and twenty catkins from each of five or ten trees per population were measured, and two or three adjacent populations in each district were sampled where possible. This method was used in preference to the collection of one leaf per tree since populations were often small.

Mean dimensions of leaves and catkins for any one tree in the Arran and Chippenham populations were found to be constant from year to year.

Data from the eighteen populations sampled are summarised in Tables 1 and 2. The location of the populations is shown in Figure 1. The same data have also been presented graphically elsewhere (McVean 1953).



Fig. 1. Location of populations shown in Tables 1 and 2.

TABLE 1
Alder leaf measurements

Population	Mean	Regional mean	Mean	No. of trees measured
	Length (mm.)		Breadth (mm.)	
1. Matley Bog, Hants.	54.8 ± 6.1	(54.8)	53.8 ± 6.9	10
2. Chippenham Fen, Cambs.	71.7 ± 13.5		59.3 ± 11.7	10
3. Santon Downham, Norfolk	65.2 ± 8.2	66.7	59.0 ± 11.5	5
4. Ranworth Broad, Norfolk	63.3 ± 6.7		57.1 ± 7.2	10
5. Conway Valley, N. Wales	59.8 ± 8.5		54.1 ± 9.9	10
6. Portmadoc, N. Wales	57.2 ± 7.9	61.9	54.1 ± 8.0	10
7. Chester	68.9 ± 6.5		56.9 ± 8.3	10
9. North Arran	58.6 ± 7.1	(58.6)	52.7 ± 7.4	20
11. Glen Nevis	59.8 ± 9.8		55.5 ± 8.0	10
12. Ballater, Deeside	47.4 ± 6.0	53.2	40.6 ± 5.0	5
13. Kinord, Deeside	45.4 ± 5.5		46.0 ± 8.6	5
15. Garmouth, Spey Bay	60.2 ± 6.3		52.5 ± 6.3	10
16. Sutherland i	52.1 ± 6.5		52.0 ± 7.2	10
17. Sutherland ii	49.8 ± 7.4	52.3	45.3 ± 5.5	10
18. Sutherland iii	55.0 ± 6.1		48.0 ± 5.1	10

TABLE 2
Alder pistillate catkin measurements

Population		Mean Length (mm.)	Regional mean	Mean Breadth (mm.)	No. of trees measured
1.	Matley Bog	10.8 $\pm$ 2.1	11.0	7.6 $\pm$ 1.6	10
	Holmesley Bog	11.2 $\pm$ 2.0		7.7 $\pm$ 1.1	5
2.	Chippenham Fen	15.0 $\pm$ 3.6	13.9	10.4 $\pm$ 1.8	10
3.	Santon Downham	13.7 $\pm$ 2.9		10.0 $\pm$ 1.8	5
4.	Ranworth Broad	13.1 $\pm$ 2.5		9.1 $\pm$ 1.0	10
5.	Conway Valley	12.9 $\pm$ 2.3	11.9	9.1 $\pm$ 1.5	10
6.	Portmadoc	11.4 $\pm$ 2.0		7.7 $\pm$ 1.0	10
7.	Chester	11.5 $\pm$ 2.1		8.4 $\pm$ 1.0	10
8.	Mugdock, S.W. Stirling	10.8 $\pm$ 2.2	11.2	8.0 $\pm$ 1.8	10
9.	N. Arran i	10.8 $\pm$ 2.9		8.0 $\pm$ 1.3	20
10.	N. Arran ii	11.0 $\pm$ 2.4		8.1 $\pm$ 1.5	10
11.	Glen Nevis	10.1 $\pm$ 2.5	10.7	7.7 $\pm$ 1.7	10
12.	Ballater	11.9 $\pm$ 1.8		7.7 $\pm$ 1.4	5
13.	Kinord	9.3 $\pm$ 1.1		6.6 $\pm$ 0.9	5
14.	E. Loch Ness	11.1 $\pm$ 1.9	9.2	8.2 $\pm$ 1.4	10
15.	Garmouth	11.3 $\pm$ 2.2		8.1 $\pm$ 1.0	10
16.	Sutherland i	10.5 $\pm$ 2.5		8.2 $\pm$ 1.3	10
17.	Sutherland ii	8.5 $\pm$ 1.5	9.2	7.4 $\pm$ 1.2	10
18.	Sutherland iii	8.6 $\pm$ 1.9		7.1 $\pm$ 1.4	10

Moss (1914) recognised three varieties of *Alnus glutinosa* in Britain on the basis of leaf and catkin sizes.

Var. *macrocarpa* Loudon. Laminae about as long as broad (7.8 cm.) and with larger and coarser serrations. Pistillate catkins about 3 cm. long at maturity.

Var. *typica* Moss. Laminae intermediate in shape and size (5.6 $\times$ 4.5 cm.). Pistillate catkins 1.7-2.0 $\times$ 1.0-1.4 cm. "Believed to be the common south and lowland form and not yet known for Wales, Scotland or Ireland."

Var. *microcarpa* Rouy. Laminae 4.5 $\times$ 3.5-4.0 cm. and with smaller and finer serrations. Pistillate catkins 1.5 $\times$ 1.0 cm. "Common form in hilly and northern localities though it also occurs to some extent in the south of England down to Somerset and Suffolk."

The variation is actually continuous so that the above varieties merely cover arbitrary ranges on the gradient. Furthermore, though correlation coefficients have not been calculated, it is apparent in the field that the largest catkins do not necessarily grow on the trees with the largest leaves, and the same applies to the small forms. Neither are the large-cone trees more robust in growth and with more coarsely toothed leaves as Moss suggests.

The largest catkins obtainable during 1949-52 at Chippenham Fen, Cambs., the *locus classicus* of var. *macrocarpa*, have been 27 and 28 mm. long (Plate 3). The mean dimensions for twenty randomly gathered catkins from this tree were found to be 19 $\times$ 12 mm.

Catkins of *typica* size have been collected in Arran and Glen Nevis though mean dimensions for each tree were below the *typica* limit.

It is apparent from the data that there is a decrease from south to north and from east to west in both leaf and catkin size. The gradient is not a smooth one unless populations are grouped regionally, as for leaf and catkin length in Tables 1 and 2. The decrease in catkin length amounts to over 5 per cent per degree and leaf length to almost 4 per cent per degree of longitude.

In Figures 2 and 3 the size distribution of 200 catkins from each region studied is

presented in histogram form. Catkin and length breadth have been multiplied together to give simple numbers which express size more adequately than either linear dimension. It can be seen from histogram $\Sigma 1-7$ that catkin size forms a unimodal curve slightly skewed towards the smaller sizes.

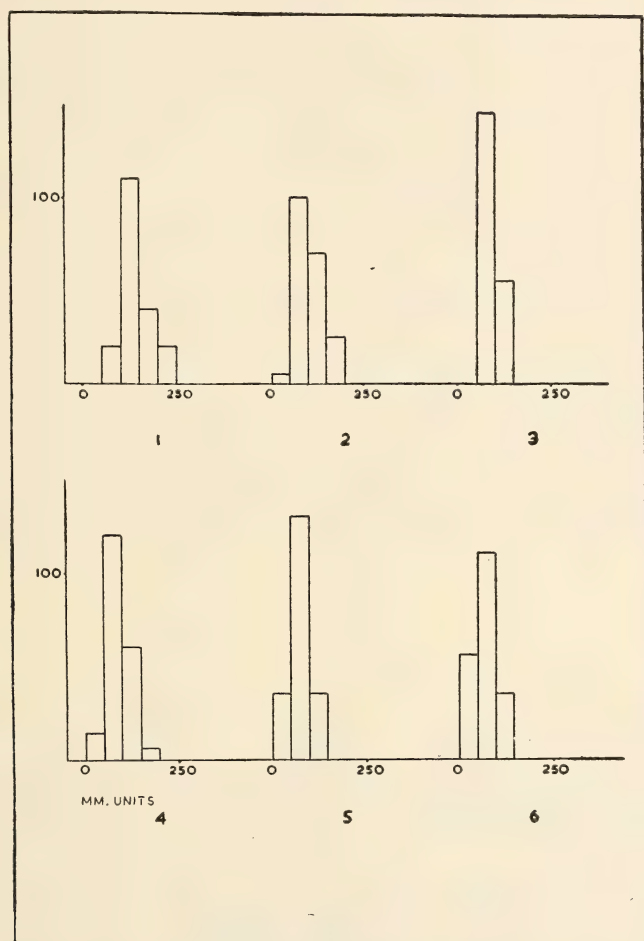


Fig. 2. Size distribution of alder catkins in each district studied. Catkin length $\times$ catkin breadth is expressed as "mm. units" on the abscissa, and the ordinate gives number of catkins measured.

- | | | |
|----------------------------|----------------|-----------------|
| 1. East Anglia | 2. North Wales | 3. Mid Scotland |
| 4. N.E. Scotland | 5. Deeside | 6. Glen Nevis |
| 7. Sutherland (see Fig. 3) | | |

Since the method of sampling has resulted in the variation studied being non-homogeneous (compounded of that "within a tree" and "between trees") only differences in means of at least three times the standard error have been regarded as significant (i.e. a level of significance of 0.27 per cent).

It has been found that each population is not significantly different from its near neighbours but that significance increases with distance. Thus Santon Downham, Chippenham Fen and Ranworth Broad populations are not significantly different nor are those of Sutherland, but any one of the first group is significantly different from any of the second.

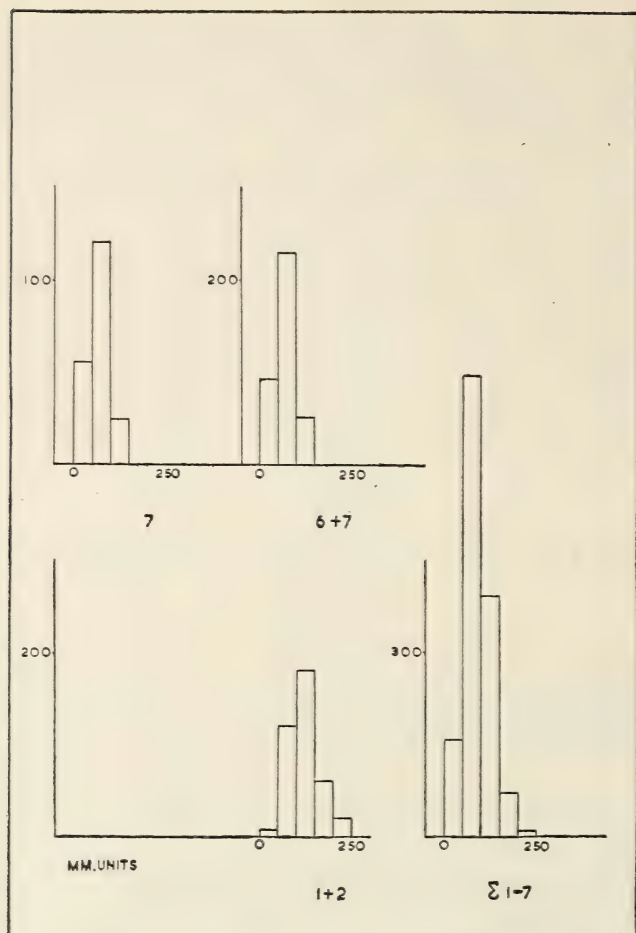


Fig. 3. Histograms 6 + 7 and 1 + 2 show the different size distributions in north and south respectively, and $\Sigma 1-7$ is a summation of all populations.

The Sutherland populations are also significantly less variable than those of S.E. England.

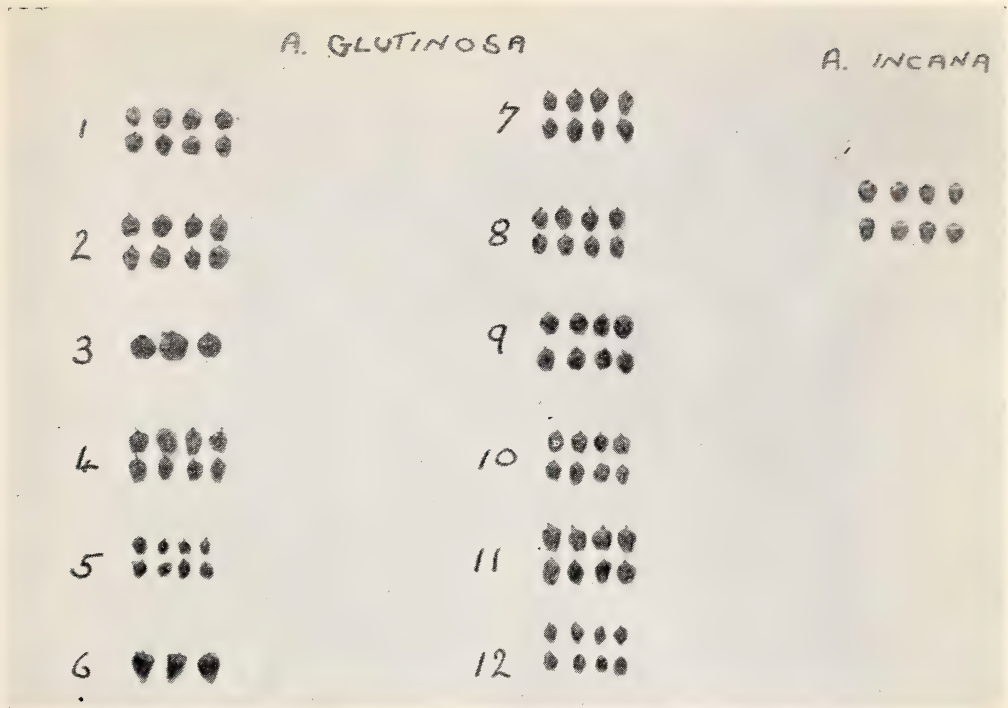
The New Forest populations of Matley and Holmesley Bogs are anomalous (see discussion).

Leaf and catkin measurements were also made over an altitudinal range of 1300 ft. (397 m.) in W. Inverness-shire (Table 3), but no variation with altitude was detected.

TABLE 3
Altitudinal variation in leaf and catkin size

Locality	Altitude (m. O.D.)	Mean Leaf size (mm.)	Mean Catkin size (mm.)
Loch Treig	260	52.5 × 46.3	8.5 × 8.0
Loch Treig	351	51.4 × 51.9	7.9 × 7.9
Loch Treig	460	58.6 × 52.4	8.9 × 8.1
Glen Nevis	61	59.8 × 55.5	10.1 × 7.7
Glen Nevis	275	66.9 × 65.2	9.3 × 7.9

PLATE 2.



(c. nat. size). Alder fruits from different British populations. 3 and 6 are abnormal (galled).

PLATE 3.



($\times \frac{1}{2}$) Pistillate alder catkins. Left to right : "microcarpa," Woodwalton Fen, Hunts.; "macrocarpa," Chippenham Fen, Cambs.; "microcarpa," N. Arran.

CYTOLOGY

Chromosome counts, in seedling root tips, of "macrocarpa," "microcarpa" and "typica" material from Chippenham and the West of Scotland all gave $2n = 28$, the diploid number. Larsen has reported the occurrence of tetraploid alders in Denmark (Ording 1939), and Johnsson (1950) has described colchicine-induced chimaeras, with diploid and tetraploid layers, as being stunted in growth, with large, irregularly lobate, deeply toothed leaves which are often asymmetric, while wholly triploid plants had more robust growth than diploids and strikingly large leaves.

RACE DIFFERENTIATION

There are some references in the literature to the occurrence of races of different provenance in *Alnus glutinosa* and to growth disturbances following the cultivation of certain races in alien territory.

Larsen (Ording, 1939) cites the losses suffered by Danish forestry through importation of a type of alder, of more southern European origin, apparently not suited to the northern climate. At Frijsenborg the local race of *A. glutinosa* develops much better than offspring of even extremely fine trees at Meilgaard where the mother trees were even supposed to be of the Frijsenborg race.

Rubner (1934) refers to the poor growth of southern stock at Memel, Germany. The plants grew very quickly and produced fruit prematurely. They were attacked by the fungus *Valsa oxystoma* and died at the early age of 12-20 years.

In the present work the only indication of this phenomenon, apart from the morphological differences described above, has been given by the different photoperiodic responses obtained from populations from different latitudes.

In 1950, seedlings, which had been raised in the greenhouse and hardened off in the cold frame, were transferred to side-shaded plots at the Cambridge Botanic Garden on April 27th. In the transfers some groups were subjected to greater temperature changes than others, with the result that the different growth rates and final sizes attained could not be attributed to racial differentiation.

Difference in the time of leaf fall in November 1950 was, however, independent of the initial differences in treatment. On October 31st the leaves of the Arran seedlings had begun to brown while those of the Chippenham and North Wales plants were still green. A background of fallen chestnut leaves made a useful, though primitive, colour comparator, and on November 7th the Scottish seedlings were not visible against the carpet while the remainder were. The colour difference was hardly visible after mid-November, but the Scottish seedlings had by then shed more of their leaves.

The difference in time of loss of leaf function was estimated at 2-3 weeks for four degrees of latitude. About 75 seedlings were under observation.

A smaller number of Arran and Chippenham seedlings were also grown together in a plot near Glasgow where the different responses were even more marked than at Cambridge, the native seedlings browning and losing their leaves about three weeks before the others.

In 1951 seedlings from West Inverness, Arran, Lancashire, North Wales and East Anglia were grown in pots out of doors for one season. Significant differences in growth rates could not be detected but differences in time of leaf fall were again apparent, the leaves browning in the above order.

The 1950 plants, now 1-3 ft. high, again showed three weeks' difference in time of leaf fall between the Arran and southern groups. In the spring of 1952 the saplings of southern origin were markedly earlier in flushing.

Wareing (1948) summarises present knowledge of photoperiodic phenomena in

trees. He notes that northern races of pine grown in southern regions show reduced height and needle length, and first-year seedlings respond to shorter days by hastened dormancy, as compared with the home region. After the first year of growth, duration of extension-growth is unaffected by day length.

In the *Annual Report of the Swedish Association for Forestry and Tree Breeding*, 1942, variation in photoperiodism is reported for both two-year and one-year *A. glutinosa* seedlings. The Västerbotten long-day type showed marked differences in increment, in time of leaf fall and in lignification of the annual shoots compared with central and southern Swedish races.

DISCUSSION

There seems little doubt that in Britain the alder exhibits clinal variation in some features of its morphology and physiology, and that these variations tend to take place along the main climatic gradient S.E.-N.W. This would seem to belong to the large scale, geographical character gradients designated topoclines by Gregor (1938-39). (Morphological variation has not yet been demonstrated on the plants grown under uniform conditions in the experimental garden.)

There may be a continual selection for small leaves and catkins in the north-west by some factors, possibly climatic, or the situation may have arisen in the selective elimination of genes during post-glacial migration north-westward across the country. The smaller variability of the northern type indicates that some gene elimination has taken place.

The failure to establish similar morphological gradients altitudinally strengthens the belief that the differences are genotypic, since there are no barriers to gene flow over the short distances here involved. The morphological gradients exist as an alteration in the mean values of leaf and catkin size ranges rather than as a polymorph-ratio cline involving the three varieties cited above (p. 28).

Habitat preferences in the species encourage the formation of isolated local colonies which tend to intra-breed rather than inter-breed. This, along with some past planting by man, may account for the occurrence of populations of small-catkin types in an otherwise large-catkin region and *vice versa*.

It should perhaps be noted that the most serious discrepancy occurs in the New Forest populations, which lie south of the maximum extent of the Pleistocene glaciation.

ACKNOWLEDGMENTS

This paper comprises part of a study of the common alder submitted for the degree of Ph.D. at Cambridge University. I wish to express my thanks to Dr. A. S. Watt and Dr. H. Godwin for their interest and encouragement while supervising the work. My thanks are also due to Dr. A. Berrie, formerly of the Glasgow Botany Department, for confirming my chromosome counts.

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PLATE 4.



Epipogium in Buckinghamshire.

Photo : R. C. L. Burges

EPIPOGIUM APHYLLUM Sw. IN BUCKINGHAMSHIRE

By R. A. GRAHAM

While searching for *Epipogium* on July 18th, this year, in one of the very many woods in Bucks, v.c. 24, which would appear to be suitable for it, I was luckily rewarded in finding what later turned out to be a scattered colony of twenty-two plants, with a total of twenty-five flowering shoots. The spot is one of the many in this and neighbouring counties that I had searched without success on several previous occasions. Most of the flowering shoots were small, less than three inches in height above ground level, but two were fine examples, attaining five inches and bearing three flowers.

The locality, which is necessarily a closely-kept secret, is a typical Chiltern wood where beech predominates. The canopy, locally heavy, is on the whole rather more open than what one might have expected to be ideal for this orchid, and a few plants grew in comparatively light conditions and amongst the type of ground vegetation that invades these woods whenever light gives a chance. In no way did the wood appear to be markedly different from many others in this general area.

The soil was clearly well drained, though moist, and whereas a few plants grew in a deep mat of decaying leaves, some were on patches where there was practically no leaf whatsoever. It was noted by a careful parting of the soil, that the underground system was apparently not growing in decaying leaf mould, but actually in the mineral soil. Except in one case, chalk was either at or nearly at the surface – in the single exception the soil appeared to be a rich sand, though no doubt in capillary contact with chalk below.

In general appearance, this orchid is delicate, attractive, and very pallid. The stem is a pale straw colour, with one or two scales of the same colour or slightly darker. The flowers are rather large – about the size of a nickel threepenny bit when fully extended – and nod slightly on their short stalks.

The lip, which is uppermost, is the palest possible pink, with raised markings of what is perhaps magenta. The sepals and petals, which together give a somewhat palmate appearance, are aureolin yellow* – perhaps better described as a very pale yellowish-straw colour. The larger examples look more than anything else like a plant-ghost, due to the pallid colouring in the darker surroundings.

A specimen was presented to the Kew herbarium, where hitherto no British *Epipogium* existed. A second specimen was cut and presented to Mr. Lousley so that he could take photographs in the more satisfactory conditions of his home – some of these were included in the *Illustrated London News*. Both these two specimens bore only one flower. A third specimen with two flowers was cut for my own herbarium. It was not intended to take any more, and those who saw the plant *in situ* were asked to make do with a photograph record. However, slugs were active, and three examples were found eaten through at the base but fresh enough for general purposes. One of these, a splendid plant with three flowers, is now also in my herbarium. Of the remaining two, which each had two flowers, one is to be presented to the Cambridge University herbarium, while the other was circulated to Professor Tutin and Dr. Butcher for purposes of illustration, and will remain finally in the herbarium of Leicester University. My own specimens will eventually go to Oxford University.

A later visit showed that the activity of slugs had continued. One plant was, however, found which clearly showed that seed had been produced and dispersed. This specimen is now in the British Museum (Natural History).

* Royal Horticultural Society's Colour Chart

ARCTIC PLANTS NOT YET FOUND IN BRITAIN

By NICHOLAS POLUNIN

Gray Herbarium, Harvard University, U.S.A.

In the rightly appreciative reviews that have so far been published of the welcome new *Flora of the British Isles* (Clapham, Tutin and Warburg, 1952), there does not appear to be any mention of the omission, even as addenda, of the two most important additions to the known British flora that have been made in recent years. These were *Koenigia islandica* L., a genus new to Britain, and *Diapensia lapponica* L., a family new to Britain; both are now considered "undoubtedly native on remote hills in Scotland" (Lousley, 1952). Both discoveries stirred public interest far beyond the British scientific press; that of *Koenigia* was announced in 1950 from material collected in 1934 (Burt, 1950) and that of *Diapensia* was made in 1951 (Blakelock, 1952). More detailed accounts of the *Koenigia* (Raven, 1952) and of the *Diapensia* (Roger, 1952) in Scotland have now been published, as have reports in *The Times* and elsewhere; the former plant has since been refound also in neighbouring localities (Raven, 1952) and the latter is abundantly confirmed (Roger, 1952). It has also been reported (Lousley, 1951; Ribbons, 1952) that *Homogyne alpina* (L.) Cass. has been confirmed as occurring in the British Isles, although the elder George Don's "reputed discovery" (cf. *Notes Roy. Bot. Gard. Edinburgh*, 3, 112-3, 1904) of it had latterly been taken with so little seriousness that the species is not even mentioned in recent floras. Further additions are reported or reviewed by Lousley (1953), some of which were actually made after the new flora was published last year; the reason for the lack in that work of any mention of the others was evidently that it was an excessively long time in the press.

These discoveries, like several of other species, make one wonder again how many more of these arctic, etc. plants, hitherto unsuspected as members of the native British flora, may still remain to be detected on remote Scottish mountains and isles in habitats that seem to fall within their normal range. It may be noted that most of these 'additions' are to a considerable extent 'open soil' plants growing best in the virtual absence of competition (Polunin 1939a, 1939b, 1941); and it may be suggested that other species, often of similar ecological requirements, which might possibly repay closer search of suitable habitats in these regions, may perhaps include (apart from some already recorded without confirmation but including the two marked with an asterisk of which there are old and very doubtful reports): *Equisetum scirpoides* Michx., *Botrychium boreale* Milde, **B. lanceolatum* (S.G.Gmel.) Rupr., *Sparganium hyperboreum* Laest. ex Beurl., *Agrostis borealis* Hartm., *Phippsia algida* (Solander) R.Br., *Trisetum spicatum* (L.) Richt., *Vahlodea atropurpurea* (Wahlenb.) Fries, *Carex brunnescens* (Pers.) Poir., *C. glareosa* Wahlenb., *C. mackenziei* Krecz., *C. rufina* Drej., *Kobresia myosuroides* (Vill.) Fiori & Paol., *Luzula confusa* Lindeb., *Salix glauca* L. s.l., *S. polaris* Wahlenb., *Arenaria sajanensis* Willd. ex Schlecht., *Lychnis apetala* L., *Stellaria calycantha* (Ledeb.) Bong., *S. crassifolia* Ehrh., *Ranunculus glacialis* L., *R. hyperboreus* Rottb., *R. pygmaeus* Wahlenb., *Cardamine bellidifolia* L., *Draba alpina* L., *D. nivalis* Liljebl., *Sedum annuum* L., *Saxifraga foliolosa* R.Br., *Potentilla nivea* L. s.l., **Rubus arcticus* L. s.l., *Astragalus frigidus* (L.) A. Gray s.l., *A. norvegica* Grauer, *Viola biflora* L., *V. selkirkii* Pursh ex Goldie, *Epilobium davuricum* Fisch. s.l., *E. hornemannii* Reichenb., *E. lactiflorum* Hausskn., *Cassiope hypnoides* (L.) D.Don, *Pyrola grandiflora* Radius, *Androsace septentrionalis* L., *Primula stricta* Hornem.,

Gentiana aurea L., *G. tenella* Rottb., *Pedicularis lapponica* L., *Veronica longifolia* L., *Pinguicula villosa* L., *Galium trifidum* L., *G. triflorum* Michx., *Petasites frigidus* (L.) Fries, and *Taraxacum lapponicum* Kihlm. Of all the accepted native arctic species not yet found in Britain, these are the 50 whose continental European (especially Scandinavian) ranges, with some other considerations, seem to allow them the best chance of occurring in the British Isles. What a delightful holiday sport to hunt for them in the lesser-known parts of Scotland or the accompanying isles!

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A 17TH CENTURY CONTRIBUTION TO THE SCOTTISH FLORA

By F. H. PERRING

School of Agriculture, University of Cambridge

About the year 1695 Martin Martin, Gent., native of Skye and sometime scholar of Leiden University, made a tour of the Inner and Outer Hebrides, visiting almost every island personally, including St. Kilda. In 1698 he published *A Late Voyage to St. Kilda, the Remotest of all the Hebrides*, and five years later in 1703 appeared the first edition of the work for which he is justly famous, *A Description of the Western Islands of Scotland*. Both works have long been valued by students of Hebridean history for the acute account of life in the islands in the late 17th century, but as far as can be gathered the many plants mentioned by Martin have been overlooked.* For this reason the plants have been extracted and are listed according to the Island on which they are said to grow by Martin. In most cases he gave an English or Scots name. An attempt has been made to identify the plants more exactly and notes, giving reasons, are added. The main source of information for identification has been Britten & Holland (1886) and unless otherwise stated the notes are based on that work.

LEWIS, v.c. 110

Birch

Hazel : *Corylus avellana*

Nettle

Reed : Probably *Phragmites communis*. *Typha latifolia* is mentioned elsewhere and is called "Cat's Tail."

Golden Rod : *Solidago virgaurea*

All Heal : May be *Stachys arvensis* which is the name given by Lightfoot (2) although it is well to remember he is "a Lecturer of Uxbridge," as Thomas Pennant delightfully describes him. He received his information mostly at second-hand from Stuart, who spoke Gaelic, and who was the third member of the party which comprised Pennant's (1776) *Voyage to the Hebrides*. However, Clown's All Heal is *Stachys palustris*, and we may perhaps accept the family likeness.

HARRIS, v.c. 110

Daisy : *Bellis perennis*

Clover

Wild White Carrot : *Daucus carota*

Allium latifolium : *Allium ursinum*; no other *Allium* has been recorded in v.c. 110.

BERNERAY, v.c. 110

Slake-like plant growing on land [slake = seaweed]

HERMETRAY, v.c. 110

Milkwort

* Neither N. Douglas Simpson nor Canon C. E. Raven with whom I have corresponded on the subject is aware of references to the book in botanical literature.

NORTH UIST, v.c. 110

- Braggir : *Fucus* sp. according to Ray (1724)
 Flamula Jovis : *Ranunculus flammula*
 Linarich : Sea plant, perhaps *Enteromorpha* sp.
 Shunnish : Suinas or Shunas. *Ligusticum scoticum*
 Alexander : *Smyrnium olusatrum*. This was probably a garden escape; it is not found wild in v.c. 110 today. It was once widely used as a pot-herb and Sibbald mentions it in his list of Scottish Garden Plants.

BARRA, v.c. 110

- Curran-Petris : *Daucus carota*. In Gaelic Curran = carrot

SKYE, v.c. 104

- Oak
 Groundsel : *Senecio vulgaris*
 Corkir : Lichen. Probably Corkin which is *Lecanora tartarea*
 Crostil : Another Lichen. Martin may have meant Crotal or Crottle - *Parmelia omphalodes*. Both these lichens are used for dyeing cloth.
 Slake : Seaweed
 Dulse : *Rhodomenia palmata*
 Alga marina : Tangle - *Laminaria digitata*

SOAY (Soa Brettil - Martin), v.c. 104

- Mertillo : *Vaccinium myrtillus*
 Red Garden Currant : *Ribes spicatum*? This is the only *Ribes* species recorded for V.C. 104

EILEAN NAN GILLEAN - near Kyle of Lochalsh (Ilan Nan Gillin - Martin), v.c. 105

- Erica baccifera* : *Empetrum* (Ray, 1690)

GUILLAMON - near Scalpay (Gilliman I - Martin), v.c. 104

- Erica baccifera* : *Empetrum* (Ray, 1690)

RONA, v.c. 104

- Erica baccifera* : *Empetrum* (Ray, 1690)
 Mertillus : *Vaccinium myrtillus*

AN t-IASGAIR - near Rudha Hunish, v.c. 104

- Scurvy Grass : "Of an extraordinary size, and very thick." *Cochlearia officinalis*.

MINGAY I - near Vaternish Pt. (Mingoy - Martin), v.c. 104

- A red, short type of dulse

COLONSAY, v.c. 102

- Erica baccifera* : *Empetrum* (Ray, 1690)
 Juniper
 Cat's Tail : In the south of England - Devon, Hampshire, Sussex - this is the name for catkins of hazel or willow. In Aberdeenshire *Eriophorum vaginatum* and *E. angustifolium* are called Cat's Tail. Prior (1863) says it is the name for *Phleum pratense* or *Typha latifolia*. The latter is the name given by Lightfoot (1777) and is the plant most likely meant by Martin.

ST. KILDA, v.c. 110

Sorrel : *Rumex acetosa*. "It (the compost) produces much Sorrel where the compost reaches."

Lapathum vulgare : *Rumex obtusifolius*. Sibbald (1684) says "Lapathum vulgare folio obtuso J.B. Folio subrotundo B.P."

Scurvy Grass : *Cochlearia officinalis*

Mille-foil : *Achillea millefolium*

Bursa pastoris : *Capsella bursa-pastoris*

Silver weed or argentine : *Potentilla anserina*

Plantane

Sage : see under "Plants used for medicines." *Teucrium scorodonia*?

Chicken weed : *Stellaria media*

All hail or siderites : This may be All Heal (see under Lewis). However, *Sideritis* is a genus of the Labiatae and a name given in Parkinson (1640) to various labiates.

Lindley & Moore (1876) say that *Sideritis* is *Galeopsis tetrahit*. This was present as a cornfield weed on St. Kilda as late as 1931.

Sea Pinck : *Armeria maritima*

Tormentil : *Potentilla erecta*. "Their leather is dressed with the roots of tormentil."

All but *Teucrium scorodonia* of the above have been recorded from St. Kilda this century.

NOTE ON DRYAS

In a section devoted to "The diseases known and not known in Skye and the adjacent Isles" we find the following entry :

"Caryophyllata Alpina Chamedrois fol. It grows on marble in divers parts, about Christ Church in Strath; never observed before in Britain, and but once in Ireland, by Mr. Hiaton (Heaton). Morison's Hist. Ray Synopsis, 137 (139)."

Caryophyllata Alpina Chamaedryos folio, to give the spelling in Ray (1724), is *Dryas octopetala*. This reference is to a locality for the plant on the Broadford Marble in Strath Parish, Skye. Christ Church is now a ruin and is marked 'Gill Chriosd' on the Ordnance Survey map, though it is also known as Kilchrist. It is about 3 miles S.W. of Broadford and 1,000 yards from a hill called Ben Suardal, upon which *Dryas* is reported as growing at least three times in subsequent literature. In 1776 Thomas Pennant (1776) wrote that the two other members of his party, Lightfoot and Stuart, "ascend the high limestone mountain of Beinn Shuardal, and find it in a manner covered with that rare plant the *Dryas octopeta* [sic]." On the opposite page is a charming drawing of the plant very correctly drawn and more correctly named. Lightfoot (1777) himself refers to the locality in his book published a year later : "Plentifully upon the Limestone rocks of Ben Suardal, etc. in the Parish of Christ Church, in Strath Swardle(s) in the Isle of Skye."

Dryas was still growing in the same locality 140 years later. Salmon (1916) wrote "*Dryas* extremely abundant on Limestone about Ben Suardal, near Broadford."

The question arises whether this paragraph in Martin is the first record for *Dryas* in Britain. No reference is made to *Dryas* in Sibbald (1864). In the first and second editions of Ray's *Synopsis* (1690, 1696) the only locality given for the British Isles is "in Ireland on the mountains between Gort and Galloway" where it was found by Heaton in 1650. Martin was probably referring to the edition of 1696 when he mentions Ray's *Synopsis*, although the actual page on which *Dryas* appears is 139 and not 137 as stated by Martin. Martin, then, had access to a copy of the second edition of Ray's *Synopsis*

before writing his book in 1703. By the time the third edition of Ray's *Synopsis* was published in 1724, *Dryas* was apparently known from a number of localities in the Scottish mountains: "Hujus plantae speciminibus me ditavit D. Lhwyd, in montibus Hibernicis juxta Sligo collectis, quae et in omnibus altissimis Scotiae occidentalis montibus abundat, ut mihi retulit idem." D. Lhwyd is almost certainly Edward Lhwyd, Ray's friend, who visited Sligo in 1700 and sent Ray a collection of plants amongst which *Dryas* is not mentioned. However it seems likely that this note in the third edition was made by Ray himself. This view is supported by the fact that it appears in brackets and not in the small type used by Dillenius to distinguish his own additions from Ray's original work. The note would have been made between 1700 and 1704 when Ray died. It is possible that Ray knew of the existence of *Dryas* in Scotland before Martin published the fact in 1703, though the latter's statement about its abundance is surprising.

The mystery of who first found the plant growing on Ben Suardal and who told Ray still remains. Martin may have written to Ray or to the Royal Society, to which he had already contributed a paper on Medicine in 1697, and to which he contributed another in 1707. His knowledge of Ray's *Synopsis* and his deep interest in natural phenomena may have led him to pass on his information, whether self-acquired or overheard. It is just possible that Ray saw Martin's book before he died and made the note about *Dryas*, but this alone cannot explain "abundat."

PLANTS USED FOR MEDICINES IN SKYE AND ADJACENT ISLES

Presumably wherever possible wild plants were used. *Conium maculatum* is not recorded from v.c. 104 and it may have been cultivated or imported from the mainland.

Violets

Chickweed : *Stellaria media*

Foxglove : *Digitalis purpurea*

Crowfoot : Any species of *Ranunculus* other than *Batrachian* according to Lightfoot (1777).

Wild Garlic : *Allium ursinum*

Carmel : Carmele, Carmeil, or Carmill. *Lathyrus montanus*

Knaphard : Knapperts or Knapparts, from knab, a knob, and urt, wort, referring to the rhizome of *Lathyrus montanus*.

Wild Sage : No *Salvia* species is recorded from the Hebrides, but Lightfoot (1777) refers to wood sage – *Teucrium scorodonia* : "An infusion of it stands recommended in the dropsy." In Martin wild sage is used to kill horse worms.

Shunnis : *Ligusticum scoticum* (see under North Uist).

Myrtillus : *Vaccinium myrtillus*

Plantain

Flamula Jovis : *Ranunculus flammula*

Hart's tongue : *Phyllitis scolopendrium*

Maidenhair : This is a name applied to many very different plants : *Narthecium ossifragum*, *Galium verum*, *Briza media*, *Cuscuta epithymum*, *Glechoma hederacea*, *Adiantum capillus-veneris*, and species of *Asplenium*. The fact that it is mentioned in the same sentence as Hart's tongue suggests a fern. Lightfoot (1777) gives the common name of *Asplenium* spp. as Maidenhair. *Adiantum capillus-veneris* is not found in V.C. 104 and it is therefore most likely that Martin was referring to a species of *Asplenium*.

Yarrow : *Achillea millefolium*

Betonica Pauli : *Veronica officinalis*

St. John's Wort : *Hypericum perforatum*[†]. Lightfoot (1777) says " An oil or tincture of the flowers is esteemed a good vulnerary." Martin says that St. John's Wort, Betonica Pauli and Golden Rod, are made into an ointment with Sheeps' grease and laid on a wound. Later Fuga daemonum is mentioned; this is again a reference to St. John's Wort which was used on the eve of St. John's day (21st June) for " putting the devil to flight." The plant was hung up at windows as a protection against thunder and evil spirits.

Mercury : *Chenopodium bonus-henricus*

Golden Rod : *Solidago virgaurea*

Flags : *Iris pseudacorus*

Oak

Hemlock : *Conium maculatum*; found in v.c. 110.

The author wishes to thank Mr. N. D. Simpson for his kind help in supplying a list of references which proved invaluable.

[†] Very rare in v.c. 104 where it is only known from Rhum. Some other species of *Hypericum* may have been used.—ED.

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PROLIFERATION OF SPIKELETS IN BRITISH GRASSES

I. THE TAXONOMY OF THE VIVIPAROUS RACES

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1. INTRODUCTION

The gramineous inflorescence may be resolved into units termed spikelets. Each spikelet consists of an axis bearing bracts or glumes. Except for the sterile glumes (two in most British grasses) which are inserted lowest upon the spikelet axis, the glumes bear florets in their axils. In this paper the terminology approximately follows that of Arber (1934). Glume will be used to denote any bract directly inserted upon the spikelet axis, but a glume subtending a floret is termed a lemma.

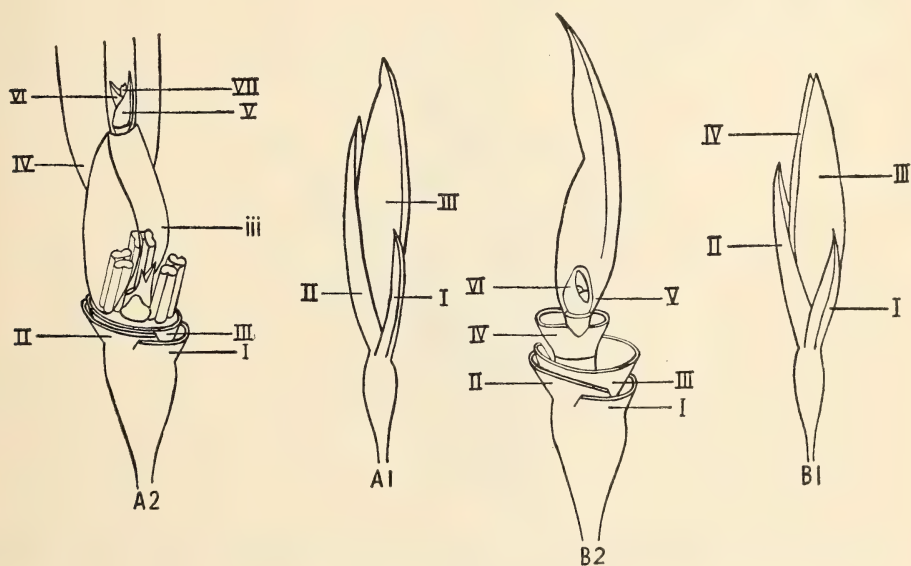


Fig. 1

A. *Festuca ovina* L. 1. Young spikelet ($\times 10$); 2. Basal portion dissected to show floret development ($\times 25$); I-VIII Glumes (I-III cut away); iii. Palea of lowest floret. B. *Festuca vivipara* Sm. 1. Young spikelet ($\times 10$); 2. Dissected to show vegetative apex of the spikelet axis ($\times 25$); I-VI Glumes (I-IV cut away).

Arber calls the continued growth of the spikelet axis, and the bearing of leaves distally upon it, 'vegetative proliferation.' The glumes are found in various stages of metamorphosis from their normal structure to foliage leaves. If the normal lemma has the upper portion of its midrib separated dorsally as an awn, then in proliferated spikelets transitions from awn to leaf-blade are found. The morphological significance has been discussed by Philipson (1934). The florets subtended by the glumes of the proliferated spikelets may be almost normal, male- or female-sterile, aborted or completely absent. Figure 1 shows young proliferated and flower-bearing spikelets of *Festuca*.

* The substance of this paper formed part of a thesis approved by the University of London for the Ph.D. degree.

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The plants showing this proliferation may be divided into two classes. Firstly, those whose spikelets are usually proliferated; secondly, those in which proliferation is an ephemeral character.

In the first class the proliferated condition appears season after season, even when plants are transplanted from their natural habitats; their offspring, moreover, inherit the characteristic. In this group the cause is primarily genetic, and environmental factors are apparently secondary. The plants of this type form the 'viviparous races,' propagating themselves by plantlets formed from the deciduous leafy upper part of the proliferated spikelets.

2. TERMINOLOGY

Before discussing the viviparous races and, later, the problem of proliferation as a whole, it is necessary to review the terminology used in relation to this phenomenon.

The detached leafy buds are often described as bulbils, but *Poa bulbosa* L. var. *vivipara* Koel. is the only grass in which they are truly "bulbous." Bulbifery is not a satisfactory term, since it is applied to plants which bear bulbils in parts other than the inflorescence, e.g. *Dentaria bulbifera* L.



Fig. 2. *Festuca ovina* L. Carmarthen Fan, 14.ix.1950. Seed of an upper floret germinating in situ. Note the coleoptile ($\times$ c.7).

'Chloranthie' is found in the French literature and in German 'auswachsende Ährchen,' 'Laubsprossen' and 'Vergrünung' are used. However, in literature in Dutch, English, French, and German may be found words derived from the Latin 'viviparus' and 'prolifer.' Unfortunately there is confusion in their use.

The derivatives of 'viviparus' were introduced by Linnaeus (1737). It is not clear from his description if this was because of a superficial likeness to an undetached seed germinating, or if he actually thought this to be the case. The term does indicate the ecologically significant fact that the propagules are dispersed in a 'living' (i.e. not dormant) condition in most cases. Nannfeldt (1940) restricts the use of the term 'vivipary' to those races in which the deciduous buds form the regular diaspores.

'Vivipary' is restricted by Pope (1949) to embryos developing continuously without any dormant period. He induced this in barley by supplying water directly to exposed germs. Such uninterrupted growth occurs in maize with defective endosperms (Eyster

1931). Germination of an undetached seed is included by Arber in 'true vivipary,' and she quotes *Spartina townsendii* H. & J. Groves as a British example. Germinating seeds may be distinguished from proliferated spikelets by the coleoptiles of the seedlings, see Figure 2.

The use of derivatives of 'prolifer' as recommended by Arber, has the support of antiquity. Tournefort (1700) used 'proliferum' in a synonym of *Poa bulbosa* var. *vivipara*. The viviparous forms of *P. alpina* L., *P. bulbosa* L. and *Festuca vivipara* (L.) Sm. are discussed by Scheuchzer (1719) under the general heading "... *Locustis foliaceis proliferis*" – proliferated leafy spikelets. However, 'proliferation' unless prefaced by 'vegetative' is not free from ambiguity. Among Arber's references to this phenomenon, a hybrid wheat of Biffen & Engledow (1926) is quoted. This wheat bore numerous florets on an elongated axis, but was innocent of vegetative development. Proliferation has been used to describe various pathological forms (e.g. in *Agrostis canina* L., Philipson, 1935) which do not bear leafy shoots.

Other sources of confusion are provided by vegetative shoots terminated by a group of many axillary buds separated by very short internodes. Especially when the buds grow out, the whole presents an appearance superficially resembling a proliferated culm, see Figure 3. The 'mop' habit of Arber falls into this category. The absence of glumes distinguishes these from proliferated culms, but the margin between extremely metamorphosed inflorescences and vegetative shoots is not sharp.



Fig. 3. *Puccinellia maritima* (Huds.) Parl. Blakeney, June 1950. A tuft of many shoots upon an elongated stolon, similar to 'mop' (Arber) ($\times c. \frac{2}{5}$).

In this paper it seems natural to follow the general usage in the literature. 'Viviparus' derivatives will be used in ecological discussions, because they are strongly entrenched in the taxonomic literature and they emphasize the fact of growth at the time of dispersal. But, whenever morphological and physiological aspects are under review, the more accurate 'prolifer' words must be used.

3. THE BRITISH RACES OF VIVIPAROUS GRASSES

The following are included in the British flora, but *Poa bulbosa* L. var. *vivipara* Koel. is almost certainly not native and the present author has never seen it growing wild.

Festuca vivipara Sm.

Poa bulbosa L. var. *vivipara* Koel.

Poa alpina L. var. *vivipara* L.

Poa × *jemtlandica* (Almq.) Richt.

Deschampsia caespitosa (L.) Beauv. var. *pseudalpina* (Syme) Druce

Deschampsia alpina (L.) Roem. & Schult.

A K L O

K L W

K L

L

L

K L O

The initials after the plant names indicate Aberystwyth, Kew, London, Oxford and Wageningen. At these places transplanted specimens have retained their vivipary. The ranges of the viviparous races and related seminiferous forms overlap, confirming that environment is not a primary cause of the manifestation of vivipary in these races. The degree of constancy of vivipary will be discussed for each species or variety separately.

4. TAXONOMY OF *FESTUCA VIVIPARA* (L.) SM.

4.1. *Historical outline*

Figure 4 shows seminiferous and partially and fully viviparous spikelets.



Fig. 4. *Festuca* spikelets.

A. *Festuca ovina* L., seminiferous (× c. 4). B. *Festuca vivipara semiviviparae* Turess. (× c. 4).

C. *Festuca vivipara viviparae* Turess., with a sketch to show dehiscence (× c. 2).

Ray (1690, 184) mentioned *Gramen montanum spica foliacea graminea* and recorded its growth amidst the summit detritus of the Welsh mountains. In 1703, p. 178, he was more certain his plant was Bauhin's *Gramen arvense panicula crispa*; since the latter was almost certainly *Poa bulbosa* var. *vivipara*, this identification was an error, but an error redeemed by an accurate description of the replacement of the flowers in the panicle by leaves.

Linnaeus (1737, 56) named this plant *Poa spiculis angustis, acutis vivipara*. The second comment is the ambiguous "*Loco feminum folia angusta, flore longiora protrudit, hinc instar qui in ipsa planta germinat, more animalium viviparum.*" Linnaeus (1745, 33) renamed this species *Festuca spiculis viviparis*, but in the *Species Plantarum* (1753, 73) he reduced it to a variety of *Festuca ovina*.

Specific rank was again conferred by Smith (1800, 114) as *Festuca vivipara* with the comment "*Videtur species a priore distincta.*" However, the property that so clearly marked the species was not its specialised mode of reproduction, but according to Smith (1824, 140) the shape and pubescence of the glumes. It was also noted that sometimes the spikelets are not fully viviparous, the lower florets being unmetamorphosed.

Hackel (1882, 88) put all viviparous plants into a subvariety thus : *F. ovina* subsp. *eu-ovina* var. *supina* subvar. *vivipara*. In 1925 Howarth revised the sheep's fescues in Britain and found viviparous specimens of *F. capillata* Lam. (i.e. *F. tenuifolia* Sibth.), *F. ovina* L. *sensu stricto*, *F. supina* Schur and *F. longifolia* Thuill. (he raised Hackel's subspecies to species). He suggested that perhaps only specimens of *F. supina* were constant in their vivipary.

Virtually the only vegetative character that divides *F. supina* from *F. ovina* is that the radical sheaths are entire over their lower third in the former, but completely split in *F. ovina*. Better subepidermal sclerenchyma development was found by Howarth in *F. supina*. Extensive cultivation of seminiferous and viviparous specimens convinced Turesson (1926-7) that it was impossible to group all constant viviparous forms under one head and the distinction between *F. supina* and *F. ovina* had no value. Subsequent works have not revived *F. supina* as an important taxon.

Tutin (1952, 1426) gives specific rank to four segregates of *F. ovina* agg., namely : *F. ovina* L. (of which two subspecies, subsp. *ovina* and subsp. *tenuifolia* (Sibth.) Tutin are admitted), *F. vivipara* (L.) Sm., *F. trachyphylla* (Hack.) Krajina [non Hack.] (i.e. *F. longifolia* Thuill.) and *F. glauca* Lam. This is satisfactory except for the statement that viviparous plants resemble vegetatively *F. ovina* subsp. *tenuifolia*, which is the *F. capillata* of Howarth.

The characters of the segregates are tabulated in Table 1. Fully viviparous fescues must be determined by vegetative characters. Robustness of the laminae and length of inflorescence parts increases from subsp. *tenuifolia* via subsp. *ovina* to *F. trachyphylla*.

TABLE 1

Characters to distinguish *Festuca ovina* subsp. *tenuifolia*, *F. ovina* subsp. *ovina* and *F. trachyphylla*

	<i>tenuifolia</i>	<i>ovina</i>	<i>trachyphylla</i>
Width of the leaf-blade in millimetres	0.3-0.5	0.3-0.7	0.6-1.1
Length of leaf proportional to culm height	Long, $\frac{1}{2}$ culm or more	Short	
Auricles	Markedly lobed	Rounded	
Length of spikelet mm	3-6	4-8	6-10
Length of lemma mm	2.5-4	3-5	4-5.5
Points of lemmæ	Mucronate	Awned Awn - 1 mm	Awned Awn - 3 mm

Sometimes hairy leaf-sheaths and scabrid rhachides are given as additional *F. trachyphylla* characters, but they are neither constant for *F. trachyphylla* nor always absent in the *F. ovina* subspecies. Leaf length and auricle characters for *F. trachyphylla* are not given, but the present author finds that they approach the subsp. *ovina*.

4.2. Observations

Thirty-eight specimens of *F. vivipara* (both partly and fully viviparous) were collected in different parts of the British Isles. Twenty-nine have survived transfer to London, twenty-two have since produced culms. In addition twenty-seven other living specimens, of which twenty-four survived, were assembled; some were gifts from other collections. Seminiferous fescues have also been grown.

Vivipary was retained by both fully and partially viviparous plants, the latter bearing both florets and bulbils as in nature. Thus vivipary and partial vivipary are constant.

Under the rather dry pot-cultivation in London the leaf-blades are shorter and thicker. Perhaps owing to this thickening, the lobing of the auricles, which is a *tenuifolia* character, appears to be less. However, cultivated plants did not acquire the glaucescence commoner in *F. trachyphylla* than in *F. ovina* subsp. Fully viviparous plants must be assigned to a category by leaf characters, and there is an overall tendency for cultivated plants to gain an appearance further to the right in the relationship :-

F. ovina subsp. *tenuifolia* → *F. ovina* subsp. *ovina* → *F. trachyphylla*

This is most marked in life, but dried leaves reflect the same bias. Where it was possible to examine inflorescence characters, they were found to be more conservative.

In Table 2 the thirty-eight specimens are classified, using all available characters.

TABLE 2
Classification of fescues

	<i>tenuif.</i>	<i>tenuif.-ovina</i>	<i>ovina</i>	<i>trachy.</i>	<i>rubra-like</i>
Completely viviparous	7	12	10	1	
Partially viviparous	3		4		1

The groupings are: *Festuca ovina* L. subsp. *tenuifolia*, plants of mixed or intermediate characters subsp. *tenuifolia-ovina*, *F. ovina* subsp. *ovina*, *F. trachyphylla* and lastly a plant with many characters closer to *F. rubra* agg. than *F. ovina* agg.

Howarth (1948) states that vivipary is known in all varieties of *F. tenuifolia* Sibth. and *F. ovina* L. and in the var. *genuina* of *F. longifolia* Thuill.

Leaf-length/culm-height ratios are probably liable to environmental variation and pot-culture throws doubt on leaf characters. Clearly, then, it is impossible to confine the constantly viviparous fescues to one form approaching that of one of the lower seminiferous taxa.

In order to include all British viviparous fescues, Smith's description should be amended to admit plants with glaucous leaves or with lower glumes metamorphosed. The viviparous fescues are a group of asexually reproducing forms restricted in range by their mode of propagation. It is useful ecologically and systematically to include all under one specific name. It is not departing from general usage to adopt *F. vivipara* Sm. for this purpose.

4.3. Subdivision of *F. vivipara* (L.) Sm.

Turesson (1926-7, 1930 & 1931) named the seminiferous forms amphimicts, the viviparous forms which had at any time borne flowers amphi-apomicts, and one group of fully viviparous plants, on which he had never found flowers, apomicts. He distinguished between the usually partially and fully viviparous plants by the names *semiviviparae* and *viviparae*. The former are amphi-apomicts, and because of occasional serotinous flower-bearing culms most of the *viviparae* are also amphi-apomicts.

The *viviparae* were divided by Turesson into 18 types constant in cultivation. Wilmott (in Campbell, 1945) applied this classification to specimens gathered in the field and added a further type. However, many characters such as culm rigidity, shape and laxity of the panicle, size of the bulbils and root development are likely to depend on

the time and place of collection. This in no way detracts from the value and importance of Turesson's original work, but renders inadvisable the use of the key for wild specimens.

The groups *semiviviparae* and *viviparae* are useful to denote partially and fully viviparous plants. The two are easily determined, appear to be constant and have differing potentialities. Both may be included in *F. vivipara*.

4.4. Cytology and Origin

All Turesson's seminiferous plants of *F. ovina* had a chromosome number of $2n = 14$, but the *viviparae* had numbers of $2n = 21, 28$ and 42 . Stählin (1929) and Church (1936) give $2n = 14$ for "*F. capillata* Lam." (= subsp. *tenuifolia*). They find or quote for various seminiferous segregates of *F. ovina* agg. the following numbers: $2n = 14, 28, 42, 56$ and 70 . Thus polyploidy is not peculiar to the viviparous forms.

Flovik (1938) investigated Spitzbergen plants and found: *F. ovina* var. *brevifolia* $2n = 28$, *F. rubra* var. *arenaria* $2n = 42 \pm 1f$ and *F. vivipara* $2n = 49$. Tromsø and Narvik plants gave: *F. ovina* $2n = 14$, *F. vivipara semiviviparae* $2n = 21$, *F. vivipara viviparae* $2n = 28$ and *F. rubra* var. *arenaria* $2n = 42$. On the basis of chromosome morphology and numbers and the morphology of the glumes he suggested that *F. vivipara* on Spitzbergen was the hybrid ($2n = 49$) of an unreduced *F. ovina* var. *brevifolia* gamete ($n = 28$) and a reduced *F. rubra* var. *arenaria* ($n = 21$) gamete. In Norway he visualised the reduced gametes of *F. ovina* ($n = 7$) and *F. rubra* ($n = 21$) giving rise to a fully viviparous fescue ($2n = 28$), which by means of an occasional flower (see also Jenkin, 1922) backcrosses with *F. ovina* yielding the semiviviparous plant ($2n = 21$).

Jenkin & Thomas (1949) report sickly seminiferous hybrids ($2n = 42$) of *F. ovina* and *F. rubra*. Nannfeldt criticises Flovik's hybridisation schemes, because the general form and growth habit of *F. vivipara* is not intermediate between the supposed parents.

Seed was obtained by Jenkin (1922) from late-arising inflorescences of viviparous fescues, pollination being possibly by nearby seminiferous *Festucae*. Four plants were raised from seed, two being virtually normal seminiferous plants. The other pair showed strong signs of the parental vivipary. One would appear to have been a fairly normal *semiviviparae* form; the second was somewhat monstrous.

The occurrence of flower-bearing by *viviparae* and the existence of the *semiviviparae* permit of genetic exchange between the viviparous forms and their seminiferous relatives. Thus, even if vivipary originated among the fescues but once, there is no reason to expect uniformity to have remained. The origin of *F. vivipara* is unknown, but its variation is certain.

5. *POA BULBOSA* VAR. *VIVIPARA* KOEL.

Caspar Bauhin (1620, 6) described *Gramen arvense panicula crispa* and illustrated it by a woodcut. Tournefort (1700, 1, 523) quoted this, but renamed it as *Gramen paniculatum, proliferum*. Scheuchzer (1719, 45) cited both the former authors and Jean Bauhin, and included the plant in his group of proliferated grasses. It is difficult to tell if Bauhin meant only the viviparous form, although the already mentioned error by Ray indicated that he believed this plant to be viviparous. Bauhin's plant was certainly of *Poa bulbosa* agg. and a seminiferous form was separately described by Scheuchzer (1719, 40) under Lobel's name *Gramen xerampelinum*.

The specific name *Poa bulbosa* was due to Linnaeus (1753, 1, 70) and all the above names are quoted. Halperin (1933) has reviewed the subsequent literature, stating that all except one of Linnaeus' specimens were viviparous. Halperin concluded that the correct name is *Poa bulbosa* var. *vivipara* Koel. (Koeler, 1802, 189).

Figure 5 illustrates spikelets of both forms.

Since the early authors agree that Bauhin's plant was viviparous, the first reference to the phenomenon may be due to him, although the present author has yet to discover a clear description of it in his works.

Parkinson (1640, 1157) included *Gramen arvense panicula crispa* (joined with a grass which was probably *Apera spica-venti* (L.) Beauv.), but the description concluded thus: "I have thought good to adde the figure of that Grasse that Lugdunnensis calleth *Bulbosum Dalechampij*, because Bauhinus saith it is this, but not well expressed, but surely I doubt it is another sort." This cannot therefore be counted the first record of *P. bulbosa*, viviparous or otherwise, in Britain.

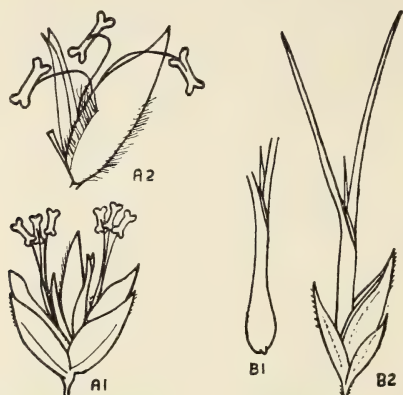


Fig. 5. A. *Poa bulbosa* seminiferous; 1. Spikelet ($\times 4.5$); 2. floret ($\times 7$). B. *Poa bulbosa* var. *vivipara* 1. Spikelet ($\times 3.5$); 2. base of bulbil.

Syme (1872, 112) knew that continental *P. bulbosa* was sometimes viviparous, but stated that only the seminiferous form was British. All references previous to Riddelsdell (1907) apparently refer to seminiferous *P. bulbosa*. Riddelsdell's plant was viviparous, found on a pebbly shore near Barry, Glamorganshire, S. Wales. At that time Barry was already a well-developed port.

With material of French and Dutch origin both the seminiferous and viviparous forms have been found constant in London. Schuster (1910) found vivipary in *Poa bulbosa* to be constant, although in culture occasional temporary 'reversions' to flowering occurred.

Åkerberg (1942) gives the chromosome number of *Poa bulbosa* (seminiferous) as $2n = 28$ and 45. Tutin (1952) mentions for the viviparous plant $2n = 35$.

6. *POA ALPINA* VAR. *VIVIPARA* L. AND *P. \times JEMTLANDICA* (ALMQU.) RICHT.

The species *Poa alpina* was first designated by Linnaeus (1753, 1, 67) quoting in his description his own earlier work (1745, 28) and Scheuchzer (1719), who recorded a seminiferous plant (p. 40, no. 4) and a proliferated plant (p. 45, nos. 2 and 3a). Linnaeus makes the second of these his β variety and inserts the adjective 'vivipara' into Scheuchzer's name.

In addition to mentioning that *P. alpina* in Britain is usually viviparous, Syme (1872, 114) drew attention to a plant he considered to be *P. stricta* Lind., a subspecies of *P. laxa* Hænke (*eu-laxa* not being viviparous). Druce (1903) named this plant *P. alpina* L. var. *acutifolia* Druce. However, Nannfeldt (1937) has traced the history in detail. The plant was given the name *P. alpina* subsp. *jemtlandica* by Almquist (1883); Richter (1890) raised it to a species, *P. jemtlandica*. It is considered to be a hybrid between *P. alpina* and *P. flexuosa* Sm., and non-viviparous specimens are not known.

P. × jemtlandica bears florets low in the spikelets, but the sex organs are always sterile in contrast to *P. alpina*. Seminiferous forms and male fertile florets in the viviparous inflorescences are known in *P. alpina*. Table 3 gives the main characters to distinguish the two viviparous forms. Figure 6 shows seminiferous *P. alpina* and viviparous *P. × jemtlandica* spikelets.

TABLE 3

	<i>Poa × jemtlandica</i>	<i>Poa alpina</i> var. <i>vivipara</i>
Leaf sheath	Persistent	Very persistent in nature
Cauline sheath	Smooth waxy green	Green with yellow ribs
Ligules	Usually all long and pointed	Upper long and pointed; lower often blunt
Leaf blades	Green, flat, tapering to a point gradually	(Often glaucous), green; usually folded, narrowing abruptly to a hooded tip
Uppermost knot	Covered	Exposed

The authorities are not agreed upon any clear glume features that may be used to distinguish the species.



Fig. 6. A. *Poa alpina* seminiferous: 1. Spikelet ($\times 3$); 2. floret ($\times 4.5$); 3. floral organs ($\times 4.5$). B. *Poa × jemtlandica*: 1. Spikelet ($\times 3$); 2. lower glumes; 3. bulbil and lowest floret; 4. as 3, but lemma removed to show the aborted nature of the sex organs.

In London, seminiferous *P. alpina* was constant. Few viviparous plants of these *Poae* were collected in this investigation, because of their rarity. Three of *P. alpina* and two of *P. × jemtlandica* were taken; they survived only one year, but produced viviparous culms. Bulbils of *P. alpina* var. *vivipara* bore flowers at the end of the summer in which they were borne and struck, but produced viviparous inflorescences next spring. Exo (1916) reported an exactly similar experience with this variety. Schuster found this variety constant in vivipary, except for occasional 'throw-backs' as in *P. bulbosa*, especially on poor soil.

Seminiferous *P. alpina* is recorded with chromosome numbers of $2n = 19-46, 49, 51-54, 57, 64, 65, 67, 72$ and 74 (see Nannfeldt's review (1940)). Apomixis has been demonstrated by Åkerberg (1942), Engelbert (1940) and Müntzing (1933, 1940).

P. alpina var. *vivipara* has $2n = 26, 33 \pm 1$ (Müntzing, 1940), 35 (Tutin, 1952) and $42 \pm 4ff, 44$ (Flovik, 1938). *P. \times jemtlandica* has $2n = 37, (39)$ (Nygren, quoted by Å. & D. Löve, 1948).

7. THE VIVIPAROUS DESCHAMPSIAE

7.1. Historical outline

Linnaeus (1753, 1, 64-5) named *Aira cespitosa* and *A. alpina*. The characters given for the former were flat leaves, a spreading panicle and short straight awn, but in *A. alpina* the leaves were described as subulate, the panicle as thick and the glumes as silvery with a very short awn. These were synonymous with species 63 and 69 in the *Flora Suecica* (1745, 23 and 26). The further details were given that sp. 63 (*A. cespitosa*) has a β variety found in wet places in Lappland and whose long thin panicle is often viviparous. Thus the first mention of vivipary in this genus was for a variety of *A. cespitosa*.

The character given by most subsequent authors as the mark of *A. alpina* is the dorsal insertion of the awn above the middle of the lemma, i.e. not basal as in *A. cespitosa*. Linnaeus however, did not discuss the point of insertion; it can only be inferred from the statements that the awn is short in *A. cespitosa* and very short in *A. alpina*. No mention of vivipary in *A. alpina* was made.

A note by Davies was quoted by Smith (1800, 85) that a viviparous variety of *A. caespitosa* (note changed spelling) is found in alpine places. Smith (1811) received from Don viviparous plants from Clova and a seminiferous plant from near Dundee, which were named *A. laevigata*. The main characters are that roughness is confined to the lamina edges, the base of the floret is bearded, but the rhachilla is very short and smooth (in *A. cespitosa* the rhachilla is long and hairy). *A. laevigata* bears culms a month earlier than *A. cespitosa*, is usually viviparous and never attains more than a foot in height.

P. de Beauvois (1812) split the genus *Aira* and designated the group including *A. cespitosa* and *A. alpina* as *Deschampsia*. The following viviparous forms are given by Roemer & Schultes (1817, 685 et seq.): *D. cespitosa* Beauv. γ var. *alpina*, *D. alpina* (L.) Roem. & Schult. and *D. laevigata* (Sm.) Sm. In 1824 (p. 105) Smith states that *A. laevigata* is within *A. alpina* L., which is now *D. alpina*.

Roemer & Schultes defined the insertion of the awn on the lowest lemma in *D. alpina* as somewhat below the open bifidity. Further details given were: the awn scarcely projects beyond the glumes, the upper lemmas bear terminal awns, the back and edges of the glumes are smooth. These features contrast with the sub-basal awn insertion and scabrid glume keels in *D. cespitosa*. The leaves of *D. alpina* are said to be short, always rolled, yellow-green and subulate.

Discussing the *Deschampsia* section of *Aira*, Syme (1872, 63-6) gave a variety γ *pseudalpina* (Syme's spelling was *Pseud-alpina*) of *A. cespitosa*, which is distinguished from the main form by smoother panicle branches and larger spikelets which are nearly always viviparous. He then described *A. alpina* L., stating that the panicle branches are smooth, the keels of the glumes are sometimes rough towards the apex but otherwise smooth and the awn is from about the middle of the lemma. He observed that all his specimens of *A. alpina* were viviparous and this species had often been confused with *A. cespitosa* var. *pseudalpina*. He considered the presence or absence of roughness on the lower portion of the glume keels the key to distinguishing the viviparous forms, and the point of insertion of the awn the main point for distinction of *D. alpina* from *D. cespitosa*.

Later it will be seen that difficulties arise because the state of the awn in viviparous forms other than *D. alpina* has never been defined, and the lower portion of the glume keels is quite smooth in all viviparous plants met with in this study.

Druce (1888) mentions *D. cespitosa* Beauv. var. *pseudalpina* (Syme). This is the

earliest reference found by the present author, in which *pseudalpina* is given as a variety of *D. cespitosa*, and not of *A. cespitosa*. Thus, strictly, *D. cespitosa* (L.) Beauv. var. *pseudalpina* (Syme) Druce is correct.

Seminiferous specimens of *D. alpina* are rare, although Linnaeus never mentioned vivipary in *A. alpina*. Don sent a flower-bearing plant to Smith (1811). Parnell (1842) describes and illustrates only seminiferous forms. Nygren (1949) received a sexual seed-bearing plant. The present author found a plant most of whose spikelets bore florets only. Another plant in culture (see below) produced a completely flower-bearing culm, although strongly viviparous when gathered in Harris.

7.2. Morphological observations

During the course of this study no viviparous specimens have been seen with a basally inserted awn. The awn is sometimes inserted about the middle of the third glume (i.e. the lowest lemma); this is the typical *D. alpina* arrangement. Often the

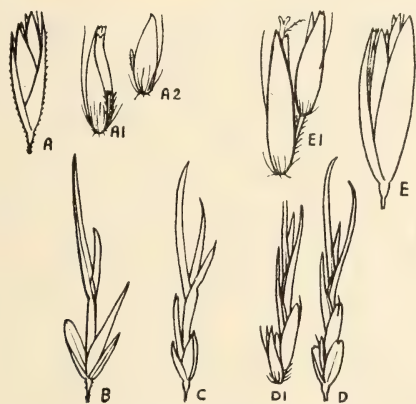


Fig. 7. *Deschampsia* spikelets.

A. *Deschampsia caespitosa* seminiferous ($\times 5.5$): 1. lower floret; 2. upper florets. B. *Deschampsia cespitosa* var. *pseudalpina*; C. *Deschampsia* 'intermediate' viviparous type. D. *Deschampsia alpina* viviparous; 1. lower glumes removed to display the poorly developed floret (B, C and D are all $\times 1.4$).

E. *Deschampsia alpina* seminiferous ($\times 7$); 1. lower glumes removed.

third glume is so metamorphosed that the awn appears as a terminal bristle or is absent. This, being the only other widespread form, is presumably the *D. cespitosa* var. *pseudalpina* condition.

There is an intermediate group, in which the awn is a hair lying between the twin ear-like terminal lobes of the third glume. In these intermediate forms there is a very short subterminal awn which is not clearly separated from the glume; it neither appears 'to arise' nor 'to be inserted.' Argument for inclusion with either of the main forms may be advanced, perhaps more strongly for *D. alpina*. In Figure 7 these types are illustrated.

The specimens in the herbaria of Linnaeus and Smith (Linn. Soc. Lond.) and of Syme (B.M.) were consulted. There are no specimens labelled *A. alpina* by Linnaeus but in his collection are two viviparous plants, apparently *D. alpina* with slight intermediate tendencies, labelled 'Lapp' and joined to *A. cespitosa*.

The plants in Smith's collection appear to be a seminiferous *D. alpina* labelled *A. alpina*; viviparous 'intermediate' plants marked '*A. laevigata*,' which he later considered *A. alpina*; and finally a viviparous plant of var. *pseudalpina* placed under *A. cespitosa*. (To avoid damage the specimens could not be very closely examined.)

Syme had two viviparous plants of 'intermediate' type from North Wales under *A. cespitosa*, which in the absence of others are presumably his var. *pseudalpina*. There are forty-seven Scottish viviparous specimens, all labelled *A. alpina*, but including in the present author's opinion the var. *pseudalpina*, intermediate plants and *D. alpina*. Evidently Syme used glume-keel smoothness as a key character. But this course includes in *A. alpina*, as interpreted by Syme, many plants hard to bring into *D. alpina*, and in fact all viviparous *Deschampsiae* in this present study.

In order to escape from this impasse of conflicting and overlapping definitions and the lack of any other names free from ambiguity, awn-insertion is used here as the criterion and an 'intermediate' category maintained.

All the seminiferous plants with basally inserted awns (*D. cespitosa*) have been found to have markedly scabrid leaves, panicle branches and glumes.

Since var. *pseudalpina* is a segregate of *D. cespitosa*, a gradation of certain characters from seminiferous *D. cespitosa* through the var. *pseudalpina*, the 'intermediate,' to the typical *D. alpina* might be expected.

Forty-six viviparous *Deschampsia* specimens have been classified by the condition of their third glume's awns at the time of collection. Other features were not consistently distributed, so this one major criterion was selected. Even so, the spikelets in a panicle are not all the same, and in deciding the category the whole was considered. It is partly for this reason that the 'intermediates' have not been lumped with *D. alpina*, and also because the specimens placed by Syme in *A. cespitosa* are intermediate.

In Table 4 the numbers of the plants with different characters are given, and in the first column the condition in seminiferous *D. cespitosa*.

The leaves and panicle branches are rougher in proportionately more var. *pseudalpina* than *D. alpina* plants, but smooth forms occur in both, although the trend is in agreement with the postulated gradation.

The midribs of lower glumes of all viviparous plants are innocent of roughness in their lower portions, hence this character from Roemer & Schultes, and Syme, does not separate these plants. Hairiness about the floret base is typical of seminiferous *D. cespitosa*, but only var. *pseudalpina* plants were naked.

Living portions of the plants discussed above were also collected; sixteen bore culms in London the next year. In April the *Deschampsiae* were making poor growth and were brought into a glass cabinet, where they obtained additional warmth and illumination. This speeded shooting and was responsible probably for the greater degree of floret-bearing in these conditions than in nature. Except the *D. alpina* plant which became fully flower-bearing, none of the inflorescences were completely free of proliferation. Established bulbils also bore viviparous culms. Here vivipary is a hereditary character modified by environment. The inflorescences obtained in culture are classified by awn type in the lower part of Table 4. It will be seen that there has been a shift towards *D. alpina* features.

It is suggested that this tendency towards *D. alpina* is associated with the bearing of more floral organs in the forced plants. These plants were further studied and it was noted, especially in the 'intermediate' group, that, where fully-floret-bearing and viviparous spikelets occurred in the same panicle, the floret lemmas were of a *D. alpina* character, but the proliferated spikelets usually bore third glumes of an 'intermediate' or *pseudalpina* type. As flower-bearing increases, so the awn becomes more clearly distinguished, longer, and inserted lower. Thus decreasing proliferation is accompanied by an approach to *D. alpina*, and if the trend could be continued, to the typical seminiferous *D. cespitosa* form.

Conversely, increasing vivipary causes a transition from the seminiferous *D. caespitosa*

TABLE 4
Characters of viviparous *Deschampsiae*

		D.c.	Dcp.	D.i.	D.a.
Forty-six as originally collected :—					
Third glume awn-insertion	Sub-basal Subterminal/central dorsally Slightly subterminal Terminal (or awn absent)	×	20	9	17
Leaves	Rough Slightly rough Smooth	×	1 12 7	1 3 5	8 9
Panicle branches	Rough Slightly rough Smooth	×	9 11	4 5	3 14
Lower portion of glume keels	Rough Smooth	×	20	9	17
Hairs at floret (or third glume) base	Many and long Few and short Absent	×	10 5 5	6 3	13 4
Sixteen plants which bore culms in culture :—					
Classified by their original awn-insertion :—			8	3	5
Awn-insertion after cultivation in London	Dcp. D.i. D.a.		4 2 2	2 1	1 4
Classified by their final awn-insertion			4	5	7

Typical condition of seminiferous plants indicated by '×'

Abbreviations : D.c. – *Deschampsia cespitosa* seminiferous type; Dcp. – *Deschampsia cespitosa* var. *pseudalpina*; D.i. – *Deschampsia* intermediate viviparous type; D.a. – *Deschampsia alpina*.

Waviness of panicle branches, leaf rolling, blade/sheath lengths ratio and leaf/culm height ratio were tried, but abandoned as they vary within seminiferous *D. cespitosa* as well as amongst the viviparous forms.

through *D. alpina* to the extreme var. *pseudalpina* type, in which the third glume has lost all lemma-like qualities and resembles a foliage leaf. Morphologically the var. *pseudalpina* is farther from normal *D. cespitosa* than *D. alpina*.

Ecological discussion is deferred, but, briefly stated, seminiferous *D. caespitosa* in all its forms is the most widely distributed ecologically and geographically. In Britain, var. *pseudalpina* has the greatest range among the viviparous *Deschampsiae* and *D. alpina* the least. 'Intermediate' forms are found mainly within the range of *D. alpina*, but also beyond, as in North Wales. Some botanists report *D. alpina* in N. Wales; they may either have found this species in the strictest sense, have been unaware that all viviparous specimens are not within *D. alpina*, or have taken a broader view on the 'intermediate' types, which is reasonable.

7.3. Cytological Observations

Seminiferous *D. cespitosa* has chromosome numbers of : $2n = 26$ (Lawrence, 1945), $2n = 28$ (Avdulow, 1931; Nielson & Humphrey, 1937; and Hagerup, 1939). Seminiferous *D. alpina* $2n = 26$ (Nygren, 1949). Slightly or partly viviparous *D. alpina* $2n = 39$ (Flovik), strongly or fully viviparous *D. alpina* $2n = 41, 49, 52$ and 56 (Flovik, 1938; Hagerup, 1939; and Nygren, 1949). Nygren traced a series of increasing vivipary with polyploidy.

In the present work, various root squash techniques were unsuccessfully attempted. Therefore root-tips were sectioned and the chromosomes in metaphase plates counted by means of a camera lucida (total magnification $\times 1,000$). Chromosomes were about 5μ long. In sectioned material there is no certainty that plates are complete or that long chromosomes have not been cut into parts. In practice the best plates were counted and the modal number taken. The numbers in Table 5 are given as approximate and not as a critical study. But they are adequate to demonstrate that cytology is a poor key to the classification of the viviparous *Deschampsiae*.

TABLE 5
Approximate Diploid Chromosome Numbers of *Deschampsiae*

Location	var. <i>pseudalpina</i>	"intermediate"	<i>D. alpina</i>
West Mayo	44, 44, 47, 47, 49	34, 37	34
North Wales	37		
Lake District	32		
Grampians	(31-32), 41		38
Western Isles	36	39	36

The numbers are erratic. The morphological characters are also somewhat randomly arranged if awn-type is used as a key. This suggests that there is considerable variation due to occasional sexual reproduction. In *D. alpina* especially, good stamens are common and not infrequently well-formed pistils are found.

7.4. The employment of the names *Deschampsia alpina* (L.) Roem. & Schult. and *Deschampsia cespitosa* var. *pseudalpina* (Syme) Druce

All facets of the subject, historical, morphological and cytological, show how weak is the distinction between the two forms. All forms cannot be brought within *D. alpina* (L.) R. & S., unless absence of an awn due to metamorphosis is counted as insertion above the middle of the third glume. This is supported by the transition series and that, in this series, *D. alpina* stands closer to seminiferous *D. caespitosa* than the var. *pseudalpina*, which is allegedly a segregate of the latter.

The different ranges argue for their retention and fuller knowledge may be lost by failing to distinguish them, especially as these observations are confined to the British Isles.

Two forms are recognized : *Deschampsia alpina* (L.) Roem. & Schult. in which the awn is inserted about the middle or upper part of the dorsal rib of the third glume (lemma of the lowest floret), and *D. cespitosa* var. *pseudalpina* (Syme) Druce in which proliferous metamorphosis prevents the distinction of a separated awn. There are intermediate forms between them, and spikelets of the same panicle may not all fall into one category.

The literature yields no well defined name free from ambiguity which covers either all the viviparous *Deschampsiae*, or all those other than *D. alpina*.

8. SUMMARY

8.1. The continued growth of the spikelet axis and the bearing of foliage leaves distally upon it is termed the vegetative proliferation of spikelets. If these leafy shoots form deciduous plantlets, which are the regular diaspores of the plant, the phenomenon is called vivipary by many authors.

The history and confusion of these terms is traced. Proliferation is an older and more accurate usage and should be employed in morphological and physiological discussions. Vivipary is useful in its restricted sense to describe regular propagation in this manner, as it has ecological meaning.

8.2. Five races of viviparous grasses are native in Britain; these have an arctic-alpine range about the North Atlantic.

Festuca vivipara (L.) Sm.

Poa alpina L. var. *vivipara* L.

Poa × *jemtlandica* (Almq.) Richt.

Deschampsia cespitosa (L.) Beauv. var. *pseudalpina* (Syme) Druce.

Deschampsia alpina (L.) Roem. & Schult.

Poa bulbosa L. var. *vivipara* Koel., a plant of dry disturbed places, is an alien in the British flora.

8.3. The names of the *Poae* are accepted without discussion.

8.4. *Festuca vivipara* is clearly of the *F. ovina* agg. The vegetative variation within *F. vivipara* is almost as wide as in *F. ovina* agg., thus *F. vivipara* cannot be placed as a subspecies or variety of a segregate of *F. ovina*.

F. vivipara includes both fully and partially viviparous forms, which may be distinguished by Turesson's names *viviparae* and *semiviviparae* respectively.

8.5. *Deschampsia cespitosa* var. *pseudalpina* and *D. alpina* are recognized. Although only the latter is at all well defined, and transition forms exist between the two. Neither vivipary nor the characters that distinguish the forms are completely constant. The forms are not separate cytologically.

An argument is advanced that the more proliferated var. *pseudalpina* is further from seminiferous *D. cespitosa* than *D. alpina*. They are left separate, partly in view of their differences in ecological range and partly because of the lack of a suitable well known name.

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THE DISTRIBUTION OF *DRYOPTERIS BORRERI* NEWM. IN THE BRITISH ISLES

By J. P. PUGH

INTRODUCTION

The fern that has been called *Dryopteris filix-mas* var. *paleacea* has been well known to botanists for many years. Manton (1950, 54) has given reasons for raising this fern to specific rank as suggested by Newman (1854, 189) and the plant is now known as *Dryopteris borrieri* Newm. in Britain. This work was undertaken with a view to determining the distribution of *D. borrieri* in the British Isles, correlating this with its distribution on the continent, and comparing it with the distribution of *D. filix-mas*. A general account is given in this paper ; detailed cytological work has been started and will be reported at a later date.

DESCRIPTION OF *D. BORRERI* NEWM.

The distinguishing characters of *D. borrieri* are :—

- (1) The large number oframenta (scales) extending along the abaxial side of the rachis of the frond from base to apex, which tend to be red-brown in colour as opposed to those of *D. filix-mas* which are far less abundant and yellow-brown in colour.
- (2) The pinnules tend to be truncate and less toothed than those of *D. filix-mas* and also they are incompletely separated at the base (fig. 1).



Fig. 1. Ventral view of pinnules of *D. borrieri* (left) and *D. filix-mas* (right) ($\times 2$).

- (3) The fronds of *D. borrieri* tend to be tougher than those of *D. filix-mas*, persisting long into the autumn and often overwintering.
- (4) In the spring the indusium is tucked under the edges of the sorus, whereas in *D. filix-mas* the indusium lies flat on the surface of the frond around the sorus (fig. 2).
- (5) Fresh specimens exhibit a small area of black pigment at the base of the pinna rachis where it joins the main rachis of the frond. This pigment is absent in herbarium specimens and has been found to disappear within a month of collection.
- (6) *D. borrieri* reproduces apogamously, the sporophyte arising directly from the tissues of the gametophyte without the formation of archegonia. Hence there is no sexual fusion, although fertile male gametes may be formed. Reproduction is quite normal in *D. filix-mas*.

Wide variation occurs throughout this species, and the most reliable character seems to be the large number of rameta on the rhachis. It has been known for some time that the fronds of *D. borrieri* tend to overwinter whereas those of *D. filix-mas* do not, and this characteristic is obvious in winter when green plants of *D. borrieri* are most prominent amidst brown, tangled remains of *D. filix-mas*.

In spring, the indusial character, as shown in fig. 2, is unmistakable, but this condition does not persist for long.

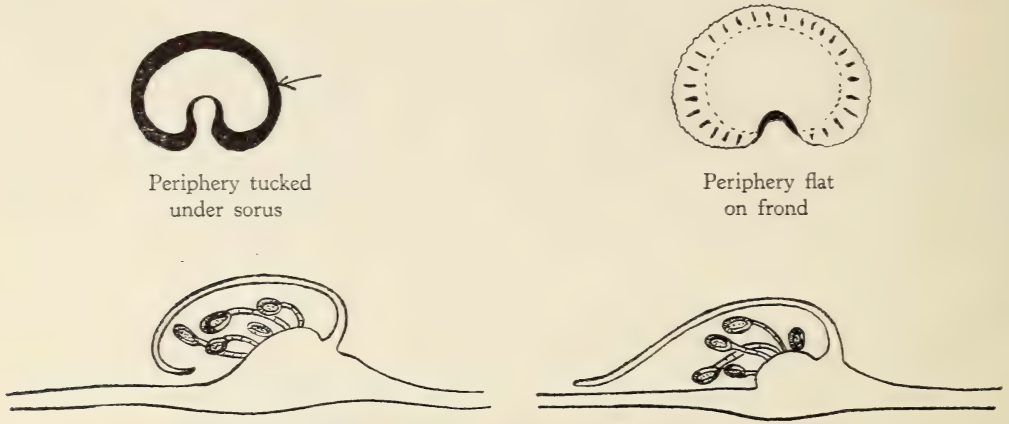


Fig. 2. Surface views and diagrammatic longitudinal sections of the sori of *D. borrieri* (left) and *D. filix-mas* (right) ($\times 20$).

The truncate nature of the pinnules is sometimes very marked, but a gradation series between the truncate form and the tapering form characteristic of *D. filix-mas* has been observed. However, in specimens of *D. borrieri* which exhibited more or less tapering pinnules, the periphery of the pinnules was more entire and less toothed than comparable pinnules of *D. filix-mas*.

D. borrieri has been described as yellow-green in colour (Newman, 1854, 191; Warburg, 1952, 38). Manton (1950, 54) records it as often more yellow-green. Material is abundant in the British Isles and on the continent which is definitely dark green. Therefore colour is not a reliable diagnostic character and conditions affecting the colour are being investigated.

Information regarding the distribution of *D. borrieri* in the British Isles is still very incomplete and any records of localities would be most welcome, especially from Ireland. The inclusion of a small note regarding topography and geology (where possible) would also be useful, as these will greatly assist in the determination of ecological requirements.

DISTRIBUTION

The following list shows the records as they are known at present; it is composed of all the localities for which there is an herbarium specimen; these localities are represented on the map (fig. 4) as solid dots. The open circles on the map represent all the localities mentioned in the literature and a list of these has been deposited in the Cryptogamic Room of the British Museum (Natural History). I am indebted to the following for personal communication of several localities:— D. E. Allen, O. Buckle, J. G. Dony, Miss E. J. Gibbons, J. D. Grose, J. W. Heslop-Harrison, H. A. Hyde, R. M. Payne, H. Milne-Redhead, Miss C. M. Rob, W. A. Sledge and A. E. Wade.

KEY TO HERBARIA

Aberdeen University	(Ab U)	C. B. Burt at Kew	(K.Burt)
British Museum (Nat. Hist.)	(B.M.)	Moore at Kew	(K.Moore)
Boswell-Syme at B.M.	(B.M.Bosw.)	Watson at Kew	(K.Wats)
Sowerby at B.M.	(B.M.Sow.)	A. J. Lacey	(Lacey)
Ley at Birmingham University	(B.U.Ley)	Luton Museum	(Lut)
Cambridge University	(Cam)	National Museum (Ireland)	(NMI)
Carlisle Museum	(Car)	Norwich Castle Museum	(Norw)
Royal Botanic Garden, Edinburgh	(E)	Oxford University	(Ox)
Royal Albert Museum, Exeter	(Ex.Hiern)	R. M. Payne	(Payne)
J. Gibbons	(Gibb)	J. P. Pugh	(Pugh)
Brody at Gloucester Museum	(Glo.Brod.)	F. Rose	(Rose)
Kew	(K)	P. Taylor	(Tayl)
Borrer at Kew	(K.Borr.)	Welsh National Herbarium	(WNH)

RECORDS WITH HERBARIUM SPECIMENS

- V.c. 1. W. CORNW. : nr. Chygarkye, 1936, *R. Melville*, (K); Madron, 1946, *E. Milne-Redhead*, (K); Penryn, 1856, *G. Dawson*, (K.Moore); Penzance, 1887, *A. Bennett*, (B.M.).
2. E. CORNW. : Callington, 1936, *R. Melville*, (K); Charlestown, 1926, *E. Thurston*, (K); nr. Egloskerry, 1915, *E. Thurston*, (K); nr. Fowey, 1949, *J. P. M. Brenan*, (K); Lostwithiel, 1839, *Babington*, (Cam); Veryan, 1938, *A. H. G. Alston*, (B.M.).
3. S. DEVON : Cockington, Torquay, 1943, *G. V. C. Last*, (K); between Colebrooke and Shaugh, 1878, *T. R. Archer Briggs*, (B.M. & K.Wats); Kilminster, 1937, *A. H. G. Alston*, (B.M.); nr. Plymouth, 1877, *T. R. Archer Briggs*, (B.M.); Sidmouth, 1935, *J. W. Wyatt*, (K); bank of Tavy, 1884, *J. Vaughan*, (Ox).
4. N. DEVON : Barnstaple, 1859, *Jackson*, (K. Moore); Bratton Fleming, 1918, *A. J. Wilmott*, (B.M.); nr. Brendon, 1917, *W. C. Barton*, (B.M.); Clovelly, 1890, *F. R. Terrast*, (Cam); Combe Martin, 1839, *Babington*, (Cam); Lynmouth, 1902, *C. B. Green*, (Ox); Lynton, 1879, *W. J. Lawson*, (Ab U); North Molton, 1939, *Hiern*, (Ex.Hiern); Rodney, nr. Lynmouth, 1919, *H. W. Pugsley*, (B.M.).
5. S. SOM. : Dulverton, 1892, *R. P. Murray*, (B.M.); Elworthy, 1865, *T. Moore*, (K.Moore); West Lyn Valley, 1913, *F. Long*, (Norw); Otterford, 1949, *E. Milne-Redhead*, (K).
6. N. SOM. : Badgworth, 1886, *H. W. Pugsley*, (B.M.); Portbury, 1899, *H. W. Pugsley*, (B.M.); Stourton Woods, 1892, *E. F. Linton*, (B.M.); Clifton, 1951, *P. Taylor*, (Tayl); Hallatrow, 1918, *I. M. Roger*, (Cam & Ox); Weston-Super-Mare, 1860, *Mrs. Walker*, (K.Moore).
8. S. WILTS. : Landford, several localities, 1952, *J. P. Pugh*, (Pugh); nr. Stourton, 1892, *R. P. Murray*, (B.M.).
9. DORSET : Bovington, 1818, *J. Ladbrook*, (B.M.Bosw); Charmouth, 1848, *H. D. Geldart*, (Norw); Halstock, 1918, *I. M. Roper*, (Norw).
10. WIGHT : Alum Bay, 1889, *C. E. Palmer*, (Ox).
11. S. HANTS. : Islands Thorns Inclosure, 1952, *J. P. Pugh*, (Pugh); Pondhead Inclosure, Lyndhurst, 1952, *J. P. Pugh*, (Pugh).
13. W. SUSSEX : Horsham, 1864, *F. J. Broods*, (K).
14. E. SUSSEX : Eridge, 1950, *A. H. G. Alston*, (B.M.).
15. E. KENT : Dungeness, 1952, *F. Rose*, (Pugh).
16. W. KENT : nr. Bidborough, 1883, *F. H. Ward*, (B.M.Sow); nr. Hawkhurst, 1952, *F. Rose*, (Pugh); Tunbridge Wells, 1850, *Miss Beever*, (K.Moore); nr. Goudhurst, 1952, *F. Rose*, (Pugh).
17. SURREY : nr. Haslemere, 1938, *A. H. G. Alston*, (B.M.); Kew, 1879, *G. Nicholson*, (Ab U); Leith Hill, 1952, *J. P. Pugh*, (Pugh); Pirbright, 1870, *H. C. Watson*, (K.Wats); Woking Heath, 1870, *H. C. Watson*, (K.Wats).
18. S. ESSEX : Epping Forest, 1951, *R. M. Payne*, (Pugh).
19. N. ESSEX : Stour Woods, 1951, *J. P. Pugh*, (B.M. & Pugh).

25. E. SUFF. : Bentley Long Wood, 1951, *J. P. Pugh*, (B.M. & Pugh).
27. E. NORF. : Aylmerton, 1952, *J. P. Pugh*, (B.M. & Pugh); Little Plumstead, 1952, *J. P. Pugh*, (B.M. & Pugh); Rockland, 1952, *J. P. Pugh*, (B.M. & Pugh); Walsham, 1952, *J. P. Pugh*, (Pugh); Bacton Wood, 1952, *J. P. Pugh*, (Pugh).
30. BEDS. : Chiltern Green, 1946, *P. Taylor*, (B.M. & K); Heath & Reach, 1946, *P. Taylor*, (Lut); Kings Wood, 1946, *P. Taylor*, (Lut); Luton Hoo, 1946, *P. Taylor*, (Lut).
31. HUNTS. : Holme Fen, 1951, *F. Rose*, (Rose).
33. E. GLOS. : Driffield Wood, 1910, *W. C. Barden*, (B.M.); Hareshfield Beacon, 1926, *C. B. Burt*, (K.Burt).
34. W. GLOS. : Huntley, 1946, *P. Taylor*, (B.M. & Tayl); Mitcheldean, *A. Ley*, (Glo.Brody); Putten Edge, *A. Ley*, (B.U.Ley).
35. MON. : Black Mts, 1871, *A. Ley*, (B.M.Bosw, K.Wats, Ox); Buckholt Wood, 1945, *S. G. Charles*, (WNH); Cross ash, 1944, *S. G. Charles*, (WNH); Cwn Glyn, nr. Pontypool, *T. H. Thomas*, (WNH); Dingestow, 1948, *S. G. Charles*, (WNH); Grossmont Wood, 1944, *S. G. Charles*, (WNH); Kilgwrrwg, 1908, *W. H. Shoolbred*, (WNH); Llandogo, 1944, *S. G. Charles*, (WNH) Newport, *E. Newman*, (B.M.); Reddings Enclosure, nr. Monmouth, 1945, *R. Lewis*, (B.M., K, WNH); Talycoed, 1943, *S. G. Charles*, (WNH).
36. HEREF. : nr. Bromyard, 1951, *P. Taylor*, (Tayl).
40. SALOP : nr. Broseley, 1855, *Maw*, (K.Moore, Ab U, Norw); Quillus Wood, 1883, *G. C. Druce*, (Ox).
41. GLAM.: Caerphilly Mt., *H. A. Hyde & A. E. Wade*, (WNH); nr. Maersaraul Ely, 1873, *T. Moore*, (K.Moore); Merthyr Tydfil, 1839, *Babington*, (Cam); Mountain Ash, 1904, *W. C. Barton*, (B.M.); Taffs Well, 1928, *A. E. Wade*, (WNH).
42. BRECON: nr. Cefn, 1903, *W. C. Barton*, (B.M.); Grwyne Valley, 1944, *S. G. Charles*, (WNH); Llandetty, 1946, *E. Milne-Redhead & H. K. Airy Shaw*, (B.M.); Taren yr Esgob, 1942, *S. G. Charles*, (WNH).
44. CARM. : Ammanford, 1951, *H. Davies*, (Pugh); Ystrad ffyn, 1950, *H. A. Hyde & A. E. Wade*, (WNH).
45. PEMB. : Cilgwyn, 1932, *A. H. G. Alston*, (B.M.); Castle Malgwyn, 1856, *W. Hutchinson*, (K); between Narbeth and St. Clears, 1931, *A. H. G. Alston*, (B.M.).
46. CARD. : nr. Aberystwyth, 1951, *P. Taylor*, (Tayl).
47. MONT. : Casseinion, 1951, *P. Taylor*, (Tayl); Cwm Einion, 1945, *P. W. Richards* (Cam).
48. MER. : Abergwynant, 1951, *P. Taylor*, (Tayl); nr. Barmouth, 1857, *W. A. Leighton*, (Cam); Cader Idris, 1948, *P. Taylor*, (K); nr. Cymeron Falls, 1941, *J. A. Webb*, (WNH); N. of Dyffrydau, 1948, *E. Milne-Redhead*, (K, WNH); between L. Gwernan and Dolgelley, 1951, *W. C. Barton*, (B.M.); Moel Cynwch, 1886, *W. Moyle Rogers*, (B.M.); Dolgelley, 1854, *T. Hawley*, (D, NMI).
49. CAERN. : nr. Bangor, 1945, *I. Manton*, (B.M.); Beddgelert, 1869, *Steele*, (NMI); nr. Capel Curig 1863, *Mrs. Battersby*, (K.Moore); Dolgarrog, 1928, *A. Wilson*, (WNH); Llanberis, 1875, *A. Bennett*, (B.M.); lower slopes of Moel Hebog, 1951, *P. Taylor*, (Tayl); Waenfawr, 1909, *C. W. Welfitt-Nicholls*, (K).
50. DENB. : Pentre-Foelas, 1854, *C. E. Palmer*, (Ox); Ruthin, 1855, *T. Pritchard*, (K.Moore).
53. S. LINCS. : Norton Disney, 1951, *J. Gibbons*, (Gibb); Stapleford Moor, 1951, *J. Gibbons*, (Gibb).
54. N. LINCS. : Croppers Gorse, 1951, *J. Gibbons*, (Tayl); Holton le Moor, 1951, *J. Gibbons*, (B.M.); Raithby Brackens, 1951, *J. Gibbons*, (Gibb); Roxton Wood, 1951, *J. Gibbons*, (Tayl); Walesby, 1951, *J. Gibbons*, (Gibb); Welton le Marsh, 1945, *A. H. G. Alston*, (B.M.).
57. DERBY : Edlaston, 1887, *W. R. Linton*, (Cam).
60. W. LANCS. : nr. Thrang End, 1951, *P. Taylor*, (Tayl).
62. N.E. YORK : Beckdale, 1841, *J. G. Baker*, (K.Wats); Kirkleatham, 1862, *J. Duncan*, (K.Moore).
63. S.W. YORK : nr. Barnsley, 1880, *H. Johnson*, (B.M.); Bilberry, nr. Holmfirth, 1894, *R. S. Standen*, (B.M.).
64. M.W. YORK : Bolton Abbey, 1946, *P. Taylor*, (Tayl); nr. Buckden, 1934, *A. H. G. Alston*, (B.M.); Harrogate, 1837, *C. A. Stevens*, (Car); Ingleborough, 1879, *E. Newman*, (B.M.Sow).

65. N.W. YORK : Cautley Spout, 1934, A. H. G. Alston, (B.M.); Holwick, 1925, C. I. & N. Y. Sandwith, (K).
66. DURHAM : High Force, 1886, H. J. Muswell & A. Bennett, (B.M.).
67. NORTHUMB. S. : nr. Featherstone Castle Ravine, 1951, P. Taylor, (Tayl).
68. CHEVIOTL. : Beanley, 1867, (K.Moore).
69. WESTMORL. : Barbondale, 1946, P. Taylor, (Tayl); Hilton Rigg Wood, 1951, P. Taylor, (Tayl); Hodge Hill, Cartmell Fell, 1929, L. Baker, (K); Kentmere, 1886, F. H. Ward, (B.M.Sow); Pennybridge, 1863, R. Morris, (K.Moore); Troutbeck, 1879, G. Nicholson, (Ab U); Windermere, 1859, W. C. Barton, (B.M.); Whitbarrow Scar, 1951, P. Taylor, (Tayl); St. Helens, Dalton, 1921, W. H. Pearsall, (Ox).
70. CUMB. : Carlisle, 1885, P. Shepherd, (Car); Eskdale, 1927, R. H. Williamson, (Car); Grange, Borrowdale, 1951, A. J. Lacey, (Lacey); Keswick, 1926, Mrs. Reynolds, (K); Skiddaw, 1870, E. F. Linton, (B.M.); St. Bees Head, 1950, C. W. Muirhead, (Car).
72. DUMFR. : Moffat, 1860, J. Anderson, (K.Moore); Penton, 1949, P. Taylor, (K).
73. KIRKC. : nr. Mainsriddle, 1951, P. Taylor, (Tayl).
75. AYR : Kilmarnock, 1881, W. Birrell, (K).
77. LANARK : Biggar Shiels Wood, 1868, N. Fraser, (E); Lamington Glen, 1863, N. Fraser, (E).
78. PEEBLES : nr. Mossfenman, 1868, N. Fraser, (E).
80. ROXB. : Newcastleton, 1951, P. Taylor, (Tayl).
83. EDINB. : Hawthornden, 1865, T. Moore, (K.Moore); Pentland Hills, Edinburgh, 1841, H. C. Watson, (K.Wats); nr. Cramond, 1833, W. MacGillivray, (Ab U); Bavelaw Wood, 1902, W. E. Evans, (E); Roslin, 1837, (E); Lasswade, 1859, W. R. McNab, (NMI); nr. Edinburgh, 1858, R. Brown, (Ab U).
85. FIFE : Balmuto, 1874, J. Boswell-Syme, (B.M., Cam, Ab U); Glassmane Hill, Kilrie, 1874, J. Boswell-Syme, (B.M.Bosw); Kinross, 1874, M. Ridley, (K.Moore); Orrock Hill, 1874, J. Boswell-Syme, (B.M.Bosw); Cullalo, 1874, J. Boswell-Syme, (B.M.Bosw).
86. STIRL. : Campsie, 1851, (Ab U); Inversnaid, 1854, T. Moore, (K.Moore).
87. W. PERTH : Pass of the Trossachs, 1854, T. Moore, (K.Moore); Loch an Balloch, 1855, T. Moore, (K.Moore); Tillicoultry Glen, 1876, J. Boswell-Syme, (B.M.Bosw); Callander, 1864, N. Fraser, (E).
88. MID PERTH : Ben Lawers, 1855, T. Moore, (K.Moore); Cairnie, 1910, J. Farquharson, (Car); Glenturret, nr. Crieff, 1899, C. B. Clarke, (K); Loch-na-Larige, 1932, G. Taylor, (B.M.); Perth, 1946, A. H. G. Alston, (B.M.).
89. E. PERTH : nr. Ballinluig, 1888, E. S. Marshall, (Cam).
90. FORFAR : Clova Mts, 1835, J. Backhouse, (K); Glen Fiagh, Clova, 1923, R. H. Williamson, (Car); cliffs by Loch Brandy, Clova, 1921, H. W. Pugsley, (B.M.); nr. Loch Long, 1947, A. H. G. Alston, (B.M.); Shieldhill, 1924, (B.M.).
92. S. ABERD. : Robslaw Den, nr. Aberdeen, 1876, J. W. H. T., (Ab U).
94. BANFF : nr. Fordyce, 1949, A. H. G. Alston, (B.M.).
95. ELGIN : Dunphail, nr. Forres, 1859, F. Browne, (K.Moore); Moseley, nr. Birnie, 1863, N. Fraser, (E).
96. EASTERNESS : nr. Drumnadrochit, 1947, C. C. Townsend, (B.M.); Dalwhinnie, 1839, H. C. Watson (K.Wats); Dunean Hill, 1866, N. Fraser, (E); Badger Fall, Fasnakyle, 1947, N. Y. Sandwith, (K).
97. WESTERNESS : nr. Arisaig, 1950, M. E. D. Poore & C. D. Pigott, (B.M.); Cairndow, 1855, T. Moore, (K.Moore); Glen Cripesdale House, 1884, (B.M.); Glen Spean, 1891, G. C. Druce, (Ox); by L. Sunart, 1884, E. F. Linton, (B.M.).
98. MAIN ARGYLL : Ardchattan, 1860, W. Haliday, (Ox); Ardrishaig, 1855, T. Moore, (K.Moore); Glen Coe, 1855, T. Moore, (K.Moore); Glen Croe, 1855, T. Moore, (K.Moore); Glen Gillip, T. Moore, (K.Moore); Glen Kinglas, 1855, T. Moore, (K.Moore).
99. DUNB. : Luss, 1857, A. O. Brodie, (E); Tarbet, 1855, T. Moore, (K).
100. CLYDE ISLES : Glen Shant, Brodick, Arran, 1852, (Ab U); Bute, 1827, Greville, (E).

101. KINTYRE : Campbeltown, 1950, *M. H. Cunningham*, (B.M.).
 104. N. EBUDES : S.W. of Kil-Marie, Strathaird Peninsula, Skye, 1951, *D. J. Griffiths*, (B.M.); Armadale, Skye, 1903, *W. C. Barton* (B.M.); Quiraing, Skye, 1884, *E. F. Linton*, (B.M.).
 105. W. ROSS : Diabaig, 1936, *A. J. Wilmott*, (B.M.); Strome Ferry, 1884, *E. F. Linton*, (B.M., Ox Cam).
 106. E. ROSS : Isle of Cromarty, 1881, (Ox).
 108. W. SUTH. : Ben Hope, 1833, *W. R. McNab*, (NMI); Lochinver, 1890, *E. S. Marshall*, (Cam); Melvich, 1886, *E. S. Marshall*, (Cam).
 111. ORKNEY : E. Corrie, on N.W. face of Hoy Hill, 1880, *H. H. Johnston*, (NMI); Hammers, Syradale, Firth, 1883, *H. H. Johnston*, (Ox); Houton, 1952, *J. T. Syme*, (K.Wats); Ramsdale, Swanbister, 1873, *J. T. Boswell-Syme*, (B.M.Bosw); Swartages, Birsay, 1921, *H. H. Johnston*, (E); nr. Wastdale Mill Farm, Firth, 1880, *J. T. Boswell-Syme*, (B.M.Bosw).
- H. 1. S. KERRY : nr. Cloonee Loughs, 1952, *A. H. G. Alston*, (B.M.).
2. N. KERRY : Killarney, 1952, *A. H. G. Alston*, (B.M.).
 3. W. CORK : Inchigeelagh, 1952, *A. H. G. Alston*, (B.M.).
 4. MID CORK : E. of Macroom, 1952, *A. H. G. Alston*, (B.M.).
 7. S. TIPP. : Newcastle, 1882, *J. Britten & C. Nicholson*, (B.M.).
 8. LIM. : Foynes, 1902, *C. G. Brien*, (NMI).
 9. CLARE : Glen at Ennistymon, 1865, *Hb. Churchill*, (K); Kilfenora Bog, 1947, *J. G. Dony*, (K).
 12. WEXF. : nr. Mt. St. Benedict, 1952, *A. H. G. Alston*, (B.M.).
 15. S.E. GALW. : Slieve Aughty, Dalystown, 1945, *I. Manton*, (K).
 16. W. GALW. : Clifden, 1907, *J. W. White*, (Cam); banks of Glen Inagh, 1900, *J. S. Gamble*, (K); Kylesmore, 1855, *R. Barrington*, (K.Moore).
 20. WICKLOW : Ballyarthur, 1894, *R. Lloyd Praeger*, (NMI); nr. Enniskerry, 1894, *R. Lloyd Praeger*, (NMI); Templemichael, Arklow, 1882, *W. Fawcett*, (B.M.); nr. Up. Lough Bray, 1855, *R. Barrington*, (K.Moore).
 22. WESTMEATH : Knock Drin, 1895, *E. S. Gregory*, (B.M.).
 27. W. MAYO : Ballycray Mts, 1855, *R. Barrington*, (K. Moore); Inishturk, 1906, *R. Lloyd Praeger*, (WNH, NMI).
 28. SLIGO : Lough Gill, 1855, *R. Barrington*, (K.Moore).
 33. FERM. : Slieve Rushen, 1949, *P. Taylor*, (Tayl).
 35. N. DON. : Killybegs, 1855, *R. Barrington*, (K.Moore).
 36. TYRONE : Omagh, 1896, *M. C. R.*, (NMI).
 38. DOWN : Sandy Warren, Newcastle, 1893, *S. A. Stewart*, (NMI).
 40. DERRY : below Glenbourne Pass, on road to Maghera, 1930, *M. M. Whiting*, (K).

DISCUSSION

Von Wolf (1936) produced the map (fig. 3) to show the northern limits of *D. borrieri* Newm. in Europe :

The map (fig. 4) showing the detailed distribution of *D. borrieri* in the British Isles, is in agreement with von Wolf's. From this map it can be seen that this species occurs rather irregularly throughout the British Isles and, like most native ferns, is more abundant in the west than in the east, since the higher humidity in the west offers a more favourable habitat for this group of plants. The vice-comital distribution also requires comment. *D. borrieri* may well be absent from Cambridgeshire, since there are so few woods in this county, but would be expected to occur fairly frequently in Yorkshire, Northumberland and Durham. The alkalinity of the soil in East Anglia may, in some measure, inhibit *D. borrieri*, although there is a small, isolated fen in the

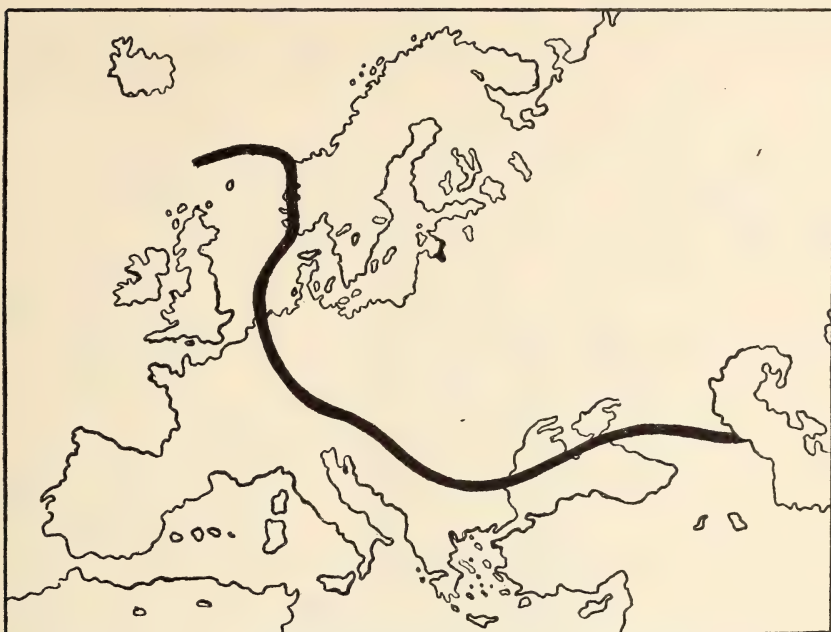


Fig. 3. Northern limit of *Dryopteris borrieri* in Europe.

south of England in which this fern is present. The pH of the soil has not yet been investigated and, therefore, no definite information on this point is available. Of the several localities in Norfolk and Suffolk, in which this fern has been found, none is markedly alkaline and it is probable that *D. borrieri* occurs in many other localities which have not yet been recorded. Lee (1933) reports that *D. borrieri* is common in Ayrshire and a few localities in the south-east corner of Kirkcudbrightshire. The latter localities have been confirmed by representative specimens collected in 1951 by P. Taylor. It therefore seems most improbable that this fern is entirely absent from Wigtown although there are, as yet, no records. The apparent absence of this fern from Caithness, East Sutherland and East Ross as well as from North Aberdeenshire seems surprising and is probably due to the failure of botanists to distinguish *D. borrieri* from *D. filix-mas*, since the latter is recorded from these vice-counties. The apparent distribution in Ireland is also unexpected and a similar explanation probably applies here.

Detailed work on the ecology of this species may prove interesting since *D. borrieri* is usually found in damper and more shaded situations than *D. filix-mas*, although not invariably so. It is hoped that this will be touched on in the investigation of the distribution of polyploid races which is now being undertaken. Manton (1950, 59) has demonstrated diploid and triploid strains; it will be interesting to see if there are any other chromosome races and also if chromosome number has any bearing on the ecological requirements.

Local populations of *D. borrieri* may be almost pure, being in fact clonal, and may exhibit differences in small details of the characters which are given above in the paragraph on description, from populations of other localities. Owing to the absence of gametic fusion, gene exchange does not occur, and hence small genetic changes within a plant are retained throughout succeeding generations and local stands may exhibit remarkable similarity among themselves but dissimilarity from other stands. It is important to remember these facts when identifying plants of *D. borrieri*. Hybrids between *D. borrieri*

and *D. filix-mas* may also be formed where these plants occur in close association. *D. filix-mas* is always the female and *D. borrieri* the male parent since fertile spermatozoids of *D. borrieri* are formed but no ova; such hybrid plants are being investigated.

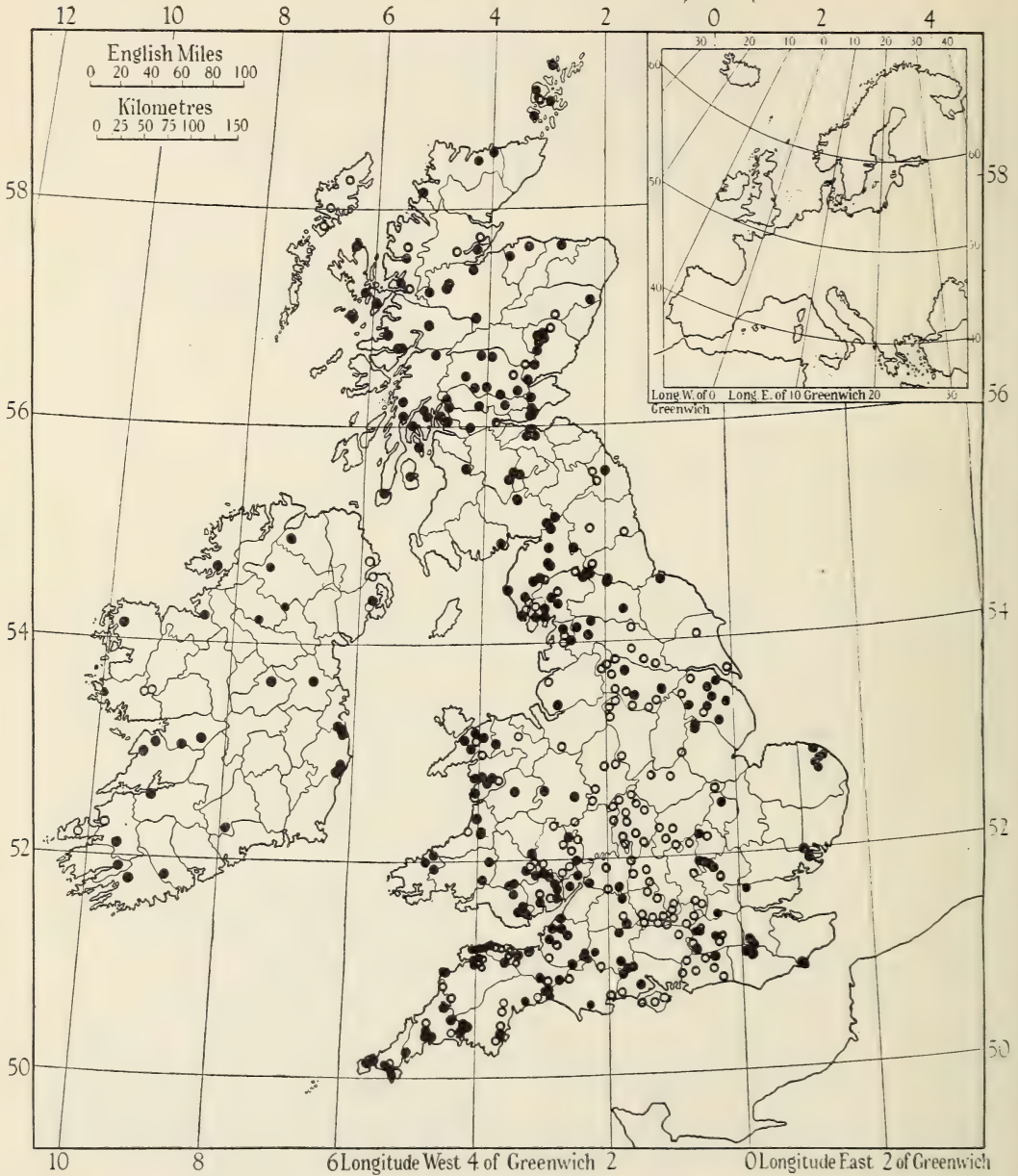


Fig. 4. Distribution of *Dryopteris borrieri* in the British Isles.

It is evident that much more work on this species is required but, as was mentioned in the introduction, this is only a general account and from this it can be seen that *D. borrieri* is distributed throughout the British Isles, and that some important facts may ensue from a study of the polyploid races.

SUMMARY

- (1) The characteristics of *D. borrieri* Newm. are given.
- (2) All the existing records of the occurrence of *D. borrieri* in the British Isles are presented on a map and a list is given of herbarium specimens.
- (3) Von Wolf's map showing the northern limits of *D. borrieri* in Europe is reproduced: the occurrence of this species throughout the British Isles (except the Shetland Islands) agrees very well with its distribution on the continent.
- (4) The scarcity of this fern in some parts of the British Isles is discussed and accounted for mainly by the lack of distinction from *D. filix-mas* by collectors.
- (5) *D. borrieri* seems to prefer damper and shadier situations than *D. filix-mas*.
- (6) Some points which may be clarified by cytological work now being undertaken are mentioned.

I am most grateful to the Trustees of the British Museum (Natural History) for a vacation studentship; to the keepers or owners of the herbaria listed above for lending material for inspection; to the staff of the European and Cryptogamic Herbaria at the Museum for much help; and especially to Mr. Alston, without whose help this work would not have been carried out.

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 VON WOLF, 1936, Ein neuer Farn der Pfalz, sein Vorkommen und seine systematische Stellung, *Pollichia*, **5**.

NOTES ON CAREX FLAVA AND ITS ALLIES

I—A SEDGE NEW TO THE BRITISH ISLES*

By ELIZABETH W. DAVIES

University College of Leicester

A sedge known to Scandinavian botanists as *C. pulchella* (Lönnr.) Lindman was recognised in Scotland during the summer of 1952. This name is now found to be invalid owing to the existence of an earlier homonym, and the new name chosen is *C. scandinavica* E. W. Davies. A description of the species follows.

Carex scandinavica E. W. Davies, nom. nov.

C. oederi Ehrh. subsp. *pulchella* Lönnroth, 1854, *Obs. Crit. Pl. Suec.*, 24.

C. pulchella (Lönnr.) Lindman, 1918, *Svensk Fanerogamflora*, 152; non Berggr. 1878.

A tufted glabrous perennial, (2-) 10-15 (-25) cm. high. Stems trigonous, smooth. Leaves 0.5-2 mm. wide, inrolled, channelled, dark green, usually shorter than the stems; ligule 1-2 mm., triangular or rounded. Lower sheaths often dark brown becoming fibrous. Male spike 1, 2-20 × 1-2 mm., usually with a short peduncle. Male glumes 3-4 mm., ovate or oblong, acute or obtuse, brown with a pale midrib. Female spikes 2-3 (-5), 3-10 × 3-5 mm., somewhat distant, rarely contiguous, sessile, or the lower shortly peduncled. Lower bracts leaf-like, spreading, usually shorter than the inflorescence, sheathing. Female glumes 2-3 mm., ovate, subacute, keeled, dark brown, with a pale or green midrib. Perigynia (1.0-) 1.5-2.5 mm., straight, feebly 2-3-ribbed, greyish green, very abruptly contracted into the short (0.25 mm.) beak. Nuts 1.5 mm., obovoid-trigonous, completely filling the perigynia. Fl. 5-7. Fr. 6-8.

This species, hitherto known only from N. Russia, Finland and Scandinavia, was first recognised in Britain during the summer of 1952, from one inland and four maritime localities in north-western Scotland, where it appears to replace the closely allied *C. serotina* Mérat (see distribution map, fig. 2.) The main characters distinguishing these two species, which have the same chromosome number ($2n = 70$), are given below.

Characters	<i>C. serotina</i> Mérat (Plate 5a)	<i>C. scandinavica</i> E. W. Davies (Plate 5b)
1. Leaves	1.5-3 mm. wide, canaliculate, grey-green, usually longer than the stems.	0.5-2 mm. wide, inrolled, dark green, usually shorter than the stems.
2. Spikes. a. Male	1, or sometimes absent, sessile, occasionally female at the base.	1, always present, usually with a short peduncle.
b. Female	(3-) 4-5 (-6), contiguous and sessile, frequently crowded round the male spike, occasionally the lowest remote and peduncled.	2-3 (-5), often separate, and somewhat distant, rarely contiguous, sessile or the lowest shortly peduncled.
3. Bracts	Lowest bracts leaf-like, upright or spreading, exceeding the inflorescence.	Lowest bracts leaf-like, spreading, usually shorter than the inflorescence.

* Part of a thesis approved for the degree of Ph.D. by the University of London.

Characters	<i>C. serotina</i> Mérat (Plate 5a)	<i>C. scandinavica</i> E.W. Davies (Plate 5b)
4. Female glumes	Pale yellow-brown	Dark brown, with a pale or green midrib.
5. Perigynia (Fig. 1)	(1.75-) 2.0-2.5 (-3.0) mm., straight, yellow-green, more or less inflated; beak 0.25-0.5 mm.	(1.0-) 1.5-2.5 mm., straight, grey-green, never inflated; beak 0.25 mm.
6. Nuts	Never completely filling the perigynia.	Completely filling the perigynia.
7. Periodicity	Flowers 6-8. Fruit 7-9.	Flowers 5-7. Fruit 6-8.



Fig. 1. Perigynia : left, *Carex serotina*; right, *C. scandinavica*.

These two allied species have different distributions in the British Isles, and as can be seen in the distribution map *C. scandinavica* appears to replace *C. serotina* in N.W. Scotland. The map is based on data obtained from Nelmes (1947) and from specimens seen in the field and from the following herbaria : Kew, Oxford, Cambridge University College, Leicester and J. E. Lousley. The details of the localities and their vice-counties not given by Nelmes are listed below.

LOCALITIES IN THE BRITISH ISLES

C. SCANDINAVICA E. W. Davies

- V.c. 88. MID PERTH : Fearnan Pier, Loch Tay, 1952, E.W.D.
 97. WESTERNESS : Arisaig, 1951, E.W.D.
 104. N. EBUDES : shore at Drynoch, Skye, 1938, J. E. Lousley.
 105. W. ROSS : Loch Carron, 1952, E.W.D.; the mains, Loch Torridon, 1952, E.W.D.; shore, Ob Mheallaidh, Shildaig, Upper Loch Torridon, 1947, R. Mackechnie & E. C. Wallace.
 108. W. SUTH. : Kylesku Ferry, 1952, E.W.D.
 110. OUTER HEBRIDES : Berie Sands, Uig, Lewis, 1946, E. F. Warburg; Meall Geal, Uig, Lewis, 1946, E. F. Warburg.
 112. ZETLAND : bog, Fair Isle, 1949, E. A. G. Duffey.

C. SEROTINA Mérat

- V.c. 4. N. DEVON : Braunton Burrows, 1952, E.W.D.
 6. N. SOM. : Shapwick Peat Moor, 1951, E.W.D.
 9. DORSET : Littlesea, 1951, E.W.D.; South Haven, Poole Harbour, 1937, E. C. Wallace.
 11. S. HANTS. : Hatchet Pond, Beaulieu, 1952, E.W.D.; Sowley Pond, 1913, J. Comber.
 12. N. HANTS. : Fleet Pond, 1952, E.W.D.
 17. SURREY : Frensham Little Pond, 1952, E.W.D.
 23. OXON. : Port Meadow, Oxford, 1946, J. E. Lousley.
 26. W. SUFF. : Poor's Fen, Lakenheath, 1951, S. M. Walters.
 28. W. NORF. : Wretton Fen, 1925, J. E. Little; Shouldham Warren, 1919, J. E. Little; Derby Fen, 1951, E.W.D.; Leziate Fen, 1951, E.W.D.
 29. CAMBS. : Fulbourn Pond, 1951, E.W.D.; Wicken Fen, 1951, E.W.D.
 31. HUNTS. : Woodwalton Fen, 1909, G. C. Druce.
 33. E. GLOS. : South Cerney gravel pit, Cirencester, 1951, E.W.D.
 41. GLAM. : Kenfig, 1935, J. E. Lousley; Oxwich Burrows, 1948, J. E. Lousley; Port Talbot, 1903, G. C. Druce.



Fig. 2. The distribution of *C. serotina* Méral ● ; *C. scandinavica* E. W. Davies x.

PLATE 5.



(a) *C. serotina* Mérat from L'Ancresse Common, Guernsey ($\times \frac{1}{2}$).

(b) *C. scandinavica* E. W. Davies from Fearnam Pier, Loch Tay, Perth ($\times \frac{1}{2}$).

46. CARD. : Ynyslas, 1948, P. W. Richards.
48. MER. : Castle Harlech, 1880, C. Bailey.
51. FLINT : shore of Llyn Helyg, 1906, J. A. Wheldon.
52. ANGL. : Rhosneigr, 1949, A. P. Connolly; Cors Goch, 1951, P. W. Richards; Llyn Maelog, 1947, A. R. Clapham.
56. NOTTS. : quarry near Shire Oaks, 1946, J. Brown.
58. CHESHIRE : sandhills on shore, Wallasey, 1887, T. Smith; Oakmere, 1868, S. Bickham.
59. S. LANCS. : coast sandhills, Formby, 1892, C. R. Billups; dune slacks, Aifhsdale, 1937, J. E. Lousley; dune slacks, Southport, 1940, E. Dovaston.
60. W. LANCS. : between Blackpool and St. Anne's, 1906, J. A. Wheldon.
68. CHEVIOTL. : Ross Links, 1938, J. E. Lousley.
69. WESTMORL. : Hale Moss, Bentham, 1952, E. W. D.
75. AYR : Ardeer Sands, Stevenston, 1898, A. Somerville.
90. FORFAR : Sands of Barry, 1916, E. S. Marshall; Rescobie Loch, 1882, G. C. Druce.
95. ELGIN : Culbin Sands, 1938, N. Y. Sandwith.
107. E. SUTH. : Cambusavie, Loch Fleet, 1931, J. E. Lousley.
- H. 9. CLARE : Lough Bunny, 1952, T. G. Tutin.
25. ROSCOMMON : Annaghmore, 1952, T. G. Tutin.

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NOTES ON CAREX FLAVA AND ITS ALLIES

II—CAREX LEPIDOCARPA IN THE BRITISH ISLES*

By ELIZABETH W. DAVIES

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Carex lepidocarpa grows in isolated and scattered areas throughout the country, wherever suitable localities occur. It shows considerable variation in form and size over its range, but this can usually be correlated with its different habitats, and its regional adaptation to climate and topography. In fact this species seems to form a discontinuous topocline in the British Isles (Huxley, 1939) and the character gradient in this case is clearly associated with latitude and altitude. Thus the southern lowland and Scottish mountain plants represent the extreme forms. The former, confined to the fens and calcareous marshes in southern England, is very different from the latter, a plant of base-rich flushes on high mountains, and these forms remain distinct even in cultivation. However, as some populations in the Midlands and northern England (the carboniferous limestone of the Pennines, in Derbyshire, Yorkshire, Durham and Westmorland) show intermediate characters and are difficult to classify, it seems best to regard these extreme forms as subspecies. A short description of the species and the two subspecies found in the British Isles now follows.

C. LEPIDOCARPA Tausch, 1834, *Flora*, 17, 179. *C. flava* L. sec. Host, 1801, *Gram. Aust.*, 1, t. 63, (pl. florifera), non L.

A tufted glabrous perennial (20-) 30-50 (-60) cm. high, generally smaller and more slender in all its parts than *C. flava* L. Stems stout and erect, or slender and slightly pendulous. Leaves (1.5-) 2-2.5 (-4) mm. wide, usually about half the length of the stems or less; ligule c. 1 mm., truncate or nearly so. Lower sheaths green, sometimes becoming brown and fibrous. Male glumes 3-3.5 mm., obovate or obovate-lanceolate, brownish-hyaline, midribs green or brown, not distinctly keeled. Female spikes 1-3 (-4), 8-12 × 5-7 mm., rarely contiguous, often somewhat distant, sessile, or lower shortly peduncled. Bracts leaf-like, slender, equalling or sometimes exceeding the inflorescence. Female glumes 2 mm., ovate, acute, dark brown or yellow-hyaline. Perigynia (3.5-) 4.25-4.5 (-5.0) mm., obovoid-trigonus, narrowed gradually into a beak, all but the upper arcuate-deflexed when ripe; beak 1.5 mm., attenuate, serrulate. Nuts 1.5 mm., broadly obovoid-trigonus or almost round. Fl. 5-7. Fr. 7-9.

(1) C. LEPIDOCARPA Tausch subsp. LEPIDOCARPA. Plate 6a.

I have not seen Tausch's type from Bohemia. Tausch, however, refers to Host's plate (see above), and suggests that it is similar to his own plant. This plant resembles the lowland form of *C. lepidocarpa* in every way. I have, therefore, assumed that Tausch's plant is the same subspecies.

A tufted perennial (20-) 30-50 (-60) cm. Stems slender and often curved when in fruit. Leaves 1.5-2.5 (-3.5) mm. wide, herbaceous, usually about half the length of the stems. Female glumes pale brown-yellow, hyaline, caducous. Perigynia (3.5-) 4.25-4.5 (-4.75) mm. (Fig. 1). Fl. 5-6. Fr. 7-8. $2n = 68$.

* Part of a thesis approved for the degree of Ph.D. by the University of London.

This subspecies is confined in the British Isles to calcareous districts including base-rich marshes in the lowlands of Scotland. It is locally abundant on the carboniferous limestone of the Pennine range, and on the oolite of the Cotswolds and Northamptonshire; and fairly common in the fens and on the chalk and chalky boulder clay of S.E. England (Distribution map).



Fig. 1. Perigynia of *Carex lepidocarpa*; left, subsp. *lepidocarpa*; right, ssp. *scotica*.

(2) *C. LEPIDOCARPA* Tausch subsp. **scotica** E. W. Davies subsp. nov. Plate 6b.

Similis subsp. *lepidocarpa*, sed culmis validis, rigidis, semper erectis, 8-30 cm. altis, foliis 2.5-4 mm. latis, plerumque brevissimis, coriaceis; glumis femineis fusco-castaneis, persistentibus; utriculis saepe longioribus, 4-5 mm. longis, differt. Typus in Herb. Mus. Brit. 88, Mid Perth: calcareous flush at 1,000 metres, Creag-an-Lochain, E. W. Davies, 4 Sept. 1951.

A robust tufted perennial (8-) 15-20 (-30) cm. Stems stout, rigid, usually remaining erect throughout fruiting. Leaves 2.5-4 mm. wide, usually very short, tough and fibrous. Female glumes dark chestnut-brown, seldom caducous. Perigynia (4.0-) 4.25-4.5 (-5.0) mm., often longer than in subsp. *lepidocarpa* (Fig: 1). Fl. 6-7. Fr. 8-9. $2n = 68$.

In contrast to subsp. *lepidocarpa*, this plant is normally confined to base-rich flushes on mountains in northern England, Scotland and Wales, and is usually found between 660 and 1,000 metres. However, at Inchnadamph in West Sutherland it grows only a few metres above sea level, together with many other high mountain plants (distribution map, fig 2).

The distribution map is based on data obtained from Nelmes (1947), from specimens collected in the field, which are now preserved at University College, Leicester, and from others seen at the following herbaria: Kew, Oxford, Cambridge and J. E. Lousley. This shows a composite distribution of the two subspecies, and their intermediate members of the topocline, but separate details of the localities and vice-counties of the two subspecies not already given by Nelmes are listed below.

LOCALITIES IN THE BRITISH ISLES

C. LEPIDOCARPA Tausch subsp. *LEPIDOCARPA*

- V.c. 8. S. WILTS.: Bulford, 1941, J. E. Lousley.
 11. S. HANTS.: St. Clair's Farm, Droxford, 1952, E. W. D.
 12. N. HANTS.: marsh near Greywell Waterworks, 1936, J. E. Lousley.
 22. BERKS.: Cothill Fen, 1935, J. E. Lousley; Frilford, 1938, A. R. Clapham; Cumnor, 1938, A. R. Clapham.
 23. OXON.: Latchford, 1938, A. R. Clapham; Eynsham, 1913, G. C. Druce.
 26. W. SUFF.: Market Weston Fen, 1936, J. E. Lousley; Redgrave Fen, 1933, J. E. Lousley; Hinderclay Fen, 1933, J. E. Lousley.
 27. E. NORF.: Roydon Fen, near Diss, 1934, E. C. Wallace

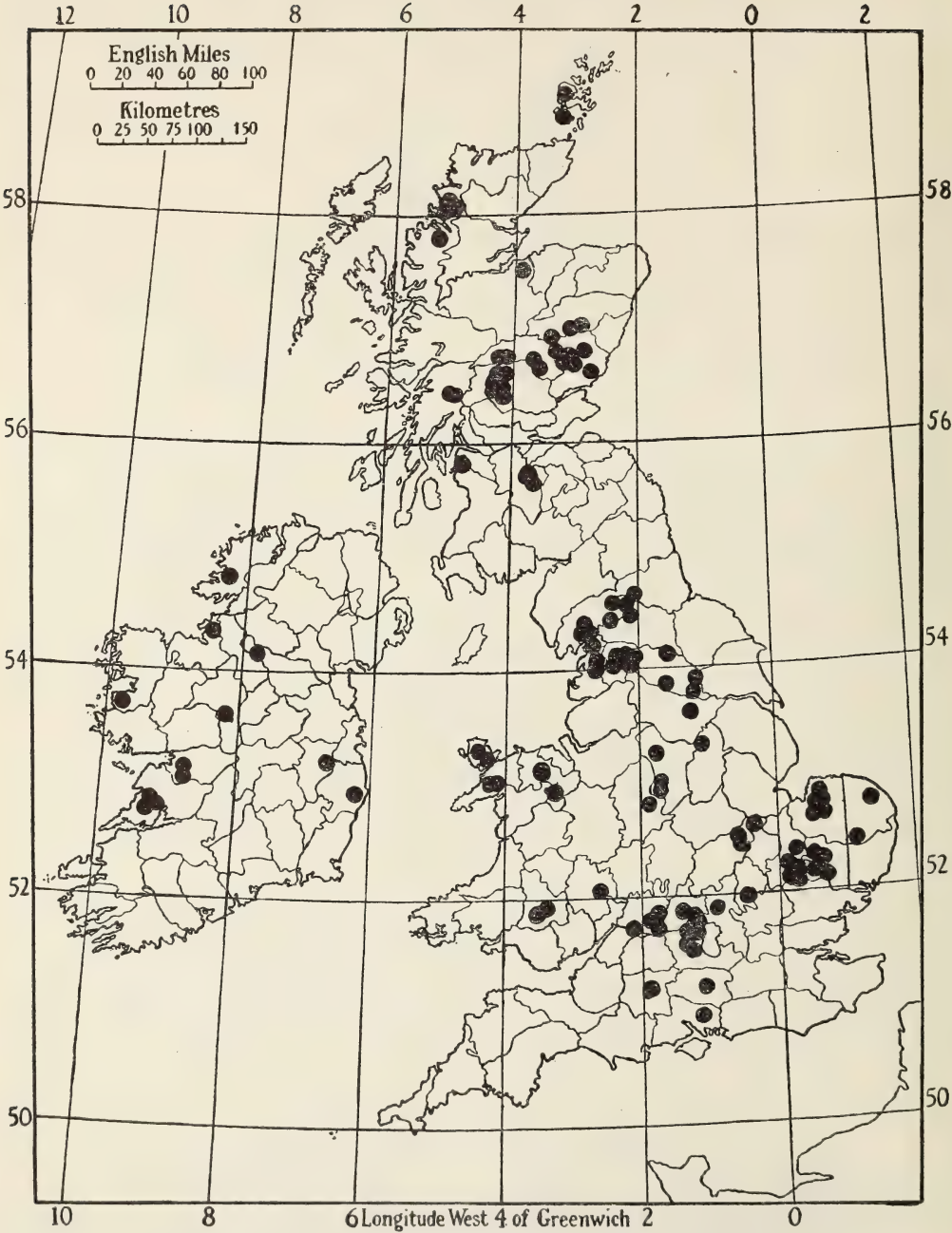


Fig. 2. The distribution of *C. lepidocarpa* Tausch in the British Isles.

PLATE 6.



- a. *C. lepidocarpa* Tausch subsp. *lepidocarpa* from Wicken Fen, Cambs. ($\times \frac{1}{4}$).
b. *C. lepidocarpa* Tausch subsp. *scotica* E. W. Davies from Creag-an-Lochain, Meall Tarmachan, Perth.
($\times \frac{1}{4}$).

28. W. NORF. : Derby Fen, 1951, *E.W.D.*; Foulden Common, 1936, *J. E. Lousley*; Caldecote Fen, 1919, *J. E. Little*; Blo Norton Fen, 1934, *J. E. Lousley*; near Oxborough, 1936, *J. E. Lousley*.
29. CAMBS. : Wicken Fen, 1951, *E.W.D.*; Fulbourn Pond, 1951, *E.W.D.*; Chippenham Fen, 1951, *E.W.D.*; meadow, Whittlesford, 1946, *S. M. Walters*.
30. BEDS. : The Litany, Totternhoe, 1952, *E.W.D.*
32. NORTHANTS. : Wittering Marsh, 1952, *E.W.D.*; Barnack Quarries, 1946, *F. J. Taylor*; Hornstock, 1913, *G. C. Druce*; marsh near Bedford Purlieus, 1913, *G. Chester*.
33. E. GLOS. : S. Cerney gravel pit, Cirencester, 1951, *E.W.D.*
42. BRECON : Penderyn, 1946, *H. K. Airy Shaw & E. Milne-Redhead*.
48. MER. : Llanaber, 1921, *G. C. Druce*.
50. DENB. : Trevor Rocks, Llangollen, 1933.
52. ANGL. : Cors Bodeilio Fen, 1951, *P. W. Richards*; Cors Goch, 1937, *J. H. Chapple*.
57. DERBY : Millersdale, 1908, *C. R. Billups*; Monsal Dale, 1947, *A. P. Conolly*.
64. MID W. YORK : Askham Bog, near York, 1946, *E.W.D.*; near Ripon, 1950, *C. West*; Great Close Mire, Malham, 1951, *E.W.D.*; outflow of Malham Tarn, 1951, *E.W.D.*; Gordale Scar near Malham, 1951, *E.W.D.*; Ribbleshead, 1947, *E.W.D.*; limestone flush, Moughton Scar, 1951, *E.W.D.*; Clapham Beck, Ingleborough, 1952, *E.W.D.*; Kilnsey, 1946, *J. E. Lousley*.
65. N.W. YORK : flush, Cronkley Scars, Teesdale, 1947, *E.W.D.*
66. DURHAM : Widdybank Fell, 1951, *E.W.D.*; Langdon Beck, 1947, *T. G. Tutin*.
69. WESTMORL. : flush between Sedbergh and Kirkby Stephen, 1952, *E.W.D.*
76. RENFREW : stream near Brother Loch, Newton Mearns, 1936, *R. Mackechnie*.
77. LANARK : source of Medwin, Pentlands, 1938, *J. E. Lousley*.
- H. 15. S.E. GALWAY : Newtown, Gort, 1937, *J. E. Lousley*.
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NOTES ON CAREX FLAVA AND ITS ALLIES

III—THE TAXONOMY AND MORPHOLOGY OF THE BRITISH REPRESENTATIVES*

By ELIZABETH W. DAVIES

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This group of closely related species included in the section *Extensae* of the sub-genus *Carex* is represented in Great Britain by:—*C. flava* L., *C. lepidocarpa* Tausch, *C. demissa* Hornem., *C. serotina* Mérat, *C. scandinavica* E. W. Davies (E. W. Davies 1953a). These species have for many years caused difficulty and been the subject of much misidentification. And although certain characters have been found useful for distinguishing the species, and their nomenclature has been elucidated (Nelmes 1945, 1947; Wiinstedt 1947; Senay 1950; Tutin 1952; and Davies 1953a and b), no detailed taxonomic or ecological study had been made, and no cytogenetical survey carried out. For this reason an investigation of this kind was begun, and the biometric and morphological aspects of the problem will be briefly discussed here. A key to the European members of this group and *C. viridula* Michx. is given opposite.

A range of forms of each species was collected from as many different localities as was possible. These plants, after their chromosome numbers had been determined, were planted out in an experimental garden, where conditions were as uniform as possible, so that any effects of differences in the environment on the phenotype were to a great extent eliminated; and the genotypes of the individuals and species could be compared directly.

These transplant experiments have shown how much variation within the species is due to environmental conditions. As was to be expected, certain characters, such as absolute size of the plant and its vegetative organs, have proved to be subject to considerable phenotypic modification, while in contrast the floral parts appear to be much more constant. The main morphological study, and detailed measurements given in Table 2, have been made on herbarium specimens gathered from the same plants in the field.

1. HEIGHT

On the whole this has proved an unreliable character, as much variation in height and size is found not only between plants of the same species from the different habitats, but also in the same plant during one year, and in successive seasons growing in the same locality. Thus, *C. serotina*, seen at Wicken Fen, Cambridgeshire, in August 1951, had fertile stems ranging from 2-25 cm. on one plant. This species at Frensham Pond, Surrey, had shoots 25 cm. long in July 1951, while in the same month in 1952 these plants were very dwarf and the fertile stems were only 2 cm. in length.

This variation in absolute size of the plant from season to season, and from different localities, can usually be correlated with a change in ecological conditions, as after they had been grown under uniform conditions for two years they showed very much less range of size.

Although there is considerable variation, it is possible to make some general statements about height. *C. flava* is normally the tallest member of the group, and the

* Part of a thesis approved for the degree of Ph.D. by the University of London.

KEY TO THE EUROPEAN SPECIES INCLUDED IN *C. FLAVA* AGGREGATE

1. Perigynia 4-7 mm. long, arcuate-deflexed with a long attenuate beak.
 2. Female spikes 3-4, upper sessile contiguous, lower sometimes distant and peduncled; perigynia 5·25-7 mm., beak 2-2·25 mm. *flava*
 2. Female spikes 1-3, somewhat distant, rarely contiguous sessile, lower usually long-peduncled; perigynia 4-5 mm., beak 1·5-1·75 mm. *lepidocarpa*
 3. Female spikes short, sub-rotund, with rather few lax spreading perigynia; beak 1·75 mm., attenuate. subsp. *jemtlandica*
 3. Female spikes ovoid, or shortly cylindrical, with rather dense crowded perigynia; beak 1·5 mm.
 4. Stems 20-60 cm., rather slender and often curved in fruit; leaves half the length of the fertile stems, narrow, 1·5-2·5 mm. wide; female glumes pale yellow-brown, hyaline, caducous; perigynia 3·5-4 mm. subsp. *lepidocarpa*
 4. Stems 8-30 cm., stout, rigid, erect in fruit; leaves short, 2·5-4·5 mm. wide; female glumes dark chestnut-brown, usually persistent; perigynia 4-5 mm. subsp. *scotica*
1. Perigynia 1-4 mm. long, usually straight, or only slightly deflexed, with a short beak.
 5. Stems 20-60 cm. erect; leaves blue-green, less than the length of the stems; lower sheaths red-brown becoming fibrous and sometimes coriaceous. *mairii*
 5. Stems 2-30 cm., erect or semi-decumbent; leaves bright yellow-green, more than half the length of the stems; lower sheaths sometimes becoming fibrous, but never coriaceous.
 6. Stems often curved and semi-decumbent; leaves flat, 3·5-5 mm. wide. *demissa*
 6. Stems erect; leaves inrolled, 1·5-2 mm. wide.
 7. Perigynia 3-3·25 mm. long, all but the upper slightly arcuate-deflexed; beak 1 mm. *dyrrachiensis*
 7. Perigynia less than 3 mm. long, straight; beak 0·25-0·5 mm.
 8. Perigynia 1·5-2·25 mm., never inflated; nut completely filling the perigynium; leaves shorter than the stems; female spikes often separated, seldom contiguous to the shortly peduncled male spike. *scandinavica*
 8. Perigynia 1·75-3 mm., more or less inflated; nut filling only three-quarters of the perigynium; leaves usually longer than the stems; female spikes usually contiguous with the sessile male spike.
 9. Plant pale grey-green; stems 5-35 cm., erect; bracts exceeding the inflorescence, upright; male spike sessile, often female in the middle. *viridula*
 9. Plant bright yellow-green; stem 2-25 cm., erect; bracts exceeding the inflorescence upright or often spreading; male spike sessile, sometimes female at the base.
 10. Plant 2-20 cm.; male spike always present; perigynia 1·75-2·5 mm. *serotina*
 10. Plant 15-25 cm.; male spike absent or frequently at the top of the uppermost female spike; perigynia 2·5-3·0 mm. *serotina* var. *cyperoides*

species descend in height in the following order :— *C. lepidocarpa*, *C. demissa*, *C. serotina*, *C. scandinavica* (Plate 7).

2. LEAVES

The dimensions of the leaves, unlike other vegetative parts of the plant, have proved a reliable and a surprisingly constant character, which shows little variation in cultivation.

(a) Length

The leaves of *C. flava* are much longer and broader than those of the other species, and, as in *C. serotina*, they often exceed the fertile shoots. This is likewise a useful

means of distinguishing *C. serotina* and the rather similar *C. scandinavica*, for although in contrast to *C. flava* the leaves of both these species are narrow and canaliculate, those of *C. scandinavica* are always shorter than the stems.

C. demissa has broad leaves, about three-quarters the length of the culms, while the leaves of both subspecies of *C. lepidocarpa* are short and comparatively narrow. Subsp. *lepidocarpa* has leaves that are about half as long as the stems; while those of the subsp. *scotica* E. W. Davies are even shorter.

(b) Width

The leaves of *C. flava* and *C. demissa* in this order are broadest, and usually flat, while both subspecies of *C. lepidocarpa* have narrower leaves. However, those of subsp. *lepidocarpa* are grass-like and herbaceous, while subsp. *scotica* has tough fibrous leaves, which retain this texture in cultivation, a character which is associated with the severe climatic conditions in the north and at high altitudes. The leaves of *C. serotina* and *C. scandinavica* are very narrow, and in contrast to all other members of this group they are inrolled.

3. SPIKES

(a) and (b) Arrangement and number of male and female spikes

The arrangement and number of the spikes are reliable characters, which show little phenotypic variation under normal conditions, and remain constant in cultivation. However, occasionally irregularities have been noticed when culms are produced as a second crop at the end of the season. This is unusual and these late fertile shoots are unreliable for identification.

As can be seen from Table 1, and in Plate 8, *C. flava* and *C. serotina* show a similarity in the number and arrangement of their spikes. Both species have a comparatively short sessile male spike, which is occasionally partly female, while the female spikes (3-4 in *C. flava* and 3-5 in *C. serotina*) are usually contiguous and crowded round the male spike. In contrast the male spikes of *C. lepidocarpa*, *C. demissa* and *C. scandinavica* are considerably longer and the female spikes (1-3 in *C. lepidocarpa*, 2-4 in *C. demissa* and 2-3 in *C. scandinavica*) are often separated from the male spike, and sometimes from each other (Fig. 2). In *C. demissa* there is frequently one remote basal spike with a long peduncle (Fig. 2d).

4. PERIGYNIA OR UTRICLES

(a), (b) and (c) Length and shape of perigynia and length of beak

The dimensions and shape of the perigynia have provided the most reliable biometric character, as they show very little variation and are seldom influenced by environmental conditions (Plate 9). In fact it is possible to identify the members of this group from the length of the perigynia alone. For although a slight overlap can be seen in the accompanying histograms (Fig. 1), in most well-grown specimens there is at least a difference of 1 mm. between any two of the species. Thus the perigynia lengths are as follows :-

<i>C. flava</i>	mode 6.0, range 5.25-7.0 mm.
<i>C. lepidocarpa</i> ssp. <i>lepidocarpa</i>	mode 4.25, range 3.5-4.5 mm.
<i>C. lepidocarpa</i> ssp. <i>scotica</i>	mode 4.5, range 4.0-5.0 mm.
<i>C. demissa</i>	mode 3.25, range 3.0-3.5 mm.
<i>C. serotina</i>	mode 2.25, range 2.0-2.5 mm.
<i>C. scandinavica</i>	mode 1.75, range 1.0-2.25 mm.

TABLE 1. Characters for distinguishing British species

Species:	I. <i>Carex flava</i>	IIa. <i>Carex lepidocarpa</i> ssp. <i>lepidocarpa</i>	IIb. <i>Carex lepidocarpa</i> ssp. <i>scotica</i>	III. <i>Carex demissa</i>	IV. <i>Carex serotina</i>	V. <i>Carex scandinavica</i>
1. Height of plant	(15-) 50-70 (-90) cm.	(20-) 30-50 (-60) cm.	(8-) 15-20 (-30) cm.	(5-) 10-20 (-30) cm.	(2-) 5-15 (-25) cm.	(2-) 10-15 (-25) cm.
2. Leaves						
(a) Leaf length	As long or longer than fertile shoots.	About half the length of fertile shoots.	Very short.	About three-quarters the length of fertile shoots and flat.	Canaliculate, often longer than fertile shoots.	Inrolled, usually shorter than the fertile shoots.
(b) Leaf width	3.5-5 mm.	1.5-2.5 (-3.5) mm.	2.5-4 mm.	(2.5-) 3.5-4 (-5) mm.	1.5-2 mm.	0.5-2 mm.
3. Spikes						
(a) Male	Short and sessile, sometimes ♀ in the middle.	Fairly long and peduncled.	Fairly long and peduncled.	Fairly long and peduncled.	Sometimes absent, or occasionally ♀ at the base, sessile.	Always present, peduncled, never female at the base.
(b) Female	3-4, upper sessile and contiguous, lower sometimes distant and shortly peduncled.	1-3, upper sessile, rarely contiguous, occasionally one lower and peduncled.	1-3, usually close together but seldom contiguous to the ♂ spike.	2-4, usually 3, upper two ± distant sometimes contiguous, lowest often remote and peduncled.	3-5, usually 4, contiguous and sessile, frequently crowded round the ♂ spike, occasionally lowest remote and peduncled.	2-3 (-4) often separated, somewhat distant, rarely contiguous, sessile, or lowest shortly peduncled.
4. Perigynia						
(a) Total length	(5.25-) 5.75-6 (-7.0) mm.	(3.5-) 4.25-4.5 mm.	(4-) 4.25-4.5 (-5) mm.	(2.5-) 3-3.5 (-4) mm.	(1.75-) 2-2.5 (-2.75) mm.	(1.0-) 1.5-2.5 mm.
(b) Beak length	2.0-2.5 mm.	1-5 mm.	1-5 mm.	1 mm.	0.25-0.5 mm.	0-25 mm.
(c) Shape	Arcuate, deflexed.	Arcuate, deflexed.	Arcuate, deflexed.	Straight, or very slightly curved.	Straight, inflated. Nut only three-quarters filling the utricle.	Straight, not inflated. Nut completely filling the utricle.
5. Female glumes	Pale brown.	Pale brown-yellow, hyaline, caducous.	Dark brown. Seldom, and only very late in the season, caducous.	Brown.	Pale yellow-brown.	Dark brown, with pale or green midrib.

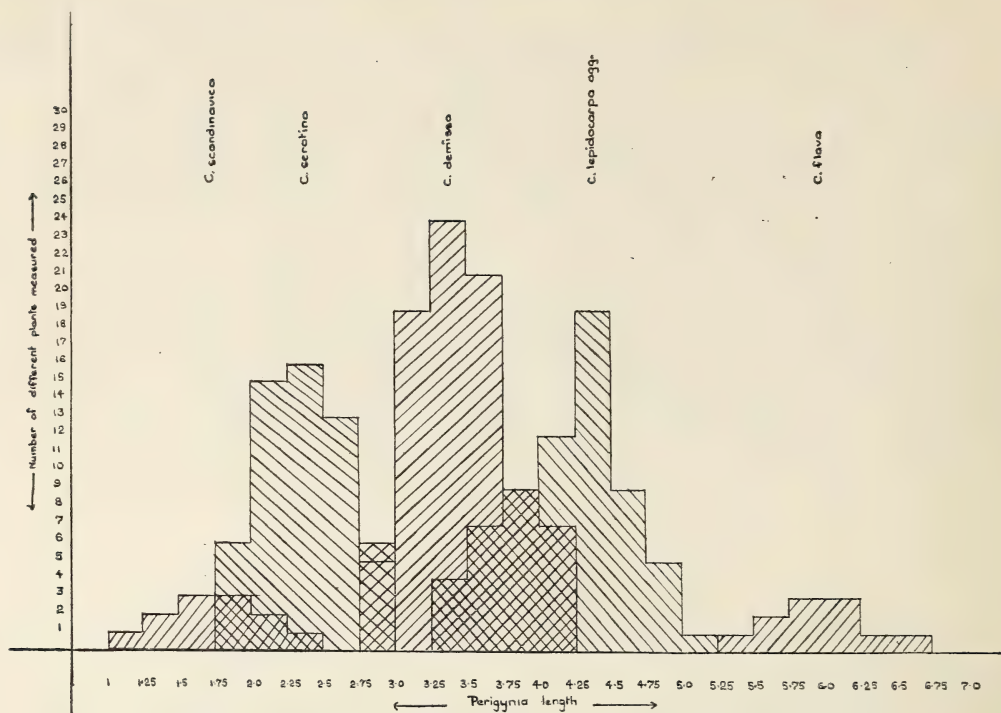


Fig. 1. Histograms showing the range in perigynia length.

The data used in drawing the histograms were obtained from collections made during the past two years in this country, and augmented by European herbarium material.

The shape of the perigynia is another good character, for *C. flava* and *C. lepidocarpa* have arcuate-deflexed perigynia, which are gradually attenuate into a beak, while those of *C. demissa* are only slightly curved, and the remaining two species have straight perigynia. In contrast to the other species the perigynia of *C. scandinavica* are not inflated, but tightly enclose the nut.

Finally the beak length is a useful character, and, as might be expected, decreases proportionately with the decrease in perigynia length. Thus the beak lengths of the five species are as follows :-

<i>C. flava</i>	2.0 -2.5 mm.
<i>C. lepidocarpa</i> ssp. <i>lepidocarpa</i>	1.5 mm.
<i>C. lepidocarpa</i> ssp. <i>scotica</i>	1.5 mm.
<i>C. demissa</i>	1.0 mm.
<i>C. serotina</i>	0.25-0.5 mm.
<i>C. scandinavica</i>	0.25 mm.

5. FEMALE GLUMES

Finally the colour of the female glumes, normally a rather unreliable and variable character, has been found useful in distinguishing certain members of the complex. Thus the female glumes of *C. lepidocarpa* ssp. *lepidocarpa* are pale brown, hyaline and caducous, while those of the ssp. *scotica* are dark chestnut-brown and usually persistent, so giving the female spikes a characteristic dark appearance.

PLATE 7.



(Left to right) : (a) *C. flava*; (b) *C. lepidocarpa* subsp. *lepidocarpa*; (c) *C. lepidocarpa* subsp. *scotica*; (d) *C. demissa*; (e) *C. serotina*; (f) *C. scandinavica*.

PLATE 8.



Male and female spikes of (left to right) : (a) *C. flava*; (b) *C. lepidocarpa* subsp. *lepidocarpa*; (c) *C. lepidocarpa* subsp. *scotica*; (d) *C. demissa*; (e) *C. serotina*; (f) *C. scandinavica*.

PLATE 9.



Perigynia of (left to right) : (a) *C. flava*; (b) *C. lepidocarpa* subsp. *lepidocarpa*; (c) *C. lepidocarpa* subsp. *scotica*; (d) *C. demissa*; (e) *C. serotina*; (f) *C. scandinavica*.

Likewise the colour of the female glumes is useful in separating *C. serotina* and *C. scandinavica*, for the glumes of *C. serotina* are frequently pale yellow-brown and hyaline, while those of the latter species are dark brown.

This character has always been found to remain constant in cultivation and shows little variation under different ecological conditions.

CONCLUSIONS

This morphological and biometric study and the transplant experiments have shown that the phenotype may be modified much more profoundly by environment in the vegetative parts of these sedges than the floral parts; in the latter the appearance of the phenotype is almost entirely the expression of their genotype. For this reason the arrangement and the spikes, and the dimensions and shape of the perigynia have been found the most reliable criteria for identification and classification, while the growth form and size of the plant, and length and breadth of the leaves have proved useful auxiliary characters.

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NOTES ON CAREX FLAVA AND ITS ALLIES

IV—GEOGRAPHIC DISTRIBUTION*

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Detailed information about the world distribution of the *C. flava* aggregate is rather fragmentary. However, in spite of the group being represented in both hemispheres, as a whole it seems to have circumboreal tendencies and the members were described by M. Raymond in 1951 as amphi-atlantic species. Although they are found on both sides of the Atlantic Ocean their European distribution is usually more extensive than their American one (Fig. 1). The British representatives are clearly components of the Northern European flora, and are rare in the Mediterranean region, where *C. mairii* Coss. & Germ. and *C. duriei* Steud., two closely allied species, seem to replace them, and are locally abundant.

C. flava is a plant with oceanic tendencies, but although it is scattered locally throughout Eurasia it is absent in the Mediterranean region. It occurs in Central Europe, extending to Iceland and Lapland in the North, and is to be found occasionally in the mountainous regions of Scandinavia, the Alps, and the Auvergne in Central France. Its eastern limits are Russia, where it is fairly common in the North, and in the west Caucasus, while it has been doubtfully recorded from near Lake Baikal. In contrast, however, this species is pronouncedly continental in North America, and extends throughout Canada, as far as British Columbia and Vancouver Island.

C. lepidocarpa, unlike the last species, has not a boreal circumpolar distribution, but is a more abundant species in Central Europe. This sedge, which is very rare in southern Europe, is distributed from Central France, Switzerland and Germany northwards to the Arctic Circle, but only extends to Finland, north-west Russia and the Balkans in the east, and to Newfoundland, Quebec, and the Magdalen Islands in the Gulf of St. Lawrence in eastern Canada in the west.

Likewise the commonest British species, *C. demissa*, has a limited distribution outside northern Europe. This sedge extends from Scandinavia and Finland southwards to North Spain and Portugal, but is totally absent from Russia, unless the Russian species *C. flavella* Krecz. is conspecific with it. In North America, *C. demissa* is described as a relic Atlantic species, and is only recorded from the maritime regions of Quebec and New Brunswick and some of the islands in the Gulf of St. Lawrence, where the flora is Atlantic in character. This species seems to be the only member of the aggregate known from Greenland.

In contrast to *C. demissa*, *C. serotina*, a rather local plant in the British Isles, is the most abundant member of this group, with a rather scattered distribution. Thus, this species, which appears to be a relic with a much wider distribution in the past, occurs in lowland and open habitats throughout Europe, Siberia as far as Lake Baikal, Turkestan, Iran, and North Africa, Madeira and the Azores. Reports of its occurrence from Newfoundland and the Magdalen Islands are doubtful and still need confirmation, for these records are probably really *C. viridula* Michx. The characters separating these two species are still obscure, although it seems likely that they are worthy of specific rank.

* Part of a thesis approved for the degree of Ph.D. by the University of London.

Lastly, the only other British representative is *C. scandinavica*. This species has a very limited and local distribution and is confined to northern Europe including north-west Russia, Norway, Sweden, Denmark, Finland and western Scotland.

There are two other non-British representatives which are so closely allied to these species that they cannot be ignored. These are first *C. dyrrachiensis* Nelmes, a plant discovered in Central Albania in 1935 by N. Y. Sandwith, and secondly *C. mairii* Coss. & Germ., which appears completely to replace *C. lepidocarpa* in southern Europe (Italy, South France and Spain) (Fig. 2).

This account would not be complete without a brief mention of other members of the group found outside Europe (Fig. 2). *C. viridula* Michx., with many characters similar to *C. serotina*, is probably the best known and studied ally of the European representatives. This species is locally abundant and widespread throughout the United States and Canada, reaching California, Mexico and Alaska on the west coast, and extending across the Pacific to Kamchatka, Japan and eastern Asia.

Finally, there are three species, about which as yet little is known, *C. philocrena* Krecz. from Turkestan and Kashmir with characters intermediate between *C. demissa* and *C. serotina*; *C. flavella* Krecz. from Russia, a plant which may prove to be a form of, or even identical with, *C. demissa*; and *C. cataractae* R. Br. from the southern hemisphere (S. America, S. Africa, Tasmania and New Zealand) a plant that in many characters resembles *C. flava*. These species cannot be disregarded for, although so far they have not been studied experimentally or cytologically, they appear on morphological grounds to be closely related to the European representatives, and undoubtedly must be included in this aggregate.

The distribution maps and information given in the brief geographical survey of this group are based on data obtained from Nelmes (1949), Senay (1950a, b, 1951) and M. Raymond (1951); from specimens collected in the field, which are now preserved at University College, Leicester; and from others seen at the following herbaria :— Kew, Oxford, Cambridge and Paris.

I have pleasure in recording my gratitude to Professor T. G. Tutin for his advice and encouragement throughout the preparation of these four short papers. I am also much indebted to Mr. J. E. Lousley, to the Director of the Royal Botanic Gardens, Kew, and to the Curators of the herbaria at Oxford and Cambridge, for generously lending me material. Finally I wish to express my thanks to the Research Board, University College, Leicester for the award of a scholarship during the period 1950-53, and for giving considerable financial help towards my field work during that period.

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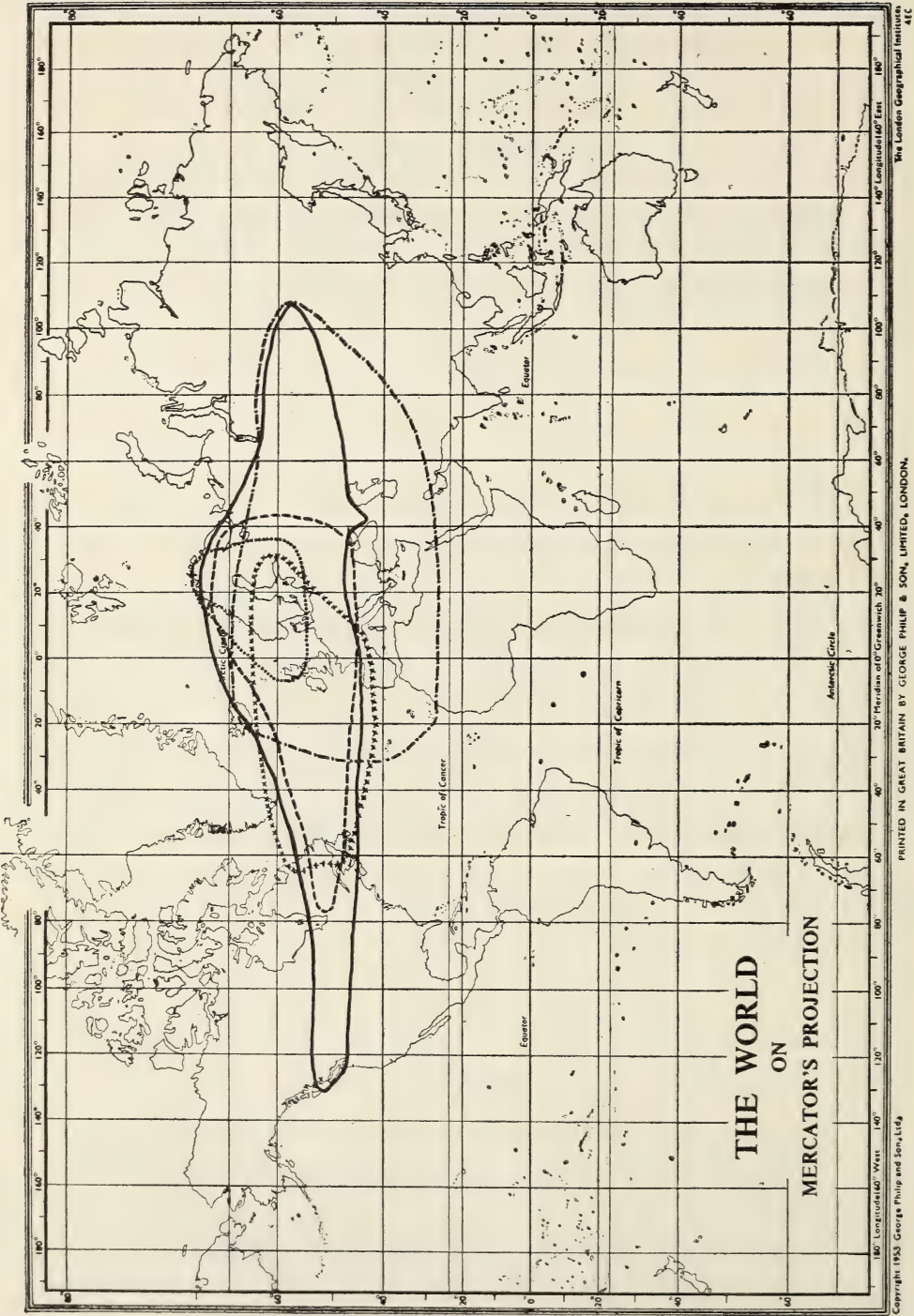


Fig. 1. Map showing distribution of the British representatives of the *C. flava* agg.
— *C. flava* L.
--- *C. lepidocarpa* Tausch
..... *C. scandinavica* E. W. Davies
xxxxxxx *C. demissa* Hornem.
- - - - - *C. serotina* Métat

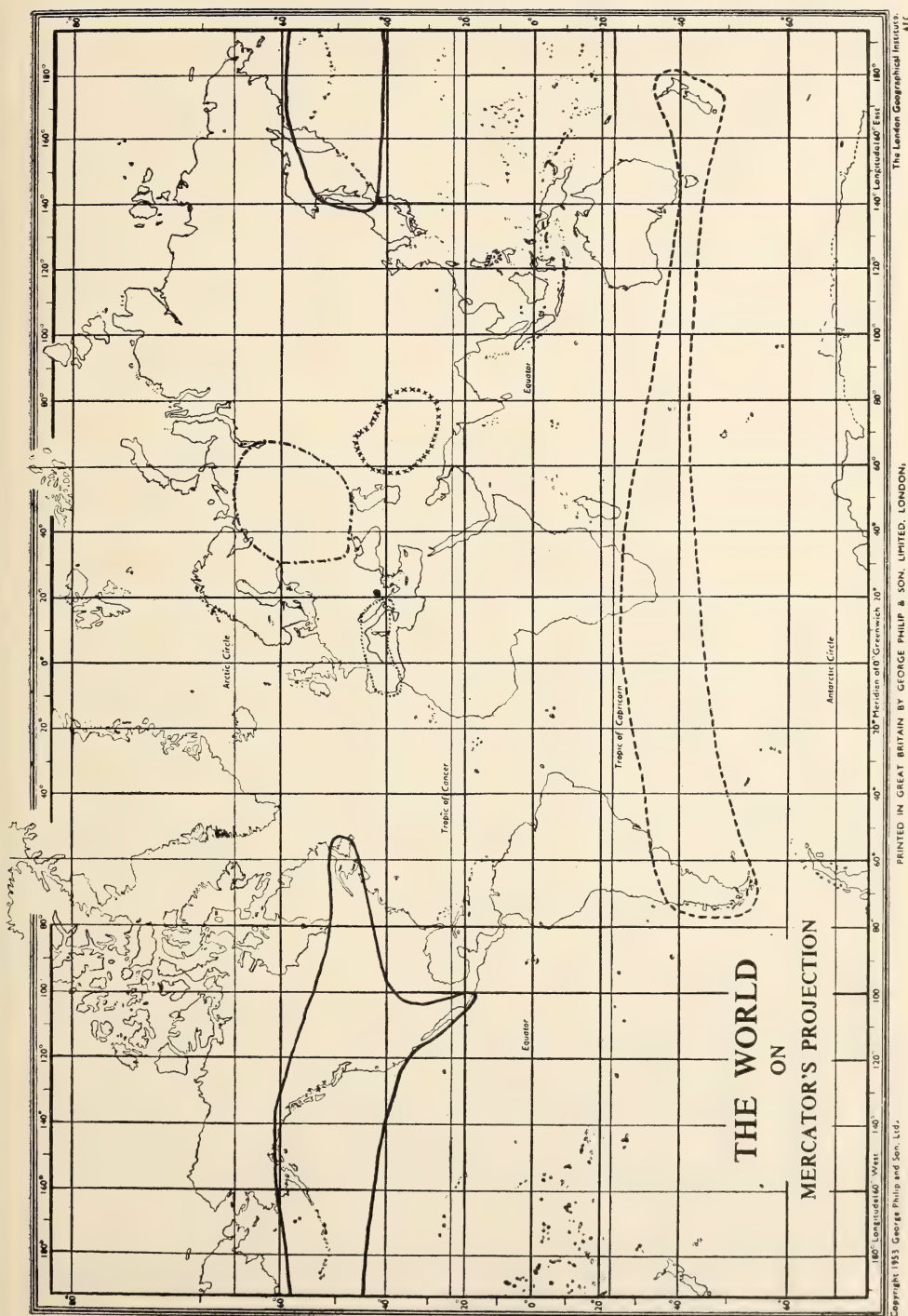


Fig. 2. Map showing distribution of the non-British representatives of the *C. flava* agg.

————— *C. viridula* Michx.
 - - - - - *C. flavella* Krecz.
 xxxxxxxxxx *C. philocrena* Krecz.
 - - - - - *C. cataractae* R. Br.
 *C. mairii* Coss. & Germ.
 ● *C. dyrrachiensis* Nelmes

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are invited both from members of the Society and others. They should have a bearing on the taxonomy or distribution of British Vascular Plants or Charophytes. Papers should be typed. They should be double-spaced and typed on one side of the paper only. The form adopted in this part should be used for citations and references. Full references should be put at the end, except where special reasons exist (e.g., the citation of place of publication of a plant name) or in very short papers. Illustrations, which may take the form of line drawings or photographs, will be considered for publication. Twenty-five separates of each paper are given free to the author, and further copies may be obtained on payment; requests for extra copies should be made when proofs are returned. Papers should be sent to the Editor, Dr. E. F. Warburg, University Department of Botany, South Parks Road, Oxford.

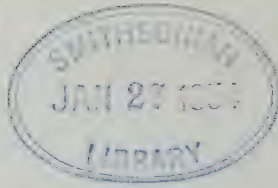
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Editor : E. F. WARBURG, M.A., Ph.D.

Vol. 3

SEPTEMBER 1954

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June 1954

The Society has launched a five years' scheme to produce an Atlas of Distribution Maps of British flowering plants and ferns on a basis of the presence or absence of each species in the 10 kilometre grid squares of the Ordnance Survey National Grid. There are about 3,500 such squares and approximately 2,000 native species in the British Flora; our task is therefore to accumulate some 2,500,000 records for vascular plants in a convenient form for map-making. In this task we need the co-operation of all field botanists, professional and amateur, in schools, local natural history societies

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sending lists or indicating what information you hope to be able to contribute. An attempt is being made to write individually to all Vice-County recorders and others actively at work on a local Flora. If you are engaged on such work, and have not already heard from us, we should like to have your suggestions as to ways in which you might co-operate. All help will be acknowledged and we will gladly give more detailed advice on any suggestions you may have.

A more detailed account of the Scheme is being prepared for the Proceedings, and will appear in the next issue.

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There are many ways in which you could help. Here are a few:-

- (1) Existing plant lists, which can be localised, would be gratefully received, and could be promptly returned if desired.
- (2) Similar lists could be compiled of the plants found in a particular 10 kilometre grid square (one of the big squares of about 6" side on the 1" O.S. map; or a single sheet of the $2\frac{1}{2}$ " O.S. map). Some indication of locality and habitat could be given for the less common plants, e.g.:-
Lychnis flos-cuculi, marsh by river, X, Grid Ref: 52/326485. 21.6.1953.
- (3) Lists of plants growing in, say, 6 particular habitats (e.g. a wood, a meadow, an arable field, a roadside, a pond, and a marsh) could be made within the same 10 kilometre grid square. In this way all the more common plants are likely to be recorded. Record Cards, on which are listed all species likely to be found in a particular Region (group of vice-counties) are available. These can be filled in quickly and easily in the field. Please indicate areas in which you would be able to use such cards.
- (4) Precise localities (with Grid Reference to 100 m.) of any rare or local plants would be very useful; such information can if desired be treated as confidential. Individual records, based on herbarium specimens or on field knowledge, could be sent in on small record cards, which we can supply; or, if you prefer, in the form of a list. (The card index is to form the basis of a permanent recording system for the Nature Conservancy, for whom this type of information is obviously of great importance).
- (5) Ecological data submitted with field lists will, where possible, be incorporated in the records, and would be welcomed.
- (6) Help will particularly be needed in certain under-worked areas, which can be suggested on request.

Important Points.

- (a) Correct identification is essential. If you have any doubt, please use the Society's system of referees. For any critical group, confirmation by a specialist is desirable and in many cases necessary. It is not necessary to make a complete list; omit any doubtful identifications.
- (b) Information on common plants is more important to us than localities for rarities. The simplest lists of roadside or field, carefully made, are exactly what we need. A specially-designed 'Common Species Record Card' is available; this would be suitable for the less experienced observer.
- (c) For purposes of standardisation, we prefer the nomenclature in Clapham, Tutin and Warburg: Flora of the British Isles. If, however, you wish to use any other reference work (e.g. Benthams & Hooker), it will be quite convenient to use your data, provided we know which book you are using.

If you would like to help, please write to:-

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sending lists or indicating what information you hope to be able to contribute. An attempt is being made to write individually to all Vice-County recorders and others actively at work on a local Flora. If you are engaged on such work, and have not already heard from us, we should like to have your suggestions as to ways in which you might co-operate. All help will be acknowledged and we will gladly give more detailed advice on any suggestions you may have.

A more detailed account of the Scheme is being prepared for the Proceedings, and will appear in the next issue.

BOTANICAL SOCIETY OF THE

VARIATION IN *PEPLIS PORTULA* L.

By D. E. ALLEN

INTRODUCTION.

It has long been known that *Peplis portula* L. varies considerably in the length of the outer calyx teeth. Although there is a general acceptance of the fact that this variation has some geographical significance, little attempt has hitherto been made to discover how far this assumption is justified. The present study was undertaken primarily to plot the distribution of the variation in the British Isles, but in the course of the work a number of interesting features have come to light and are discussed in this paper.

The first notice of the variation in Britain was given by Dunn (1896), who, however, made the surprising assertion that var. *longidentata* Gay, a local race on the Continent, appeared to be the only form occurring in this country. It is difficult to account for this error, for Dunn is known to have been familiar with parts of Surrey and Warwickshire; his statement would have been understandable had his experience been confined, say, to the Cornish Peninsula. The next mention was by Druce (1911) who, misunderstanding the true nature of var. *longidentata* and misled by only finding specimens that did not display the calyx character to an extreme degree, created a new variety *dentata* for the British plants, which in his opinion formed a passage to the (supposedly) Mediterranean var. *longidentata*. Druce's name was challenged by Thompson (1917), who rightly claimed that perfectly good examples of var. *longidentata* were to be found in Britain and also questioned the value of giving varietal names to "passages." Furthermore, in 1916 W. C. Barton had distributed through the Watson Botanical Exchange Club excellent material from Radnor of both the typical plant and what he correctly named var. *longidentata*. Even so, Druce persisted in using his epithet and the interesting nature of the variation soon relapsed into the oblivion from which it had emerged.

TAXONOMY

As reported by Bennett (1917), Gay's type is in the Kew Herbarium, where it is described as follows: "Dentibus calycinis interioribus brevibus, exterioribus longioribus, valde elongatis, filiformibus." The specimens were collected in 1825 near Banyuls-de-mer in Roussillon, close to the Franco-Spanish border, and sent to Gay, who later (1832) published an account of the new variety. Afterwards, he seems to have considered it a distinct species, for he raises to it this rank in his herbarium.

The synonymy is as follows:—

- P. *PORTULA* var. *LONGIDENTATA* Gay, 1832, *Notic. sur Endress*, 38; 1832, *Ann. Sci. Nat.*, 26, 226; *P. fradini* Pomel, 1860, *Matér. Fl. Atlant.*, 156; *P. portula* *[ssp.] *longidentata* (Gay) Boiss. & Reut. ex Nym., 1879, *Consp. Fl. Eur.*, 2, 252; *P. longidentata* (Gay) Batt. 1890, in Batt. & Trab., *Fl. Alg.*, 1, 320; *P. portula* "forme" *P. longidentata* (Gay) Rouy & Camus, 1901, *Fl. Fr.*, 7, 167; *P. portula* proles *longidentata* (Gay) Rouy, 1927, *Consp. Fl. Fr.*, 107.

The outer calyx teeth in Gay's type specimens are 1.5-2 mm. long, and this is the extreme reached in various parts of the plant's range. In var. *portula* the outer teeth are not at all elongated and consequently only attain 0.5 mm. in length at the most. Between these two extremes—the latter always well-marked, the former somewhat less so—every intergradation can be found. The continuity of this variation tends to be obscured by

the very small range (only one millimetre) that is involved. H. Stuart Thompson, in a note in his herbarium, also came to the conclusion that every form occurs between the type and var. *longidentata*, but he failed to realise that this intergradation follows a definite pattern. The manner, in fact, in which one extreme gradually gives way to the other following a broadly recognizable geographical trend suggests that a cline of some kind may be distinguishable.

In the earlier determinations of herbarium material during the present study, the two extremes were treated as subspecies – a view which later had to be abandoned. The case for subspecific rank rests not only on the very distinct geographical range of var. *longidentata*, but also on a number of other characters which various authors have claimed to be associated with the elongation of the calyx teeth. Thus, Knerskon (1874) has asserted that the variety is also characterised by sessile (rather than subsessile) flowers and longer, subherbaceous (rather than scarious) bracteoles. Battandier & Trabut (1890) mention a strongly papillose stigma and sublinear (not ovoid) placentas as additional features. It has not been possible to check these alleged correlations (which would have to be done by a biometric analysis, preferably of fresh material), and it is by no means out of the question for the gene or genes determining the elongated character of the calyx teeth to possess a pleiotropic effect, or even for linkage to be involved. However, since the variation between the two extremes of the calyx character evidently forms a single continuum, the maintenance of two distinct subspecies seems inappropriate.

It should be stressed that while var. *portula*, with almost obsolete calyx teeth, is a well-defined extreme, the boundary between var. *longidentata* and the various intermediate grades is a somewhat arbitrary one. Even so, by studying the variation in an area such as Cornwall, where only two out of the eleven gatherings seen fail to exhibit extreme elongation of the calyx teeth, the limits of var. *longidentata* can be comprehended and defined with reasonable precision. Moreover, there are specimens of the variety in Gay's herbarium which he records having grown from seed in 1845. In the British Isles it is not uncommon to find both var. *portula* and intermediates growing together in abundance without any sign of var. *longidentata*; I have personally encountered this in populations in Dorset and the Isle of Man, and it is reflected in a number of herbarium gatherings. It was this phenomenon, no doubt, that led Druce to the belief that the true variety of the Iberian Peninsula was not to be found in Britain.

In the meantime, it seems best to treat these two extreme forms as varieties; those who like to use a name for the medial part of a continuous series might find var. *dentata* Druce convenient for the purpose.

DISTRIBUTION

A study of the distribution of the variants reveals a fairly well-marked geographical trend: var. *longidentata* is prevalent in the west, but becomes gradually replaced eastwards, first by specimens exhibiting various degrees of intermediacy and then by the well-marked extreme of var. *portula*. It is possible that climate operates effectively in producing a balance between the varieties, and for this reason it is of interest to see how far the isophenes coincide with any particular climatic feature.

In order to assess the degree of oceanicity of the climate, Greig-Smith (1950) has employed Amann's Index of Hygrothermy. This is obtained by dividing the annual precipitation (in centimetres) multiplied by the annual mean temperature by the mean temperature of the coldest month subtracted from that of the hottest month, the values of these last three being expressed in degrees Centigrade. On comparing the values for this index in various parts of the British Isles with the variation in *Peplis portula* as plotted on the map (see fig. 1), there would appear to be some correlation in Great Britain between

the line joining places with a hygrothermic value of about 70 and those areas in which the two varieties are represented in approximately equal proportions ; in Ireland, however, no such correlation is perceptible, though little can be argued from this owing to the small amount of material seen from the eastern part of that country.

It would be premature, in view of the so far scanty evidence adduced, to make too emphatic an assertion about the nature of this geographical trend. It does, however, appear that a cline, albeit a rather ill-defined one, is to some extent recognisable. This cline is remarkable for the fact that one extreme, var. *longidentata*, has a " Lusitanian " type of distribution. The direction of the cline – or topocline, as it should perhaps be more accurately termed – is also interesting. Most topoclines so far recognised in the British Flora seem to extend from north to south. The only other recorded examples of a true east-west cline are apparently those exhibited by *Ulmus stricta* Lindl. (Melville, 1939, 1944, 1948) and by *Orchis fuchsii* Druce subsp. *hebridensis* (Wilmott) Clapham (Harrison, 1949, 1952).

Material from the following herbaria has been examined :

Hb. Univ. Birmingham (B), Hb. Univ. Cambridge (C), Hb. Carlisle Museum (Cl), Hb. Royal Botanic Gardens, Kew (K), Hb. Manchester Museum (M), Hb. British Museum (Natural History) (N), Hb. Univ. Oxford (O), Hb. N. Douglas Simpson, Bournemouth (S), Hb. National Museum of Wales, Cardiff (W).

The extra-British distribution will be considered first.

var. *longidentata* :

FRANCE : Banyuls-de-mer, Roussillon, 1825, *M. Petit* (K).

SPAIN : Manzanares, 1841, *G. F. Reuter* (N).

PORTUGAL : Manteigas, 1881, *J. Daveau* (C) ; Golleça, 1886, *A. R. da Cunha* (N) ; Near Oporto, 1889, *R. P. Murray* (N).

ALGERIA : near Lake Houbera, La Calle, 1841-4, *J. Gay* (K).

AZORES : Caldera, Fayal, 1842, *H. C. Watson* (C) and 1929, *T. G. Tutin* & *E. F. Warburg* (C).

Rouy & Camus (1901) record this variety as occurring " here and there " in the departments of France nearest the Pyrenees. In Spain it has been recorded by Knerskon (1874) from Escorial and by Willkomm (1893) from the Sierra de Palma ; it is probably more plentiful than the sparsity of the records suggests. Wolley-Dod (1914) noted that it had been recorded from Gibraltar, although his only gathering belonged to var. *portula*. In Algeria (Battandier & Trabut, 1890, 1902) it is said to be " frequent in the east," while Jahandiez & Maire (1931) report it as more frequent than the type in Morocco. In the Azores Trelease (1897) records it on Flores, Fayal, Pico, Terceira and San Miguel. All these authors, however, do not distinguish between the extreme type and the probably equally frequent intermediates. I have seen material of the latter from :—

SPAIN : near Madrid, 1844, *M. Willkomm* (K) ; La Granja, Sierra de Guadarrama, 1858, *E. Boissier* & *G. F. Reuter* as *P. longidentata* (K).

PORTUGAL : Coimbra, 1848, *F. Welwitsch* (C) ; near Manteigas, 1881, *J. Daveau* (N).

Var. *portula* is the only form outside Macaronesia, North Africa and the Iberian Peninsula. Material of this has been seen from most of Europe, including Italy, Sicily, Sardinia, Corsica, many parts of France (including La Vendée) and a single gathering from Pico in the Azores.

BRITISH ISLES

A considerable amount of material lacked ripe capsules and could not be determined satisfactorily. In the far north the species tends to become aquatic and evidently does not fruit readily.

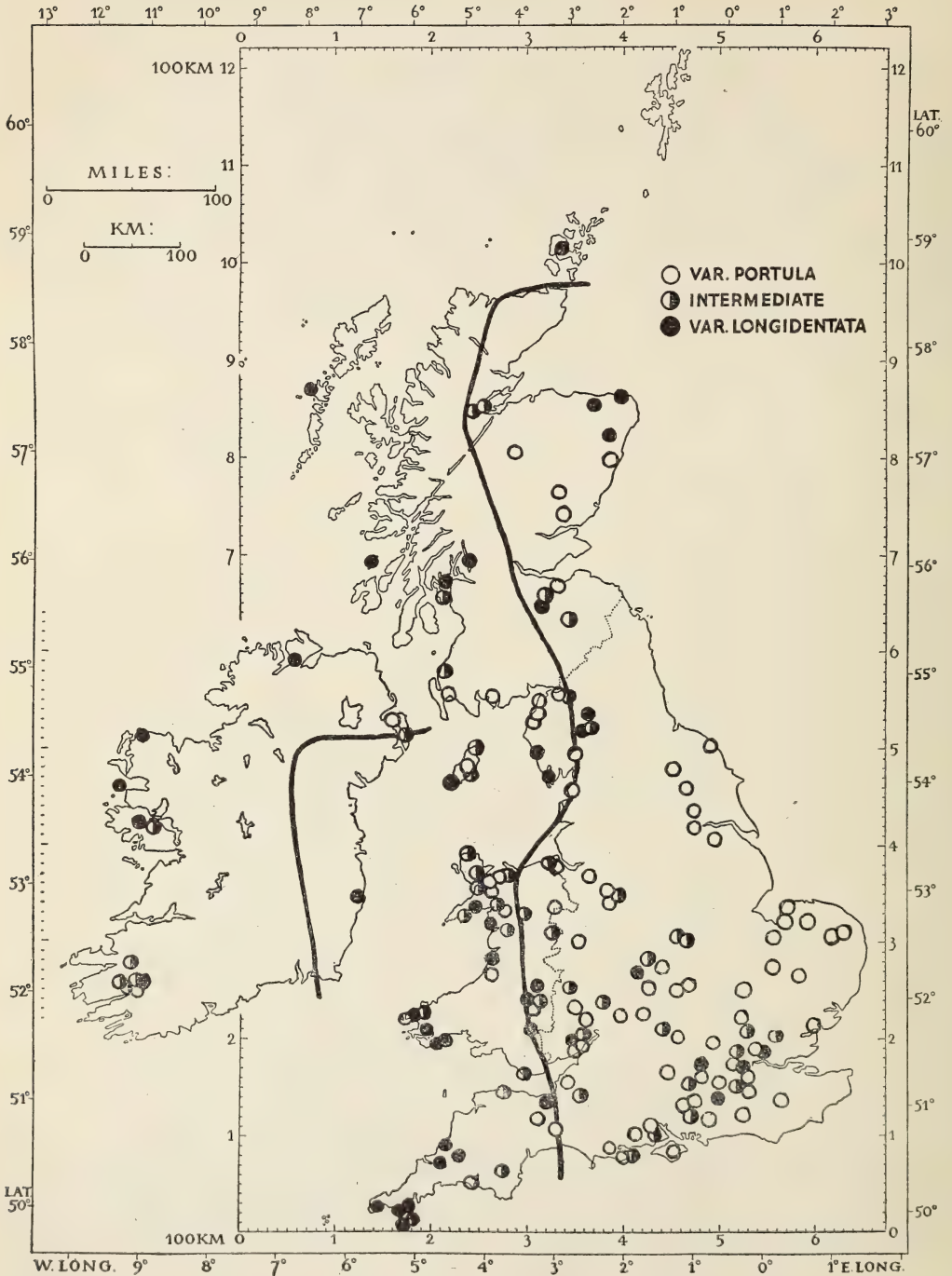


Fig. 1. Distribution of the three forms of *Peplis portula* L. in the British Isles. The line indicates the approximate eastern limit of the areas where the values of the hygrothermic index exceed 70 (copied from Greig-Smith, 1950). Base-map by courtesy of "New Naturalist" Series.

VAR. LONGIDENTATA :

- V.c. 1. W. CORNW. : pond near Lcoe Pool, Helston 1870, *G. C. Druce* (O) : near Penzance, 1875, *E. A. Lomax* (M) and 1880, *H. S. Thompson* (B) : Lizard Head, 1882, *R. P. Murray* (N) and 1887, *C. A. Wright* (N) : Helston, 1891, *F. R. Tennant* (C).
2. E. CORNW. : Boscastle, 1906, *G. C. Druce* (O) : Lank Valley, 1923, *R. Melville* (W) : Egloskerry, near Launceston, 1943, *J. H. Davie* (N).
5. S. SOM. : stream near Quantock, 1890, *H. S. Thompson* (B, N).
17. SURREY : Wimbledon Common, 1860, *H. Trimen* (N) : wealden copse near Witley, 1888, *E. S. Marshall* (C) : Ham Common, 1928, *C. E. Hubbard* (K).
18. S. ESSEX : Woodford Forest, 1839, *J. Freeman* (Cl).
22. BERKS. : Bulmarsh Heath, 1804, *S. Rudge* (N).
35. MON. : Trelleck Bog, 1944, *A. E. Wade* (W).
38. WARW. : Earlswood Reservoir, 1893, *H. S. Thompson* (B).
42. BRECON : The Ystrad, Taffechan, 1900, *A. Ley* (B) : Cae-pandy Wood, near Builth, 1928, *A. E. Wade* (W).
43. RADNOR : wet places on hillside, Llandrindrod, 1890, *W. H. Purchas* (N) and 1916, *W. C. Barton* (various herbaria).
45. PEMB. : Haverfordwest, 1848, *C. C. Babington* (C) : Saundersfoot, 1873 (B) : Dowrog Moor, near St. David's, 1937, *H. A. Hyde & A. E. Wade* (W) : near Llanerch, Gwaen Valley, 1939, *A. E. Wade* (W) : woods near Tenby, 1945, *F. L. Rees* (W).
46. CARD. : cliff-top near Upper Borth, 1930, *H. M. Montford & W. B. Turrill* (K).
48. MER. : Barmouth, 1867, *M. A. Lawson* (O).
49. CAERN. : Criccieth, 1931, *H. Hall* (W).
69. WESTMORL. : Poaka Beck Reservoir, Dalton-in-Furness, 1913, *W. H. Pearsall* (C, O, N, W) : marsh, Rough Hill, near Askham, 1925, *L. B. Hall* (S) : moor north of Rough Hill, 1925, *C. E. Salmon* (N).
70. CUMB. : pond near Melmerby, 1919, *C. E. Salmon* (N) : Seascale, 1928, *R. H. Williamson* (Cl).
71. MAN : field near Fleshwick, 1952, *D. E. Allen*.
76. RENFREW : Glen Dam Abbey, 1886, *E. S. Gregory* (N).
78. PEEBLES : near West Linton, 1790, *W. McRitchie* (N).
- 86 or 99. Loch Lomond, 1868, *J. Storrie* (W).
93. N. ABERD. : Old Meldrum, 1879, *F. C. King* (C, N) : Drowning Pot, Pitsligo, 1888, *J. Fraser* (K).
94. BANFF : Alvah, 1838, *W. A. Stables* (Cl).
98. ARGYLL : Dunloskin Loch, near Dunoon, 1868, *J. C. Hutcheson* (N).
102. S. EBUDES : Isle of Colonsay, ante 1916, *M. McNeil* (N) and 1929, *Mrs. Lockhead* (K).
109. CAITHN. : Kirk of Stones, 1905, *D. Douie* (N).
110. HEBRIDES : ditches, west side of North Uist, 1896, *W. A. Shoolbred* (W).
111. ORKNEY : "Orkney," *J. Miers* (N).
- H. 1. S. KERRY : Poulgorm Bridge, 1952, *S. M. Walters* (C).
- H. 2. N. KERRY : near Finow Bridge, Lough Guitane, 1935, *S. Ross-Craig & al.* (K).
- H.16. W. GALWAY : Recess, Connemara, 1900, *J. S. Gamble* (K).
- H.20. WICKLOW : Wicklow, *J. Ball* (C).
- H.27. W. MAYO : Clare Island, 1903, *R. L. Praeger* (N) : mouth of R. Glenamoy, Lough Feeagh, 1903, *H.H.S.* (W).
- H.34. E. DONEGAL : Buncrana, 1894, *H. E. Fox* (O).

INTERMEDIATE :

0. JERSEY : St. Brelade's, 1842, *W. W. Newbould* (C) : Grouville Common, 1900, *L. V. Lester-Garland* (K).
1. W. CORNW. : Goonhilly Downs, 1910, *H. E. Fox* (O).
3. S. DEVON : Holne Chase, near Ashburton, *H. T. Mennell* (N).
4. N. DEVON : Lynton, 1831, *C. C. Babington* (C) : Badgeworthy Valley, 1917, *W. C. Barton* (M).
6. N. SOM. : Melcombe Wood, Wells, 1918, *H. S. Thompson* (B).
9. DORSET : Wareham, 1889, *E. F. Linton* (N) : near Littlesea, Studland, 1911, *H. E. Fox* (O) and 1951, *D. E. Allen & N. D. Simpson*.
11. S. HANTS. : New Forest, 1882, *F. T. Mott* (M) : Brockenhurst, 1885, *R. P. Murray* (N) and 1889, *J. D. Gray* (C) : Petersfield Lake, 1911, *F. Stratton* (D) : Blashford, 1921, *N. D. Simpson* (S).
12. N. HANTS. : Mattingley, 1934, *J. F. G. Chapple* (D, M).

17. SURREY : Abberley Hills, 1840, *H. Newman* (N) : Wandsworth Common, without data (M) : wealden copse near Witley, 1888, *E. S. Marshall* (C) : Ashted, 1890, *C. B. Clarke* (K) : Ham Common, 1928, *A. R. Horwood* (K) and 1928, *C. E. Hubbard* (K) : Lost Pond, Richmond Park, 1933, *H. M. Montford & al.* (K).
19. N. ESSEX : Norton Heath, 1910, *A. J. Wilmott* (N).
20. HERTS. : Hertford Heath, 1910, *J. E. Little* (C).
21. MIDDX. : Hampstead Heath, 1866, *H. E. Fox* (O) : Stanmore Common, 1905, *H. P. Reader* (W).
22. BERKS. : Mortimer Common, 1930, *G. C. Druce* (O).
23. OXON. : Bladon Heath, near Woodstock, 1943, *W. B. Turrill* (K).
34. W. GLOS. : near the Buckstone, Coleford, 1874, *A. Ley* (B).
35. MON. : Trelleck Bog, 1876, *A. Ley* (B, N) and 1944, *A. E. Wade* (W).
36. HEREF. : Lower Pool, Shobdon, 1887, *A. Ley* (B).
37. WORCS. : Great Malvern, 1907, *J. S. Gale* (O).
38. WARW. : Coleshill Pool, 1893, *H. S. Thompson* (B).
39. STAFFS. : Rudyard Reservoir, 1887, *C. Bailey* (M).
41. GLAM. : Pilton, 1903, *H. J. Riddelsdell* (N) : Mynydd-y-Glew, St. Donats, 1907, *E. Vachell* (W) and 1921, *A. E. Wade* (W).
43. RADNOR : Llandeilo Hill, Aberedw, 1927, *A. E. Wade* (W).
45. PEMB. : Dowrog Moor, near St. Davids, 1937, *H. A. Hyde & A. E. Wade* (W) : Llanbed, near Mathry, 1939, *A. F. Wade* (W).
46. CARD. : bog near Llantrissant, 1893, *I. H. Burkill & J. C. Willis* (C).
47. MONT. : between Craig Breidden and Craig Moel-y-Golfa, 1832, *W. A. Leighton* (C).
48. MER. : near Tan-y-bwlch, 1854 (M) : Dolgelly, *Mrs. Berkeley* (N) : near Abercorys, 1875, *A. Ley* (B) : Lake Bala, between Llan-y-Cil and Bala, 1877, *C. Bailey* (M, N) : Barmouth, *G. C. Druce* (O).
49. CAERN. : Caernarvon, 1830, *C. C. Babington* (C) : Criccieth, 1884, *H. C. Levinge* (K) : Pwllheli, 1904, *C. T. & E. Vachell* (W) : Ro Wen, near Conway, 1931, *A. Wilson* (W).
52. ANGL. : Llyn Pwmp, Llangefni, 1884, *J. E. Griffith* (W) : near Cemmaes Bay, 1931, *A. Wilson* (W).
55. LEICS. : Ulverscroft, 1896, *F. T. Mott* (M) : Cropstone Reservoir, 1913, *W. Wade* (W).
58. CHES. : Mere mere, 1870, *J. L. Warren* (N) : Irby, 1876, *J. H. Lewis* (D).
69. WESTMORL. : Cliburn Moss, 1905, *T. J. Foggitt* (N) : Poaka Beck Reservoir, Dalton-in-Furness, 1913, *W. H. Pearsall* (C, M, W).
70. CUMB. : Cronkley Fell, 1873, *H. E. Fox* (O) : Melmerby, 1920, *W. W. Mason* (O) : Moorhouse, near Carlisle, 1949, *C. W. Muirhead* (Cl).
71. MAN : Gat-y-Whing, Andreas, 1921, *C. I. Paton* (Hb. Manx Mus., Douglas) : Smeale ; Clypse Reservoir, 1951 ; near Fleshwick, 1952, *D. E. Allen*.
- 73 or 74. "Galloway," 1836, *R. K. Greville* (C).
75. AYR : Currarie Glen, Ballantrae, 1902, *A. Somerville* (N).
79. SELK. : near Caddonfoot, 1872, *A. Brotherston* (M).
83. EDINB. : Harlaw Reservoir, 1878, *W. Horton-Smith* (M).
93. N. ABERD. : Drowning Pot, Pitsligo, 1888, *J. Fraser* (K).
100. CLYDE IS. : Bute, 1823 (K).
106. E. ROSS. : Loch Ussie, Strathpeffer, 1877, *Thomson* (D) : near Achilty Inn, 1909, *W. A. Shoolbred* (C, N, W).
- H.1. S. KERRY : Gap of Dunloe, 1901, *G. C. Druce* (D).
- H.2. N. KERRY : Killarney, 1858, *C. C. Babington* (C), 1901, *H. J. Riddelsdell* (N) and 1908, *C. Bucknall* (K) : ditches, Dicksgrove, 1895, *R. M. Middleton* (N) : near Finow Bridge, Lough Guitane ; between Ross Island and mouth of R. Flesk, Killarney, both 1935, *S. Ross-Craig et al.* (K).
- H.16. W. GALW. : ditches near Maam, 1885, *C. Bailey* (B, D, M, W).
- H.38. DOWN : Kircubbin, 1918, *C. H. Waddell* (N).

Material of var. *portula* is too numerous to cite individually ; it has been seen from the following vice-counties : 0, 2, 4-6, 9-24, 26-29, 32-36, 38-43, 45, 46, 48-50, 54, 55, 58, 60-63, 69-71, 73, 74, 80, 83, 90, 92, 96, H1, H38, H40. It should be noted that from the Channel Isles five gatherings of var. *portula* have been seen, two of the intermediates, but none of var. *longidentata*.

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VASCULAR PLANTS COMMON TO THE ARCTIC AND THE BRITISH ISLES : ENUMERATION OF SPECIES

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The availability of (a) a 'working' delimitation of the Arctic (Polunin 1951), (b) a manuscript 'Circumpolar arctic flora' in which I have treated all of the recognized species of vascular plants known to reach the prescribed area, and (c) a modern British flora (Clapham, Tutin and Warburg, 1952, hereafter referred to as '*F.B.I.*'), has made it desirable, with much further exploration in the Arctic and botanical discovery in the British Isles (cf. Lousley 1951, 1952; Polunin 1953), to undertake a more adequate treatment than was formerly available (Polunin 1939a, 1939b) of the subject of 'arctic plants in the British Isles.' The bases and results in outline of this revised analysis of the vascular plant species common to the Arctic and the British Isles have recently been published (Polunin 1954), and it now seems desirable, as on the former occasion before the war, to offer also details of the plants concerned in the various ecological (or sometimes phytogeographical) categories.

In the lists given below the order is that of *F.B.I.*, as are in general the orthography and nomenclature. Where the nomenclature differs from that used in *F.B.I.*, or where this last supplants some more familiar designation, sufficient synonymy is given to orientate the reader : this is especially necessary with some widely inclusive species (indicated by "s.l.") which have been maintained here for reasons either of taxonomic preference or personal uncertainty (e.g. where insufficient material has been available for demonstration of conspecificity or for satisfactory appraisal of the situation in the British Isles and the Arctic together). This has allowed the inclusion in some instances of different subspecies, admittedly with probably different ecological relationships, as representatives of a species in the north and south ; but there are doubtless more segregations and discoveries to come. There were also occasional needs for changes (usually indicated by citing authorities) in accordance with the *International code of botanical nomenclature* as recognised in my 'Circumpolar arctic flora' or otherwise in relation thereto, though in general where matters of mere personal preference were concerned I have given precedence in the present lists to the *F.B.I.* and merely indicated by adding synonyms that other opinions exist.

Worse difficulties have been encountered in the assignment of some species to their proper ecological, etc., category ; and indeed the categories, like all too many biological entities, are somewhat nebulous and apt to overlap. When the entire picture is considered as a whole, however, these components stand out with fair clarity, and it is certainly hoped that anyone interested in the subject will supplant the old analysis with this new one which is much more worthily based. Especially has it a far less restricted and more logical and scientific 'Arctic' as its basis.

A single asterisk before the name of a plant indicates that it is, supposedly, introduced in the Arctic, and a double asterisk at the end of a plant's treatment indicates that it appears to be introduced in the British Isles : a few species are both. Introduced plants are taken as those of which the ancestral disseminules were supposedly transported by man to the region concerned, whether in ancient or modern times, so long as they appear to be established and able to persist from generation to generation without his continued intervention. When an otherwise introduced species appears to be native in any place in a

region it is counted as native, but in cases of serious doubt – as for instance when collection data have been inadequate – such species have been counted as introduced.

The symbols following plant names indicate the numbers of vice-counties of Great Britain (112 in all) and Ireland (designated “H” and 40 in all) in which the species concerned is known to occur. Usually these numbers are taken from *F.B.I.* but in a few cases in which the species concerned or at least the numbers are lacking in that work, they have been supplied from other sources – in particular Druce (1932). In some other instances, recent finds have had to be added to bring the vice-county numbers more nearly up-to-date. Further symbols have been employed in the case of group 2, comprising plants of sea-shore, lake-margin, aquatic and allied habitats: these indicate the group and sub-group to which each species would have been assigned if it had not been so specially selected.

There follow the detailed results of this analysis which, although it is in general based on that published in 1939, has the first and third categories somewhat broadened in other ways besides the geographical. There are also unfortunately many of the seemingly inevitable nomenclatural changes. It may be noted that further field experience and general considerations have led to (1) the omission of *Luzula arcuata* owing to prevailing doubts about its being in full development in the Arctic, (2) changing of *Carex lachenalii* from a plant of open soil to one characteristically of closed habitats though sometimes found in open areas, (3) changing of the polymorphic and often apomictic *Poa pratensis* s.l. in precisely the reverse manner, (4) the ‘sinking’ of *Cochlearia groenlandica* (which apparently differs from *C. scotica* and never was a British plant) in the polymorphic *C. officinalis* s.l., (5) the omission of *Senecio congestus* (R.Br.) DC. (*S. palustris* (L.) Hook.) as being apparently extinct in Britain, and (6) the changing of *Eriophorum angustifolium* from the category of plants of closed communities to that of plants to be found in open areas though characteristic of closed ones.

1. Plants commonly of open soil or rocky, etc., habitats with little or no competition (although humus may be plentiful) at least in the Arctic.

- (a) found in all three latitudinal arctic zones and of wide distribution meridionally in the Arctic (occurring in at least 5 of the 10 sectors – cf. Polunin 1951, 1954).

Lycopodium selago – 89, H40.
Equisetum variegatum – 34, H21.
E. arvense s.l. – 112, H40.
Cystopteris fragilis s.l. (incl. *C. dickieana*) – 90, H34.
Woodsia alpina – 6.
Cardamine pratensis s.l. – 112, H40.
Arabis alpina – 1.
Silene acaulis – 25, H5.
Cerastium alpinum s.l. – 20.
Sagina intermedia – 2.
Minuartia rubella (Wahlenb.) Hiern (*Arenaria rubella* (Wahlenb.) Smith) – 5.
M. stricta (Sw.) Hiern (*Arenaria uliginosa* Schleich. ex DC.) – 1.
Potentilla crantzii – 21 (incl. recent addition).
Dryas octopetala – 19, H10.
Sedum rosea – 45, H17.
Saxifraga nivalis – 16, H1.
S. hirculus – 10, H6.
S. cernua – 2.
S. rivularis – 4.
S. cespitosa – 3.
S. aizoides – 33, H6.
S. oppositifolia – 35, H7.
Koenigia islandica L. – 1 (not mentioned in *F.B.I.*)

Polygonum viviparum - 35, H4.
Oxyria digyna - 31, H8.
Salix herbacea - 38, H17.
S. reticulata - 5.
Diapensia lapponica L. - 1 (not mentioned in F.B.I.)
Armeria maritima s.l. - 82, H27.
Matricaria maritima s.l. (*M. inodora* L. s.l.) - 112, H40.
Juncus castaneus - 9.
J. biglumis - 5.
J. triglumis - 25.
Kobresia simpliciuscula - 6.
Carex capillaris s.l. - 20.
C. saxatilis - 14.
C. glacialis - 1.
C. atrofusca - 2.
C. bigelowii - 39, H15.
C. rupestris - 6.
Festuca vivipara - uncertain but indicated as widespread and locally common.
Poa alpina - 17, H2.
P. glauca - 14.
P. pratensis s.l. - 112, H40.
Deschampsia cespitosa - 112, H40.
D. alpina - 17, H3.
Alopecurus alpinus s.l. - 7.

TOTAL = 47.

- (b) occurring northward at least to the middle-arctic zone and found in at least three sectors (cf. Polunin 1951, 1954).

Woodsia ilvensis - 9.
Thalictrum alpinum - 80, H5.
Draba norvegica s.l. (incl. *D. rupestris* at least of some authors) - 6.
D. incana - 32, H9.
Cardaminopsis petraea (L.) Hiit. (*Arabis petraea* (L.) Lam.) - 20, H2.
Viscaria alpina (L.) Don (*Lychnis alpina* L.) - 3.
Cerastium cerastoides - 8.
Arenaria ciliata s.l. - H1.
Montia lamprosperma - widespread in the British Isles.
Chamaenerion angustifolium (L.) Scop. (*Epilobium angustifolium* L.) - 108, H11 (H17 according to Druce, 1932).
Rumex acetosella - "widespread and common."
R. graminifolius Georgi ex Lambert (if incl. *R. tenuifolius* (Wallr.) Löve) - "probably widespread."
Arctous alpinus (L.) Niedenzu (*Arctostaphylos alpinus* (L.) Spreng.) - 9.
Veronica alpina s.l. - 10.
Pinguicula vulgaris - 100, H38.
Thymus serpyllum s.l. - widespread.
Plantago maritima s.l. - 86, H29.
Gnaphalium supinum - 16.
Juncus trifidus - 21.
Luzula spicata - 21.
Carex bicolor - 1 (by some considered an introduction).
C. microglochin - 1.
C. capitata s.l. - 1 (by some considered doubtful).

TOTAL = 23.

- (c) limited to the low-arctic zone or otherwise of restricted distribution in the Arctic.

Asplenium viride - 49, H12.
Athyrium alpestre - 14.
Dryopteris filix-mas - 112, H40.
Polystichum lonchitis - 30, H6.

- **Ranunculus repens* – 112, H40.
- **Chelidonium majus* – 96, H40, according to Druce (1932).
- **Thlaspi arvense* – 101, H19.
- **Capsella bursa-pastoris* – 112, H40.
- Rorippa islandica* – 93, H38
- Erysimum cheiranthoides* – 76, H18**
- Viola canina* s.l. – at least 106, H38.
- Cerastium arvense* – 81, H12.
- C. holosteoides* Fries ampl. Hylander (*C. vulgatum* of many authors) – 112, H40.
- **Stellaria media* – 112, H40.
- Sagina procumbens* – 112, H40.
- S. saginoides* – 11.
- S. nodosa* – 106, H40.
- Minuartia verna* (L.) Hiern (*Arenaria verna* L.) – 31, H3.
- **Erodium cicutarium* – 111, H25.
- **Potentilla norvegica* – 47**.
- Alchemilla alpina* – 28, H2.
- Sedum acre* – 111, H40.
- S. villosum* – 34, according to Druce (1932).
- Saxifraga stellaris* – 45, H18.
- Parnassia palustris* – 90, H33.
- Polygonum aviculare* s.l. (incl. *P. heterophyllum* Lindm.) – 112, H40.
- **P. lapathifolium* – 110, H38.
- Rumex maritimus* – 57, H4.
- Arctostaphylos uva-ursi* – 34, H8.
- Gentianella amarella* s.l. (*Gentiana amarella* L.) – at least 89, H30.
- **Asperugo procumbens* – “rare and usually casual” according to F.B.I.**
- **Myosotis arvensis* – 112, H40.
- Veronica fruticans* – 5.
- **V. persica* – 112, H40**.
- Thymus drucei* Ronn. (*T. arcticus* (E. Durand) Ronn.) – 70, H13.
- **Lamium amplexicaule* – 105, H26.
- **L. moluccellifolium* – 42, H25.
- **L. purpureum* – 112, H40.
- **Plantago major* – 112, H40.
- Galium boreale* – 46, H24.
- **Senecio vulgaris* – 112, H40.
- Tussilago farfara* – 112, H40.
- **Gnaphalium uliginosum* – 112, H40.
- Erigeron acris* – 72, H17.
- **Matricaria matricarioides* – 91 (incl. recent addition), H40**.
- **Artemisia vulgaris* – 112, H40, according to Druce (1932).
- **Cirsium arvense* – 112, H40.
- Allium schoenoprasum* s.l. – 12, H1.
- Juncus bufonius* – 112, H40.
- J. filiformis* – 5.
- J. balticus* – 17.
- J. alpinus* – 9.
- Eleocharis pauciflora* – 104, H34.
- Festuca* [cf.] *ovina* – 112, H40.
- **Puccinellia distans* – 74, H12.
- **Poa annua* – 112, H40.
- P. laxa* s.l. (incl. *P. flexuosa* Sm.) – 2.
- **Agropyron repens* – 112, H40.
- **Hordeum jubatum* – “occasionally as a casual.”***

TOTAL = 59.

2. Plants of sea-shores or lake, etc., margins (including aquatics) with little or no competition.

Isoetes lacustris – 42, H18 – group 1 (c).

- I. echinospora* s.l. – 21, H5 – group 1 (c).
Equisetum fluviatile – 110, H40 – group 1 (c).
Ranunculus reptans – 5 – group 1 (b).
R. trichophyllus – probably 112, H40 – group 1 (a).
Cakile maritima – 69, H19 – group 1 (c).
Cochlearia officinalis s.l. – 87, H25 – group 1 (a).
Subularia aquatica – 32, H6 – group 1 (c).
Honkenya peploides (L.) Ehrh. (*Arenaria peploides* L.) – 83, H24 – group 1 (a).
Atriplex [cf.] *glabriuscula* – 80, H24 – group 1 (c).
Suaeda maritima – 74, H24 – group 1 (c).
Lathyrus maritimus (L.) Bigel. (*L. japonicus* Willd.) – 11, H1 – group 1 (b).
Myriophyllum spicatum s.l. – 108, H39 – group 1 (b).
M. alterniflorum – 100, H39 – group 1 (c).
Hippuris vulgaris s.l. – 102 (incl. recent addition), H40 – group 1 (a).
Callitriche verna – 47, H8 – group 1 (b).
C. intermedia s.l. (incl. *C. hamulata* Kütz. ex Koch) – 99, H23 – group 1 (c).
C. hermaphrodita L. (*C. autumnalis* L.) – 43, H18 – group 1 (b).
Cicuta virosa – 36, H16 – group 1 (c).
Ligusticum scoticum – 29, H5 – group 1 (c).
Menyanthes trifoliata – 111, H40 – group 1 (c).
Mertensia maritima – 37, H7 – group 1 (a).
Limosella aquatica – 56, H2 – group 1 (c).
Utricularia intermedia – 39, H23 (or more) – group 1 (c).
U. minor – 87, H39 – group 1 (c).
Zostera marina – 63, H26 – group 1 (c).
Potamogeton natans – 112, H40 – group 1 (c).
P. gramineus – 77, H36 – group 1 (c).
P. alpinus – 88, H27 – group 1 (c).
P. berchtoldii Fieb. (*P. pusillus* of many authors) – 72, H35 – group 1 (c).
P. filiformis – 21, H13 – group 1 (b).
P. pectinatus – 94, H29 – group 1 (c).
Lemna trisulca – 80, H36 – group 1 (c).
L. minor – 109, H40 – group 1 (c).
Sparganium angustifolium – 53, H25 – group 1 (c).
Eleocharis acicularis – 79, H24 – group 1 (b).
Carex rostrata – 110, H40 – group 1 (c).
C. aquatilis – 31, H13 – group 1 (a).
C. maritima s.l. – 19 – group 1 (a).
Puccinellia maritima – 81, H23 – group 1 (c).
Catabrosa aquatica – 104, H40 – group 1 (c).
Elymus arenarius s.l. – 54, H5 – group 1 (b).
Alopecurus aequalis – 38 – group 1 (b).

TOTAL = 43.

3. Plants to be found in open areas but characteristic of closed habitats.

- Lycopodium clavatum* – 101, H27.
L. alpinum – 70, H13.
Selaginella selaginoides – 61, H33.
Equisetum trachyodon – 2, H16.
E. palustre – 111, H40.
E. pratense – 23, H4.
Dryopteris austriaca s.l. (incl. *D. spinulosa*) – 112, H40.
Thelypteris phegopteris (L.) Slosson (*Dryopteris phegopteris* (L.) C. Chr.) – 84, H21.
Botrychium lunaria – 107, H38.
Caltha palustris – 112, H40.
Ranunculus auricomus – 87, H36.
Viola palustris – at least 104, H40.
Polygala serpyllifolia – 110, H40.
Stellaria palustris – 67, H21.

- **Trifolium repens* – 112, H40.
- Astragalus alpinus* – 3.
- Oxytropis campestris* – 2.
- Lathyrus palustris* – 19, H13.
- Rubus saxatilis* – 70, H31.
- Potentilla fruticosa* – 4, H4.
- Sibbaldia procumbens* – 22.
- Alchemilla vestita* (*A. minor* of many authors) – 4, H1.
- A. filicaulis* – mountains in Great Britain.
- A. acutidens* s.l. (incl. *A. wichurae* (Buser) Stéfanss.) – 7.
- Chrysosplenium alternifolium* s.l. – 81.
- Drosera rotundifolia* – 108, H40.
- Epilobium palustre* – 112, H40.
- E. anagallidifolium* – 23.
- Chamaepericlymenum suecicum* (L.) Aschers. & Graebn. (*Cornus suecica* L.) – 20.
- **Carum carvi* – 49, H26.**
- Angelica archangelica* – “locally abundant.”**
- Polygonum bistorta* – 102, H20 (or more).
- Rumex acetosa* – 112, H40.
- **R. longifolius* DC. (*R. domesticus* Hartm.) – 48.
- **Urtica dioica* – 112, H40.
- Salix lanata* – 3.
- S. myrsinites* – 13.
- Loiseleuria procumbens* – 19.
- Phyllodoce caerulea* – 1.
- Vaccinium vitis-idaea* – 73, H19.
- Pyrola minor* – 82, H12.
- Primula farinosa* s.l. – 14.
- Gentiana verna* – 4, H5.
- G. nivalis* – 2.
- Myosotis palustris* – 108, H40.
- M. alpestris* – 2.
- **Veronica serpyllifolia* – 112, H40.
- Bartsia alpina* – 6.
- Campanula glomerata* – 54.
- C. rotundifolia* s.l. – 111, H28.
- Galium verum* – 112, H40.
- **G. uliginosum* – 100, H18.
- **G. aparine* – 112, H40.
- Senecio integrifolius* – “local in England” (23 according to Druce, 1932).
- Solidago virgaurea* – 111, H40.
- Erigeron borealis* – 3.
- Achillea millefolium* s.l. – 112, H40.
- **Chrysanthemum leucanthemum* – 112, H40.
- **Cirsium heterophyllum* – 55.
- Leontodon autumnalis* – 112, H40.
- Hieracium alpinum* L. – 4.
- Triglochin palustris* – 111, H40.
- T. maritima* – 80, H27.
- Lloydia serotina* – 1.
- Luzula multiflora* s.l. – 112, H40.
- Coeloglossum viride* (L.) Hartm. (*Habenaria viridis* (L.) R. Br.) – 108, H40.
- Leucorchis albida* s.l. (*Habenaria albida* s.l.) – 61, H25.
- Eriophorum angustifolium* – 112, H40.
- Trichophorum caespitosum* (L.) Hartm. (*Scirpus caespitosus* L.) – 104, H40.
- Eleocharis palustris* s.l. – 112, H40.
- Carex buxbaumii* s.l. – 1.
- C. atrata* – 14.
- C. norvegica* – 3.
- C. chordorrhiza* – 1.

- C. lachenalii* - 5.
Festuca rubra s.l. - 112, H40.
 **Lolium perenne* - 112, H40.
Poa nemoralis - 106, H21.
Deschampsia flexuosa - 111, H38.
Agrostis canina - 110, H39.
 **A. tenuis* - 112, H40.
A. gigantea - "44 (incomplete)."
A. stolonifera - 12, H40.
 **Phleum pratense* - 112, H40, according to Druce (1932).
P. alpinum s.l. (incl. *P. commutatum* Gaudin) - 10.
 **Alopecurus pratensis* - 111, H40.
 **A. geniculatus* - 112, H40.
Hierochloa odorata - 3, H1.
Anthoxanthum odoratum - 112, H40.

TOTAL = 89.

4. Plants usually restricted to closed habitats.

- Lycopodium annotinum* - 24.
Equisetum sylvaticum - 103, H37.
Cystopteris montana - 10.
Thelypteris dryopteris (L.) Slosson (*Dryopteris disjuncta* (Rupr.) Morton) - 84, H5.
Juniperus communis s.l. - 82, H18.
Trollius europaeus - 56, H3.
Ranunculus acris s.l. - 112, H40.
Geranium sylvaticum - 56, H1.
 **Vicia cracca* - 112, H40.
V. sepium - 112, H40.
Filipendula ulmaria - 112, H40.
Rubus chamaemorus - 42, H1.
Potentilla palustris - 107, H40.
Geum rivale - 104, H35.
Alchemilla glomerulans - 8.
Sanguisorba officinalis - 70, H4.
Betula pubescens s.l. - 105, H40.
B. nana - 14.
Ledum palustre - 2** (or possibly native).
Andromeda polifolia - 35, H27.
Vaccinium myrtillus - 102, H40.
V. uliginosum - 23.
Oxycoccus palustris s.l. (*O. quadripetalus* Gilib.) - 76, H34.
O. microcarpus - 6.
Pyrola rotundifolia - 34 (incl. recent addition), H1.
Ramischia secunda (L.) Garcke (*Pyrola secunda* L.) - 33, H3.
Moneses uniflora - 11.
Empetrum nigrum s.l. (incl. *E. hermaphroditum*) - at least 77, H34.
Trientalis europaea - 43.
Rhinanthus minor - 112, H40.
R. borealis - 17, H1.
Euphrasia arctica Lange (*E. frigida* Pugsl.) - 13 or more.
Linnaea borealis - 18.
Adoxa moschatellina - 105, H1.
Gnaphalium norvegicum - 5.
Saussurea alpina - 31, H9.
Tofieldia pusilla - 18.
Juncus squarrosus - 109, H40.
Listera cordata - 65, H26.
Corallorhiza trifida - 19.
Eriophorum vaginatum s.l. - 94, H39.
E. brachyantherum - " ? Native. In peat bogs on mountains, rare."

Carex panicea - 112, H40.

C. vaginata - 16.

C. magellanica s.l. (incl. *C. paupercula* Michx.) - 18, H1.

C. rariflora - 6.

Calamagrostis neglecta s.l. - 6, H4.

Nardus stricta - 111, H39.

TOTAL = 48.

Extinct are :

Pinguicula alpina - formerly 1.

Senecio congestus - formerly 8, according to Druce (1932).

There are thus 309 species of vascular plants which are common to the Arctic and the British Isles - at all events according to my computation and rather broad view of specific limits. Of these a total of 172, or 55.66%, are to at least a considerable extent 'open soil' plants or ones commonly to be found in habitats where there is little or no competition, while a further 89, making a total of 84.98%, are fairly frequently to be found growing in such circumstances. These percentages are lower than in the former analysis, particularly owing to the extension southward of the coverage into regions where open habitats no longer preponderate, although the higher one is only slightly lower than its earlier counterpart. Altogether this affords solid confirmation of the earlier contention that the majority of British vascular plants which reach the Arctic grow largely in the absence of competition, while many more, comprising in all the vast majority, are fairly frequently to be found in open habitats. Moreover, many of the above-mentioned 48 species that are normally restricted to closed habitats are occasionally to be seen growing in open ones, though not to an extent which would seem to warrant any suggestion that this circumstance might be phytogeographically significant.

The further circumstance that many of the predominantly boreal plants which extend far south do so largely on calcareous substrata has been noted e.g. by Patton (1923); at least in some cases it seems likely that this may be due to the tendency for more open vegetation and less competition in such areas, especially where precipitation and temperatures are relatively low, although this would seem a worthy subject for future investigation.

In all, 874 species of vascular plants are so far known to inhabit the Arctic, of which 833 are native and 41 apparently alien. Of these last, as indicated in the above lists, at least 33 are natives of the British Isles, 6 more being considered aliens there also, while at least 3 native arctic species appear to have been introduced into Britain. It seems that only a single plant which has been introduced in the Arctic, *Agrostis scabra*, is unknown in Britain in anything approaching a wild state, though presumably others will be added when the arctic parts of the U.S.S.R. become better known to western civilisation. The above figures also indicate that in the present-day native British flora there are represented no less than 267 of the 833 recognized species of native arctic vascular plants; this is a percentage of just over 32. If aliens are included in the calculations, the percentage rises considerably.

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THE CYTOLOGY OF BRITISH SPECIES OF *EUPHRASIA*

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The counting of the chromosomes of *Euphrasia* species was undertaken in connection with an investigation of the breeding system and fertility relationships of the British species.

PREVIOUS WORK

There has been little previous work on the cytology of European species of *Euphrasia*, and as far as is known to the author, none of this has been on British material.

Four species were counted by von Witsch (1932); they were as follows : *E. minima* Jacq. subsp. *minima* (not British), $n=22$; *E. rostkoviana* Hayne subsp. *rostkoviana*, $n=11$; *E. montana* Jord., $n=11$; *E. salisburgensis* Funck, $n=22$. In addition Á. & D. Löve (1948) report that Sörensen and Westergaard found $n=22$ in *E. frigida* Pugsl., in Greenland. Maude (1939) records $2n=44$ for "*E. confusa* Pugsl. (*minima* auctt. angl.) von Witsch, 1932," but as shown above, it was *E. minima* Jacq. that von Witsch counted. Finally, Tischler (1950) gives the entry "*E. brevipila* Burn. et Gremli (*E. montana* Fries) $n=11$, von Witsch (1932)." This must refer to von Witsch's count of *E. montana* Jord. All the names used by von Witsch are current names for well-known species and there seems no reason to suppose that he cited his authorities wrongly.

METHOD

(1) Material

The use of root tips was not attempted. Root tips would be very difficult to obtain from wild plants owing to the slenderness of the roots, and their consequent fragility. They could, however, have been obtained from young seedlings, but when this work was started the few seedlings available were wanted for cultivation. Work was therefore confined to the use of pollen mother cells.

(2) Collecting

Observations on cultivated plants showed that flowers at successive nodes open at intervals of three or four days, or, in the case of *E. pseudokernerii*, five to seven days. Meiosis thus occurs in any one spike with this frequency, and takes place roughly four or five nodes above that of the flower open at the time. It should thus occur periodically from about a fortnight before flowering starts until a fortnight before it ceases. Actually it probably ceases earlier, because flowers at the last few nodes open at shorter intervals, and there may be flowers open at two or three successive nodes simultaneously, so that just before it stops flowering the plant becomes very floriferous. Meiosis seems to be farther advanced when flowering is about to end, since it is found to have taken place in smaller flower-buds than usual. For fixing, therefore, good solid shoot apices with plenty of young bracts have to be chosen. These occur on the more luxuriant plants. If the plants are growing under unfavourable conditions, flowers may be produced at only three or four nodes, and then meiosis may be over when the first flower opens. As a result of this, material of *E. cambrica* obtained in 1952 proved completely useless.

* The work reported in this paper was carried out during the tenure of a Research Scholarship at the University College of Leicester.

The time taken by meiosis is evidently less than the interval between the opening of the flowers, and thus one is not bound to find meiosis in a particular spike, even if it has not occurred in that spike for the last time. In addition, therefore, to selecting spikes of the kind described, an adequate quantity must be collected. The same fact also makes obtaining counts a time-consuming process, though the chance of getting a count is increased by the fact that the two pairs of anthers of each flower are at different stages, and also that various stages are sometimes found in the same anther.

(3) *Fixing*

Buds were fixed in acetic acid and ethyl alcohol, mixed in the proportions 1 : 3, or more usually, in acetic acid, alcohol, and chloroform in the proportions 1 : 3 : 4. In the case of wild plants, buds were fixed either at the end of a day's collecting, the plants having been kept in the vasculum, or as soon as the gathering was complete, or they were cut off the plants *in situ*. The last method was always used for cultivated plants.

(4) *Storage*

Fixed material was preserved in a refrigerator at about -15°C ., as described by Davies (1952). The oldest material used had been stored in this way for six or seven months.

(5) *Staining and Mounting*

The acetocarmine squash method was used, iron alum or iron acetate being used as a mordant. For permanent preparations triacetin was used. A drop is placed at the edge of the coverglass and as the acetic acid of the stain evaporates the triacetin takes its place. This is relatively involatile and allows the preparation to be studied at leisure without it drying up, while the removal of the carmine eliminates the danger of the cytoplasm becoming stained. After the removal of excess triacetin the coverglass is ringed with "Euparal".

CHROMOSOME COUNTS

These are based on any stage of meiosis at which the chromosomes could be counted. In *Euphrasia* prophase does not yield satisfactory counts, though at late diakinesis counts can occasionally be obtained. Metaphase and early anaphase of the first division yield counts most easily. In tetraploids ($n=22$) the later stages can rarely be counted reliably; of these, late anaphase of the first division (anaphase I) is the most likely to give a count. In diploids ($n=11$), however, late anaphase I, metaphase II, and anaphase II can frequently be counted without difficulty.

There was not time to work on all the material available, and species on which no counts had been made previously (in particular British endemics) were given preference.

All the plants were determined by the writer. In some cases the fixed specimens were kept separate from others in the same gathering, and these are either in the writer's herbarium, or at the Department of Botany, University College of Leicester. Where the fixed individuals were not separated, the gathering concerned is represented in both these herbaria, and a number are also at the Cambridge Botany School.

(1) *E. micrantha* Reichb. Wild material fixed at Withypool, S. Somerset, in August 1952 proved to have finished meiosis. Seeds from this locality (specimen No. E185A) were grown in 1953, but too few spikes were fixed. As a result no meiotic metaphases were obtained, but diakinesis was observed which, though not quite unambiguous, can be interpreted as showing 22 bivalents.

(2) *E. scotica* Wettst. Material from Lawers, Mid Perth (E261) shows $n=22$.

(3) *E. foulaensis* Towns. A count was obtained from cultivated material (E227) showing $n=22$. The seed came from live plants sent from N. Uist, Outer Hebrides, in 1952, by Mr. R. G. West.

(4) *E. marshallii* Pugsl. E311, Bettyhill, W. Sutherland, showed $n=22$.

(5) *E. curta* Fries var. *rupestris* Pugsl. Cultivated material (E100) showed $n=22$. E100 was collected in Cwm Idwal, Caernarvon, in June 1952, and consisted of herbarium specimens of *E. cambrica* Pugsl., and turves. The only plants that persisted in the turves were *E. curta* var. *rupestris*, which was not generally in flower at the time the turf was collected. Seeds were collected from the plants in the turves and grown in 1953. The plants gave a small number of buds from which the count was obtained. E100 therefore consists of herbarium specimens of wild *E. cambrica*, and cultivated *E. curta* var. *rupestris* from which the chromosome number was obtained.

(6) *E. occidentalis* Wettst. $n=22$, from E192, Rame, E. Cornwall.

(7) *E. nemorosa* (Pers.) H. Mart. emend. Löhr. Two counts were obtained, both of $n=22$, one from E134, Bedford Purlieu, Northants., the other from E149, Banstead Downs, Surrey.

(8) *E. confusa* Pugsl. $n=22$, E175, from Withypool, S. Somerset.

(9) *E. pseudokernerii* Pugsl. $n=22$; plants from the Devil's Dyke, near Brandon, W. Norfolk (Plate 10, fig. 3) (E136), and Risby Poor's Heath, W. Suffolk (E143).

(10) *E. brevipila* Burnat & Gremli. $n=22$, E245, Sparrowlee Halt, near Waterfall, Stafford. In one cell observed, there is an indication that one pair of chromosomes is represented by two univalents instead of a bivalent, but this is not certain.

(11) *E. brevipila* var. *notata* Pugsl. Two lots of material (E254 and E256) from colonies about half a mile apart at Lawers, Mid Perth, were worked on. In both, $n=22$ was observed, but some buds showed $2n=44+1$, the extra chromosome appearing as a univalent, most frequently either at the edge of the metaphase plate, or well away from it. The occurrence of an extra univalent can be accounted for by supposing that, in one of the parents of an individual possessing it, there occurred a failure of disjunction at meiosis, and that as a consequence of this both members of the pair went to one pole at anaphase, giving pollen grains with twenty-three chromosomes, instead of twenty-two. No anaphases showing evidence of this unsymmetrical distribution were seen, but pairing failure in one pair of chromosomes at metaphase was rather frequent. Plate 10, fig. 4 shows a metaphase in E254 with twenty-one bivalents and three univalents. This has the extra chromosome and shows the pairing failure that probably gives rise to it. It will be noted that all three univalents are of approximately the same size, and that they are about as large as the largest chromosomes among the bivalents. That these chromosomes were univalents was confirmed by Dr. J. R. S. Fincham, upon inspection of the photographic negatives. The only suggestion that the two univalents are members of a bivalent that have separated early is that they are in every case near one another. Dr. Fincham pointed out, however, that as the univalents are almost always found at the edge of the metaphase plate they are probably forced into this position by lack of a spindle attachment, and thus have a good chance of appearing in the same part of the cell in the preparation. The shape of these chromosomes indicates that they are true univalents.

In fixing, more than one spike was usually taken from each plant, and all were fixed together. Thus it is not known whether more than one plant in each gathering had the extra chromosome, and, at least in the case of E256, not all the fixed material was worked through. However, the extra univalent was found in both gatherings, and pairing failure was observed in both, being seen several times in E254.

(12) *E. brevipila* var. *reayensis* Pugsl. This form, and *E. brevipila* var. *notata*, are the only European forms with long glandular hairs that are not classified in the Series

Hirtellae, the members of which, as far as is known, are all diploids. However, the question whether var. *reayensis* shows, in common with var. *notata*, any irregularities at meiosis, has not been gone into. This was due to the fact that meiosis had finished in a large proportion of the spikes fixed, and work on the material was stopped after a clear count had been obtained, so that few divisions were seen. The count showed $n=22$; the material was from Bettyhill, W. Sutherland (E304).

(13) *E. rivularis* Pugsl. Plants dug up in turf in Cwm Idwal, Caernarvon, in June 1952 (E123), were grown in the greenhouse and produced seed. In 1953 the count of $n=11$ was obtained from a plant grown from this seed.

(14) *E. anglica* Pugsl. The number $n=11$ was observed in E71, plants dug up as seedlings at Holmsley, S. Hants; E150, Box Hill, Surrey; E157, Mickleham Downs, Surrey; and E168, Charnwood Forest, Leicester.

(15) *E. hirtella* Jord. var. *polyadena* (Gren. & Roux) Pugsl. Material from Lawers, Mid Perth (E253), had $n=11$ (Plate 10, fig. 5).

(16) *E. anglica* $\times$ *micrantha*. A single individual (E185C) was found on a heath near Withypool, Exmoor, S. Somerset, at a point where the parent species came into contact. The plant resembled *E. micrantha* in habit, small foliage, and dark anthocyanin pigmentation. The flower had no lilac in it, unlike those of the surrounding *E. micrantha*, and was slightly larger than those, with a larger lower lip, in this respect diverging from *E. micrantha* in the direction of *E. anglica*. The foliage had scattered rather long glandular and eglandular hairs. (*E. anglica* has dense long-stalked glands; *E. micrantha* is sub-glabrous). On the main axis it had flowered at five successive nodes, but there had been no development of any of the capsules. The percentage of normally formed pollen grains was investigated by staining with cotton blue in lactophenol. Of 998 grains from one flower 31, or 3.1 per cent, were normal in appearance.

The shoot apex from the main axis, and one from a branch of this plant, were fixed, and preparations of pollen mother cell meiosis obtained from both. The chromosomes tended to be clumped, a condition met with occasionally in other material, and this made interpretation difficult. It was clear that a number of univalents, up to eleven, was present, and also some bivalents. What appeared to be larger bodies are evidently groupings of two or three bivalents. Interpreting the chromosomes on this assumption it was possible to count most of the bivalents and univalents in four cells, there being a residue of one or two doubtful bodies. These could be interpreted as large univalents and, if this was done, the conclusion was reached that there were eleven bivalents and eleven univalents present. One of these cells is shown in Plate 10, fig. 6. Figures 1 and 2 show interpretative diagrams of two of them. These interpretations were made from the preparations themselves, but they are not certainly correct. In each of the cells illustrated there is, in fact, one body that looks like a multivalent. These are indicated in the diagrams; that in fig. 2 is very suggestive of a trivalent. The interpretations given, however, are the only ones that give a total of 33 chromosomes. Since the basic number is 11, and since the number in this hybrid is certainly in the neighbourhood of 33, an interpretation that gives exactly this number is more likely to be correct than one giving a different number.

The anaphases seen were too obscure to give any information, but at telophase univalents were occasionally present, faintly stained, at the equator. These lagging univalents usually numbered only one or two.

GENERAL OBSERVATIONS ON THE CYTOLOGY

The chromosomes are of moderate size. The size varies within the complement but in meiotic material it is difficult to describe the differences in detail, as von Witsch (1932)

found. Roughly there are large, small, and intermediate sizes, the latter apparently in the majority. Mostly there is one chiasma per bivalent, but one or more bivalents with two chiasmata occur in most cells, both in tetraploids and diploids. In the tetraploids no indications of multivalent formation were seen.

The occurrence of an extra univalent in *E. brevipila* var. *notata* was not recognized until a fair number of cells had been seen, and it is conceivable that it could have been encountered in previous work and overlooked. However, the fact that it was never detected indicates that among the species in general it is rare, whereas its discovery in two populations of var. *notata* indicates that it is relatively frequent in that form. Its accompaniment by frequent pairing failure in one pair of chromosomes suggests that it may be quite common in *E. brevipila* var. *notata*, at least around Lawers.

DISCUSSION

Relation of Chromosome Numbers to Classification

The two diploid species which von Witsch (1932) counted, *E. montana* and *E. rostkoviana*, possess long glandular hairs, and fall in the Series *Hirtellae*, a group created by Pugsley (1930), while all the other species previously counted were tetraploids with $n=22$. This suggested that probably all the *Hirtellae* were diploids, and that all the other members of the Subsection *Ciliatae*, together with the Subsection *Angustifoliae*, were tetraploids. The counts obtained in the present work confirm this pattern, as far as the *Ciliatae* are concerned. This is illustrated in the accompanying table.

Table of British species of *Euphrasia* arranged according to Pugsley's classification, with *E. minima*, showing their haploid chromosome numbers.

SECTION SEMICALCARATAE

SUBSECTION CILIATAE

Series Latifoliae		Series Nemorosae		Series Brevipilae	
<i>micrantha</i>	22	<i>rotundifolia</i>		<i>borealis</i>	
<i>scotica</i>	22	<i>marshallii</i>	22	<i>brevipila</i>	22
<i>rhumica</i>		<i>curta</i> var. <i>rupestris</i>	22	var. <i>notata</i>	22
<i>frigida</i>	22*	<i>cambrica</i>		var. <i>reayensis</i>	22
<i>foulaensis</i>	22	<i>occidentalis</i>	22	Series <i>Hirtellae</i>	
<i>eurycarpa</i>		<i>nemorosa</i>	22	<i>rostkoviana</i>	11*
<i>campbelliae</i>		<i>heslop-harrisonii</i>		<i>montana</i>	11*
(<i>minima</i>)	22*	<i>confusa</i>	22	<i>rivularis</i>	11
		<i>pseudokernerii</i>	22	<i>anglica</i>	11
				<i>hirtella</i>	11

SUBSECTION ANGUSTIFOLIAE

<i>E. salisburgensis</i>	22*
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* Chromosome number obtained from non-British material.

These results confirm Pugsley's classification of the long-glandular species in a separate group, the series *Hirtellae*. Previously they were placed partly in the *Grandiflorae* Wettst. and partly in the *Parviflorae* Wettst., both of which groups also included eglandular species. The cytological distinctness of the *Hirtellae* draws attention to the relative isolation of the group. The species have one constant and almost diagnostic character, namely the covering of long glandular hairs. In addition the capsule tends to be short and broad, the calyx and seeds to be similarly proportioned, and the flower to have a porrect lower lip, with the lobes not greatly emarginate or greatly dilated apically, and a broad upper lip. They do not diverge to any great degree from the series *Brevipilae*,

which, of the other series of the *Ciliatae*, they most nearly resemble, but they are relatively well characterized morphologically, and stand apart from the other groups, there being no borderline species. Unlike some groups, the Series *Hirtellae* does not seem to include species that appear to relate it to more than one other group. In contrast to this, not only do the other Series within the Subsection *Ciliatae* tend to grade into one another, but the Subsections *Ciliatae* and *Angustifoliae* are scarcely discontinuous, members of the Series *Alpinae* in the *Ciliatae* approaching quite close to *E. salisburgensis* of the *Angustifoliae*.

The Series *Hirtellae*, it seems, ought both on morphological and cytological grounds to be raised to the rank of subsection, and the definition of the Subsection *Ciliatae* amended to exclude them.

Pugsley (1930) excluded the long-glandular forms known as *E. brevipila* var. *notata* and var. *reayensis* from the *Hirtellae*, and this proves to be justified by the cytology.

Hybridisation

Although diploid and tetraploid species were reported as long ago as 1932, there appears to have been no consideration of these counts in relation to the hybrids reported to occur. The existence of diploid and tetraploid species imposes a limitation on hybridisation and enables members of the two series to exist together, and remain distinct. In fact the results of diploid-tetraploid hybridisation appear to go beyond the formation of an occasional triploid, and it is intended to devote a future paper to this subject. Here it may be added that diploid and tetraploid species commonly grow together and that triploids are rare, that described above being the only one I have found in two seasons of active field work.

Origin of Tetraploids

The situation in the triploid *E. anglica* $\times$ *micrantha* indicates that homology exists between the set of chromosomes present in *E. anglica* and half the set in *E. micrantha*. *E. micrantha* must therefore be an allotetraploid. The simplest inference would be that *E. anglica* at some time crossed with a distantly related diploid, and that as a result of chromosome doubling in the offspring, *E. micrantha* arose. However, owing to the close relationship of the various tetraploids, as evidenced by their morphological similarity and the frequent occurrence of fertile hybrids among them, it is possible that an inference of this type may apply to the group of tetraploid species as a whole, and that *E. micrantha* is a subsequent descendant of the original tetraploid. Similarly *E. anglica* itself may not have been concerned in giving rise to tetraploids; a related present-day or ancestral species may have been responsible.

Another possibility is the repeated formation of tetraploid forms from different pairs of diploids from the same two groups.

It is probable that one should consider the origins of groups of species rather than of individual species. The question arises whether the other diploid group exists today, and if so, where. The only European groups not found in Britain are the Series *Pectinatae* and *Alpinae*; these fall within the *Ciliatae* and include species which form a series linking the *Ciliatae* with *E. salisburgensis* in the *Angustifoliae*. It is therefore unlikely that they include diploid species. Within the *Angustifoliae*, however, there is a sharp discontinuity between the *salisburgensis* complex, and the two closely related species *E. cuspidata* Host and *E. tricuspidata* L. A chromosome survey is needed, including these two species, and covering the other subsections of the Section *Semicalcaratae*, namely the *Alpicolae* and *Japonicae* Pugsley (1936) of Japan, and also the Section *Atlanticae* Pugsley (l.c.) of the Azores. It is doubtful if the *Alpicolae* and *Japonicae* are very distinct from one

another. They possess rounded, cuneate-based leaves with rounded teeth, and the former includes both eglandular and long-glandular forms. The mere discovery of other diploid groups would not, of course, identify that which was concerned in giving rise to the European tetraploids.

Endemism

Euphrasia shows a high rate of endemism. Thus of the species counted, *E. foulaensis*, *E. marshallii*, *E. occidentalis*, *E. confusa*, *E. pseudokerneri*, *E. rivularis*, and *E. anglica* are endemic to the British Isles, or almost so. (*E. occidentalis* occurs in Brittany and probably in Belgium, and *E. confusa* and *E. foulaensis* occur in the Faeroes.) The cytological work shows that in these cases variation in chromosome number is not the cause of the multiplicity of species, many of which are very localized in distribution. Uniformity of chromosome number appears to be the rule, so that it seems improbable that any other British endemics owe their existence to the possession of different chromosome numbers.

SUMMARY

Chromosome counts at pollen mother cell meiosis were made in fifteen British *Euphrasia* forms, covering thirteen species.

The method used is outlined and the selection of material for fixing described.

The numbers $n=22$ and $n=11$ were observed. All previously reported numbers are listed, and a table of all known numbers is presented (p. 105). In addition to the regular numbers, *E. brevipila* var. *notata* showed pairing failure in one pair of chromosomes, and plants were found with $2n=44+1$, presumably caused by this pairing failure; also a single triploid individual was observed, which most probably forms 11 bivalents and 11 univalents at metaphase. This plant was a hybrid between *E. micrantha* and *E. anglica*.

The relation of chromosome numbers to classification is discussed. The division between diploids and tetraploids coincides with one of the divisions of Pugsley's classification, the Series *Hirtellae* being diploid and other groups tetraploid. The raising of the *Hirtellae* to the rank of Subsection is recommended on morphological as well as cytological grounds. The anomalous forms *E. brevipila* var. *notata* and var. *reayensis* are tetraploids; this confirms their exclusion by Pugsley from the Series *Hirtellae*.

The existence of diploid and tetraploid series makes it possible for certain pairs of species to grow in company and remain distinct. This they frequently do; triploids, however, are very rare.

The cytology of the triploid shows that *E. micrantha* is an allotetraploid. In considering the origin of tetraploids, groups should be probably considered as a whole, since the species they comprise are closely related to one another. *E. anglica* is perhaps not a direct ancestor of a tetraploid, and *E. micrantha* is probably derived by divergence from a primitive tetraploid.

A chromosome survey of other groups of *Euphrasia*, particularly those within the Section *Semicalcaratae*, is needed.

Differences of chromosome number are not the cause of the multiplicity of *Euphrasia* species.

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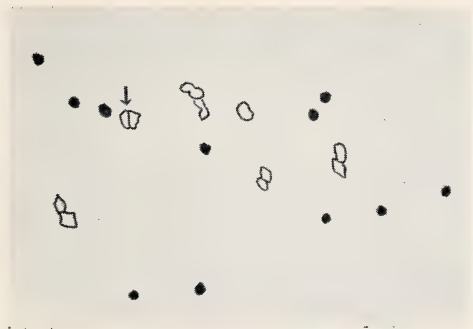


Fig. 1.



Fig. 2.

Figs. 1 & 2. Meiosis in *Euphrasia anglica* $\times$ *micrantha* (185C), $\times$ 1000. Interpretative diagrams of two cells; fig. 2 corresponds with fig. 6. Univalents are shown solid, bivalents in outline. The arrows indicate bodies that look like multivalents (see text).

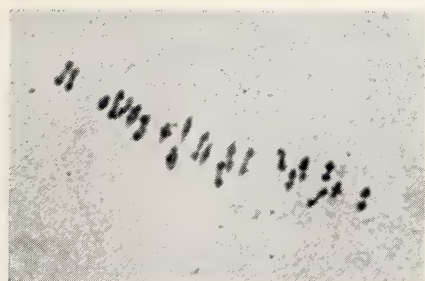


Fig. 3.

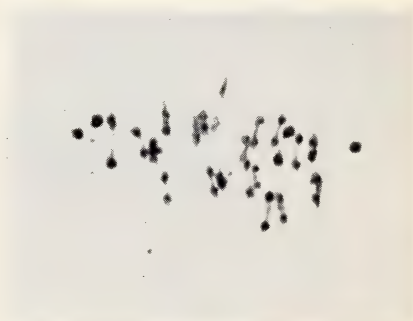


Fig. 4.

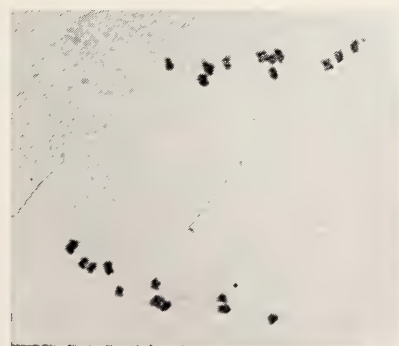


Fig. 5.

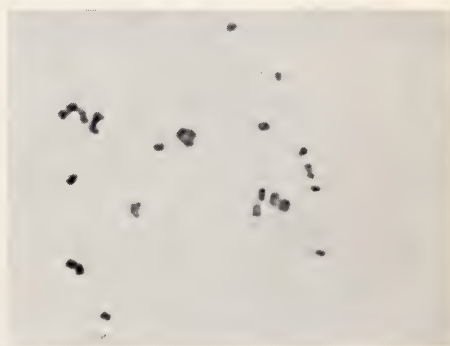


Fig. 6.

Figs. 3-6. Pollen mother cell meiosis in *Euphrasia*. Metaphase I, except fig. 5, $\times$ 1000.
 Fig. 3. *E. pseudokernerii* (E136). Fig. 4. *E. brevipila* var. *notata* (E254).
 Fig. 5. *E. hirtella* (E253), metaphase II. Fig. 6. *E. anglica* $\times$ *micrantha* (E185C).

MINT NOTES

By R. A. GRAHAM

V. MENTHA AQUATICA, AND THE BRITISH WATER MINTS

Water mints differ essentially from other British mint groups in having a *capitate* inflorescence, the capitulum being borne terminally and with or without underlying, axillary verticils. Rarely the inflorescence is very elongated to form a thick spike, the contiguity of the underlying verticils contributing to such an appearance. Certain hybrids of *M. aquatica* L. with *M. spicata* L. em. Huds., *M. longifolia* (L.) Huds. and *M. arvensis* L. sometimes produce capitate forms, and these will be dealt with in papers on the respective groups.

M. AQUATICA L., 1753, *Sp. Pl.*, 1, 576

Mentha floribus capitatis, foliis ovatis serratis petiolatis, staminibus corolla longioribus . . . Planta non hirta, Verticilli terminales in capitulum s. spicam obtusam conferti.

There is, in my opinion, no Linnean specimen that can be satisfactorily accepted as type or lectotype. Specimen No. 730/9 (Savage, 1945, *Catalogue*), which bears the name *aquatica* in Linnaeus' hand, is one of those mint oddities whose exact status cannot be ascertained without observation under cultivation, and cytogenetical investigation. Undoubtedly it has some connection, through hybridity, with a water mint, and it agrees with the description, in that (1) the stamens are exerted, and (2) that the inflorescence is somewhat subspicate due to a close arrangement of the verticils, *which are however far more numerous (up to 10) than is usual in a water mint*. From its general appearance, this specimen is *probably* an unusual form of *M. × verticillata* L. (*M. aquatica* × *arvensis*). Smith (1800, 198-9) considered it to be a connecting link between *M. hirsuta* Huds. and *M. paludosa* Sole, and, believing it to represent the mint described as *M. aquatica* in *Sp. Pl.*, he abandoned this binomial in favour of *M. hirsuta* to designate the water mint group. There can, in my opinion, be no reasonable doubt that by *M. aquatica*, Linnaeus intended the mint known to us as Water Mint, though to be sure he described a particular form. His citations point to this, and, further, water mints grow quite commonly in Sweden so that it is only reasonable to assume that Linnaeus knew them. This specimen is best regarded as a misidentified oddity – several of the Linnean mints are queer plants.

It is, perhaps, not strange that Linnaeus' description, being so short, agrees with the specimen in certain respects. But I do not believe it to be the plant from which his description was framed, and as this is of fundamental importance I give my reasons below for rejection.

(1) Linnaeus *accurately describes a normal water mint*, which has a capitate inflorescence composed either of a terminal capitulum alone, or with underlying verticils of which the uppermost one or two are contiguous or subcontiguous to the capitulum thus giving the appearance of an obtuse spike.

(2) The Linnean specimen *is a verticillate mint*. There is no capitulum, but an apical verticil smaller than the many underlying verticils. There is thus no appearance whatever of a capitate inflorescence, though it could be described as a spike or subspike (but of very different appearance to the "spike" of a water mint).

(3) It is clear, from his descriptions of other mints, that Linnaeus accurately recognised capitate and verticillate types of inflorescence. Had this specimen been the original *M. aquatica* it is hard to understand why he used the words *floribus capitatis* when *floribus verticillatis* would be much more correct.

(4) Linnaeus accurately described his *M. hirsuta* as *floribus capitatis*. His specimen of this is a normal but very hairy water mint. It is described as differing from *M. aquatica* only in being more hairy and with shorter petioles, and yet his specimen of *M. hirsuta* is very unlike that named as *M. aquatica*.

(5) Water mints apparently always have a hairy calyx tube. For this reason I do not think that "*Planta non hirta*" can imply a wholly glabrous state. But the specimen named *M. aquatica* is altogether too hairy reasonably to be described in these terms.

From Linnaeus' description of *M. aquatica* and from his comments in comparison with *M. hirsuta* (see under var. *hirsuta* below), together with inferences from his specimen of the latter mint (No. 730/8), the original *M. aquatica* L. can be suggested as a water mint with the following characters: *Whole plant subglabrous in appearance, though not wholly so in detail; leaves ovate, serrate, basally rounded to $\pm$ cordate, on petioles long enough to be obvious; inflorescence either a terminal capitulum only, or with underlying verticils which may be contiguous to give the appearance of a blunt spike.* His specimen probably owes its identification to some character in which it appeared to Linnaeus to agree with his original *M. aquatica*.

Many British water mints, especially from riparian areas, are largely subglabrous and can, in my opinion, be regarded as typical of Linnaeus' original *M. aquatica*. I have placed in the Oxford herbarium an example which indicates my conception of a typical plant in every character except that the upper part of the stem is perhaps a little too hairy although the whole plant is outwardly subglabrous. Gathered from Marlow river-side, Bucks., v.c. 24, it can be described as follows:

Stem green, branched, a little bearded at the nodes, otherwise almost glabrous below but becoming progressively more hirsute upwards with retrorse, white hairs; internodes up to 5.5 cm. *Leaves* ovate to oblong-ovate, thin in texture, obtuse to sub-acute, abruptly rounded and sometimes $\pm$ truncate at the base, usually with a small wedge at the junction with the petiole; up to 5.5 $\times$ 3.3 cm.; generally subglabrous but with whitish hairs on the nerves of both surfaces – more numerous on the upper, more immature leaves; serratures shallow, blunt, forward-directed, $\pm$ regular in spacing, up to 1 mm. deep, and to 14 in number. *Petioles* up to 2.5 cm. long, with a few, scattered, white hairs. *Inflorescence* consisting of a terminal, $\pm$ rounded capitulum of medium size, 2 cm. in diameter, with one pair of under-lying, non-contiguous, axillary, shortly-pedunculate verticils. *Calyx* tubular, shortly ciliate with $\pm$ ascending hairs. *Pedicels* rather shaggy with retrorse, white hairs. *Corolla* with a few scattered hairs externally. *Stamens* exserted.

Whereas typical *M. aquatica* L. is suggested as a mint with the general characters set out in the previous paragraph, it will become clear to anyone who consults the many specimens in our national herbaria and in private collections that water mint is extremely variable. The following paragraph is therefore devoted to a description of water mint forms in the aggregate, indicating variation in certain characters.

Stem squarish, simple or branched, green to red, glabrous to densely hairy with long, white hairs. *Leaves* orbicular to narrowly elliptical, very acute to rounded at the apex, cordate to long attenuate at the base, glabrous to densely pilose – the lower surface having sometimes a matted indumentum giving the appearance of a coarse tomentum (the upper, less mature leaves tend to be more hairy than the lower which have arrived at full maturity); serratures very few to very many, shallow to deep, sometimes salient, blunt and sometimes $\pm$ crenate to jagged. *Inflorescence* essentially capitate, of either a

terminal capitulum only, or commonly with up to two pairs of underlying, axillary verticils, occasionally with as many as eight pairs which are contiguous at least at the apex thus forming an obtuse spike (such a form is the example recorded by Miss Muirhead from R. Eden, Cumberland, v.c. 70, in 1952, *Watsonia*, **2**, 204, which I tentatively, and erroneously, named as *M. × palustris* Sole). *Calyx* glandular, ribbed, always tubular, shortly ciliate to densely shaggy with usually ascending hairs, probably never quite glabrous or even essentially so, the teeth $\frac{1}{4}$ - $\frac{1}{2}$ the length of the tube, occasionally rather longer. *Pedicels* shortly to densely hairy with white or whitish, usually retrorse hairs, apparently never glabrous. *Peduncles* of axillary verticils usually short, sometimes long and very noticeable. *Corolla* 4-fid, sometimes deeply so, varying somewhat in size (depending perhaps on sexuality), usually with a few scattered hairs externally and sometimes with a ring of hairs in the throat. *Stamens* exserted or included, sometimes perhaps absent. (See Schultz (1896, 433-434) for an interesting correlation of stamen development with the size of the leaves and capitula). *Scent* minty, but rather dull and not sweet, nor pungent as in *M. spicata* and *M. piperita* L. Very rarely examples are found with the scent characteristic of *M. citrata* Ehrh. and it is possible that these may be hybrids although they show no morphological indications of this. Those who wish for an anatomical account should consult A. & E. G. Camus (1911).

Typical *M. aquatica* L. is, in my opinion, only a form that, by a combination of certain characters set out in the foregoing paragraph, can be selected out of the innumerable forms that occur. But the different combinations of characters are so endless, and the variation thereby so wide, and yet so gradual – indeed it is only seldom that one can exactly match examples from different localities – that I believe *M. aquatica* L. to be a polymorphic species whose division into the grades *variétas* and *forma* is taxonomically unsound. It is perhaps unfortunate that a great many different forms have received names from eminent specialists of the past.

The causes of the great polymorphism are not very clear. Cytological investigation indicates that $2n=96$ in most plants – if not all. Reproduction is largely vegetative, by runners, and no doubt many mutants become perpetuated in this way as clones. Seed is produced to a certain extent. No doubt also seasonal, edaphic and other environmental factors play their part in influencing the final characters of any given form, and it is clear that some of the named forms owe their status to such causes only. That the degree of hairiness of the stem and leaves is controlled, at any rate in part, genetically, is suggested by occasional occurrences of subglabrous and very hirsute forms sharing a habitat.

Strail, Braun, Briquet and Topitz are among those who have divided the water mints into many named forms, using *species*, *variétas* and *forma* as grades for the purpose. Indeed Topitz (1913, 168-179) contrived to recognise no less than 40. Leaf characters, degree of hairiness, size of the capitula, presence of axillary verticils, and degree of branching are among the chief criteria used for differentiation. Strail regarded the exsertion or inclusion of the stamens as an important character, but this is probably a matter of sex-function. In my view, all the varieties listed by these and other authors (except var. *memorosa* Fr.) are merely examples selected from the great variational range. Many are closely allied, and identification according to any of these four authors, or all, becomes a task of distracting difficulty. This is particularly so in view of intermediates, because, no matter how many named forms there are, intermediates will always be found in a species as polymorphic as this, and with so many names to choose from the correct placing of any given intermediate often becomes taxonomically impracticable.

This paper, in view of the complexity of the problem, should be regarded as a preliminary attempt to simplify the British water mints as a whole – to restore a semblance

of order out of chaos. The great tangle of the past is thereby reduced to a basis whereon future constructive work can be based.

It may be convenient for herbarium purposes to separate the various forms into different groups. I therefore give below all the varieties and forms that have been included in British lists, with a few others that can be recognised by a simple character. It is necessary to deal in some detail with all the varieties, etc., recognised by Fraser (1925 and 1927), as some of his descriptions differ in certain details from the originals – this being due to Fraser's having framed his texts on examples identified by Briquet, but apparently without adequate reference to the original descriptions in each case. But it must be remembered that, within the reasoning of this paper, no importance is attached to these varieties, etc., with the possible exception of var. *nemorosa* Fr.

Distribution and status

Water mints in the aggregate are common throughout the British Isles, being recorded from every vice-county. Essentially lowland plants, they inhabit marshes, ditches, river-sides, and other types of habitat where damp conditions prevail, and they tend to become stunted or die out in the wild state if the accustomed humidity becomes permanently denied them. Although mentioned in certain horticultural works, they do not appear to have been seriously cultivated, if at all, and it is unlikely that their status is other than native – as on the Continent. Information on medical properties is rather scanty, but Sole mentions the use of his *M. aquatica major* in cases of hysteria.

SOME WELL-KNOWN FORMS OF *MENTHA AQUATICA* L.

1. *With a rounded to cordate leaf-base*

(a) *Mentha aquatica* L., *sensu stricto* (see above).

(b) var. *hirsuta* (Huds.) Hudson, 1778, *Fl. Angl.*, ed. 2, 252.

'*Mentha floribus capitatis, foliis ovatis serratis subsessilibus pubescentibus, staminibus corolla longioribus.*' Hudson, *loc. cit.*

M. hirsuta Hudson, 1762, *Fl. Angl.*, ed. 1; Linnaeus, 1767, *Mantissa*, 81

"*Differt a M. aquatica foliis magis sessilibus hirsutis; convenit staminibus corolla longioribus, et toto facie. Pistillum corolla longius. Corolla profunde 4-fida, fere regularis. Calyces ciliati.*" Linnaeus, *loc. cit.*

No specimen of Hudson's appears to exist. But the Linnean specimen No. 730/8, named as *hirsuta* in Linnaeus' hand, agrees with the description and can be regarded as typical of this variety. It is described as follows:

Stem square, simple, reddish, covered – especially thickly above – with retrorse, whitish hairs. *Leaves* ovate, $\pm$ acute, basally subcordate, up to 3×2.8 cm., very hairy and dark green above, paler below and thickly matted with grey-white hairs forming a coarse tomentum; nerves of the upper, and midrib of the lower surface whitish; serratures unequal in spacing, size, and shape, shallow but jagged and rather salient, up to 1 mm. deep, and up to 14 in number. *Petioles* short, up to 8 mm. long, shaggy. *Inflorescence* of a terminal capitulum and two pairs of axillary verticils, the upper subcontiguous with the capitulum. *Corolla* with scattered hairs externally (not examined within). *Stamens* exerted. *Calyx* and *pedicels* shaggy.

This specimen is very hirsute throughout, and thereby has a very different appearance from typical *M. aquatica* L. But between the two there is every degree of intermediate in this character, and it is impossible to draw a distinctive line. Short petioles are often found in the more hirsute forms, but they are not restricted to them, and provide a most unreliable character. Probably Linnaeus thought little of *M. hirsuta*, and many writers

since have held a similar view. For those who wish to differentiate between them, Grenier & Godron (1850, 651) provide the following succinct distinction: *M. aquatica* "var. *genuina*" having leaves "*munies de poils épars ou presque glabres*," and var. *hirsuta*, "*couvertes de longs poils blancs presque tomenteuses*." Such a distinction is easy when extremes are handled, but the bulk of the material lies between the two. I regard var. *hirsuta* as merely a hirsute form of *M. aquatica*.

(c) var. *tomentosa* Sole (1798, 55, no fig.).

"*Mentha spicis glomeratis, caule erecto villosa non ramoso, foliis cordato-ovatis serratis petiolatis, incanis, mollioribus, staminibus corolla brevioribus: odore aromatico.*"

This variety seems to have been largely neglected, perhaps due to its secluded position at the end of Sole's fine book. There are several authentic specimens, those at the British Museum and the Linnean Society being apparently the same sort of mint, and no doubt from the same habitat. I have been unable to find any good distinction from var. *hirsuta*. The leaves may be a trifle softer but this feature is difficult of assessment when a specimen is stuck down. Sole's specimens are rather paler green in colour, but this may be due to difference in drying conditions. I regard var. *tomentosa* as a softly hairy form of var. *hirsuta*, the two being questionably differentiable.

(d) var. *chaixii* Timbal-Lagrange (1860, 332).

... leaves "*couverte surtout en dessous de poils blancs gros et brillants, ce qui n'y a lieu ni dans l'hirsuta ni dans l'aquatica.*"

This variety, whose additional characters are a simple, hirsute stem, with elongate-oval, acute, basally subcordate leaves with fine and unequal serratures, is characterised chiefly by the *long, brilliantly white hairs of the leaves*. I have seen no British examples that answer exactly to the description, but they are quite likely to occur, and this variety is included here as perhaps representing the extreme of hairiness in the water mint group.

(e) var. *grandidentata* (Strail) Briquet (1891, 78).

M. grandidentata Strail (1887, 96)

According to Briquet's description, which follows Strail closely, this variety is a very hirsute form, distinguished by *leaves little longer than broad with deep, regular, sharp serratures*. I possess specimens from the periphery of Braunton Burrows, v.c. 4, which can be named as this variety, which I regard merely as a form of var. *hirsuta* with the above-mentioned leaf shape and serrature characters.

(f) var. *denticulata* (Strail) H. Braun (1890, 420).

M. denticulata Strail (1887, 104)

M. aquatica var. *lupulina* Briquet (1891, 79)

Stengel . . . mit etwas zurückgekrümmten Haaren bekleidet. Blätter oberseits zerstreut behaart, unterseits hauptsächlich an den Nerven behaart, alle gestielt, breit-oval, am Grunde fast herzförmig, lang spitz nach vorn, 4 cm lang, 3 cm breit, am Rande wenig tief gesägt, mit spitzen und genäherten Sägezähnen. Köpfchen nicht breit . . .

This variety, which Braun regarded as a minor variant of his *M. aquatica* L. is characterised by the *many, small, sharp serratures*. It is evidently only thinly hairy, and Fraser was perhaps in error in describing the upper leaves as densely hairy with a grey

tomentose subsurface. Still (in correspondence with me) regarded this variety as a very hirsute form, but this would seem to be incorrect although hirsute forms with serratures as described above certainly occur. At its best this variety can be easily told by the saw-like leaf edges, but there is every degree of variation in serrature characters, and no distinction can be adequately described between this and forms with fewer serrations except as a matter of extremes.

Fraser considered the miniature examples from Braunton Burrows dunes to be this variety, a view with which I have never been able to agree, as the number of serratures on the reduced leaves of these small plants seems to be relatively insufficient for agreement with var. *denticulata*. Furthermore, these specimens are shaggy with hairs. In my view they are more likely to be reduced examples of var. *grandidentata*, which evidently has fewer though deeper serratures in its normal state than var. *denticulata*.

Briquet's var. *lupulina*, which would appear to have been chosen to replace the earlier, valid name (Braun's various forms are clearly to be regarded as of *varietal* grade), has a slightly different description from that of var. *denticulata*. Those who wish to do so can seize the chance to differentiate between them, but it would seem preferable to regard the two as essentially the same sort of water mint, as Briquet no doubt intended.

(g) var. *pedunculata* Persoon (1807, 119).

Hirsuta, foliis subinciso-serratis, capitulis lateralibus longe pedunculatis subfastigiatis.

This variety probably owes its state to luxuriance. It is told primarily by the long-pedunculate axillary verticils, which would probably appear as lateral capitula rather than verticils. A further character is the subincise leaves. I possess a specimen from near Westerham, v.c. 17 (D. B. Fanshawe), which has subascending peduncles no less than 8 cm. long at maturity – these being the longest I have yet seen. But this example differs from Persoon's description in being markedly subglabrous throughout, and in having very shallow serratures.

(h) var. *purpurea* (Host) Pérard (1870, 340).

Plante plus ou moins velue. Tige et feuilles rougeâtres. M. purpurea Host (1831, 141). *Folia petiolata, subcordata . . . Folia, caules, rami, bracteae sunt plerumque colore purpureo tincta.*

This more or less hairy water mint is purely a colour form, dependent no doubt for its colour on the chemical content of the ground water. Such highly coloured forms will be met with quite often, perhaps more commonly amongst subglabrous material.

(i) var. *minor* Sole (1798, 23-24, fig. 10).

For a general description see Sole's text, with which his specimens at the Linnean Society and British Museum agree. In this variety, which is quite easily recognised at its best, the stems are usually reddish; the leaves rather small (up to 4.2×2.8 cm.), ovate, acute, basally rounded or subcordate, with neat, rather jagged serratures, sparsely hairy above and more thickly so below; the inflorescence a large, showy, terminal capitulum, with or without axillary verticils; the stamens exserted. The large terminal capitulum, especially during anthesis, affords a somewhat topheavy appearance to the plant owing to its surmounting the rather small leaves. Sole's specimen called *Mentha aquatica decumbens* appears to be essentially the same sort of water mint as var. *minor* but with included stamens. (Water mints are essentially erect plants, and a decumbent state is presumably due to an artificial factor). Despite its name, var. *minor* is not necessarily a small plant. One of the Linnean Society specimens is 32 cm. tall,

- (j) var. *weiheana* (Opiz) H. Braun (1890, 424).

Stengel . . . mit kurzen Haaren, und kurzen blüthentragenden Zweigen bekleidet. Blätter beiderseits dicht behaart, alle gestielt, breit-oval, am Grunde abgerundet, nicht an den Blattstiele herablaufend, an der Spitze lange und allmählig verschmälert, 5-6 cm. lang, 3-3.5 cm breit, tief gesägt, Sägezähne spitz, gleich weit von einander entfernt . . .

This variety is characterised chiefly by the long, drawn-out leaf apex, and no doubt approaches var. *acuta* (below) in this respect. The serratures are deep, well spaced. Fraser's comment that the leaves are thinly and shortly hairy disagrees with *beiderseits dicht behaart*, and other discrepancies between his text and Braun's will be noticed.

- (k) var. *nemorosa* Fries (1828, 183).

Glabriuscula. Caules altiores, virentes. Folia ovata s. oblonga, sparsim pilosa. Capitula minus congesta. Pili pedicellorum brevissimi, subadpressi. Calyx passim glabra. (The comparatives are in distinction from var. *hirsuta*).

This variety differs from all others that I have seen described in literature (except *M. citrata* Ehrh. which is doubtfully a true water mint), in that the calyx is quite glabrous. Such a feature is clearly most unusual in a water mint. I have examined a great wealth of material, both British and Continental, but have failed to find a single example of an undoubted water mint with a glabrous or essentially glabrous calyx, indeed in only two instances were the cilia so short as to give a glabrous appearance. Fries' specimen has not been traced, and it is not at present known to me whether it exists. Information was requested from certain Swedish botanists, but unfortunately no reply has to date been received.

In my view, a mint with a glabrous calyx and morphological resemblance to a water mint can arise only as a result of hybridity. *M. citrata* Ehrh., which will be the subject of a later paper, is very like a water mint in appearance, and has been classed as a variety of *M. aquatica* L. by several authors. Its calyx is essentially glabrous, and it is likely to have arisen either as a sport or form of a hybrid, or as a double hybrid, of *M. aquatica* with *M. spicata*. It is clear that var. *nemorosa* cannot be the same sort of mint as *M. citrata*, as Fries describes the two separately. The only mint known to me which might bear relationship to var. *nemorosa* is the well-known "Roydon mint," from near Roydon, v.c. 20, which has a wholly glabrous calyx, and is indeed almost glabrous throughout. But this is very likely also to be a hybrid of the two parents suggested for *M. citrata*, or possibly a sport of the latter.

According to present knowledge it is not possible to be definite about var. *nemorosa*. The solution can only lie in the original specimen. This much, however, can be said, that on account of the glabrous calyx var. *nemorosa* is unlikely to be a true water mint, and is probably a hybrid of which one parent is *M. aquatica* L. It will be noted that Fries cites this latter as a synonym of var. *nemorosa*, but I have doubts as to the accuracy of this view.

2. With an attenuate leaf base

- (l) var. *ortmanniana* (Opiz) H. Braun (1890, 421).

M. Ortmanniana Opiz (1826, 437)

Stengel dünn, schlaff, aufrecht, unterwärts kahl oder an den Kanten behaart, Blattstiele zerstreut mit weisslichen Haaren bekleidet. Blätter ziemlich lang gestielt, dünn, klein oder mittelgross, die obersten am Stengel klein, beiderseits wenig aber hauptsächlich nur an den Nerven behaart, nach oben spitz, öfter in eine längliche Spitze vorgezogen, eiförmig-lanzettlich, in den Blattstiel fast rhombisch zugeschweift,

am Rande fein und öfter stumpflich gesägt. Blütenstiele und Kelche von kurzen Härchen fläumich. Blütenquirle ziemlich klein; Kelche oft violett überlaufen. Durch die kleinen, dünnen, eilanzettlich geformten, spitzen Blätter und die kurz fläumiche Behaarung der Blütenstiele und des Kelches sehr ausgezeichnet.

Evidently a weak, thinly hairy form, with a slender stem; long-stalked, thin, ovate-lanceolate, acute, small leaves, often with a long point; and with small capitula. Braun also stresses the downy petioles and calyx. Fraser gives rather different leaf characters, describing the bases as rounded, which scarcely agrees with *fast rhombisch zugeschweift*, nor can his "broadly ovate" be found in the above text. I possess specimens from the Oxted area, v.c. 16 (D. B. Fanshawe), which can be regarded as this variety, and it is likely to be met with in damp habitats.

Braun's description follows that of Opiz generally, the latter referring to the leaves as *fere internodiis brevioribus* – another indication of their small size. Braun no doubt consulted Opiz' specimens, which are extant in Germany (*Mit Ausnahme der Linné'schen Sole'schen und Hudson'schen Arten und Formen habe ich fast alle nachfolgend besprochenen Menthen in Original-Exemplaren vorliegen gehabt* – Braun (1890, 352)).

(m) var. *elongata* Pérard (1870, 340).

Plante velue. Feuilles ovales-oblongues, larges, très longuement petiolées.

Evidently a hirsute form, with large, oval-oblong leaves on very long petioles. The right hand specimen on sheet No. 15 of Sole's set of mints at the Linnean Society is perhaps this variety, in a slightly smaller state but having noticeably long petioles.

It would seem that var. *ellipticifolia* Loret (1880, 268) is nearly allied to var. *elongata*, being, according to its description, a luxuriant water mint with broadly elliptic-oblong leaves, *nearly as broad towards the apex as towards the base*, and with petioles that are *as long on the upper leaves as on the lower*. As leaves of water mints develop, their petioles usually become longer, and a water mint such as Loret's variety would present rather an unusual appearance.

(n) var. *major* Sole (1798, 25-26, fig. 11).

This well-known variety has usually been regarded as a luxuriant water mint with a distinctly attenuate leaf base. It is probable that Sole had luxuriance in mind when describing it. But close attention to his text, and examination of his specimens, indicate that this variety comprises several forms, and can be taken as synonymous with *M. aquatica* L. in an aggregate sense.

In his description Sole says of the leaves . . . *pointed, green, hairy, broad, ovate, elliptical, and oblong; for nature sports much in the habit of this plant according to the variety of soils and situations . . . at Twiford . . . with broad elliptical leaves almost smooth. . . . about Bath . . . exceedingly hairy, with ovate leaves . . . on our downs . . . procumbent, hoary, and its leaves acuminate*. The above words cover a wide range in leaf shape, and this is borne out by the specimens. There are three at the Linnean Society, all different from each other, and none agreeing with the figure. Two have leaves with rounded bases, whereas in the figure they are distinctly attenuate. At the British Museum there is a specimen that agrees well with the figure, and it is perhaps this one that Fraser (1927, 228) means when he refers to *type*. It is thus possible to select a type specimen to agree with the figure, and with the description in part, but to do so amounts, in my opinion, to a denial of Sole's concept of his variety, which is, more than anything, merely a strong, luxuriant plant.

I cannot, therefore, regard var. *major* as a precise form of *M. aquatica* L., and propose to relegate it to synonymy with this latter in its aggregate sense.

(o) forma *cana* Fraser (1927, 228).

Fraser's specimens, at Kew, indicate that this form is a hirsute variant of var. *major* *sensu* Fraser. The leaves are *ovate-lanceolate*, *grey-white with matted pile on the under-surface*. The whole plant is generally rather hoary, and agrees with Fraser's description, and, apart from its hairiness, with Sole's figure of his var. *major* (*Mentha aquatica major*).

3. Forms whose leaf base is somewhat intermediate between rounded and *attenuate*

(p) *M. dunensis* Strail (1887, 102).

Tige . . . couverte de longs poils étalés . . . Feuilles très velues sur les deux faces . . . elliptiques, aigues ou subaigues, arrondies à leur base et un peu décurrentes sur les pétioles, de 3 à 5 cent. de longueur sur 2½ de largeur, peu profondément dentées, à dents aigues et écartées . . .

This "variety", originally described from terrain reclaimed from the sea, can perhaps be applied to certain forms from Branton Burrows and similar habitats. It is a *very hairy water mint*, with *elliptic, subacute leaves, basally rounded or narrowed to the petiole, and with ± shallow but sharp and well-spaced serratures*. One would imagine that var. *grandidentata*, in a reduced state, would produce a form such as this, though this latter variety would not, according to its description (above), apply to examples with an attenuate leaf base. With regard to specimens from Branton Burrows with a rounded leaf base, I must leave it to others to decide whether they are to be classed as *M. dunensis* or reduced forms of var. *grandidentata*.

(q) var. *inciso-serrata* (Strail) Briquet (1891, 80).

M. inciso-serrata Strail (1887, 101).

M. aquatica var. *foliis inciso-serratis* Wirtgen, *Herb. Ment. Rhen.*, ed. 3, No. 37.

Plante robuste . . . Tige couverte de poils réfléchis . . . à rameaux ascendants allongés et florifères. Feuilles modérément ovées, vertes et hérissées sur les deux faces, très aigues ou un peu acuminées au sommet, très convexes à la partie inférieure, très brièvement atténuées, subarrondies ou arrondies à leur base . . . serrature consistant de dents assez nombreuses, ± irrégulières, saillantes, formant des triangles hauts de 1.3-2 mm., ondulés ou dentés extérieurement, à sommets aigus ou légèrement étalés, séparés par une distance de 4-6 mm. Capitules ordinairement hérissées.

The chief character for this variety is clearly the deeply-cut (incised), salient serratures. Briquet's above description follows that of Strail closely, the latter describing the serratures as *profondément incisées-serrées, à dents très aigues et irrégulièrement écartées*. The specimen in the Oxford herbarium, which was thus identified by Briquet and qualified with the word *forma*, corresponds quite well with the description though the serratures are rather more salient than they are deep. This also applies to Wirtgen's specimens at the British Museum, whose serratures are also more irregular in their depth. I possess an example from Kempford, Glos. v.c. 33 (C. C. Townsend), which has very irregular serratures, some of them gashes to a depth of 5 mm., and which can be loosely regarded as var. *inciso-serrata*. Such a water mint is extremely strange in appearance, and this variety is perhaps easy of identification. But the variation in serrature characters is unending.

(r) var. *nicaeensis* Briquet (1891, 97).

. . . Tige robuste, ± rameuse, rougeâtre, pourvue surtout sur les angles d'un indument relativement peu scabre . . . Pétiole velu, atteignant 2.5 cm. de longueur dans les régions moyennes de la tige. Feuilles ovées-elliptiques, allongées, ayant leur

plus grande largeur près de la base, à marges fort convexes en cet endroit, convergeant ensuite suivant une ligne $\pm$ droite pour former au sommet une pointe aigue ou un peu acuminée, arrondies ou très brièvement atténuées à la base, vertes et $\pm$ poilues sur les deux faces . . . serrature consistant en dents assez régulières, nombreuses, formant des triangles hauts de 1-1.5 mm., droits intérieurement, presque tous nettement dentés extérieurement, à sommets très aigus, séparés par une distance de 3-4 mm. Capitules $\pm$ velus . . . Cette variété est fort voisine de la var. *inciso-serrata* dont elle diffère surtout par sa serrature double.

Briquet regarded this variety as a near ally of var. *inciso-serrata*, the chief distinction from the latter being the small, intermediate denticles on the exterior surface of the serratures. The Oxford specimen, identified by Briquet, agrees with the description to a certain extent, but the double serration occurs only on the lower leaves, while on the upper the serratures are fewer (up to 4), and, apart from the question of immaturity, show no clear indication that double serration will develop. Frankly, I can see extremely little in this variety, double serration being a not uncommon feature of many forms of water mint.

(s) var. *riparia* (Schreber ex Schweigger & Körte) H. Braun (1890, 422).

Stengel unterwärts wenig behaart oder kahl, oberwärts mit weisslichen zurückgekrümmten Haaren $\pm$ bedeckt . . . Blätter länglich-lanzettlich . . . spitz aber kurz gesägt, beiderseits zerstreut, an den Hauptnerven etwas mehr mit Haaren bekleidet . . . an der Basis zum Blattstiele kurz zugeschwefelt . . . Blütenquirle meist kleiner als bei *M. aquatica* L.

This is apparently a subglabrous form, with long-lanceolate, basally shortly-narrowed leaves, with short, sharp serratures; and with small capitula. It would seem to be nearly allied to var. *ortmanniana* (above), differing in having much larger leaves. Possibly one is a luxuriant form of the other. This variety is included in this account as it is mentioned frequently in Continental literature, although not previously listed as a British form. Many herbarium specimens can be classed as this variety.

(t) var. *acuta* H. Braun (1890, 422).

M. acuta Opiz (1852, 64), sine descr.

Stengel oberwärts dicht behaart, Blätter ziemlich lang gestielt, Blätter vor der Mitte der Lamina an in eine lange Spitze ausgezogen, Blütenquirle 2-3 cm. gross.

This variety is characterised by a long, drawn-out, acute, leaf apex, and evidently has large capitula. Braun regarded it as a minor variant of var. *riparia*, from which it differs in these two characters, and in having hairier leaves and stem. Specimens classifiable as var. *acuta* will fairly often be found, but there is every variation between a long, drawn-out, acute apex to the leaf and a short, blunt one.

The following three varieties, hitherto classed as water mints by Fraser and other authorities, are rejected as being, in my opinion, of doubtful status in this group.

(u) var. *subglabra* Baker (1865, 248).

The only reference to a var. *subglabra* attributable to Baker appears in the above-cited essay "On the English Mints." But here it is unquestionably listed as a variety of *M. sativa* (*M. × verticillata* L.), nor is there any mention of a var. *subglabra* in the section dealing with water mints. A reputedly authentic specimen at Kew, bearing a label perhaps in Baker's hand, is a verticillate – not a capitate – mint, in fact *M. × gentilis* L.

(*M. arvensis* × *spicata*). In Syme's herbarium there is a specimen from Kincardine, which may be that referred to in Baker's text, and this is a subspicate form of *M. × verticillata* L. The above evidence would seem to indicate that, whatever Baker intended by this variety, it was not a water mint.

On the other hand, this variety has been very widely treated as a water mint in many British works, and many subglabrous forms of *M. aquatica* L. have received this varietal name in our national herbaria. Further, there is in Syme's herbarium an undoubted water mint named as var. *subglabra* in Baker's hand. Fraser (1927, 228, 232), it will be noted, refers to this variety both under *M. aquatica* var. *major* and under *M. × verticillata* var. *ovalifolia* (Opiz) H. Braun.

It is likely that, whatever his original view, Baker came to regard *M. aquatica* L. and *M. × verticillata* L. as essentially the same sort of mint, differing only in the form of the inflorescence. This was Smith's view (1825, 78-82), also that of Fries. The latter's var. *suavifolia*, cited by Baker as a synonym of var. *subglabra*, is placed under a capitate-verticillate division of *M. aquatica* L., and this section would seem to comprise subspicate forms of *M. × verticillata* L. On such a basis it would be possible to regard var. *subglabra* as applicable to both groups. The two are, however, differentiable both morphologically and cytologically, and as var. *subglabra* was originally described as a variety of *M. sativa* L. it is scarcely possible to retain it also as a variety of *M. aquatica* L.

(v) var. *lobeliana* Becker (1828, 222).

Stengel krausshaarig oder häkerig, fast einfach; Blumenköpfe alle achselständig, auf Gipfel ein einzelner kleinster. Mentha cardiaca Lobel, obss. p. 271, fig. 4, ic. p. 508, fig. 1.

This variety has come down to us, chiefly through Briquet and Fraser, as a small-leaved, thinly hairy form of *M. aquatica* L. Becker places it under his *hirsuta*, which can be taken to imply *M. hirsuta* Huds. One may question whether the word *alle* may not more correctly refer to a verticillate mint, perhaps a subspicate form of *M. × verticillata* L. or of *M. × gracilis* var. *cardiaca* (Baker) Briquet. The small terminal capitulum is sometimes found in forms of these two hybrid groups, surmounting an otherwise multiverticillate inflorescence. Further, there is, in Becker's text, the clear reference to *M. cardiaca* Lobel. This – Cardiac Mint – has been known as a medical herb from pre-Linnean times, and is no doubt the *M. cardiaca* of Gerarde and Baker. Whereas the ancient *icones* may not always accurately represent the plants they purport to be, in the case of Becker's references they have every appearance of being *M. cardiaca*. This evidence would seem to indicate that var. *lobeliana* was merely another name for *M. cardiaca* Lobel, Gerard, et alior. It is quite likely that Becker regarded this hybrid mint as essentially the same sort of mint as *M. aquatica* L., differentiation in those days being often shallow in this genus.

Briquet (1891, 83) who apparently examined Becker's specimens, described one of these as the true var. *lobeliana*, and this was evidently a water mint. At the same time Briquet says that under this varietal name Becker, according to his herbarium, included many forms – whether all are water mints or not I do not at present know. Briquet's statement that the original description can be applied to all varieties of *M. aquatica* is a somewhat debatable point – one with which I am disinclined to agree. Braun, who no doubt also saw Becker's specimens, classes this variety under his *M. paludosa* Sole (*M. × verticillata* L. var. *paludosa* (Sole) Druce), a treatment with which Briquet disagreed, but one which appears to be rather nearer the truth according to Becker's text. The whole matter is very confusing, and a great deal must depend on Becker's specimens. At any rate for the time being, I would question the inclusion of this variety in the water

mint group, and would suggest its kinship to the *M. cardiaca* of the ancients as its more correct status.

(w) var. *obscura* Wimmer & Grabowski (1829, 178-9).

Caule, calycibusque violaceo-purpurascens, foliis purpurascens vel violascens. (Saepe caulis hirtus, folia subglaberrima complicata.)

From the above description, this mint is undoubtedly a colour form, and it must be regretfully pronounced that Fraser's description bears no resemblance whatsoever to that of the original joint authors.

This plant is classed as either a *variety* or a *form* under the authors' *M. aquatica* var. γ *gracilis*, which is described as *Foliis ovali-oblongis breviter petiolatis, caule elongato sub-simplici, verticillis multis, capitulo parvo*, which quite adequately describes *M. $\times$ gracilis* Sole, or perhaps its var. *cardiaca* (Baker) Briquet (= *M. cardiaca* Ger., Baker, et alior.), especially the strict, subspicate form (Graham 1950, 278). I do not know whether their *gracilis* was the same sort of mint as Sole's but from the description it would appear to be at least highly likely. Its place under *M. aquatica* L. is perhaps another example of earlier authors believing a capitate and a verticillate mint to be essentially the same. From the above evidence, var. *obscura* can scarcely be regarded as a variety of *M. aquatica* L., but would appear to be a deeply-coloured form of *M. $\times$ gracilis* Sole, or of its var. *cardiaca*.

SUMMARY

Mentha aquatica L. should be regarded as one form only of an extremely polymorphic group, known in the aggregate as Water Mint. Many forms have received distinctive names, but their retention is not recommended on scientific grounds, as their existence gives rise to a taxonomic chaos. Further, there would appear, according to present knowledge, to be no justification on a cytological basis, though in this respect it is advisable for more chromosome counts to be taken. So great is the range of variation in most characters, and so gradual is any combination of characters, that all the named varieties and forms should, in my view, be abandoned, and the whole group be regarded and determined under the single binomial *M. aquatica* L., though for herbarium purposes the different forms may, if desired, be separated under varietal names. Only one reservation should be made, i.e. in respect of var. *nemorosa* Fr., correct assessment of which must await the appearance of an original specimen.

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STELLARIA NEMORUM L. SUBSPECIES GLOCHIDISPERMA MURBECK IN BRITAIN

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INTRODUCTION

In June 1953 a short paper was published by A. Lawalrée (1953) in which attention was drawn to the existence in Belgium of subspecies *glochidisperma* of *Stellaria nemorum*. As this subspecies seems quite distinct and had been overlooked for some time in the Belgian flora, I decided to look at the material in the British Herbarium at the Royal Botanic Garden, Edinburgh, and there discovered a single specimen (Plate 1a). It had been collected at Llandogo in Monmouthshire more than a century ago and the label reads: "Ex Herb. F. Farre, Llandogo, Monmouthshire, at the falls, 32.6.29."

DISTRIBUTION

In order to confirm this record and see whether further specimens and records from Britain exist, material was studied from the following herbaria, to whose authorities grateful acknowledgment is made: Aberdeen University, Birmingham University, British Museum (Natural History), Cambridge University, National Museum of Wales and Royal Botanic Gardens, Kew. In all, collections have been discovered from four counties: Monmouthshire, Cardiganshire, Montgomeryshire and Merionethshire. The detailed localities, together with a formal description, are given at the end of this paper.

Very recently Lawalrée (1954a) has recorded the occurrence of subsp. *glochidisperma* in France and Spain, and at the conference of the Botanical Society of the British Isles, held on April 9th and 10th, 1954, Dr. Ch. H. Andréas of Groningen read a short paper in which she discussed its occurrence and ecology in Holland. These records have considerably extended the known range of the subspecies on the continent. It was originally described from Yugoslavia (from that part formerly known as Herzegovina) and is a central European subspecies, reaching in the north as far as southern Sweden and eastern Denmark, in the west to Wales, France and central Spain and in the south to Corsica and Italy (the Apennines). Its eastern limit is uncertain but it is probably the plant named from Russia as var. *subebrateolata* Fenzl (Ledebour 1842). A map showing its distribution in Scandinavia is given by Hultén (1950).

DESCRIPTION

Stellaria nemorum subsp. *glochidisperma* is most easily distinguished with certainty from subsp. *nemorum* by two characters: one of the inflorescence and the other of the seed.

In subsp. *nemorum* the bracts of the inflorescence decrease gradually in size at each dichotomy of the cyme (Plate IIb), whilst in subsp. *glochidisperma* their size decreases abruptly after the first pair. The second pair is rarely more than a quarter of the length of the first, and the third is characteristically scale-like (Plate IIa). In those specimens of subsp. *glochidisperma* investigated, the length of the second bract ranges from 10-27% of that of the first (with one robust specimen up to 50%, but even then with extremely small third bracts), and in subsp. *nemorum* from 30-85%. It is important not to mistake the small flowering branches which occur occasionally in the axils of the upper leaves for the first branches of the inflorescence (Plate IIa). The inflorescence proper always has a flower arising between the two dichotomous branches.

The edge of the ripe seed of subsp. *nemorum* is furnished with rows of rounded more or less hemispherical tubercles, whilst the margin of the seed of subsp. *glochidisperma* has long cylindrical papillae about 0.15 mm. in length, which under the microscope are seen to possess a barbate cap. A warning should be added that when the seed is immature the marginal tubercles in subsp. *nemorum* may seem longer in proportion to breadth than when mature; especially is this the case in herbarium material where the immature seed has become somewhat shrivelled.

A further characteristic, although not diagnostic in itself, is that in subsp. *glochidisperma* the uppermost leaves are stalked whilst those of subsp. *nemorum* are usually sessile or subsessile. This is an unreliable character where the specimen is either a very lush *nemorum* or a diminutive *glochidisperma*, whilst in young growth and on vegetative shoots the leaves of both subspecies are stalked. Typically, a flowering specimen of subsp. *glochidisperma* has the appearance of *Circaea lutetiana*; a figure is to be found in Hegi (1911 a or b) under the synonym, subsp. *circaeoides* A. Schwarz.

In addition to these distinguishing characters, Murbeck in his original description of subsp. *glochidisperma* (Murbeck 1892) mentioned several others which on being tested have proved to be either of little value or else to be common to both subspecies. (1) It was claimed that the stem leaves of subsp. *glochidisperma* are broader. If breadth alone is considered this is quite false, and even if breadth is considered relative to length there is no difference between the two subspecies in ordinary vegetative leaves. Only with the pair of leaves at the last node before the first branching of the cyme does there seem to be any difference, and even then it can only be said that there is a tendency for subsp. *glochidisperma* to have leaves broader in proportion to their length. In the specimens measured, the index of leaf-breadth divided by leaf-length for subsp. *nemorum* was 0.31-0.59 and for subsp. *glochidisperma* 0.39-0.70. (2) Subsp. *glochidisperma* is said to possess more cordate leaf bases. Examination again shows that this is not so in purely vegetative leaves and that only in the uppermost ones, including the first pair of bracts, is there a slight difference. In subsp. *nemorum* they are truncate to rounded, whilst in subsp. *glochidisperma* they are subcordate to truncate. Furthermore, there is a tendency in both subspecies for the leaf blade to be slightly decurrent. This tendency is greater subsp. *nemorum*, partly because the leaf base is less cordate and partly because the petiole is usually shorter. In leaves which are very shortly stalked or subsessile the decurrent wing makes the leaf base merge into the axis of the shoot. (3) The capsule is said to be twice as long as the calyx in subsp. *glochidisperma* and only a third longer in subsp. *nemorum*. This has proved a difficult character to test, as relatively little of the available material has fully ripe capsules. It seems there may be a tendency in subsp. *glochidisperma* for the capsules to be longer in proportion to the calyx length, but it is doubtful if it is as significant as has been claimed by Murbeck. (4) Another character that has not been tested is that the fruiting pedicel in subsp. *glochidisperma* lies in line with the axis whilst in subsp. *nemorum* it lies bent at an angle. It is quite impossible to observe this with certainty on herbarium material and field or experimental garden studies will be necessary.

Early in this investigation, before it was known that the chromosome numbers of both subspecies had been found to be the same ($2n = 26$, Peterson 1936), it was thought possible that one of them might be a polyploid. Had this been so it might have been reflected in the pollen grain sizes and stomatal indices of the two subspecies. No significant difference in pollen grain size between the two subspecies was found, however. The pollen of six specimens of subsp. *glochidisperma* was measured and the total range in diameter found to be $(40 -) 41-48 (-50) \mu$, whilst in nine specimens of subsp. *nemorum* the total range was $(39 -) 41-47 (-50) \mu$; ten grains per specimen were measured. No comparison has so far been possible between the stomatal indices, that is in the proportion of stomatal

cells to ordinary epidermal cells (for details of the method of calculation etc., see Salisbury, 1927 ; or Rowson in Howard & Manton, 1946), and, despite experimentation with various techniques, attempts to use herbarium material have proved unsatisfactory. Thus the only diagnostic characters so far known depend upon the plant being at least at the flowering stage.

POSSIBLE HYBRIDS

As has been mentioned, both subspecies have the same chromosome number and Peterson (1936, 324) has reported, as the result of hybridisation experiments, that they are fully interfertile, the hybrid producing well developed pollen and ovules and viable seeds. These seeds are intermediate between those of the parents. According to Dr. Andréas, the two subspecies are separated ecologically (at least in Holland) but there seems no doubt that they do cross when they happen to meet in the wild. Lawalrée (1954b) has reported intermediate specimens from Belgium and there are three herbarium sheets in the National Museum of Wales, Cardiff, and one in Birmingham University which seem intermediate in character. These four specimens are listed towards the end of this paper in the section dealing with the detailed British distribution and there seems no reason to doubt that as both subspecies have been collected and recorded from the area of the Wye Valley a number of intermediate plants may occur in that district. Only one of the four specimens cited bears seeds, and even these are immature, but the intermediate status of the plants is shown by a combination of the two characters : length of the petiole of the uppermost vegetative leaf and the proportional length of the second inflorescence bract to the first : see Table.

TABLE

Locality	Length of petiole of uppermost vegetative leaf.	Length of second inflorescence bract as a percentage of that of the first.
1. Between Bigsweir and St. Briavels	1.5-2.0 cm.	16-56%
2. Llandogo Glen	1.5-3.5 cm.	41-78%
3. Whitebrook	2-3 cm.	42-71%
4. Cwm Rhaiadr	1-1.5 cm.	32-50%

Very few abortive pollen grains were found in three of the specimens cited above and, as has been mentioned, Peterson pointed out that the pollen in the hybrid is fully developed. However, whatever its significance may be, in the specimen from Cwm Rhaiadr, Llyffnant Valley, the proportion of abortive grains is quite high.

STELLARIA MONTANA Pierrat.

Amongst the Continental material in the Herbarium at Kew, I have had my attention drawn by Mr. R. D. Meikle to three specimens collected in July 1879 at Gerbamont, Rochesson, Vosges, France (Plate IIc). This material was described as a new species : *Stellaria montana* D. Pierrat (1880, *Comptes Rendus Soc. Bot. Rochelaise*, 2, 58)*. I have

* Not the plant from Alamos, Mexico, named *S. montana* J. N. Rose (1891, *Contrib. U.S. Nat. Herb.*, 1, 93) which is the only *S. montana* at present listed in the *Index Kewensis*.

not seen this description, but mounted on the sheet with the specimen is a printed diagnosis which, though somewhat inadequate, is sufficient in itself to constitute valid nomenclatural publication. This material is undoubtedly the same taxon as *S. nemorum* subsp. *glochidisperma* and, whilst the name *S. montana* Pierrat seems to have been overlooked recently, it was apparently treated at one time as synonymous with the typical subspecies, known to-day as subsp. *nemorum* (Murbeck, 1899; Hegi, 1911a and b). However, this isotype material shows this interpretation to be incorrect. Ascherson and Graebner (1919) suggest that the two taxa may be the same but say that they have seen no authentic material of *S. montana*, whilst Rouy and Foucaud (1896) treat it as a variety and with it, but separate, list var. *subbracteolata* Fenzl. Fortunately, if we retain the subspecific rank for this plant, and there do not seem sufficient grounds for considering it as a separate species, there is no need for a change of name, *glochidisperma* being the earliest epithet in the rank of subspecies.

STELLARIA NEMORUM L. subspecies *GLOCHIDISPERMA* Murbeck, 1892, *Acta Univ. Lund.*, **27**, (5), 156-157.

An ascending or erect herb, 15-30 (—50) cm. high, usually smaller than subsp. *nemorum*. Leaves ovate, the upper ones broadly so, cordate to deeply cordate, the ultimate pair subcordate to truncate (truncate to rounded in subsp. *nemorum*); petioles longer than in subsp. *nemorum*, the lower ones up to 5 cm. long, the upper pair usually at least 1 cm. long as compared with 0.5 cm. or less in subsp. *nemorum*. Bracts of the inflorescence diminishing abruptly in size after the first dichotomy of the cyme, the second pair rarely more than a quarter the length of the first, the third pair scale-like, 1.5 (—2) mm. or less in length. Seeds furnished round the margin with long cylindrical papillae, 0.15 mm. in length.

DETAILED BRITISH DISTRIBUTION

The following specimens of *Stellaria nemorum* subsp. *glochidisperma* have been seen :

- v.c. 35, Monmouth; Llandogo, at the falls, 1832, ex Herb. F. Farre, (E); Llandogo, 1836, J. Bell, (B.M.); Llandogo Glen, 1877, A. Ley, (Birm.), (N.M.W.).
- 46, Cardigan; woods in Cwm Rhaiadr Valley, 1885, A. Ley, (Birm.); Glaspwll, Llyffnant Valley, 1924, J. H. Salter, (N.M.W.); oakwood in Llyffnant Valley, 1938, W. B. Turrill, (K.).
- 47, Montgomery; Llyffnant Valley, 1941, J. A. Webb, (N.M.W.).
- 48, Merioneth; Llechwedd Wood, nr. Harlech, 1903, W. G. Hamilton & D. A. Jones, (N.M.W.).

In addition there are the following specimens of possible hybrid origin : subsp. *glochidisperma* × subsp. *nemorum* :

- v.c. 34, W. Gloucester; streamlet in boggy wood between Bigsweir and St. Briavels, 1893, W. A. Shoolbred, (N.M.W.).
- 35, Monmouth; wooded bank of stream, Llandogo Glen, 1897, W. A. Shoolbred, (N.M.W.); Manor Wood, Whitebrook, 1942, S. G. Charles, (N.M.W.).
- 46 or 47, Cardigan or Montgomery; Cwm Rhaiadr, 1860, A. Ley (Birm.).

(The following are the abbreviations used to denote the herbaria in which the specimens listed above exist : Birm.—Birmingham University. B.M.—British Museum (Natural History). E.—Royal Botanic Garden, Edinburgh. K.—Royal Botanic Gardens, Kew. N.M.W.—National Museum of Wales, Cardiff.)

In the collection at Kew is a sheet with a mixture of specimens of subsp. *nemorum* and subsp. *glochidisperma* marked "Suffolk, Herb. Hookerianum 1867." It is difficult to believe that these plants really came from Suffolk which is right outside the range of both subspecies, and in view of the fact that the sheet is mixed and that Hooker received

a very great number of plants from correspondents it seems best to treat the "Suffolk" locality as a mistake.

In order to complete the record of distribution, determinable material of subsp. *memorum* has been seen from the following vice-counties.

4. N. Devon.	64. Mid W. York.	*82. Haddington.
35. Monmouth.	65. N. W. York.	83. Edinburgh.
36. Hereford.	66. Durham.	84. Linlithgow.
39. Stafford.	67. S. Northumberland.	85. Fife.
42. Brecon.	68. Cheviotland.	86. Stirling.
44. Carmarthen.	69. Westmorland.	87. W. Perth.
48. Merioneth.	70. Cumberland.	88. Mid Perth.
54. N. Lincoln.	72. Dumfries.	89. E. Perth.
57. Derby.	73. Kirkcudbright.	90. Forfar.
58. Cheshire.	75. Ayr.	94. Banff.
59. S. Lancs.	77. Lanark.	95. Elgin.
60. W. Lancs.	79. Selkirk.	96. Easternness.
62. N. E. York.	80. Roxburgh.	99. Dunbarton.
63. S. W. York.	81. Berwick.	

Vegetative material which is underterminable as to subspecies although probably subsp. *memorum* has been seen from

51. Flint, 91. Kincardine and 92. S. Aberdeen.

Finally *S. nemorum* has been recorded from the following vice-counties but no material has been seen by the author; in brackets are listed those from which doubtful records, which need to be confined, exist.

(37. Worcester.)	(38. Warwick.)	(40. Salop.)
(41. Glamorgan.)	49. Caernarvon.	(61. S. E. York.)
(71. Isle of Man.)	74. Wigtown.	76. Renfrew.
78. Peebles	(93. N. Aberdeen.)	(109. Caithness.)

It should also be looked for in 43, Radnor and 50, Denbigh where it may well occur but has not been recorded.

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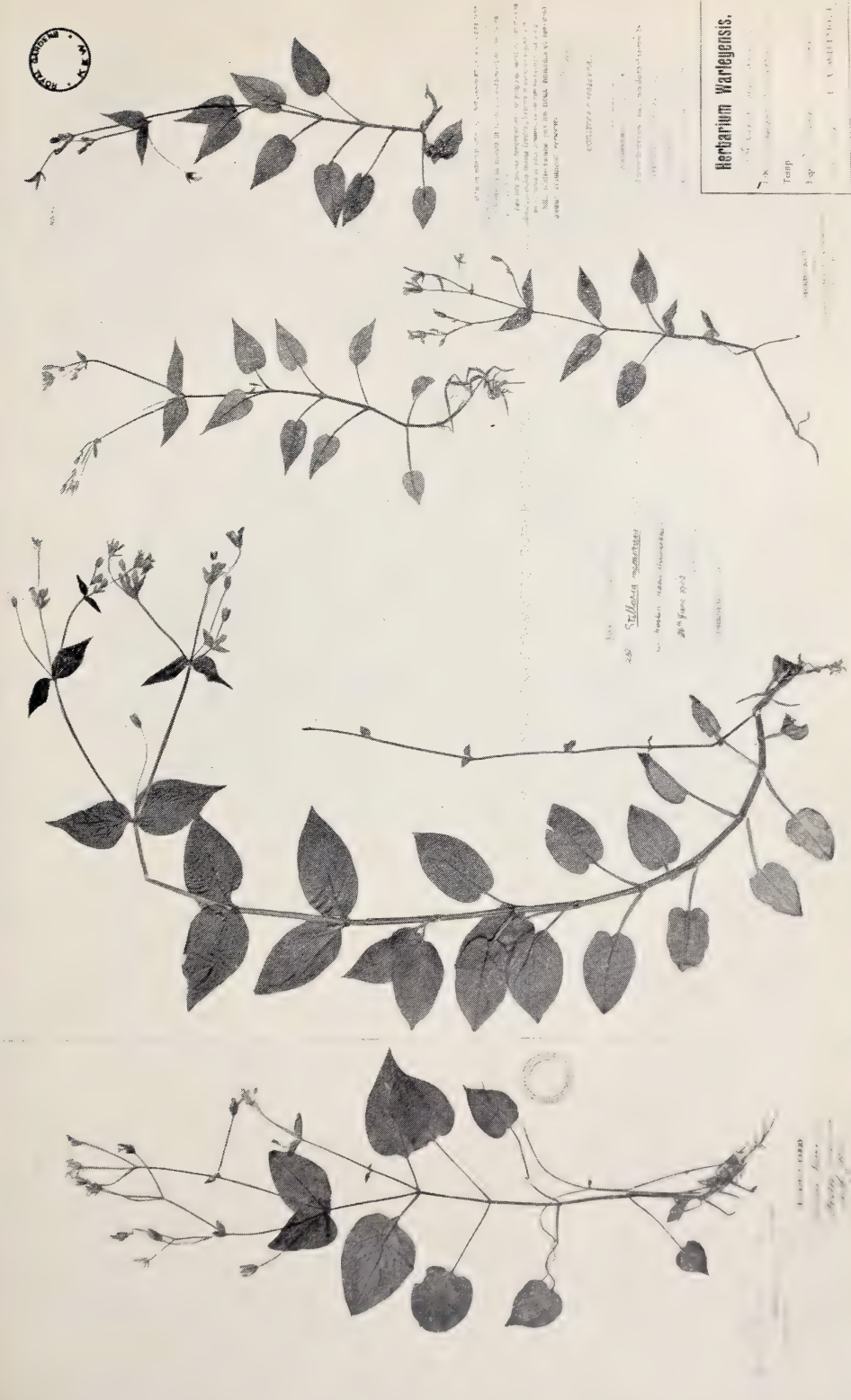


PLATE II.

a. *Stellaria nemorum* L. subsp. *gluchidisperma* Murb. ($\times \frac{5}{16}$).

b. *Stellaria nemorum* L. subsp. *nemorum* ($\times \frac{5}{16}$).

c. Isotypes of *Stellaria montana* Picrat ($\times \frac{5}{16}$).

REVIEWS

Downs and Dunes: Their plant life and its environment. SIR EDWARD SALISBURY, C.B.E., LL.D., V.P.R.S. Pp. xiii + 328, 100 text figures, 32 plates. G. Bell & Sons, Ltd., London, 1952; £2 5s.

The association of accounts of the vegetation of chalk downs and of sand dunes within the covers of a single volume has a great deal to commend it. The two types of habitat have important features in common, and contrast and comparison of their floras and ecological conditions offer scope for interesting conclusions. Sir Edward Salisbury's choice of subject is thus a happy one; there is plenty of room for a book combining the two topics.

Downs and Dunes is, in effect, two books. The first deals with chalk and limestone areas, and the second, of equal length, is an account of coastal dunes. The two are treated quite independently but treatment in both includes discussion of various ecological aspects, biological notes on, and phyto-geographical relationships of, the species represented, and brief notes on the animal life. The writer has had long experience in lecturing on his two subjects and many of those who have heard his lectures will be glad to have the subject matter and illustrations available in book form.

The book is most expensively produced, and it is a pity that some of the statements about distribution and habitats, and certain of the maps, need modification, and that there are a number of misprints. The illustrations and diagrams are lavish and most carefully reproduced. All but six are the work of the author and must evoke lively admiration of his versatility. Those of root systems and seedlings are particularly valuable and the 74 photographs include some of a very high standard.

J. E. LOUSLEY

Studies on British Beechwoods. J. M. B. BROWN, B.Sc. Forestry Commission Bulletin No. 20, London. Her Majesty's Stationery Office; 12/6.

This bulletin contains a great deal of valuable information which will interest not only foresters but also ecologists. Mr. Brown has made a wide survey of British Beechwoods during the last ten years and therefore has obtained at first hand a knowledge of the community as it exists in these islands in planted and in semi-natural state. It is of great value that an account which considers the effects of forest management on these woodlands should be available, for there is, perhaps, a tendency amongst ecologists of an academic sort to omit to consider adequately the effects of man even on British communities. The survey of some two hundred woodlands and the collection of information on the performance of the beech with respect to climate, soil, site and associated plants would alone be of great interest. In this bulletin the author has been enabled to consider much of the relevant literature on the beech together with a first-hand field knowledge to give a balanced account of the beech in these islands.

The appendices included in the Bulletin summarise in shorthand form the information gained by the field work and to many ecologists and foresters these will be of first-class value. Some parts of the account, especially those on the borders of the subject, which are unlikely to be in the forefront of interest to ecologists and foresters, are somewhat lightly passed over – for example the history of the beech as a native tree and the physiological work. Such omissions do not detract from a bulletin of this kind and this one is, for its size, excellent. It is well illustrated by fine and in some instances very artistic photographs.

J. L. HARLEY

Key to the Names of British Plants. R. D. Macleod. 8vo., pp. ix + 94. London, Sir Isaac Pitman & Sons Ltd., 1952; 12/6.

This book is largely a careful compilation from previous works dealing with the derivation and meaning of the scientific and popular names of British Flowering Plants and Ferns and is intended not for botanists but for the use of flower-lovers who have little or no knowledge of Greek or Latin. The author's botanical horizon is sufficiently indicated by his statement on page 1 that "as regards scientific names, Bentham & Hooker's list is certainly the most authoritative one available."

The main body of the book consists of three lists, the first of which includes the explanation and derivation of the generic names and of those scientific "names" (i.e. epithets) which are nouns in apposition to their generic name and are commonly spelt with a capital initial letter. The second list comprises the remaining scientific "names" and the third the common names followed by their scientific equivalents.

The first list is the one most open to criticism, since the author has endeavoured to supply derivations for all Latin plant names, confessing defeat in only a few cases, e.g. *Blechnum* and *Draba*. Some of these derivations are, to say the least, highly conjectural: no evidence is given in support of the statement that *âcer*, the Latin name of the Maple, is cognate with *âcer*, sharp – Lewis & Short (1924) say “kindred with German Ahorn.” The author suggests (pp. 3, 27) that *Armeria*, the generic name now used for the Thrifts, may be derived from “ad mare,” near the sea, with reference to the habitat of some of the species. Actually, the name *Armeria* or *Armerius* first appears in the sixteenth century and was applied primarily to certain species of *Dianthus* with aggregated flowers, namely to *D. barbatus*, *D. carthusianorum*, *D. armeria* and *D. prolifer*, also to *Dianthus arenarius*, *Silene armeria* and *Lychnis flos-cuculi*. Clusius included the plant now known as *Armeria maritima* under the name *Armerius montanus tenuifolius major*, probably because of its superficial resemblance to *Dianthus prolifer*. Caspar Bauhin (1623) states that the name *Armeria* or *Armerius* is derived from the French words “armoires” (wardrobes) and “Armoiries,” (coats of arms) but this seems very far-fetched. The origin of the name *Armeria* is quite problematical. Undue importance is attached by the author to the fanciful derivations supplied by Pliny in his Natural History.

The introduction is attractively written and the book is one which should appeal to the large non-botanical public interested in wild flowers and using Bentham & Hooker's *Handbook of the British Flora* as a text-book.

T. A. SPRAGUE

THE CHANGING FLORA OF BRITAIN

A report of the Conference held in 1952. Edited by J. E. Lousley, pp. 204 + 6 half-tone plates and 25 figures in the text. Bound in buckram. The book contains contributions covering many aspects of the subject, including ecology, palaeo-botany, plant geography, the influx of alien plants, and conservation. The contributors include Dr. Maurice Burton, Prof. A. R. Clapham, Dr. H. Godwin, Canon C. E. Raven, Sir Edward Salisbury, Sir Arthur Tansley, Prof. T. G. Tutin, Dr. S. M. Walters, and Dr. E. F. Warburg. The volume provides much information which is not easily available elsewhere, and some that is new. It should be in the hands of all interested in British field botany. The price of the publication is 15/-, plus 8d. postage, and it is obtainable from E. B. Bangerter, c/o Dept. of Botany, British Museum (Natural History), Cromwell Road, London, S.W.7.

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This book contains full accounts of the papers, exhibits and discussions at the Conference: much of the information included is not easily available elsewhere and some of it is new. The aims of the study of the distribution of British plants are discussed from various angles and the methods employed in this and other countries are described and compared. This volume should be in the hands of everyone interested in British field botany.

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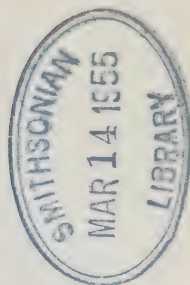
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THE CYTOGENETICS OF *CAREX FLAVA* AND ITS ALLIES*

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- I. Introduction
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1. INTRODUCTION

This group of closely allied species included in the section *Extensae* of the subgenus *Carex* is represented in Great Britain by : *Carex flava* L., *C. lepidocarpa* Tausch, *C. demissa* Hornem., *C. serotina* Mérat, and *C. scandinavica* E. W. Davies. The taxonomy of these species has caused difficulty for many years, and, although the chromosome numbers have been investigated by workers in Sweden, Japan and America, there has been considerable discrepancy in their results (see below), and no counts have previously been made on British material.

Species	Haploid Chromosome Number	Determined by :	Date
<i>C. extensa</i> Good.	30	Wulff	1937
<i>C. flava</i> L.	29	Tanaka	1942, 1948
	30	Heilborn	1939
	30	Wahl	1940
<i>C. lepidocarpa</i> Tausch	29	Tanaka	1942, 1948
	34	Heilborn	1924
" <i>C. oederi</i> Retz " = <i>C. serotina</i> Mérat	36	Heilborn	1922, 1924, 1928
	35	Tanaka	1948

2. CYTOLOGICAL TECHNIQUE

The cytological technique employed throughout this investigation is a modification of the aceto-carmin squash method by the addition of a drop of iron alum. The *Carices* have exceedingly small chromosomes and hard wiry roots, which make them difficult cytological material.

The original attempts to count the chromosomes of this genus were made at mitosis using root tips. First embedding and sectioning methods were tried and later the root tip squash technique was used, staining with Feulgen, aceto-carmin, or a combination of the two stains together. However, the results throughout were unsatisfactory, as the cytoplasm was overstained and contained oil globules, while the chromosomes remained faint and aggregated together. Thus the counts were never accurate enough to detect a difference of two chromosomes at mitosis, which is essential when examining a genus

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like *Carex* which has an aneuploid series with many allied species with consecutive chromosome numbers.

Finally young male spikes were fixed and meiosis was investigated using the modified aceto-carmin method. This produced well stained and spread chromosomes and, in contrast, a light background, as the cytoplasm absorbed little stain.

3. CHROMOSOME NUMBERS

The chromosome numbers have perhaps not proved as valuable a criterion in the taxonomy of these species as had formerly been hoped. However, the chromosomes of the British members of the *Extensae* and of *C. mairii* Coss. & Germ., a closely allied species from southern Europe, have been examined from several localities, and are remarkably similar and uniform in number and morphology (Plates 12 and 13, figs. 1-14). This is further evidence that they are a naturally closely united group distinct from the other sections, such as *Distantes*, *Acutae*, *Montanae*, etc., which differ from them in size and morphology of their chromosomes.

The chromosome numbers of these species together with their subspecies and varieties are given in Table 1. The number of plants of each species and their localities is stated in each case.

Thus this aggregate of species forms a short aneuploid series with chromosome numbers ranging from 30 to 35. If this series is ascending, the low numbered members are assumed to be primitive, while the species with more numerous chromosomes are secondary and advanced. If this is the case, *C. flava* is the oldest and original member of this aggregate, and the other species are derived and more recent in origin. This aspect of the problem will be referred to, and elaborated, later, when the curious abnormalities, found at meiosis in hybrid sedges, have been discussed in the next section.

4. HYBRIDS AND HYBRIDISATION

The study of the interspecific hybrids of a critical group such as the *C. flava* aggregate is of great importance, as it frequently yields information about the relationships of the species, their age and evolution. The natural and artificial hybrids will now be discussed separately.

(a) *Natural Hybrids*

Natural hybrids are found between members of this aggregate, whenever two or more of the species grow together and their flowering periods overlap. However this is rather infrequent in this country, except in the case of the widespread *C. demissa*, and it appears that ecological barriers prevent much introgression between the species. The hybrids found in the field are listed in Table 2, and these will be discussed later, after some of the abnormalities seen at meiosis have been briefly outlined.

The meiosis of hybrid *Carices* is always highly irregular, and cytology produces conclusive evidence of hybridity in a suspected plant. However, the arrangement of the chromosomes and their behaviour at metaphase and anaphase is very different from what is usually seen in hybrids of most genera. First, and perhaps of most fundamental importance, there are no lagging chromosomes at anaphase I, but these can usually be seen to a small extent at anaphase II. Thus the normal sequence of events generally accepted for hybrids in most genera, with the possible exception of *Luzula*, is reversed. Secondly, at metaphase I, instead of the occurrence of tri- and bi-, or univalents, depending on the nature of the hybrids, there are frequently chains or even rings formed of from 3 to 6 or even 8 chromosomes (Plate 13, fig. 16) and round the periphery of the metaphase plate univalents are often seen.

TABLE 1
Chromosome numbers of the *C. flava* aggregate

Species	Haploid number	Number of plants sampled	Locality
1. <i>C. extensa</i> Good.	30	4	Rhos Neigr, Anglesey.
2. <i>C. flava</i> L.	30	4	Roudsea Wood, Haverthwaite, Lancs.
	30	1	Malham Bog, Yorks.
	30	2	Preda, Graubünden, Switzerland.
	30	1	Lake Carezza, W. Dolomites, N. Italy.
3. (a) <i>C. lepidocarpa</i> Tausch subsp. <i>lepidocarpa</i>	34	1	Wicken Fen, Cambs.
	34	1	Fulbourn Pond, Cambs.
	34	3	Wittering Marsh, Northants.
	34	1	Gordale Scar, Malham, Yorks.
	34	1	Malham Tarn, Yorks.
	34	1	Moughton Scar, Yorks.
	34	3	Widdybank Fell, Teesdale, Durham.
	34	1	Gotland, Sweden.
	34	1	Tiefencastel, Switzerland.
	34	1	Cwm Glas, Snowdon, Caernarvon.
3. (b) <i>C. lepidocarpa</i> subsp. <i>scotica</i> E. W. Davies	34	1	Carn Eige, Cannich, Inverness.
	34	1	Inchnadamph, W. Sutherland.
	34	1	Preda, Graubünden, Switzerland.
	34	1	Albula, Graubünden, Switzerland.
	34	4	Lumbreras, Spain.
4. <i>C. mairii</i> Coss. & Germ.	34	4	Lumbreras, Spain.
	34	4	Lumbreras, Spain.
5. <i>C. demissa</i> Hornem.	35	2	Shapwick peat moor, Somerset.
	35	1	Bredon Cloud Wood, Leics.
	35	3	Strines Moor, Derbyshire.
	35	1	Little Dun Fen, Westmorland.
	35	3	Loch Tummel, Perth.
	35	2	Cannich, Inverness.
	35	1	Cwm Glas, Snowdon, Caern.
	35	1	Furnols, Echandelyse, Auvergne, France.
	35	1	Lac de la Faye, Auvergne, France.
	35	1	Issoire, Central France.
	35	1	Font Romeu, E. Pyrenees, France.
	35	1	L'Ancrese, Guernsey.
6. <i>C. serotina</i> Mérat	35	1	L'Ancrese, Guernsey.
	35	1	Frensham Pond, Surrey.
	35	2	Fulbourn Pond, Cambs.
	35	2	Rhos Neigr, Anglesey.
	35	2	Hale Moss, Benthams, Lancs.
	35	1	Monea, Ireland.
	35	2	Hökatorp, Skåne, Sweden.
	35	2	Alvar, Öland, Sweden.
	35	2	Gotland, Sweden.
	35	1	Shapwick peat moor, Somerset.
<i>C. serotina</i> var. <i>cyperoides</i>	35	1	Shapwick peat moor, Somerset.
7. <i>C. scandinavica</i> E. W. Davies	35	1	Sweden.
	35	1	Loch Torridon, W. Ross.

The meiosis appears to be more abnormal and irregular when the parents of the hybrid are very dissimilar, and have widely different chromosome numbers. The metaphase I, described above, represents a hybrid between *C. demissa* ($n = 35$) and *C. hostiana* ($n = 28$). In an interspecific hybrid between two more closely related species such as *C. demissa* ($n = 35$) and *C. lepidocarpa* ($n = 34$), or *C. demissa* ($n = 35$) and *C. serotina* ($n = 35$), meiosis is more normal, and apart from a few univalents and perhaps one conglomerate group of chromosomes forming a chain, the rest are arranged on the metaphase plate as bivalents (Plate 13, figs. 17-20). Thus a fairly high degree of homology

is indicated between these species with similar and consecutive chromosome numbers; for the pollen of hybrid plants is never completely sterile, and fertility usually ranges from 20 to 35 per cent (Table 2).

The hybrids detected in the field between British members of this aggregate will now be briefly discussed.

TABLE 2
Natural hybrids in the *C. flava* aggregate

		% Pollen fertility	Localities
1. <i>C. flava</i>	× <i>C. lepidocarpa</i>	29%	Lake Carezza, Dolomites, N. Italy.
2. <i>C. flava</i>	× <i>C. demissa</i>	22%	Roudsea Wood, Haverthwaite, Lancs.
3a. <i>C. lepidocarpa</i>	× <i>C. demissa</i>	22%	Teesdale, Durham.
subsp. <i>lepidocarpa</i>			
"	× "	24%	Derby Fen, Norfolk.
"	× "	30%	S. Cerney, Glos.
"	× "	35%	Hökatorp, Skåne, Sweden.
"	× "	25%	Krogenbund Mose, Zealand, Denmark.
b. <i>C. lepidocarpa</i>	× <i>C. demissa</i>	32%	Loch Tummel, Perth.
subsp. <i>scotica</i>			
"	× "	35%	Creag-na-Caillich, Perth.
"	× "	33%	Creag-an-Lochan, Perth.
"	× "	35%	Ben-y-Vrackie, Pitlochry, Perth.
"	× "	28%	Ben Dorain, Argyll.
"	× "	30%	Glen Doll, Clova, Angus.
"	× "	31%	Cwm Glas, Snowdon, Caernarvon.
4. <i>C. lepidocarpa</i>	× <i>C. serotina</i>	25%	Wicken fen, Cambs.
"	× "	20%	S. Cerney, Glos.
5a. <i>C. demissa</i>	× <i>C. serotina</i>	29%	S. Cerney, Glos.
b. <i>C. demissa</i>	× <i>C. serotina</i> var. <i>cyperoides</i>	26%	Shapwick, Somerset.
6a. <i>C. hostiana</i>	× <i>C. lepidocarpa</i>	0%	Chippenham Fen, Cambs.
	subsp. <i>lepidocarpa</i>		
b. "	× <i>C. lepidocarpa</i>	0%	Loch Tummel, Perth.
	subsp. <i>scotica</i>		
"	× "	0%	Waulk Mill Bay, Mainland, Orkney.
			Lech, Voralberg, Austria.
7. <i>C. hostiana</i>	× <i>C. demissa</i>	0%	Loch Tummel, Perth.
8. <i>C. distans</i>	× <i>C. lepidocarpa</i>	0%	Totternhoe, Beds.

(1) *C. flava*

This rare British plant, with its specialised ecological requirements, seldom meets the other members of the group in this country. However, at Roudsea Wood (Lancashire), *C. demissa* occurs with *C. flava*, and there is a range of intermediate forms, which are clearly of hybrid origin. These plants revealed a highly irregular meiosis, and the pollen showed between 70 and 80 per cent sterility. It certainly seemed as if back crosses with the parent species were present as well as F_1 plants, for there was a great range of forms and it appeared that, in time, *C. demissa* would completely oust *C. flava* by hybridisation, for the latter species was scarce compared with the abundance of hybrid plants and *C. demissa*. This is the only record of a *C. flava* hybrid from this country; as this species has never been found growing with or near *C. lepidocarpa*, *C. serotina* or *C. scandinavica*, and as their ecological requirements are rather different, hybrids between *C. flava* and these species seem unlikely to occur naturally. However, hybrids and back crosses between this species and *C. lepidocarpa* were abundant by Lake Carezza in the Western

Dolomites. Here, in North Italy, the habitat and the topography seemed suitable for both species and they were hybridising freely.

(2) *C. lepidocarpa*

Subsp. *lepidocarpa* frequently hybridises with *C. demissa*, and a hybrid swarm often predominates, while the parent species are comparatively rare, and sometimes difficult to detect. This certainly is the case on the lower slopes of Widdybank Fell in Upper Teesdale (Plate 13, fig. 17) and at Hökatorp (Plate 13, fig. 18), a calcareous fen by the sea in S.E. Skåne, Sweden. Likewise, on base-rich Scottish and Welsh mountains hybrid swarms between *C. demissa* and subsp. *scotica* are common at about 1,000 m. where the distribution areas of these two species overlap, whereas below and above this altitude the two species remain quite distinct.

In the same way hybrids might be expected between *C. lepidocarpa* and *C. serotina* in the few calcareous localities where these species are known to occur together. However, this hybrid is rare, apparently because *C. serotina* flowers and fruits at least one month later than the other four species. At Fulbourn Pond (Cambridgeshire), where *C. lepidocarpa* and *C. serotina* grow completely intermixed, there is no sign of hybridisation, and, in late June, the former species is in ripe fruit while the latter is still in flower.

Consequently, it was rather unexpected to find a plant at Wicken Fen, Cambridgeshire, which appeared to be a hybrid of this parentage, growing with *C. serotina* and *C. lepidocarpa*. This plant had an irregular meiosis and the pollen showed 80 per cent sterility. The only other locality examined where these two species were found growing together is a disused gravel pit on the Cotswolds near S. Cerney, and, as *C. demissa* also grows at the edge of the pit, the situation is complicated further. A complex hybrid swarm involving all three species occurs, and the range of forms is very great. Although the majority of plants seem to be intermediate between *C. lepidocarpa* and *C. serotina*, and some forms contain *C. demissa* also, there is a large stand of pure *C. serotina* at one side of the gravel pit. This can almost certainly be correlated with the late flowering period of this species, for specimens of pure *C. lepidocarpa* and *C. demissa* were not seen and these species had clearly been ousted by hybridisation.

(3) *C. demissa*

This species, which is tolerant of a wide range of habitats, is frequently found growing with, or near, the other species, and hybrids are fairly common.

The hybrids with *C. flava* and *C. lepidocarpa* have already been mentioned, but on Shapwick peat moor in Somerset, this species forms a hybrid swarm with *C. serotina* var. *cyperoides*. The latter is rather uncommon, and it seems likely that it may, in time, be lost completely, if hybridisation with *C. demissa* continues, for an enormous range of intermediate forms is now abundant on the moor, and *C. serotina* var. *cyperoides* is becoming increasingly rare. The cytology of this hybrid has been examined, and reveals a highly irregular meiosis (Plate 13, fig. 19), with a conglomerate ring of chromosomes surrounded by univalents.

(4) *C. serotina*

The few hybrids that are known between *C. serotina* and the other members of the aggregate have already been discussed, and it undoubtedly seems to be the late flowering of this species that acts as the main barrier, and keeps it distinct from the other members of the group.

(5) *C. scandinavica*

C. scandinavica, in the British Isles confined to northern and western Scotland, has

as yet never been found growing with any of the other species in this country. Hence no hybrids have been recorded.

(6) *C. hostiana* and *C. distans*

This study would not be complete without mentioning *C. hostiana* DC. and *C. distans* L., two members of the closely related section *Distantes*, for the former species very frequently hybridises with *C. lepidocarpa* and *C. demissa*. *C. hostiana* ($n = 28$), like *C. demissa*, grows in a wide range of habitats and tolerates many different soil conditions, which probably accounts for the frequency of its hybrids.

The hybrid between *C. hostiana* and *C. lepidocarpa* is sufficiently well known to have a name (*C. × xanthocarpa*), and is of fairly frequent occurrence. It grows (Table 2) at Chippenham Fen, Cambridgeshire, where the hybrid forms a large clone, which appears to multiply entirely vegetatively and now covers a considerable area, surrounded by the parent species.

Likewise *C. hostiana* hybridises with *C. demissa*. This hybrid was collected by Loch Tummel, Perthshire, and the plant showed a highly irregular meiosis with several chains of chromosomes and numerous univalents.

Lastly a hybrid between *C. distans* ($n = 37$) (Plate 13, fig. 15) and *C. lepidocarpa* was recorded from Cow Common, Totternhoe, Bedfordshire. This hybrid formed a clonal stand like *C. × xanthocarpa*, and had highly sterile pollen and a very irregular meiosis.

Thus it seems that all the members of this aggregate are capable of hybridisation, and considerable gene-flow between species is possible. It seems also that it is not genetical incompatibility but ecological and topographic barriers that keep *C. flava*, *C. lepidocarpa*, *C. demissa* and *C. scandinavica* apart, as distinct entities, while, in contrast, late seasonal periodicity seems to play the major role in the case of *C. serotina*.

(b) Artificial Hybrids

These flavoid species of *Carex*, like all those in the subgenus *Carex*, lend themselves to artificial hybridisation, as the male spike is easily removed without damaging the female organs. The crosses were carried out during May and early June, and the ripe seeds collected at the end of July and sown immediately.

The artificial hybridisations included all possible combinations between the five British members of the aggregate, and some crosses between these and *C. mairii*, *C. extensa* and *C. hostiana* (Table 3). However, although in most combinations some apparently ripe seed was produced, germination is slow and spasmodic in this genus, so as yet only a few of the hybrid seedlings have produced fertile spikes. These are listed in Table 3, and Plate 13, fig. 20 shows the very irregular meiosis of these artificial hybrids.

Thus it would seem that these five British species included in the *C. flava* aggregate, are capable of considerable gene-flow from one to another, and produce F_1 plants with between 20 and 30 per cent good pollen. They should therefore be regarded as ecospecies, and the group as a whole as one coenospecies (Gregor, 1939; Clausen, Keck & Hiesey, 1939).

6. DISCUSSION

The cytology, evolution and origin of the aneuploid series in the genus *Carex* will be discussed more fully in another paper.

However, it seems reasonable to postulate from the present cytological, ecological (Davies, 1954) and taxonomic (Davies, 1953a, b, c) evidence that, within this coenospecies,

TABLE 3
Artificial hybrids in *C. flava* aggregate

	Female Parent	Male Parent	No. of seedlings	% Pollen Fertility of hybrid
1.	<i>C. flava</i> Roudsea, Lancs.	× <i>demissa</i> Loch Tummel, Perth.	4	20
2.	<i>C. flava</i> Roudsea, Lancs.	× <i>lepidocarpa</i> subsp. <i>scotica</i> Cannich, Inverness.	1	—
3.	<i>C. lepidocarpa</i> Tiefencastel, Switzerland.	× <i>flava</i> Preda, Switzerland.	4	—
4.	<i>C. demissa</i> a. France b. Bredon, Leics.	× <i>flava</i> Roudsea, Lancs. Roudsea, Lancs.	1 2	— —
5.	<i>C. demissa</i> a. Shapwick, Somerset. b. France c. Wild Boar Fell, Westmorland	× <i>lepidocarpa</i> Teesdale, Durham. Wicken, Cambs. Wittering, Northants.	5 3 5	25 — —
6.	<i>C. demissa</i> a. Strines Moor, Derbyshire. b. France. c. Shapwick, Somerset. d. France.	× <i>C. serotina</i> Anglesey. Hökatorp, Sweden. Anglesey. Monea, Ireland.	2 1 5 1	29 30 — —
7.	<i>C. demissa</i> Strines Moor, Derbyshire.	× <i>scandinavica</i> Sweden.	3	—
8.	<i>C. demissa</i> Bredon, Leics.	× <i>mairii</i> Lumbreras, Spain.	2	—
9.	<i>C. serotina</i> Hökatorp, Sweden.	× <i>lepidocarpa</i> Pyrenees.	6	24
10.	<i>C. mairii</i> a. Pyrenees. <i>C. mairii</i> b. Pyrenees.	× <i>lepidocarpa</i> subsp. <i>lepidocarpa</i> Gordale, Yorks. × <i>lepidocarpa</i> subsp. <i>scotica</i> Cannich, Inverness.	1 2	— —
11.	<i>C. mairii</i> Pyrenees.	× <i>serotina</i> Fulbourn, Cambs.	2	—
12.	<i>C. extensa</i> Anglesey.	× <i>serotina</i> Sweden.	1	—
13.	<i>C. hostiana</i> Teesdale.	× <i>lepidocarpa</i> Pyrenees.	2	—

C. flava is the relict and primitive member, with the lowest chromosome number, specialised ecological requirements and relict distribution (Davies, 1953 d). The development of the other ecospecies from *C. flava* has been accompanied by an increase in chromosome numbers, a greater variation within the species and an ability to grow in a wider range of plant communities. Thus *C. lepidocarpa*, with four more chromosomes, is more abundant, adaptable and probably of more recent origin, although not so recent as the very widespread and variable *C. demissa* with a capacity to flourish under various ecological conditions. Lastly, *C. serotina*, with the same chromosome number as *C. demissa*, yet requiring more specialised conditions, seems to be a more primitive and possibly a reduced form, which needs the low sparse vegetation of an open habitat with little competition.

It seems likely that this species, with the widest geographical distribution (Davies, 1953 d) of the group, spread rapidly during and after the last glaciation, recolonising the open habitats produced by the retreating ice. Within recent times, owing to its specialised requirements, this species has become confined to scattered and local areas; probably the presence of different forms which are not true ecotypes (as these differences do not seem

related to ecology) can be correlated with this fact. The isolated populations throughout the British Isles show minor differences, which are retained in cultivation; the most striking examples of such isolated populations are some of the forms which are found in Ireland and the Baltic Islands of Gotland and Öland, for these plants are almost worthy of recognition as distinct taxa. This continued isolation is probably the reason for the existence of a form on Shapwick peat moor, Somerset, sufficiently different to be considered a variety (*C. serotina* var. *cyperoides*). Further results of this isolation are possibly to be seen in the origin of *C. scandinavica* and *C. viridula* Michx. (Davies 1953 d). These two plants, which are rather similar to *C. serotina* but have different and more limited geographical distributions, have only recently been considered distinct species. They may have been evolved within comparatively recent times owing to geographic separation.

6. CONCLUSION AND SUMMARY

A cytogenetical survey of the *C. flava* aggregate (*C. flava* L., *C. lepidocarpa* Tausch, *C. demissa* Hornem., *C. serotina* Mérat, *C. scandinavica* E. W. Davies) is made, and the origin and evolution of the species discussed.

These five members of section *Extensae* and *C. mairii* are found to form a short aneuploid series, with their haploid numbers ranging from $n = 30$ to $n = 35$.

The interspecific hybrids between the members of this group, with the exception of *C. demissa*, were found to be rather uncommon. This seems to be due to the different and specialised ecological requirements of the species, topographic separation and the late flowering season of *C. serotina*. Hybrids were examined and synthesised whenever possible, and in every case the pollen showed at least 20 per cent fertility; this increased when the parent species had the same or nearly similar chromosome numbers.

Thus these five closely related species, which are capable of considerable gene-flow from one to another, and produce natural and artificial hybrids with between 20 and 30 per cent good pollen, are regarded as ecospecies and the group as a whole as one coenospecies.

C. flava seems to be a relict and stable plant with an isolated and scattered distribution. *C. lepidocarpa*, with its three subspecies, namely subsp. *lepidocarpa* and subsp. *scotica*, which form a discontinuous topocline in the British Isles, and subsp. *jemtlandica*, so far only known from Scandinavia, is more widespread.

The abundant *C. demissa* appears to be a variable plant, but the range of variation is continuous, and within the limits of one adaptable species. In contrast, *C. serotina*, with its local and fragmentary distribution, has a number of forms which, owing to long isolation, seem to give rise to varieties, such as var. *cyperoides*, and eventually species; such is probably the origin of *C. scandinavica* and *C. viridula*.

7. ACKNOWLEDGMENTS

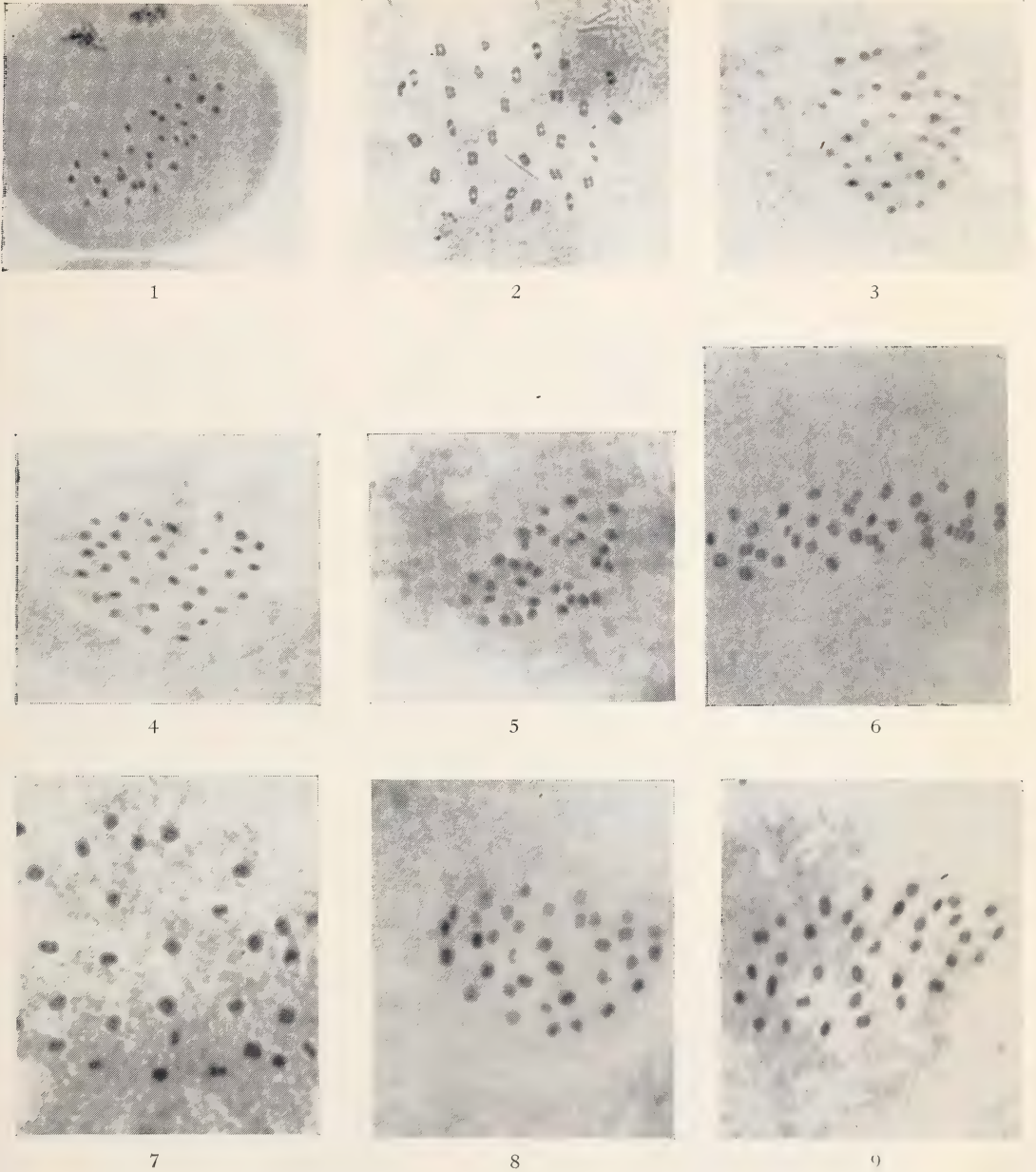
I have pleasure in recording my gratitude to Professor T. G. Tutin for his advice and encouragement throughout this work. I should also like to express my thanks to the Research Board, University College, Leicester, for the award of a scholarship during the period 1950-53, and for giving considerable financial help towards my field studies during this period.

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PLATE 12

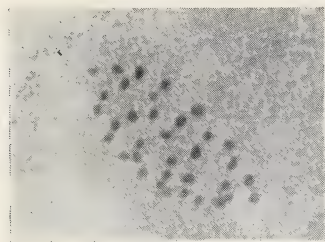
Figure 1 shows a pollen grain mitosis and two of the three aborting nuclei, and Figs. 2-9 show meiosis in the pollen mother cells. All photographs $\times 2,400$.



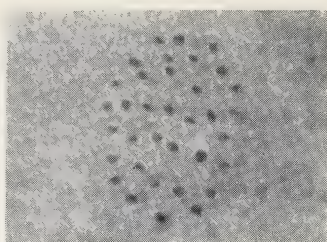
- Fig. 1. *Carex flava*, Roudsea Wood, Lancs., $n = 30$.
- Fig. 2. *C. flava*, Malham Tarn Moss, Yorks., $n = 30$.
- Fig. 3. *C. flava*, Preda, Graubünden, Switzerland, $n = 30$.
- Fig. 4. *C. lepidocarpa* subsp. *lepidocarpa*, Wicken Fen, Cambs., $n = 34$.
- Fig. 5. *C. lepidocarpa* subsp. *scotica*, Inchnadamph, Sutherland, $n = 34$.
- Fig. 6. *C. demissa*, Loch Tummel, Perthshire, $n = 35$.
- Fig. 7. *C. demissa*, Furnols, Central France, $n = 35$.
- Fig. 8. *C. serotina*, calcareous marsh, Fulbourn, Cambs., $n = 35$.
- Fig. 9. *C. serotina*, salt marsh, Hökatorp, Sweden, $n = 35$.

PLATE 13

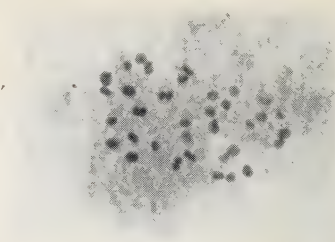
Figures 10-15 show normal meiosis in the pollen mother cells, and Figs. 16-20 show highly irregular meiosis in the pollen mother cells of some hybrid sedges, with univalents marked by arrows, and a few multivalents forming chains and rings of chromosomes. All photographs $\times 2,400$.



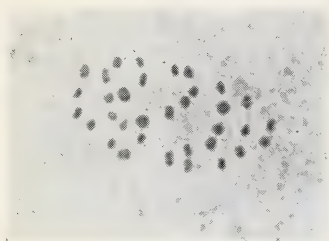
10



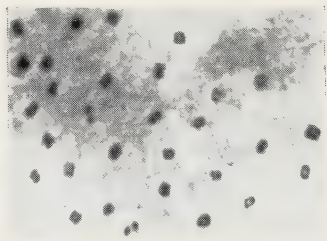
11



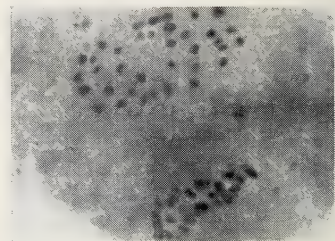
12



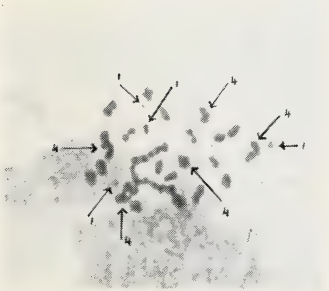
13



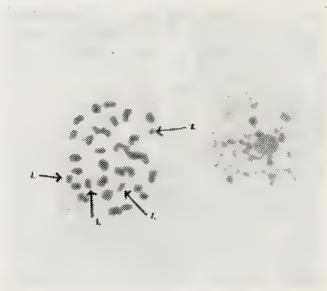
14



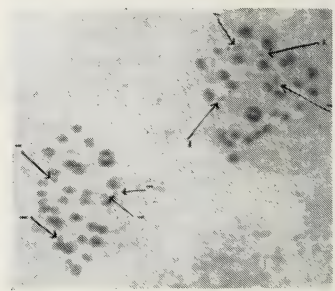
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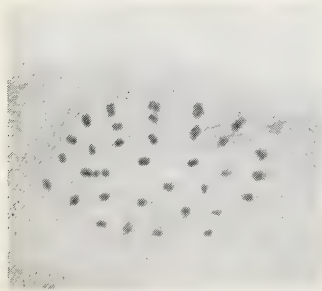
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19



20

Fig. 10. *Carex serotina* var. *cyperoides*, Shapwick peat moor, Somerset, $n = 35$.

Fig. 11. *C. scandinavica*, Loch Torridon, W. Ross, $n = 35$.

Fig. 12. *C. scandinavica*, Sweden, $n = 35$.

Fig. 13. *C. mairii*, Lumbreras, Spain, $n = 34$.

Fig. 14. *C. extensa*, Rhos Neigr, Anglesey, $n = 30$.

Fig. 15. *C. distans*, St. Nectaire, Central France, $n = 37$.

Fig. 16. *C. demissa* $\times$ *C. hostiana*, Loch Tummel, Perthshire.

Fig. 17. *C. lepidocarpa* $\times$ *C. demissa*, Teesdale, Durham.

Fig. 18. *C. lepidocarpa* $\times$ *C. demissa*, Hökatorp, Sweden.

Fig. 19. *C. demissa* $\times$ *C. serotina* var. *cyperoides*, Shapwick, Somerset.

Fig. 20. *C. demissa*, Shapwick, Somerset, $\times$ *C. lepidocarpa*, Teesdale, Durham; hybridised 10 May, 1951.

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STUDIES ON *ULMUS*

I. THE RANGE OF VARIATION OF EAST ANGLIAN ELMS

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The English elms have been taxonomically recalcitrant for over three hundred years. The present paper is an attempt to see how far a biometric analysis based on a systematic sampling survey can be used to provide an objective description of the range of variation encountered in the genus and to elucidate some of the taxonomic and other problems that it presents.

SAMPLING TECHNIQUE

The area surveyed was major square 52 of the Ordnance Survey national grid; the corners of this 100 km. square are located respectively in the vicinity of Stamford, Wymondham, Amersham and Maldon (cf. Fig. 1). This area is one of crucial importance as far as the systematics of *Ulmus* is concerned. The sampling units within the major square were the hundred 10 km. squares composing it. A site in each minor square was selected beforehand for subsequent visiting. The sites chosen were ancient parish boundary hedges with trees and within convenient access from a road. Such sites can be located on the first edition of the 6 inch to a mile Ordnance Survey maps. These mark both trees and parish boundaries. Many of these sheets were issued before the taking effect of the Divided Parishes Acts of 1876 and 1882, and these can usually be taken as giving a reliable indication of the course of the medieval boundaries. The later sheets must be used with more caution lest recent boundaries of no historic standing should be selected.

Boundaries are utilized because these are extremely permanent features of the countryside and are only alterable by Act of Parliament. It seems reasonable to suppose that the trees growing in them will usually represent the descendants of trees growing on the same site at a considerably earlier period. This supposition is supported by the fact that, in some cases, boundary trees mentioned in Anglosaxon charters are still represented today by the same species marking the same point in the boundary (cf. Stonor, 1951).

Collection is deferred till 1 June and continued till 30 September. Sampling earlier in the year is inadvisable since the leaves are apt to be immature. Each preselected locality is visited and the relevant hedge examined for elms. Ten leaves are then collected from a representative tree, or, if more than one evidently dissimilar elm is present, ten leaves from each sort. The leaves are picked from dwarf shoots growing from major branches, taking care to avoid suckers, lammas shoots, and trees heavily attacked by insect pests. The leaves chosen are the subdistal members of the dwarf shoots.

BIOMETRIC TECHNIQUE

Each leaf is measured for five quantitative characters: lamina breadth/lamina length; the number of teeth; petiole length/lamina length; the degree of basal asymmetry; and the tendency towards obverse configuration. Lamina length is measured on the longer side of the leaf. Breadth is taken as maximum breadth. Minor teeth are counted, not the major teeth on which they are superposed. Basal asymmetry is calculated from

the ratio : length between the transverse axes marking the lowest point on each side of the leaf/lamina length. The tendency towards obverse configuration, which may conveniently be termed obversity, is calculated from the ratio : length between the transverse axes marking (1) the point of maximum breadth on the shorter side of the leaf and (2) the point where the longer side runs into the petiole/lamina length.

In addition, it is noted whether the upper surface of the leaf is scabrous or smooth. Although gradations exist in this characteristic, a convenient method of measuring scabrosity was not found. Scabrous leaves will be denoted hereafter by an asterisk *, smooth leaves by a dagger †.

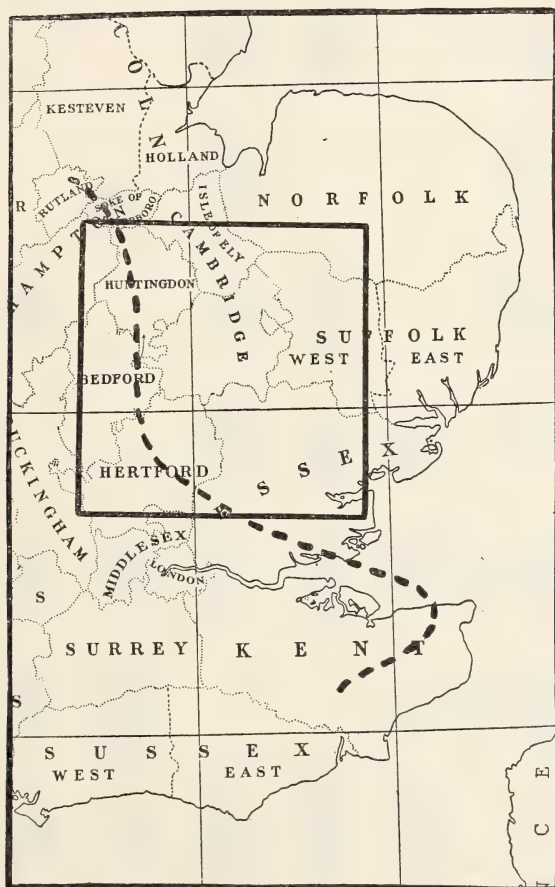


Fig. 1. Area of survey. The solid line represents major square 52 of the Ordnance Survey. The broken line represents the eastern boundary of *U. procera*.

From these primary measurements, means for each character per tree are calculated, together with their standard deviations. Then, for each pair of fairly similar trees, the *t* test for significance of difference between means ($P = 0.05$) is made for each character. A record is made of all pairs of sample trees which do not differ significantly in any of the five characters studied.

RESULTS

Specimen samples from each minor square in which elms were encountered are illustrated in Fig. 2. Where two samples were obtained from one minor square, they

are referred to as samples *a* and *b*, respectively; in Fig. 2, the *a* samples are on the left, in Table 1, the *a* samples are above the *b*. The measurements pertaining to each sample are given in Table 1. To simplify the presentation of the data, each character is expressed in terms of a scale of 10 units (0-9), the order of the characteristics being (1) relative

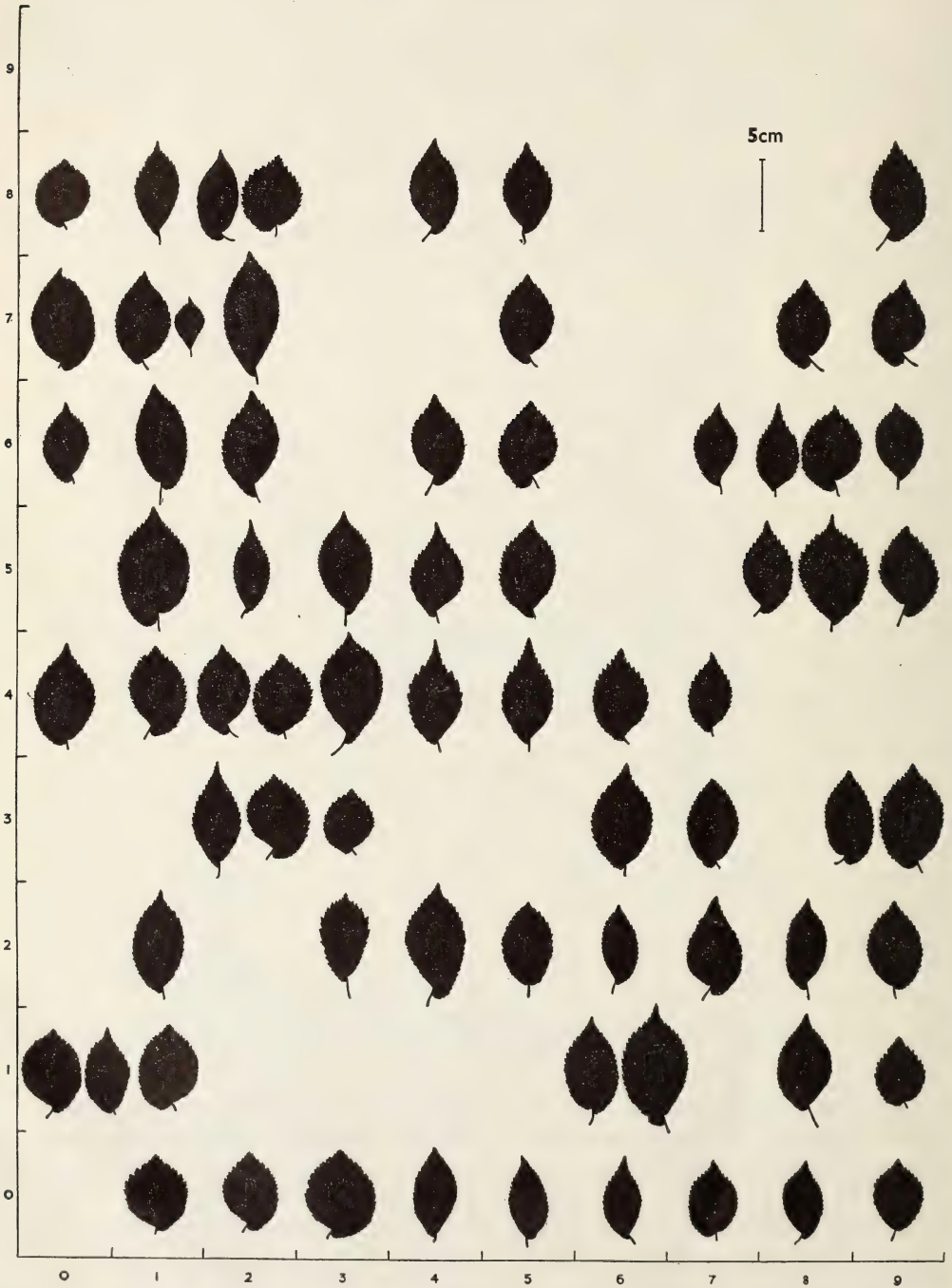


Fig. 2. Specimen leaves from major square 52. The figures are the grid reference coordinates of the minor squares.

TABLE 1.

Mean values for (1) relative breadth, (2) tooth number, (3) relative petiole length, (4) basal asymmetry, and (5) obversity, of elm leaf samples collected from major square 52. A range scale of 0-9 is used for each character. The marginal figures are the grid reference coordinates of the minor squares.

9										
8	72443*	15536†	18535† 82552*		26634†	33644†				44853†
7	57121*	44433† 33807†	16326†			53555†			45963†	44973†
6	41334†	27726*	44568†		33666†	63754†		35616†	27331* 64665†	44525†
5		49551†	06434*	27535*	36323†	45545†			34434† 59232*	65565†
4	56422*	73555*	63453† 71434*	44747†	35651†	36431†	46431*	36432†		
3			14623† 83557*	81544*			33423†	44533*		44444* 54443*
2		22323†		43929†	25646†	43704†	13617†	44641†	25557†	52834†
1	63534* 34524†	63436*					34715† 48346†		35922†	72620†
0		82325*	72436*	93344*	25325†	10514†	23522†	53631†	33545†	62915†
	0	1	2	3	4	5	6	7	8	9

breadth, (2) number of teeth, (3) relative petiole length, (4) basal asymmetry, and (5) obversity. The absolute range for each of these characters is as follows:

Relative breadth	·40-·90
Number of teeth	50-150
Relative petiole length	·00-·20
Basal asymmetry	·00-·20
Obversity	·40-·60

Thus, sample 08 in the top left-hand corner of Table 1, expressed as 72443*, relates to the following set of mean absolute values; relative breadth, ·79, tooth number, 74; petiole length, ·08; asymmetry, ·09; and obversity, ·47.

In Fig. 3, the results are presented graphically. The two most discriminant characteristics, relative breadth and number of teeth, are used as coordinates, suitably deformed for convenience of illustration, and the three other characteristics are represented as sectors in the circles or triangles pertaining to each sample. Circles are used for smooth-leaved samples, triangles for scabrous material. Sector 8-12 o'clock represents relative petiole length, sector 12-4 basal asymmetry, and sector 4-8, obversity. Each sector is

blackened in clockwise to show where the value of each characteristic lies relative to the total range.

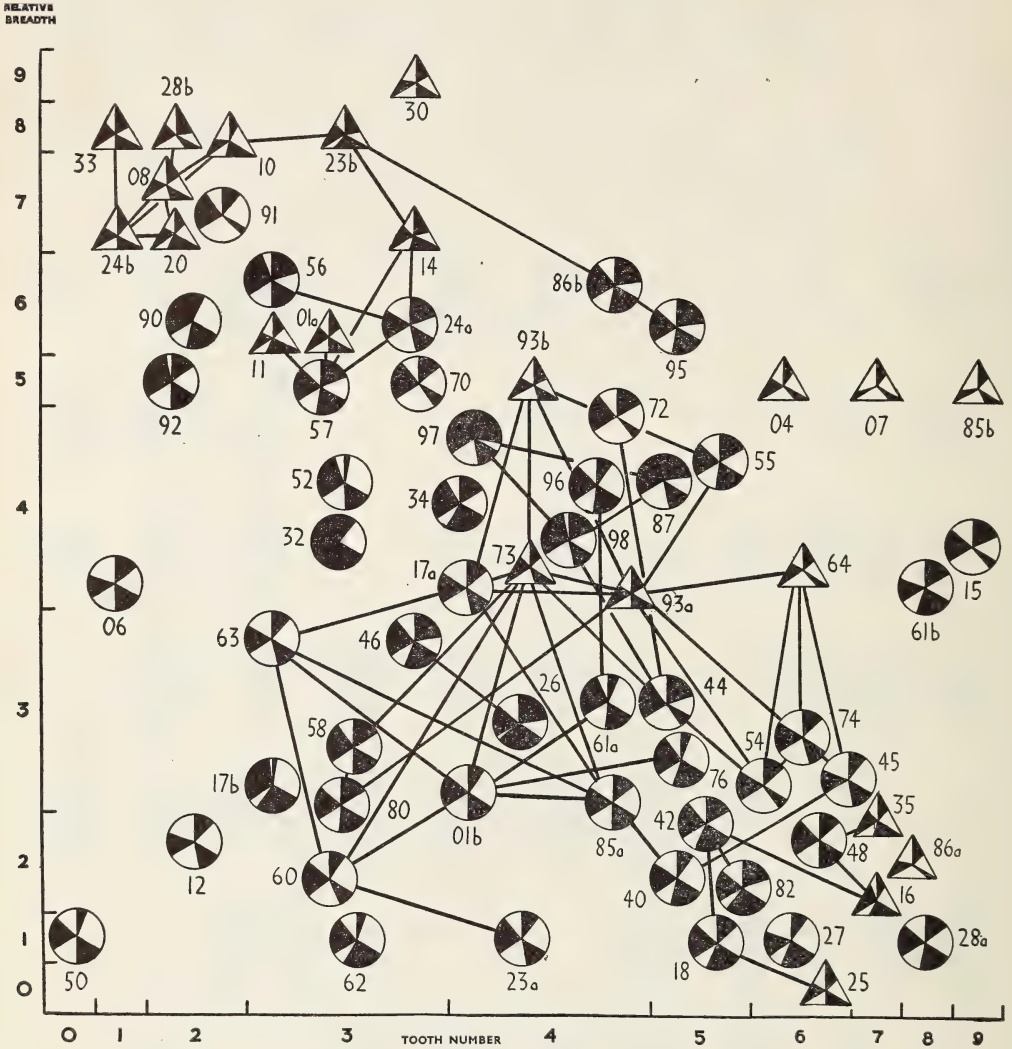


Fig. 3. Graphical representation of the affinities of the samples collected in major square 52. The coordinates indicate relative breadth and tooth number; a range scale of 0-9 is used. The widths of the shaded sectors represent three minor quantitative characters. Circles indicate smooth leaves; triangles, scabrous leaves. The bars connect samples which the *t* test fails to separate.

All samples which cannot be separated by the *t* test in any of the 5 characters are joined by a connecting bar. As a general rule, differences between the absolute means were significant if they exceeded the following values :

Relative breadth	·07
Number of teeth	10-15
Relative petiole length	·02
Basal asymmetry	·02
Obversity	·03

Tooth number is not normally distributed and the number of teeth required for a

significant difference rises with the absolute number of teeth. Since, however, comparisons are only made between closely similar samples, scale transformation is probably unnecessary.

Preliminary tests showed that comparisons between 10 leaves from each sample gave little increase in discrimination above comparisons between five leaves per sample, provided that the initial sampling procedure was rigorously followed. The data presented are therefore based on 5-leaf samples.

TABLE 2.
Taxonomic analysis of the elm samples collected from major square 52.

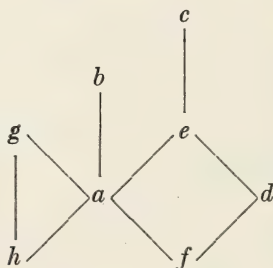
Group	Subgroup	Samples	Range	Taxonomic relations
I	a	01b, 17a, 23a, 58, 60, 63, 73, 80, 85a, 93a	13311, 46976*† 13422, 44645*†	{ <i>U. diversifolia</i> <i>U. ?aff. carpinifolia</i> sens. str. <i>U. ?aff. diversifolia</i> <i>U. ?aff. coritana</i> var. <i>media</i>
		61a, 76, 96	34515, 45726†	
	c	87, 97, 98	44853, 45973†	
	d	54, 64, 74	36431, 46432*†	
	e	44, 72	34641, 45651†	{ <i>U. glabra</i> - <i>carpinifolia</i> <i>U. ?aff. diversifolia</i> <i>U. ?aff. carpinifolia</i> sens. str.
	f	40, 45	25323, 36325†	
	g	93b	54443*	
	h	55	45545†	
II	a	01a, 08, 11, 14, 20, 23b, 24a, 24b, 28b, 33, 56, 57	51432, 85767*†	{ <i>U. procera</i> <i>U. ?aff. coritana</i> <i>U. ?procera</i> - <i>carpinifolia</i> <i>U. coritana</i> var. <i>media</i>
			51432, 84757*†	
	b	86b, 95	64565, 65665*	
III		16, 18, 25, 35, 42, 48, 82	05424, 27757*†	<i>U. carpinifolia</i> sens. str.
IV		26, 46	33566, 44668†	<i>U. ?aff. carpinifolia</i> sens. str.
V			42600, 73935†	<i>U. coritana</i> var. <i>rotundifolia</i>
	a	70, 92	52631, 53834†	
	b	52, 90	42704, 63915†	
	c	91	72620†	
VI		07, 85b	57121, 59232*	<i>U. glabra</i>
VII			48341, 49556†	{ <i>U. glabra</i> - <i>carpinifolia</i> <i>U. glabra</i> - <i>carpinifolia</i> <i>U. ?aff. carpinifolia</i> sens. str.
	a	15	49551†	
	b	61b	48346†	
VIII			10514, 13617†	<i>U. ?aff. coritana</i> var. <i>angustifolia</i>
	a	50	10514†	
	b	62	13617†	
IX		81	35922†	
X		32	43929†	
XI		06	41334†	<i>U. plotii</i> - <i>carpinifolia</i>

An examination of Fig. 3 indicates that the elms collected fall into a number of groups and subgroups. These are listed in Table 2, together with the minimum and maximum values for the five characteristics studied in each assemblage; a note is added on the probable relation of each assemblage to the elm species and varieties recognised by Tutin (1952). A hyphen is used to indicate intermediate characteristics, not necessarily hybridity.

AXONOMIC ANALYSIS

It will be assumed that the groups and subgroups listed in Table 2 are genetically diverse entities. Without transplantation experiments it is impossible to rule out the possibility that some of the differences observed are environmental rather than genetic, but it seems improbable that environmental effects are a major source of variation because (a) within a single tree or clonal stand, variation in the characteristics investigated was usually very small, (b) no correlation was detected between any particular type of variation and habitat, and (c) striking differences were frequently noted between adjacent clones in a single hedgerow.

Coming now to the groups recognised, it is evident that group I is a highly variable assemblage showing smooth intergradations between the extremes. The subgroups are interconnected thus :



Ia is a large assemblage characterised by a low tooth number and low obversity; it includes both smooth and scabrous leaved types. It is closely connected to Ig, a scabrous-leaved type with notably broad leaves, to the smooth-leaved subgroup Ib with rather long petioles but low asymmetry, and to Ih, characterised by its high tooth number.

A very homogeneous assemblage is constituted by Id, with both smooth and scabrous leaved representatives; the tooth number is high, the obversity low. Ia and Id form a ring with Ie and If. Ie resembles Id in its low obversity, while If has rather narrow leaves with shortish petioles.

Ic stands rather apart from the others. It has broad leaves with very long petioles and highly asymmetrical bases.

It is clear that I as a whole, excluding perhaps the scabrous members, comes within *U. carpinifolia* Gled. as interpreted, for instance, by Rehder (1940). In the rest of this paper, *U. carpinifolia* will denote this broad conception of the species; *U. carpinifolia* Gled. emend. Melville (1946) will be referred to as *U. carpinifolia* sens. str. The scabrous-leaved types are intermediate between *U. carpinifolia* and *U. glabra* Huds. Attempts, however, to equate the subgroups with Melville's microspecies are difficult. The type description of *U. diversifolia* Melville (1939) applies to some members of Ia, though the coexistence of asymmetrical and symmetrical leaves on dwarf shoots from the same tree was never observed. Ib and Ih also come fairly near to *U. diversifolia*. It should be pointed out, however, that the straight-sided leaf margin making a right-angle turn into the petiole, regarded by Melville (1946) as diagnostic of *U. carpinifolia* sens. str., occurs in some members of Ia and in Ih. Ic has a remote affinity to *U. coritana* var. *media* Melville

(1949), but the leaves are narrower, and the petioles longer, than in the type description of this variety. Id, Ie, and If do not correspond closely with the type descriptions of any of Melville's segregates.

The second largest group, II, is quite sharply differentiated from I. The principal subgroup, IIa, has ovate to orbicular leaves with a low tooth number. The leaves are usually scabrous but exceptions occur. Two samples with a higher tooth number are relegated to IIb; these forms have smooth leaves.

The scabrous members of IIa correspond exactly with *U. procera* Salisb. The smooth-leaved members of this subgroup are more of a problem. Their relationship with *U. procera* is obviously close. On the other hand, they might be regarded as extreme forms of *U. carpinifolia*; they bear some resemblance to the microspecies *U. coritana* but do not correspond at all closely with either var. *rotundifolia* Melville, which has fewer teeth and more symmetrical leaves, or with var. *media*, which has longer petioles and more highly asymmetrical leaves. Another possibility is to regard these forms as intermediate between *U. procera* and *U. carpinifolia*. IIb can probably be classed as a member of *U. carpinifolia*, since the high tooth number as well as the smooth leaf surface differentiate it fairly sharply from *U. procera*. It corresponds quite closely with *U. coritana* var. *media*.

III includes a set of narrow-leaved elms with high tooth numbers. They differ from If in having longer petioles. Forms with smooth and with scabrous leaves both occur. The group, in spite of its scabrous tendency, can probably be classified under *U. carpinifolia*. The allocation to a microspecies is less certain. The nearest is *U. carpinifolia* sens. str., but only some members of III show the straight leaf and right angle turn into the petiole characteristic of this segregate.

IV differs from Ia in the longer petiole, greater asymmetry and higher obversity. It clearly comes under *U. carpinifolia*, but does not correspond well with any of the microspecies. Sample 26 has the characteristic leaf shape of *U. carpinifolia* sens. str. but in other respects recedes considerably from the type description of this segregate.

Five samples, 52, 70, 90, 91 and 92, though all significantly different from each other and from II, the nearest group, resemble each other in being smooth and broad-leaved elms with relatively few teeth, markedly long petioles and low asymmetry. They are associated into group V. The two samples of Va differ from Vb in their rather shorter petioles and more pronounced basal asymmetry. Sample 91, the sole representative of Vc, has broader leaves than either of the other subgroups and very low obversity. The group as a whole comes within *U. carpinifolia*, but is far more sharply separated from the other members of this species than any of the segregates hitherto considered. As will be seen below, this group has a distinctive geographical distribution. Va is fairly close to *U. coritana* var. *rotundifolia* though having a rather longer petiole. The other two subgroups do not correspond closely with any of the previously described segregates.

The two scabrous-leaved samples 07 and 85b, though differing significantly in tooth number, agree in having broad leaves with very short petioles, low asymmetry and low obversity. They are typical representatives of *U. glabra*, and are consigned here to group VI.

Three samples were collected which were intermediate between VI and the smooth-leaved elms of I. Sample 04 has broad scabrous leaves with an intermediate tooth number, the petiole being significantly longer than in VI. It approaches close to sample 64 of Id, but the leaves are slightly more symmetrical. Samples 15 and 61b resemble VI in their high tooth number, but in other respects, including the smooth leaf surface, come fairly close to Id. These last two samples differ considerably from each other, 15 having longer petioles and much lower obversity than 61b; they are therefore relegated to separate subgroups, VIIa and VIIb, respectively, of a single group. This group and 04 are clearly

intermediate between *U. carpinifolia* and *U. glabra*; 61b has the characteristic leaf shape of *U. carpinifolia* sens. str.

Of the remaining samples, two, 50 and 62, agree in being very narrow-leaved types with low asymmetry. In other respects they are remote from one another, 50 having much fewer teeth. Both these samples differ from Ia in their low asymmetry and fairly high obversity. These samples are therefore relegated to separate subgroups VIIla and VIIlb of a single group. Both appear to pertain to *U. carpinifolia*, and 62 approaches *U. coritana* var. *angustifolia* Melville, though it is less asymmetrical than the type. Sample 50 is remote from any of the described microspecies.

Another isolated type is the smooth-leaved sample 81. It comes nearest to Id and Ie but differs in the very long petiole and rather low asymmetry. It is relegated to a separate group IX. It obviously pertains to *U. carpinifolia*, but corresponds to none of the described microspecies.

A much more extreme type, and, in fact, one of the most distinctive elms collected in the whole area, is sample 32. Its outstanding characteristics are its very long petiole and extreme obversity. In addition, the veins leave the midrib at a narrow angle and show a tendency to curve inwards at the apex. This elm, which was only encountered in the vicinity of Buntingford, appears not to have been previously recognised. It could possibly be accommodated under *U. carpinifolia*, but is very remote from the other smooth-leaved elms. It is classed here as the sole representative of group X.

It is convenient, at this point, to refer to those isolated samples which have not been referred here to any group, mainly because of the possibility that further collection will reveal intermediate types connecting them with the groups already recognised. Sample 04 has been discussed already; 12 is close to Ia but has fewer teeth; 27 is fairly close to If but is considerably narrower. Sample 30 would come into IIa were it not for its shorter petiole, while it is only the high tooth number that separates 28a from III. Sample 34 approaches IV but has a longer petiole; like 26 in this group, it has the leaf shape characteristic of *U. carpinifolia* sens. str.

Elm 17b is a small-leaved type. Although so small, its tooth number is not proportionally low, and its other salient characteristics, long petiole, low asymmetry and high obversity, may be consequences of its reduced size. It is possible that such small-leaved types occur sporadically in each of the groups recognized. In the meanwhile, 17b will not be placed in a separate group.

An unusual combination of characters is found in 86a, in which the narrow scabrous leaves have a high tooth number, short petiole and low obversity. It is possible that this sample may eventually link up with Id so that, for the time being, it is not allocated a group of its own.

The last sample to require consideration is 06. This is a type with smooth, moderately broad leaves, few teeth and shortish petioles. Its nearest subgroup is Ia, but it has the proliferating habit characteristic of *U. plotii* Druce. Typical *U. plotii*, however, which has rather longer petioles, was not collected in the area studied, and sample 06 is probably to be regarded as a form intermediate between *U. plotii* and *U. carpinifolia*. It is relegated here to group XI.

The bearing of these observations on the problem of specific discrimination in *Ulmus* is somewhat intricate. In general, the demarcation of species within a genus depends on the recognition of discontinuities in the range of variation shown by the group as a whole. It is customary, in sexually-reproducing organisms, to distinguish between species proper and hybrids, the latter being usually few in numbers compared with the putative parent species. The genus *Ulmus*, however, is atypical in that, while *U. glabra* regularly reproduces by seed, *U. carpinifolia* and *U. procera* normally reproduce vegetatively, though

seed is produced in the former species in very favourable seasons (cf. Henry, 1910). Such vegetative propagation tends to increase and conserve variability (cf. Muller, 1951), and heterozygous types, if well-adapted to their environment, may well equal or even exceed in abundance the relatively homozygous parent types. The frequency distinction, therefore; that normally subsists between species and their hybrids is liable to disappear.

Within *Ulmus*, no fundamental sterility barriers appear to exist between the English species, and hybrids are readily produced (cf. Doorenbos, 1938). The chromosome number of all the English species, is the same, as far as is known, although it is possible that triploid or tetraploid clones may occur, as they do in *U. turkestanica* Reg. (cf. Krijthe, 1939). The subdivision of the genus into species must therefore rest entirely on the discovery of discontinuities, and the data here reported support, on the whole, subdivision of the English elms into the sexually-reproducing species *U. glabra* (VI), and the two vegetatively reproducing species *U. procera* (II) and *U. carpinifolia* (I, III and IV). There are, however, forms intermediate between these species and some of these may well be hybrids, for example VII, intermediate between *U. glabra* and *U. carpinifolia*, but it would be rash to presume too far on this point without further evidence as to the range of variation of each species when not in proximity to the other. Thus, scabrosity in *U. carpinifolia*, as in 64, suggests introgression from *U. glabra*. But it has to be remembered that the juvenile leaves in *U. carpinifolia* are scabrous, and it would probably require only a slight physiological change for this character to persist to the adult condition.

The distinction between *U. procera* and *U. carpinifolia* is also blurred. The smooth-leaved elms in IIa may well be hybrids, and 24a in this subgroup occurs in the region of overlap of these two species, but the full range of variation of *U. carpinifolia* is not yet known, and it is possible that the smooth-leaved members of IIa, and even more likely, IIb, are only extreme forms of *U. carpinifolia*.

Further subdivision of *U. carpinifolia* is obviously possible. Melville (1939, 1946, 1949) partitioned it into the three microspecies *U. carpinifolia* sens. str., *U. diversifolia* and *U. coritana*, excluding for the moment *U. plotii* and *U. stricta*. The data presented here, however, suggest relationships which cut across and transcend Melville's groups. Thus the large group I includes *U. diversifolia*, forms with a somewhat remote relationship to *U. carpinifolia* sens. str. and *U. coritana* var. *media*, and forms receding considerably from any of these. Typical *U. carpinifolia* sens. str. is found in III, but samples with the characteristic leaf shape of this species appear also in I, IV and VII. *U. coritana* seems a rather artificial aggregate. *U. coritana* var. *angustifolia* is nearest to VIII; it is very remote from var. *media*, in II, and var. *rotundifolia* in V. Thus the groups derived by the present analysis include, in some cases, several of Melville's microspecies; in other cases, one microspecies has to be partitioned into several distinct groups. A more concordant return would be obtained, however, if Melville's three varieties of *U. coritana* are treated as independent microspecies with an equivalent status to the other two.

It is true that the type descriptions of Melville's microspecies relate to highly characteristic and well-defined entities, but the analysis given here raises considerable doubt as to the status of these types as foci of the populations into which the genus can most naturally be divided. It is indeed probable that further work will reveal more intermediate types and intergroup connections than those here described; this would render the status of the microspecies even more uncertain. The conclusion would seem to follow that the application of Latin names to segregates of *U. carpinifolia* is of doubtful utility.

The data given here are not adequate to discuss the status of *U. plotii* or *U. stricta*, but the indications are that these species might turn out to be nothing but extreme variants of *U. carpinifolia*. Typical *U. plotii* is a very distinct elm with a characteristic

habit, but it is probably only a single clone from among many other small-leaved elms that make up a much wider entity, widespread in north Northamptonshire and elsewhere in the northeast Midlands, and which may eventually be shown to intergrade continuously with typical *U. carpiniifolia*.

The preceding discussion has been somewhat critical of the status of the microspecies and varieties of *Ulmus* already described. Yet it is clear, in the case of the vegetatively-reproducing elms at least, that taxonomic discrimination is possible between very minute categories, and between individual clones. It is true that many of the samples can be connected into a web in which numerous pairs of samples cannot be significantly separated, but this must not be allowed to obscure the fact that most of the samples do differ significantly from each other. The final picture that emerges is that of an aggregate of clones, perhaps several hundred in East Anglia, whose interrelations can be expressed in an *n*-dimensional network such as that in Fig. 3.

Since the present treatment is perhaps unsympathetic to classical taxonomic procedures, it is pertinent to enquire what is to replace it. It is possible that further work will provide a complete series of intermediates connecting even the major species *U. glabra*, *U. carpiniifolia* and *U. procera*. Should then only a single species be recognised? It is not necessary to go so far. Should morphological discontinuities be absent, it is still possible to utilise discontinuities of another sort.

Thus, it can be seen in Fig. 3 that Ic (samples 87, 97 and 98) are only connected with the other members of I by a single bond to sample 44. That is, connectivity between Ic and the rest of I is lower compared with connectivity within Ic and within the rest of I. Such a zone of low connectivity can be regarded as a type of taxonomic discontinuity and used as a basis for discriminating between the two contiguous groups.

Should even this type of discontinuity fail, it would still be possible to fall back on relatively low frequency of individual types in the field as a basis for discrimination. Thus, even were multifarious connecting links discovered between *U. carpiniifolia* and *U. procera*, the greater frequency of elms representing the typical species as compared with the intermediates, would probably, of itself, serve to justify the discrimination between these species.

The present evidence suggests that the three species *U. glabra*, *U. carpiniifolia* and *U. procera* can be legitimately distinguished on the basis of one or other of the types of discontinuity discussed above. With regard to the subdivision of *U. carpiniifolia*, it seems best to eschew altogether the classical taxonomic categories. As an alternative, subordinate systematic groups can be conveniently defined in terms of the range exhibited in a number of selected characters. In the present paper, five quantitative characters have been principally studied. If each of these is regarded as a dimension in a 5-dimensional anisotropic taxonomic space, then, by citing the lower and upper limit for each characteristic, we define a 5-dimensional parallelepiped, which can then be used as a taxonomic category. This, in fact, is what has been done in Table 2. The highly distinctive assemblage of elms referred to as Ic can be denoted by *Ulmus* '44853, 45973' or even by *U. carpiniifolia* '44853, 45973.' This suffices to exclude all the other elms collected in the area and seems to offer a better and more objective method of characterizing the East Anglian elm population than the taxonomic methods used hitherto.

GEOGRAPHICAL ANALYSIS

The first point requiring mention is the distribution of the zones in which elms were not collected. These include the fens, but exclude the "islands" such as Ely where elms are abundant. This explains why no samples were obtained in minor squares 92 to 97. The chalk scarp, which runs diagonally across the area, is also devoid of elm,

but since the scarp is narrow, this feature has hardly affected the sampling. The Breckland (for example minor square 77) provided no elms, and elm is sparse on the limestone outcrop in the extreme north-east part of the area.

The most striking result of the survey in respect of the distribution of the various groups is the discovery that *U. procera*, in the older hedges, does not extend eastward of a line running approximately north-south from Peterborough to Waltham (cf. Fig. 1). This is especially noteworthy in view of the fact that *U. procera* is frequently planted in later hedges and grows well east of this line. It is of interest to note that this line, to anticipate the results of further work, bends round sharply south of our area, and runs eastward, parallel with the Thames, reaching the sea near Shoeburyness. It reappears in east Kent, near Herne Bay, and runs thence in a south-westerly direction, leaving a small area in south-east Kent where *U. carpinifolia* is once again the predominant elm.

U. glabra occurs only sporadically throughout the area, suggesting a relict distribution. It is fairly frequent on the oolitic limestone outcrop, for example, in minor square 07, but this formation only just comes into the area. It is possible, however, that the widespread scabrous-leaved types, here considered under *U. carpinifolia*, have resulted from introgression from this species.

U. plotii, or rather the related sample 06, was only encountered once. This is not surprising since this species is known to be characteristic of the country to the west of Stamford. It appears to reach its eastern limits around Kimbolton.

U. carpinifolia occurs throughout the whole area. It penetrates beyond the eastern boundary of *U. procera*, though with reduced frequency, but how far it extends westward has not yet been ascertained. It has been collected along parish boundary hedges as far west as Bletchley.

What is of more interest is the distribution of some of its constituent groups and subgroups. Thus *Id*, with leaves of medium breadth and high tooth number, is characteristic of the country between Royston and Clare, while the elms with very long petioles and highly asymmetrical leaves that constitute *Ic* have only been collected around Thetford. As might be expected, some of the smooth-leaved representatives of *Ila*, the subgroup which includes typical *U. procera*, are found where *U. carpinifolia* and *U. procera* overlap, for example, 24a. Samples 56 and 57, however, which also belong to this subgroup, were collected in hedges adjoining the fens.

III, the group of narrow-leaved elms with a high tooth number, is fairly widespread, but especially frequent in Huntingdonshire and the adjacent parts of Cambridgeshire, e.g. 16, 18, 25, 35 and 48. IV was only collected in Cambridgeshire.

With the broad-leaved elms in V, a totally different area is concerned. *Va* was only observed in the coastal region of Essex. Sample 90 of *Vb* grows alongside the Blackwater estuary, while 52, which is the least typical representative of the group, was the only inland specimen. Sample 91 of *Vc* also came from near the Blackwater estuary. V extends south beyond our area to the estuary of the Crouch, but is then replaced by *U. procera*. South of the Thames, it has not been found. *U. procera* occurs along the north Kentish coast as far east as Herne Bay, while in Thanet some very small-leaved elms, most nearly resembling some of the elms of the Lincolnshire limestone, appear. It is not known how far north of Colchester V extends, but the elms around Walton-on-the-Naze and along the Norfolk coast are totally different. This group, then, which is very distinct from all other elms, seems to be quite narrowly localised along the Essex coast.

The other groups of *U. carpinifolia*, VIII, IX and X, are only known from single collections. It is possible that these, especially the very distinctive sample 32, are single extremely localised clones, but more intensive sampling would be necessary to confirm this.

It is not supposed that the sampling procedure utilised in this study is at all adequate for ascertaining the precise geographical limits of the various groups recognized. There is every reason to suppose that the overall pattern of distribution is extremely complex, rather in the nature of a jig-saw puzzle involving a large number of distinct clones.

The topocline concept has been applied to East Anglian elms (cf. Melville, 1949); the present evidence suggests that this concept is too coarse and involves far too great a simplification of the data to warrant its use. None of the five quantitative characteristics studied here show any simple relationship with geographical direction.

HISTORICAL ANALYSIS

It is pertinent to inquire what light the above data throw on the history of the genus and on the general question of the sequence of postglacial vegetation in this country.

Many lines of evidence suggest that the present distribution of the three major species, *U. glabra*, *U. carpiniifolia* and *U. procera*, may be of considerable antiquity. The earliest account that differentiates satisfactorily between the British species is in the 1633 edition of Gerard's Herball, where their relative distribution appears to be more or less the same as now. Earlier than this there is little direct evidence, but it is possible to draw some inferences from the distribution of place names and surnames derived from elms, and from mention of elms in early documents, in particular charters.

In East Anglia, the surnames Elmes and Elmy occur in the seventeenth century Hearth Tax returns for Suffolk and in early wills pertaining to Essex, Huntingdonshire, Norfolk, Northamptonshire and Suffolk; the Latin rendering *de Ulmis* also occurs. Making due allowance for migration, there seems no reason to doubt that elms were sufficiently widespread in the Middle Ages to afford a basis for East Anglian surnames.

Place names take us back much further. There are three etymological roots to consider, the Anglosaxon *elm* and *wice* and Celtic *lem*. Parish names in our area thought to be based on *elm* include Elmdon and Elmswell; those based on *wice* include Witchford and Witcham (cf. Ekwall, 1947). Other parish names based on these roots occur in the adjacent regions. No examples based on *lem* have been detected in major square 52, but the River Lymn in Lincolnshire and Lypne (Rother), from which the Kentish parochial names Lypne and Lyminge originate, are believed by Ekwall (1928) to be derived from this root.

It is highly probable that all these etymological roots refer to elm in general, without restriction to particular species. The suggestion of Hoops (1903) that *elm* is *U. campestris* L. (i.e. *U. carpiniifolia* or *U. procera*) and *wice*, *U. montana* Stokes (i.e. *U. glabra*), appears to be based on very tenuous grounds; the argument from modern English usage is particularly weak since this dates back no further than the eighteenth century. In Gerard's Herball, *U. carpiniifolia* is called *wych*; earlier still in Turner's list of plant names (1548) and in the fifteenth century *Promptorium parvulorum*, *elm* and *wich* appear to be used indifferently for elms in general. Cognates of *elm* occur in High German and in the Scandinavian languages. *Wych* corresponds to the Low German *Wiecke* or *Wietzer*, also with the Slav *vyaz* and the Lithuanian *vinkšna* (cf. Pokorny, 1930). A whole series of etymological roots for the elm occur on the continent; in Germany, in addition to the two already cited, there is a root *ip*, corresponding to the Dutch *iep*, and a root *rust*, in addition to the borrowed *Ulme*. In the Slav languages, there is also a root *brest* and words based on the borrowed Teutonic root *elm*. It may well be that, at certain times and in certain places, these terms have been used differentially to discriminate between different types of elm, but there is little satisfactory evidence of any consistent discriminant usage. In England, the distribution of place names based on *elm* and on *wice* suggests different linguistic traditions in different regions rather than a reflection of regional

differentiation in the elms themselves. Thus, parish names based on *elm* are conspicuous in Kent, Essex and Suffolk, but no names based on *wice* are reported (cf. Ekwall, 1947); in Cambridgeshire, Norfolk and Northamptonshire, the reverse situation occurs. It will therefore be assumed that place names involving (1) *elm* or *wice*, or (2) the Celtic *lem* indicate the presence of elms in post-Roman and pre-Roman times, respectively, without any restriction as to species.

The next step in our argument, namely, the postulation that the species or clones, frequent in the ancient parochial hedges in localities whose names indicate the presence of elms in earlier times, are the descendants, sexual or vegetative, of the earlier elms, is obviously more hazardous. The alternative, however, would require the extinction of one type of elm and its replacement by another, which is obviously a more elaborate and less likely hypothesis.

Other lines of evidence, too, provide grounds for supposing that the present elms have persisted *in situ*, at least since Roman times. The elm played an important role in Roman agriculture as a forage plant, in addition to its use as a timber and shade tree and as a support for vines. Cato gives instructions for planting elms around fields and along roads; the somewhat discrepant accounts of Pliny and Columella indicate clearly that the Romans distinguished between different types of elm in respect of fodder value and introduced clonal material from one region into another. The value of the elm as a source of fodder is reiterated in the Middle Ages by de Crescentiis, and the fact that it was so employed in England is stated in the writings of such early English agriculturalists as Fitzherbarde (1534) and Markham (1631). It is quite feasible that a number of Roman farming practices were perpetuated after the Anglosaxon invasions. Gray (1915) has shown, with reference to field systems, that this may be particularly the case in Kent and East Anglia. It seems reasonable, therefore, to suppose that elms were extensively distributed in eastern England in Roman times and have persisted since then without major distributional change.

There is no reason to suppose, however, that the Romans are responsible for the present pattern of distribution. Elm has been a conspicuous component in the British flora since mesolithic times (cf. Godwin, 1940). The earliest type was presumably *U. glabra*. This is not a frequent species in old hedges in East Anglia, and the present distribution suggests that it may be a relict species.

U. carpinifolia is abundant in East Anglia and occurs also in East Kent; it is probably the species that gave rise to the Celtic place names based on *lem* in Kent and also to the frequent East Anglian place names based on the Anglosaxon *elm* or *wice*. The fact that this species is seldom found in woods makes it rather doubtful whether it occurred in England before the opening up of the country by neolithic agriculturists, unless, possibly, it was present in some open communities no longer extant. The failure of the species to set seed except in exceptionally favourable seasons suggests that it has been introduced, directly or indirectly, from warmer regions to the south.

The present evidence, therefore, seems to suggest that *U. carpinifolia* was introduced by, or in the wake of, settlers arriving in England from the east and settling both in Kent and East Anglia, some time in the neolithic, Bronze or Iron ages. Intensive study of the distribution of the English clones composing *U. carpinifolia* and a comparison between these and those of the European seaboard might well throw further light on the source and date of this introduction.

U. procera presents a much more difficult problem. It only occurs along the western edge of our area, and, although it is generally recognised as a Midland species, no detailed knowledge has been obtained yet as to its distribution in the Midland counties. It is known to extend eastward along both sides of the Thames estuary, severing the East

Anglian and Kentish populations of *U. carpinifolia*. It is obviously premature, therefore, to speculate as to its early history, but it may prove useful to list the following facts, which will have to be taken into consideration when adequate distributional data have been obtained. In the first place, place names based on *elm* or *wice* are rare in the Midlands, and agricultural settlement appears to have been sparse till well after Roman times (cf. Darby, 1936). It therefore seems probable that elms were relatively infrequent in this region in early times as compared with East Anglia. However, the absence of *U. procera* from East Anglia and eastern Kent suggests that this species did not migrate into England from the east. *U. procera* does not appear to be known as an indigenous tree on the continent. *U. procera* var. *australis* (Henry) Rehder from southern Europe is very remote from the typical variety and should almost certainly be excluded from the species. *U. procera* occurs in Spain, and samples from Aranjuez and Mondoñedo in the Cambridge Herbarium are indistinguishable from English material. It seems probable that the Spanish trees were, as stated by Evelyn (1679), introduced into Spain from this country.

It would therefore appear that the origin of *U. procera* must be sought somewhere in the English Midlands. Possibly it arose as a single local clone and became widely spread on account of such desirable characters as straight bole and late defoliation. Its relation to *U. carpinifolia* is problematical. Transitional forms, notably IIb and the glabrous members of IIa, occur, and, of these, samples 86b and 95 of IIb are from far beyond the eastern limit of *U. procera*. It may be, then, that *U. procera* arose from some such type of *U. carpinifolia*, the scabrous character deriving either from a persistence of the juvenile condition or from introgression from *U. glabra*. On the other hand, it is quite likely that some intermediates between *U. procera* and *U. carpinifolia* are later hybrids.

The data presented here are not adequate to discuss the history of *U. plotii*.

SUMMARY

A technique for analysing the taxonomic variation of East Anglian elms is described, based on systematic sampling of the boundary hedges of ancient parishes. Five quantitative and one qualitative leaf characters were determined for each sample, and the degree of affinity between samples was ascertained by a graphical method based on an application of the *t* test. As a result of this approach, eleven taxonomic groups could be distinguished within the genus, together with a number of subgroups. The three major species, *U. glabra*, *U. carpinifolia* and *U. procera*, were fairly satisfactorily distinguishable, but the groups here recognised both cut across and transcend the segregates of *U. carpinifolia* recognised in the new *Flora of the British Isles*. It seems probable that *U. carpinifolia* is composed of a large number of distinguishable clones, and it is doubtful whether any useful purpose is served by applying Latin names to assemblages of these. A method of characterising the clones and clonal groups numerically is described.

U. glabra occurs sparsely in the area studied; *U. carpinifolia* is widespread; while *U. procera* hardly occurs east of a line running from Peterborough to Waltham. Many of the recognised groups and subgroups of *U. carpinifolia* have characteristic geographical distributions.

The evidence suggests that *U. carpinifolia* was introduced from the east as a forage plant, sometime in the neolithic, Bronze or Iron ages. *U. procera* appears to have arisen somewhere in the Midlands, whence it is spreading eastward.

It is considered likely that an intensive study of the distribution and relationships of the individual clones of *U. carpinifolia* would throw an interesting light on the history of agricultural settlement in England.

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SOME CHROMOSOME COUNTS IN THE EUROPEAN CISTACEAE

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The Cistaceae are a small and rather homogeneous family, distributed chiefly in the Mediterranean region. A few, including the four British species, extend into central and northern Europe, and others occur in the west Asian steppes, the Arabian and north African deserts, and the Atlantic islands. In addition a number of species, which will not be considered further here, are confined to the New World. The Linnean genus *Cistus* originally included all the European Cistaceae, but these are now invariably subdivided. Grosser (1903) in his monograph of the family recognises five genera, and I follow most recent authors in adopting them throughout this paper.

A number of chromosome counts of species of Cistaceae exist in the literature, but taken as a whole they are unsatisfactory. Few have been based on wild material of known origin, and some seem certainly to be wrong. The position in *Cistus* itself is clear. Many counts have been made by several workers with the uniform result $2n = 18$ in all the species investigated (Chiarugi, 1925, 1937; Collins in Warburg, 1930; Bowden, 1940; La Cour in Darlington & Janaki Ammal, 1945). The published records for *Helianthemum* s.l. present a much more confused picture, which it is the attempt of the present paper to clarify.

Counts have been made of both mitotic and meiotic chromosomes. Mitosis was examined in root tips obtained either from germinating seeds or from pot-grown plants. The roots were cut off, pre-treated with 0.002 M 8-hydroxy-quinoline for 4-6 hours, and then fixed in Carnoy's fluid. Maceration and staining were combined by heating the roots in a little acetocarmine in a test-tube over a boiling water-bath for 5-10 minutes. Iron was introduced either by standing a needle in the test-tube for a short time or by adding a drop of an iron acetate solution. The root-tips were cut off on a slide, teased in a drop of 45 per cent acetic acid, tapped out and squashed in the usual way. Acetic orcein gave better results with pollen mother cell preparations for meiosis. A few anthers were squashed in a small drop of the stain with a fine pointed scalpel, the anther debris was removed and the preparation covered and squashed. Preparations were made permanent by inverting the slide in a dish of 50 per cent alcohol until the coverslip separated. The slide and coverslip were dehydrated separately, and recombined in a drop of 'Euparal.'

The chromosomes were drawn using a *camera lucida*, at a magnification of about $\times 1,800$. A Leica camera with a microscope adaptor was used for the photographs.

Almost all the plants used were of known wild origin, and documented herbarium specimens of most have been deposited in the Cambridge University Herbarium.

The results are listed in the following table. In general they differ from genus to genus, but within a single genus show a considerable degree of regularity. Some confirm existing counts, but in a number of cases published figures show discrepancies which will be discussed in more detail below.

*Now Nature Conservancy, Bangor.

LIST OF CHROMOSOME NUMBERS DETERMINED		<i>n</i>	<i>2n</i>
HALIMIUM (Dunal) Willk.			
<i>ocymoides</i> (Lam.) Willk. & Lange			
Sintra, Mercês, Estremadura, Portugal (Estação Agronómica Nacional, Sacavém, Portugal)			18
<i>halimifolium</i> (L.) Willk. & Lange			
Sesimbra, Apostica, Estremadura, Portugal (E.A.N.)			18
<i>umbellatum</i> (L.) Spach			
Almada, Corroios, Estremadura, Portugal (E.A.N.)			18
TUBERARIA (Dunal) Spach			
<i>vulgaris</i> Willk.			
Sintra, Mercês, Estremadura, Portugal (E.A.N.)			14
(Garden origin)			14
<i>guttata</i> (L.) Fourreau			
South Stack, Holyhead, Anglesey (D.E.C.)		c.	36
Three Castles Head, Co. Cork, Ireland (S.M.W.)			36
Baie des Trépassés, Finistère, France (C.D.P.)			36
Sintra, Mercês, Estremadura, Portugal (E.A.N.)			36
HELIANTHEMUM Adans.			
<i>apenninum</i> (L.) Mill.			
Berry Head, Brixham, Devon	10		
Purn Hill, Bleadon, Somerset (S.M.W.)			20
Les Andelys, Eure, France (S.M.W.)			20
St. Adrien, nr. Rouen, Seine-inf., France (S.M.W.)	10		
<i>chamaecistus</i> Mill.			
Hod Hill, Blandford, Dorset			20
Chilham, Kent (C.D.P.)			20
Risby Poors Heath, Suffolk			20
Holywell Mound, Lincs.			20
Millington Pastures, Yorkshire Wolds, E. Yorks. (M.E.B.)			20
Gordale Scar, Malham, W. Yorks.			20
Humphrey Head, Grange, N. Lancs.	10		
Near Aberfeldy, Perthshire (M.E.D.P.)			20
Ballintra, Co. Donegal, Ireland (S.M.W.)			20
Sta. Comba Dão, Beira Alta, Portugal (E.A.N.)			20
Domodossola, N. Italy (C.D.P.)			20
Visp, Wallis, Switzerland (C.D.P.) (<i>H. grandiflorum</i> (Scop.) DC.)			20
Donaueschingen, Baden, S.W. Germany (W.K.) (<i>H. ovatum</i> (Viv.) Dunal)			20
Bjergsted Bakker, Sjaelland, Denmark (T.W.B.) (<i>H. ovatum</i>)	10		
Mt. Trebeviča, nr. Sarajevo, Yugoslavia (W.K.) (<i>H. tomentosum</i> (Scop.) Spreng.)	10		
<i>ledifolium</i> (L.) Mill.			
Sintra, Algueirão, Estremadura, Portugal (E.A.N.)			20
<i>canum</i> (L.) Baumg.			
Rhossili, Glamorganshire	11		
Pabo, nr. Llandudno, Caerns. (S.M.W.)	11		
Cronkley Fell, Teesdale, N.W. Yorks. (H.G.)	11		
Scout Scar, Kendal, Westmorland			22
Poulsallagh, Co. Clare, Ireland (S.M.W.)			22
Poulsallagh, Co. Clare, Ireland (C.D.P.)	11		
St. Adrien, nr. Rouen, Seine-inf., France (S.M.W.)	11		
Öland, Sweden (T.G.T.)			22
Nüßenberg, N. of Naumburg, Saxony, Germany (A.H.)			22
<i>oelandicum</i> (L.) Swartz			
Öland, Sweden (T.G.T.)	11		
<i>alpestre</i> (Jacq.) Dunal			
Schynige Platte, Interlaken, Switzerland (T.W.B.)	11		
<i>lunulatum</i> (All.) DC.			
(Garden origin)			22
FUMANA			
<i>laevipes</i> (L.) Spach			
Portinho, Serra d'Arrabida, Portugal (S.M.W.)			32



Fig. 1. Chromosomes of Cistaceae ($\times 1,200$): g, i, o, p, and r are pollen mother cell meiosis; the remainder are from root tip preparations. (a) *Halimium ocymoides*, Sintra, Portugal; (b) *H. halimifolium*, Sesimbra, Portugal; (c) *H. umbellatum*, Almada, Portugal; (d) *Tuberaria vulgaris*, Sintra, Portugal; (e) *T. guttata*, Sintra, Portugal; (f) *T. guttata*, Finistère, France; (g) *Helianthemum apenninum*, Berry Head, Devon; (h) *H. apenninum*, Les Andelys, France; (i) *H. chamaecistus*, Humphrey Head, Lancs.; (j) *H. chamaecistus*, Risby, Suffolk; (k) *H. chamaecistus*, Yorkshire Wolds; (l) *H. chamaecistus*, Perthshire; (m) *H. chamaecistus*, Visp, Switzerland; (n) *H. ledifolium*, Sintra, Portugal; (o) *H. canum*, Teesdale, Yorks.; (p) *H. canum*, Rhossili, Glamorgan-shire; (q) *H. canum*, Kendal, Westmorland; (r) *H. oelandicum*, Öland, Sweden; (s) *H. lunulatum*; (t) *Fumana laevipes*, Portinho, Portugal.

(a) *Halimium*

The three species counted all have a diploid number of 18, which agrees with the counts of $n = 9$ in *H. halimifolium* and $2n = 18$ in *H. atriplicifolium* (Lam.) Spach given by Chiarugi (1925, 1937).

(b) *Tuberaria*

This genus provided two rather surprising diploid counts of 14 and 36, both, I believe, not previously recorded. Of the published figures for *T. guttata*, Bowden's $2n = 20$ (1940) is almost certainly an error due to wrongly named material. Chiarugi (1925) found $n = 24$, and this count deserves more consideration. The occurrence of as low a number as $2n = 14$ in *T. vulgaris* suggests that *T. guttata* with $2n = 36$ must have arisen as a polyploid. It seems most likely that it is a hexaploid on a basic number of 6, so that, whatever its exact mode of origin, plants with other multiples of this number, especially 12 and 24, should be sought. The four counts published here are from only a small part of the area of the *T. guttata* complex, and it is quite likely that other numbers may occur in other parts of the range. Cytological investigation both of other *T. guttata* forms, and of the remaining perennial species, *T. globulariifolia* (Lam.) Willk., would be well worth while.

(c) *Helianthemum*

Two differing chromosome numbers occur in this genus as in the last. In the species investigated, those of the subgenus *Helianthemum* have $2n = 20$, while those of *Plectolobum* have $2n = 22$. However the genus is a large one, and more counts would be needed to establish that this represents the full variation, especially as the material studied leaves several sections unrepresented. Most of the more recent published work is consistent with these results, but Bowden (1940) obtained diploid counts of 32 in *H. apenninum* and *H. chamaecistus*, and Mattick (in Tischler, 1950) 32 in *H. chamaecistus* which agree with the earlier determinations of Chiarugi (1925). It is difficult to see how a mistake can have occurred, though the triploid garden forms of *Helianthemum* reported by Snoad (1954) with a somatic chromosome number of 30 suggest one possibility. On the evidence now presented, appears to be cytologically uniform over a wide area with $2n = 20$ (Fig. 2). The forms investigated embrace the greater part of its morphological variation, and it seems unlikely that there could actually exist a chromosome race with as unrelated a number as $2n = 32$. Apart from my counts, $2n = 20$ is quoted by Å. & D. Löve (1948) from Scandinavian material, and it has been determined by K. Larsen (Dr. T. W. Böcher *in litt.*) from the following localities: dry field in *Pinus* wood between Angoulême and Bordeaux, France; dry slope in the valley at Luchon, Pyrenees, France; dry *alvar* on Gotland, Sweden. Bowden's '*H. alpestre*' with $2n = 20$ was probably a small form of *H. chamaecistus*. A plant of *H. alpestre* from Interlaken, Switzerland, agreed quite clearly with *H. canum* and *H. oelandicum* in its haploid number of 11, as would be expected from its taxonomic relationships. The counts given here for *H. canum* from Teesdale and Westmorland confirm those published by Tutin (1953) from the same localities.

(d) *Fumana*

Few counts are available for *Fumana* species. Such as there are suggest a uniform diploid number of 32, the number obtained by me for *F. laevipes*, but most are old and need confirmation.

A number of errors have been indicated in the published chromosome numbers of the Cistaceae, and some comment on accuracy in chromosome counts seems called for. Errors may arise in two ways: either through poor technique, or through wrongly named



Fig. 2. Map showing the distribution of *Helianthemum chamaecistus* (from Meusel, 1943) and the localities from which chromosome counts are given in the present paper.

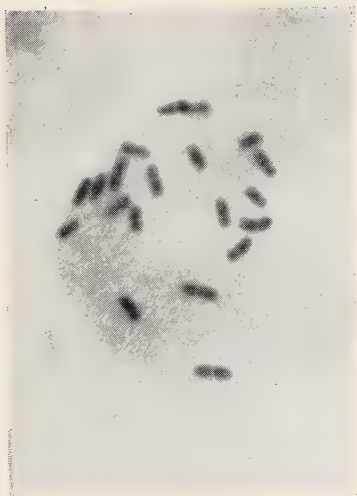
material. Cytological methods have advanced greatly in recent years, and for this reason alone too much weight must not be laid on the early counts. With careful use of modern methods there is no reason for serious mistakes to occur. Cytologists are however usually dependent on outside sources, especially botanic gardens, for their material, and this used uncritically can be a fertile source of error. I have received from two very reputable sources seed of an annual species of the *Brachypetalum* section of *Helianthemum* as *Tuberaria guttata*, and plants of *Helianthemum chamaecistus* as *H. alpestre*. Both these might have given rise to incorrectly recorded chromosome counts. The remedy lies partly with the botanic gardens and others distributing plants and seeds, but it is also a responsibility of the cytologist to be sure that his plants are correctly named. It is particularly desirable that seed should be grown on and checked very carefully, and specimens of the plants used preserved.

The distribution of chromosome numbers in the Cistaceae accords quite well with existing classifications. It seems quite clear that the four genera within *Helianthemum* s. l. are natural groups, and that they are not particularly closely related one to another. In particular *Halimium* seems in all respects to be much closer to *Cistus* than to the restricted *Helianthemum*. This is borne out by the occurrence of bigeneric hybrids between *Halimium* and *Cistus* section *Ledonia*. The chromosomes are rather small, so it has not been possible to get much help from their morphology, though a few generalisations can be made. *Halimium* has roughly equal sized chromosomes with median centromeres. The species of *Helianthemum* investigated show two or three pairs of chromosomes with obviously unequal arms, and there is some variation in size. In *Tuberaria* a large proportion of the chromosomes are asymmetrical.

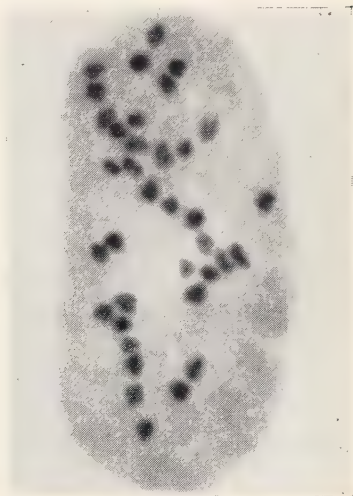
Two conspicuous characteristics of the Cistaceae are the absence of polyploid chromosome races, and the variation in basic number between the genera. Genome

PLATE 14

Metaphases in root tips pre-treated with 8-hydroxy-quinoline ($\times 1500$):

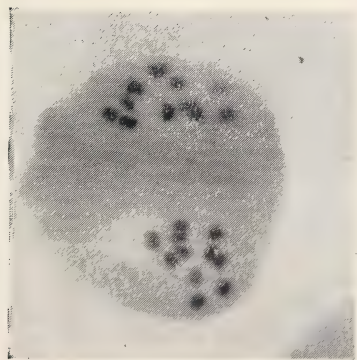


(a) *Helianthemum chamaecistus* ($2n = 20$),
Hod Hill, Dorset

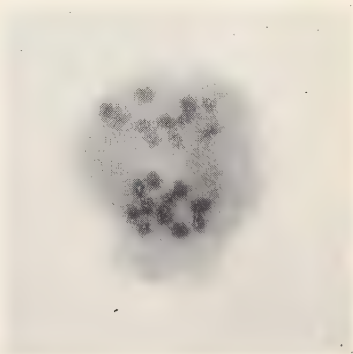


(b) *Tuberaria guttata* ($2n = 36$),
Three Castles Head, Co. Cork.

Metaphase II in pollen mother cells ($\times 1500$):



(c) *Helianthemum canum* ($n = 11$),
Poulsallagh, Co. Clare



(d) *Helianthemum alpestre* ($n = 11$)
Interlaken, Switzerland

evolution seems to have proceeded largely by aneuploid variation early in the history of the group. Polyploidy probably played a part in the origin of *Tuberaria guttata*, and perhaps of *Fumana*. Bowden (1940) comments on finding a single tetraploid cell in otherwise diploid *H. canum*, and I have found tetraploid cells in root tips of *Tuberaria vulgaris*, *Helianthemum chamaecistus* and *H. ledifolium*. However a woody plant with a limited life-span, and reproducing sexually from seed, may provide conditions hardly more favourable than an annual for polyploid types to arise. Even so, it is surprising that an annual should provide the only instance of polyploidy in a predominantly perennial family.

I gratefully acknowledge that the work on which this paper is based was carried out during the tenure of a training grant given by the Nature Conservancy. I would like to thank Dr. H. Godwin for his constant and stimulating interest in supervising my work, and the following for their kindness in providing material: Dr. T. W. Böcher, Miss M. E. Bradshaw, Dr. D. E. Coombe, Dr. A. R. Pinto da Silva, Dr. H. Godwin, Herr A. Horn, Dr. W. Krause, Dr. C. D. Pigott, Dr. M. E. D. Poore, Prof. T. G. Tutin, Dr. S. M. Walters.

SUMMARY :

42 chromosome counts from 13 species of Cistaceae are listed and briefly discussed. The distribution of the chromosome numbers in the family is as follows :

	2n
<i>Halimium</i>	18
<i>Tuberaria</i> sect. <i>Eu-tuberaria</i>	14
sect. <i>Scorpioides</i>	36
<i>Helianthemum</i> subgen. <i>Helianthemum</i>	20
subgen. <i>Plectolobum</i>	22
<i>Fumana</i>	32

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GERANIUM PURPUREUM VILL. AND G. ROBERTIANUM L. IN THE BRITISH FLORA

I. GERANIUM PURPUREUM

By H. G. BAKER

Department of Botany, University of Leeds

Geranium purpureum Vill. and *G. robertianum* L. form a valuable pair of species for ecological and cytogenetical comparison. One is a rare species whose British occurrences are at the northern limit of its Mediterranean type of distribution while the other is a widespread species with a considerable range of ecological tolerance. Since 1945 they have been grown, observed and hybridised in the Experimental Gardens of the University of Leeds. The genecological results of this study will be published elsewhere; in the present papers the subspecific units which have been established in each species as a result of the experimental and field studies are treated taxonomically and their British distributions are mapped.

A great many infra-specific taxa have been described for these two species by those who have only observed their plants in the wild. Cultivation experiments show that some of these have no genetical basis (and are modifications induced directly by the environment). Only those distinctions which are maintained in cultivation in the uniform conditions of a garden are to be considered worthy of nomenclatural recognition. With this principle in mind, those morphologically distinct forms which appear to be ecologically significant (or to possess a distinctive geographical distribution) are given subspecific rank. They are the 'ecological races' and their taxonomic treatment is thus in accordance with the principles of Clausen, Keck & Hiesey (1939). Within these subspecies, lesser morphological groupings may be made, but these more or less discrete forms usually differ from each other only in respect of individual qualitative characters. They are accompanied by other, more or less continuous, variation in quantitative characters and neither the discrete nor the continuous variation *within* the subspecies appears to have any measurable ecological correlation.

On this basis, British material of *Geranium purpureum* appears to consist of two subspecies, while *G. robertianum* contains three (which will be discussed in the second paper of this series). That there are other non-British infra-specific groupings in both species is certain and some of them will be treated elsewhere.

In the preparation of these accounts, use has been made of material contained in the following herbaria :—

H. G. Baker	(Bak.)	Royal Botanic Gardens, Kew	(K)
British Museum (Natural History)	(B.M.)	Borrer at R.B.G., Kew	(K.Borr.)
Boswell-Syme at B.M. (N.H.)	(B.M.Bosw.)	Cryer at Leeds University	(L.Cry.)
Sowerby at B.M. (N.H.)	(B.M.Sow.)	Roper at Leeds University	(L.Rop.)
Cambridge University	(Cam.)	Oxford University	(Ox.)
Marshall at Cambridge University	(Cam.Mar.)	National Museum of Wales, Cardiff	(WNH)
Royal Botanic Garden, Edinburgh	(E)	C. C. Townsend	(Town.)
Royal Albert Museum, Exeter	(Ex.Hiern)	Muséum National d'Histoire Naturelle, Paris	(Par.)

Grateful acknowledgment is made to the authorities concerned.

GERANIUM PURPUREUM Vill. (1785), *Fl. Delph.*, 72, emend. Jord. (1848)

G. PURPUREUM subsp. PURPUREUM

G. scopulicolum Jord., nom. nud.

G. lebelii Boreau (1840), *Fl. Cent. Fr.*, 1, 324.

G. modestum Jord. (1848), *Adnot. Cat. plant. Jard. Grenob.*, 3; (1860), *Bull. Soc. Bot. Fr.*, 7, 605.

G. minutiflorum Jord., *Cat. Dijon*; ex ej. (1848), *Pug. Pl. Nov.*, 39.

G. robertianum L. var. *modestum* Syme, 1863, *Eng. Bot.*, ed. 3, 2, 204, t. 306.

G. intricatum Gren. in litt. et in herb. Mus. Paris; ex Rouy (1897), *Fl. Fr.*, 4, 98.

G. purpureum Vill. var. *genuinum* Rouy (1897), *Fl. France*, 4, 97.

Type locality : Pont de Claix, near Grenoble, France.

Within the species *Geranium purpureum* as defined by Villars, there were two distinct plants, one from Le Buis (Drôme) the other from the Pont de Claix, near Grenoble. Jordan (1848) recognised this and redefined *G. purpureum* on the basis of the Pont de Claix form, separating the material from Le Buis as *G. villarsianum*. The former contains plants whose fruits carry a pattern of ridges on their backs while the latter group of forms is characterised by thick weals on the fruits. In the Paris herbarium there are several sheets from Pont de Claix. Jordan, however, came to believe that any units which were distinct, constant and true-breeding represented true species and, as a result of the cultivation experiments which he carried on with plants of various genera, he described a great number. Because *G. purpureum* is normally self-pollinated, it tends towards homozygosity and, while populations in any locality may be relatively uniform as a result, there are often well-marked distinctions between populations (Baker, 1953). Consequently, Jordan, after cultivating samples of some of these populations, was able to describe at least two new "species" within this group. Other French workers were willing to find specific diversity here. Wilmott (1921) has already pointed out that *G. purpureum*, *G. scopulicolum*, *G. modestum* and *G. lebelii* cannot be separated by any character which we should now consider to be of specific significance. Indeed after the examination of authentic material from French sources, both in British Herbaria and at Paris, they do not seem to differ even in subspecific degree from Villars' type. *G. minutiflorum* appears to represent an exposed form of this subspecies. *G. intricatum*, which is characterised by the extreme reduction in size of the leaves in the region of the inflorescence, also appears to represent only a minor variant. None of them have significantly different ecological preferences and they occur here and there within the general area of the species.

Thus, within the limits of the species, the type subspecies may be said to comprise plants which have an upright or strongly ascending habit and grow in rocky places, on cliffs and on dry hills. In the southern parts of its distribution these plants may occur in shady places, even in woodland, but in the British Isles they are rather intolerant of shade. Except in some populations where hybridisation with *G. robertianum* appears to have played a part, their fruits carry a characteristic pattern of closely-set ridges (Fig. 1). These fruits may be glabrous or hairy.

This subspecies ranges through south-western and western Europe and reaches the islands of Madeira. Its complete European distribution is not yet fully worked out but it is replaced in many Mediterranean areas by the group of forms included in *G. villarsianum* Jord. and in the eastern Mediterranean and the highlands of East Africa by a third species which has also been confused with *G. purpureum*.

As indicated by Evans (1920) and Wilmott (1921), plants agreeing in all essentials with Villars' type are found in all the south-western stations for the species in the British Isles. Here they grow particularly in rocky and stony places (but are also found in open

hedgebanks), usually near the sea, and always in a rich soil (usually derived from a limestone). Their British and Irish distribution is thoroughly in accordance with that of the Mediterranean element in our flora.

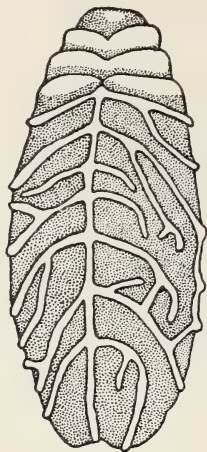


Fig. 1. Dorsal view of fruit of *G. purpureum* Vill. subsp. *purpureum* from Leigh Woods, N. Som. ($\times 20$).

The detailed distribution of this subspecies is as follows. Collectors' names are given only for the less well-known localities.

CHANNEL ISLES :

JERSEY : St. Helier, 1838, *Babington* (Cam.); La Haule; St. Brelade's; Don Bridge, 1923, *Barton* (B.M.); Quenvais; St. Peter's, 1923, *Barton* (B.M.); St. Ouen's; St. Anne's, 1920, *Druce* (Ox.); Port Mogurta, 1906, *Druce* (Ox.); L'Etac, Lester-Garland in *Fl. Jersey*, 1903, is undoubtedly correct.

GUERNSEY : Fort George, 1926, *Foggitt* (B.M.); S.W. Guernsey, 1879, *Melville* (B.M.); E. of Vazon Bay, 1878, *Fraser* (Ox., WNH); around Cobo Bay, 1878, *Fraser* (K), 1923, *Foggitt* (B.M.); Grandes Rocques, 1912, *Barton* (B.M.); Bordeaux Harbour, 1902, *Cooper* (Ox.); Vale Castle, 1883, *Fawcett* (B.M.); 1906, *Druce* (Ox.); Paradis, 1897, *Druce* (Ox.). King's Mills, Grosse Hougue and Spur Point, Marquand, *Fl. Guernsey*, 1901, are probably correct.

- V.c. 1. W. CORNW. : Scilly Isles (probably St. Mary's), 1878, *Curnow* (WNH); Hayle, 1922, *Pegler* (B.M.); around Crantock and Newquay; Padstow.
2. E. CORNW. : Wadebridge; St. Issey, 1918, *Thurston* (K), 1945, *Baker* (Bak.); between Wades bridge and St. Minver, 1945, *Baker* (Bak.); Par, 1911, *Druce* (B.M., Ox., WNH). Record from Polzeath (in Davey, *Fl. Cornwall*, 1909), and Gorran Haven (Reid 1911) are almost certainly correct.
3. S. DEVON : East Prawle, 1938, *Chapple & Rob* (K, Ox.); Brixham, 1931, *C. I. & N. Y. Sandwith* (K); between Babbacombe and Torquay, 1834, *Borrer* (K.Borr.); many stations around Torquay; Watcombe, 1914, *Larter* (Ex.Hiern); Drewsteignton, 1909, *Hiern* (Ex.Hiern); Hole's Hole, W. Bere Ferrers, 1871, *Briggs* (B.M.).
6. N. SOM. : Leigh Woods; Cheddar Gorge, 1918, *Roper* (L.Rop.), 1938, *R. & K. Tuckins* (B.M.); 1945, *Baker* (Bak.).
9. DORSET : Pumfield, near Swanage, 1882, *Ridley & Fawcett* (B.M.); near Swanage, 1884, *Murray* (B.M.) (probably the same station).
13. W. SUSSEX : Cockbush Common, 1833, *G. E. Smith* (Cam.); Clymping (Middleton), 1930, *Lousley* (Cam.).
34. W. GLOS. : Observatory Hill, Clifton (St. Vincent's Rocks), 1924, *Roper* (B.M., K, Cam., WNH, L.Rop.), 1953, *Townsend* (Towns.).
44. CARM. : near Newcastle Emlyn, 1934, *Chapple & Parry* (Ox.).
- H. 4. MID CORK : Cork, 1848, *Carroll* (B.M.).
6. WATERFORD : Dungarvan, 1881, *Britten* (B.M.), *Britten & Nicholson* (B.M., Camb., Ox.).

Fig. 2 shows the distribution in map form. This account of the distribution of this subspecies is far more complete than that given by Wilmott (1921) and differs considerably from the overall picture presented by Druce (1932) and Warburg (1952). These differences and the many incorrect references to be found in local floras are due to the extensive confusion which existed in the older literature between *G. purpureum* Vill. and the prostrate maritime race of *G. robertianum* (which was frequently miscalled *G. purpureum* by British authors prior to 1921 and occasionally since). The originator of this misconception in Britain appears to have been Syme (1864). The confusion has been increased by a beautiful photograph of prostrate *G. robertianum* growing on shingle near Rye, Sussex, which appears in Sir Arthur Tansley's great work (1939) with the statement that "*Geranium purpureum* Vill. . . . is a characteristic species of the south-eastern shingle beaches."

The earliest Sussex record of *G. purpureum* subsp. *purpureum* is from Cockbush Common on the west side of Chichester harbour. As pointed out by Wolley-Dod (1937) "Cooper (1834) gives a short description of it at Cockbush and Middleton (i.e. Clymping Sands) indicating that he found the true species there." However, we do not need only to trust Cooper's judgment, for through the years there have existed unnoticed four small specimens collected on June 3, 1833 by the Rev. G. E. Smith. At one time these plants rested in the Henslow Herbarium and they now form part of the Cambridge University collection. They were collected at the same time as prostrate maritime *G. robertianum* and were mounted on the same sheet. Their true nature was appreciated for the sheet is labelled "*Geranium robertianum* with *G. purpureum*. Cockbush Common. Sussex." In view of the fact that no subsequent collection had been made in this storm-damaged area, it is to be feared that the population is now extinct.

A rather similar story attaches to the other West Sussex record. In this case, erect specimens were collected in 1930 on shingle at Clymping (Middleton) between Littlehampton and Bognor at the station for the prostrate subsp. *forsteri* (see p. 000) by Mr. J. E. Lousley. Some of the specimens which were distributed give the impression of having grown upright in shade and, when I visited the population between 1945 and 1948 only plants shaded by concrete blocks or the wooden groyne were found growing erect. Nevertheless, Mr. O. Buckle (*in litt.*) tells me that he knows of a small population of *G. purpureum* with an ascending habit growing near Clymping so, until tests are made on these plants in culture, the record must be taken as correct.

Subsp. *purpureum* appears to be absent from Hampshire and very rare in Dorset, despite the first record for England at Swanage (see Wilmott, 1921), but begins to be locally common in South Devon. Many of the numerous localities given by Martin and Fraser (1939) are, however, incorrect, and the species occurs in only four areas, all but one of them coastal. The exception is Hiern's specimen from Drewsteignton. All records from North Devon are erroneous. The Cornish populations are all relatively well-known and this subspecies is probably more common around Newquay and by the estuary of the River Camel than elsewhere in England.

The erroneous records by E. S. Marshall and others having been discounted, it seemed for a long time that the only Somerset station was in Leigh Woods. Here the species was first seen growing under a wall by Miss A. Carpenter in 1837 whose specimen of a shade form is at Cambridge. It was first recognised, cultivated and commented upon by Moss (1912) and, since then has been repeatedly distributed, by J. W. White and others. Whether this has contributed to its apparently decreased numbers is problematical.

A record for Cheddar Gorge by H. M. Drummond-Hay was backed by a specimen collected in 1871 and lodged in the Boswell-Syme collection at the British Museum



Fig. 2. Distribution of subsp. *purpureum* ● (○ where specimen not seen) and subsp. *forsteri* ★ in the southern vice-counties of England and Wales (Southern Ireland and the Channel Isles inset).

(Natural History). It is quoted by White (1912). As expected, it proved, on examination, to be *G. robertianum*, of which several forms occur at Cheddar. However, genuine specimens of *G. purpureum* subsp. *purpureum* were collected by Miss Roper in 1918 and by R. and K. Tuckins in 1938; they do not appear to have been recorded in the literature. In 1945 I collected the plant growing on a ledge on the south side of the Gorge (and have used this material in experimental studies) and, in 1946, saw the species again growing on the roof of a greengrocers' stall in the Gorge (where seed had evidently dropped from the cliffs above). Interested by this, Mr. N. Y. Sandwith kept a look-out for the species and confirmed its presence.

The single station in Gloucestershire lies across the Avon Gorge from Leigh Woods. *G. purpureum* was first recognised on Clifton Down as recently as 1925 by C. Wall. Herbarium specimens suggest that this population has suffered some introgression from *G. robertianum*. This also applies to the relatively recent Carmarthenshire record, for, although it is referable to *G. purpureum*, the single specimen from Newcastle Emlyn has several features reminiscent of *G. robertianum*. A population-analysis in this locality might be very rewarding particularly as this is a remarkably disjunct outpost for *G. purpureum*. Similar suggestions of interspecific hybridisation apply in the Torquay area, at Bere Ferrers, and in north Cornwall.

Druce (1932) is in error in including the Isle of Wight and Breconshire in the range of *G. purpureum*.

Of the records from outside England and Wales, those from the Channel Isles are, in general, well known. The record from Bordeaux Harbour is of interest in that subsp. *purpureum* occurs there at the same station as the subsp. *forsteri* and, apparently, in circumstances reminiscent of those at Clymping, Sussex. The two Irish records are of long standing and are quite genuine although, surprisingly, they are not given by Druce (1932), nor by Praeger in any of his lists. At Dungarvan, however, there is a suggestion of natural hybridisation with *G. robertianum*. The records from Kerry, Clare and Galway (Moore & More, 1866; Colgan & Scully, 1898; Praeger, 1909, 1934a, 1934b; Scully, 1916; Warburg, 1952; Webb, 1952) are all due to confusion with prostrate maritime *G. robertianum*.

In the Scilly Isles, only *G. robertianum* is reported in the literature but Curnow's specimen in the National Museum of Wales appears to be *G. purpureum*. The literature records of *G. robertianum* (kindly supplied by Mr. J. E. Lousley) are all rather old and may also turn out to be referable to *G. purpureum*. Further collecting is very desirable.

G. PURPUREUM subsp. *FORSTERI* (Wilmott) comb. nov.

G. purpureum Vill. sec. T. F. Forster (1830), *Engl. Bot. Suppl.*, **3**, 2648.

G. robertianum var. γ Babington (1851), *Man. Brit. Bot.*, ed. 3, 62.

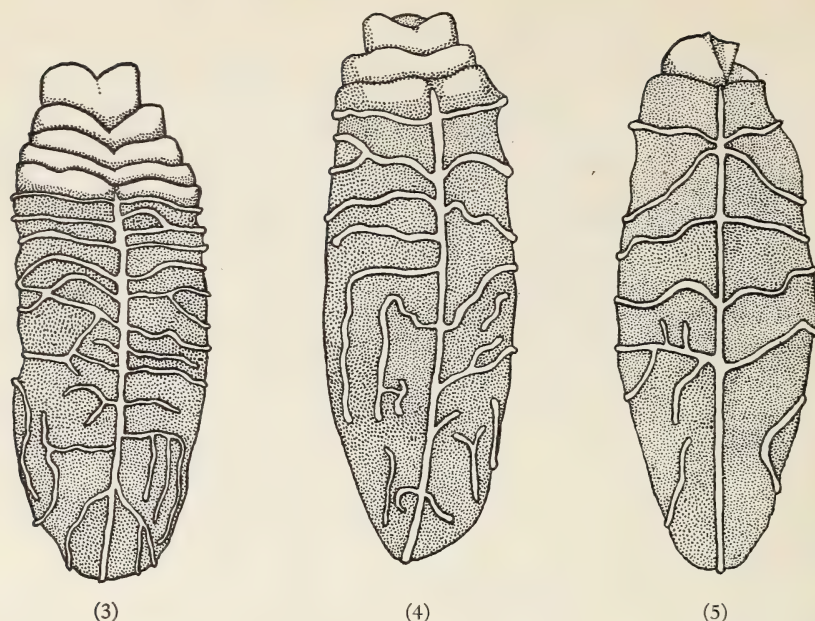
G. robertianum var. *purpureum* (Vill.) sec. Syme, 1864, *Engl. Bot.*, ed. 3, **2**, 204.

G. purpureum var. *forsteri* Wilmott (1921), *J. Bot.*, **59**, 95.

Type locality: Clymping (Middleton), W. Sussex, England.

Plants of this subspecies have a prostrate habit, for the leader soon branches and the branches run at only a slight angle with the ground although the tips ascend. The petioles of the rosette leaves are still shorter than those of subsp. *purpureum*. They grow only in the stabilised area at the rear of certain shingle-beaches. In cultivation they flower about a fortnight later than British material of subsp. *purpureum*.

While the fruits of most British representatives of the subsp. *purpureum* are quite distinctly ridged, any population of subsp. *forsteri* shows a considerable range from typical *purpureum* to fruits very like those of *G. robertianum* (Figs. 3-5) and both glabrous and hairy fruits occur together. This makes the determination of herbarium material



Figs. 3-5. Dorsal views of three fruits from the population of subsp. *forsteri* at Clymping, W. Sussex ($\times 20$), showing a transition from the typical *purpureum* pattern (left) to a *robertianum* pattern (right).

rather more difficult. There has been some doubt as to the correct name for this subspecies. Rouy (1897) describes his maritime *G. purpureum* Vill. var. *littorale* as having the petals "une fois plus longs que le calice." These petals (the measurement refers to the limb) are certainly large for *G. purpureum* and for this reason Wilmott (1921) dismisses the possibility that this represents the same taxon as his var. *forsteri*. This could not be regarded as the last word on the subject for whereas Wilmott concluded, quite unjustifiably, that the "rarement presque orangées" added to the "anthères jaunes" in the description of *purpureum* was "presumably added for the benefit of this *G. Robertianum* form" he admitted that he had seen no material from Rouy's type-locality (maritime shingle between Cayeux and le Hourdel, dept. Somme). Actually Rouy points out that it is in his var. *semiglabrum* that the anthers are rather orange.

However, there is material of Rouy's var. *littorale* at Kew from the classic locality and an examination of this sheet together with several other collections from the same population (in the Paris herbarium) shows unquestionably that it consists of the nearly glabrous prostrate maritime form of *G. robertianum* which was first described by Babington (1851) as var. *maritimum*. Consequently Wilmott's name var. *forsteri* is genuinely the first to have been given to prostrate *G. purpureum*.

The following stations for subsp. *forsteri* are represented in British herbaria :—

CHANNEL ISLES :

GUERNSEY : Bordeaux Harbour, 1892, Marquand & Groves (B.M.), 1902, Cooper (B.M.), 1912, 1914, Barton (B.M., Camb., Ox.); St. Sampson's Bay, 1894, Gray (Camb.); Fort Cumberland, 1876, Wright (B.M.); Fort Doyle, 1892, Miller (Camb.).

V.c. 11. S. HANTS. : Stoke's Bay, 1829, Borrer (K.Borr., B.M.—Syntypes), 1871, Warner (B.M.Bosw.), 1878, 1883, J. Groves (B.M.); Southsea, 1836, E. P. (B.M.); Portsmouth, n.d., Macreight (K); Calshot, 1871, Streatfield (B.M., B.M.Bosw.); Hurst Castle, 1924, Turrill (K), 1928, 1929, Marsden-Jones (K), 1934, Ballard & Hubbard (K).

13. W. SUSSEX : A pair of compact populations sampled by many collectors and variously referred to as at Clymping, Middleton, Atherington or simply "between Littlehampton and Bognor," type and syntypes, 1919, A. J. Wilmott (B.M.). Also an isolated plant "close up to the sandhills at Littlehampton," 1919, Wilmott (B.M.).

It is not certain how many separate stations were represented here, but it is virtually certain that subsp. *forsteri* has been extinguished by man's activities in its Hampshire stations with the exception of that at Hurst Castle. The Sussex populations are now very small. Wilmott (1921) discusses the possibility that this subspecies occurred at one time at Selsey (on the authority of Dillenius) and at Swanage, in Dorset (from a reference by Sherard), but no vouchers have ever been located.

The general impression given by the distribution and state of the populations of both subspecies is far from being one of expansion (as suggested by Reid, 1911). It is rather one of gradual diminution and, in the case of outlying populations, of approaching or actual extinction. Along the south coast a retraction westwards seems to be indicated while the headquarters remains in the West Country. If this be the case, subsp. *forsteri* has lingered longer than subsp. *purpureum* and their relative numbers at Clymping (before seaweed-clearing by tractor almost wiped them out) seem to substantiate the belief that subsp. *forsteri* finds the conditions less unfavourable than subsp. *purpureum* and is slower to disappear. On the other hand, the extreme localisation of this subspecies, to a group of stations in Sussex and Hampshire on the one hand, and Guernsey on the other, might suggest a separate origin for the subspecies in each. In speculating upon this it may not be without significance that subsp. *purpureum* and prostrate *G. robertianum* are both known to have occurred in relatively close proximity to these groups of the prostrate subsp. *forsteri*. A combination of the features of subsp. *purpureum* and prostrate *G. robertianum* could produce the characters of subsp. *forsteri*, both morphological and ecological (including an intermediate climatic tolerance).

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COMPARATIVE STUDY OF DIPLOID AND TETRAPLOID SPORES OF *DRYOPTERIS DILATATA* FROM BRITAIN AND EUROPE*

By FERN WARD CRANE

Summit, New Jersey

It has been noted that spore characters are diagnostic for separating various North American taxa of *Dryopteris* (Crane, 1953). Professor Irene Manton (see Manton, 1950), University of Leeds, and Dr. Stanley Walker, University of Liverpool, who have worked on the cytology of diploid and tetraploid specimens of British and European *D. dilatata* (Hoffm.) A. Gray, report it difficult to distinguish the fronds on the basis of gross morphological characters. In a recent conference, Professor Manton asked me to describe spores of such specimens in order to ascertain any correlation.

Mature spores of *Dryopteris* are protected by an alate membrane or perispore (Bower, 1928). In the "*spinulosa*" complex this perispore is spinose, the size and spacing of spinules varying with the taxon. Since there is no appreciable difference between these spores whether collected from living plants or herbarium specimens, I make comparative studies from the dried fronds. Another factor, a proper mounting medium, insures the stability of material to be examined. Permount, a synthetic resin solution, is most suitable for preparing permanent slides. This medium does not cause shrinking or swelling of the spores, but it preserves them naturally and permanently.

The accompanying figures of typical diploid and tetraploid spores of *D. dilatata* were originally plotted on graph paper according to measurement. Diploid specimens, collected in Scotland, Sweden, and Switzerland, and tetraploid plants gathered in England, Ireland, and Sweden, were made available.

There proved to be surprising dissimilarities between spores of diploid and tetraploid specimens of *D. dilatata*. While the sizes are not particularly indicative, an obvious difference in texture can be observed at first glance, even under low magnification. The spore of the diploid has a thin, tan-coloured, membranous perispore; in that of the tetraploid this structure is heavy, dark brown, and coriaceous.

A measurable difference in spinule size and spacing on the perispore of the two types is another constant criterion of discrimination. In a spore of the diploid the spinules are minute, blunt-tipped, 1μ or less in height, and more or less widely spaced on the surface of the perispore. The spinules of a tetraploid specimen are large, heavy, coarse, thick-set, blunt-tipped, irregular, up to 2μ , and crowded.

Thus it may be concluded from the above observations that spore characters are diagnostic for the diploid and tetraploid *D. dilatata* under consideration.

It is possible that a similar situation occurs in *D. spinulosa* of North America, and this problem is being studied in collaboration with Manton & Walker (1953).

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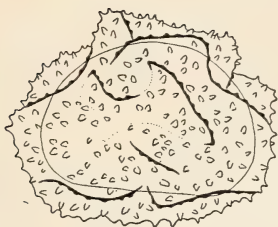


Fig. 1.

Diploid. Ben Lawers, Scotland. Crane #53141.

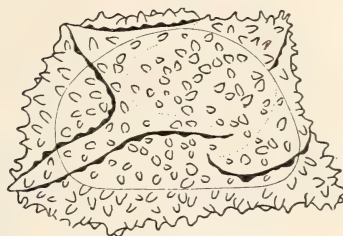


Fig. 4.

Tetraploid. England. Crane #53146.

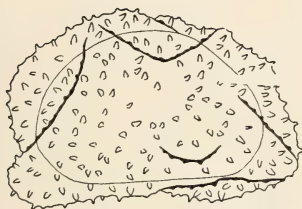


Fig. 2.

Diploid. Sweden. Crane #53139.

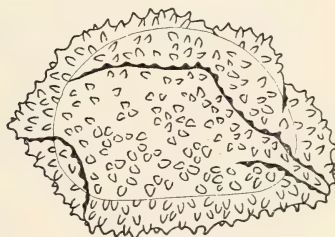


Fig. 5.

Tetraploid. Ireland. Crane #53142.

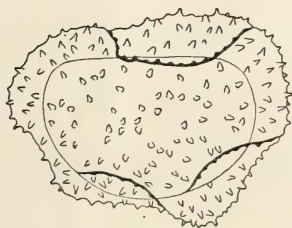


Fig. 3.

Diploid. Switzerland. Crane #53138.

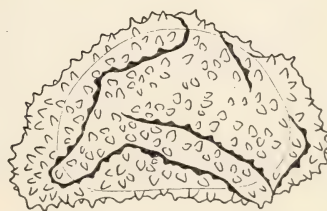


Fig. 6.

Tetraploid. Sweden. Crane #53143.

30 μ

CHROMOSOME RACES IN *CARDAMINE PRATENSIS* IN THE BRITISH ISLES

By F. HUSSEIN

Botany Department, Cairo University

INTRODUCTION

Cardamine pratensis L. is a highly variable species in its morphological characters, particularly in the type of flower. The prevailing type of flower is single, but some forms occur bearing completely sterile double flowers, with all the floral parts, except the calyx, petaloid. Another sterile double variant was recorded by Blackburn (1922) in which the flower resembles that of the double form of *Arabis caucasica* in that each flower repeats itself several times by a median bud ("Arabis type"). In 1923 she also noted, in Northumberland, the occurrence of a "semidouble" type, in which the ovary becomes swollen and bursts into a double or an incompletely fertile flower.

Early chromosome counts for the species were $2n = 32$ and $2n = 64$ by Manton (1932) for material collected from Cambridge and Southport respectively. Lawrence (1931) gives a count of $2n = 30$ for material obtained from the grounds of the John Innes Horticultural Institution. Flovik (1940) in his cytological survey of the Spitzbergen flora listed the species among those found in the polyploid form only ($2n = 64$). Guinochet (1946) recorded three chromosome numbers for material from the Jura Mountains: $2n = 16$, $2n = 30$ and $2n = 40$. Lövkqvist (1946) reported several counts for material collected from Southern Sweden. These were: $2n = 30$, 56, 60, 64, 68, 72 and 76 with a few of $2n = 58$ and 84. Banach (1950) gave a similar long list of numbers for Polish plants. Howard (1948) gave counts of $2n = 56$ for material collected from Cambridge and Cheshire. The present author (1948), working on the chromosome numbers and geographical distribution of the species in the British Isles, found only two chromosome races: $2n = 56$ and $2n = 30$.

The distribution map given in 1948 included 70 plants and it showed the restriction of the $2n = 30$ plant to the south and the prevalence of $2n = 56$ all over the country. My request for more material brought the number of investigated plants up to 113, obtained from 100 different localities, belonging to 31 vice-counties. The following account contains a more complete distribution map, a cytological study of the chromosome races and details of the relation between the different types of double flowers and the chromosome numbers.

RESULTS AND DISCUSSION

Geographical Distribution

Of the total number of plants only 19 gave counts of $2n = 30$, the rest of the material having a complement of $2n = 56$. No other chromosome race was found in the British Isles by me. Recently Mr. D. E. Allen has suggested that the $2n = 64$ count, originally made by Professor Manton for a plant from the Southport dunes, represents a third chromosome race which is readily distinguishable morphologically (Yearbook B.S.B.I., 1952, 56). The distribution map shows but one exception to the rule that the race with single flowers and lower chromosome number is restricted to the south. The exceptional plants were found in a wood in Northumberland in two different years. They may well have been due to accidental introduction with young trees since *Lilium martagon* was



found in the same wood and its presence certainly suggests planted, rather than natural, woodland. For the same reason—planting—the northern localities of the $2n = 30$ sterile doubles may not be significant as most of them were from gardens. The northern and wider distribution of the $2n = 56$ race and the virtual restriction of $2n = 30$ to the southern unglaciated regions of Britain may furnish another example of a polyploid race able to invade new regions in which its diploid relation cannot survive.

Cytological Differences

The $2n = 30$ plants had either a single, sterile double, or "Arabis type" flower. A comparison between the somatic chromosome complements of the three types did not show any obvious differences either in shape or in size of chromosomes (Fig. 1 a). Among members of the same complement shape and size differences were few. In length the

chromosomes measured about 1μ . Constrictions, seldom visible, were mainly sub-terminal or median, with a few submedian ones. There was, however, a longer pair measuring 2μ which seemed always to have a median constriction. In meiosis of the single flowers, a large diamond-shape bivalent with a median attachment was always clear and would correspond with the longest pair of somatic chromosomes (Fig. 1 b). Multivalents were found in about 2.5 per cent of cases and were either tri- or quadrivalents.

The results of anaphase separation were nearly always equal. These results agree with Lawrence's (1931) description, from which he concluded that the species is an allotetraploid.

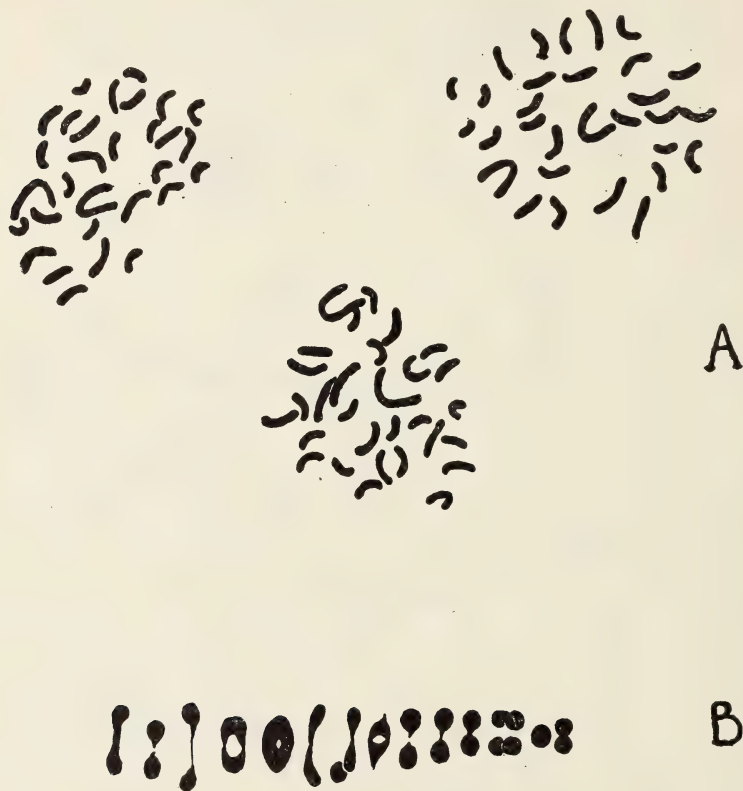


Fig. 1. (a) Somatic chromosomes of $2n = 30$ of a single, double and "Arabis" type; (b) Meiotic chromosomes of a single $2n = 30$.

Plants with $2n = 56$ had either single or semidouble flowers. The study of somatic and meiotic plates of the two types (see Fig. 2 a and b) showed no major differences.

The differences in size and shape among the chromosomes of the same complement were also few, and may be correlated with those found in the $2n = 30$ plants. However, owing to the smallness of the chromosomes, it was not possible to identify them individually and thus one could not judge the amount of similarity between the two races. The result of meiotic anaphase separation in $2n = 56$ was also equal. This race may be considered an aneuploid of an octoploid. Whether it is an auto- or allopolyploid of the $2n = 30$ race one cannot decide unless the meiotic behaviour of a hybrid and of an artificially produced $2n = 60$ is examined. Except for the aneuploidy, the case is similar to that

of *Nasturtium microphyllum* (*uniseriatum*) which proved to be an allopolyploid, rather than an autopolyploid, of *N. officinale* (Manton & Howard 1946). In such cases, smallness of the chromosomes makes it difficult to consider the lower percentage of multivalents as a definite criterion of allopolyploidy, although the high fertility of the $2n = 56$ race is suggestive. Morphological differences between the two chromosome races were quite notable and will be dealt with statistically in a following study.

Type of Flower

From the cytological data it was clear that doubleness of flower was of a different type in the two chromosome races. All sterile doubles including the *Arabis* type, were $2n = 30$, while all semidoubles were $2n = 56$.

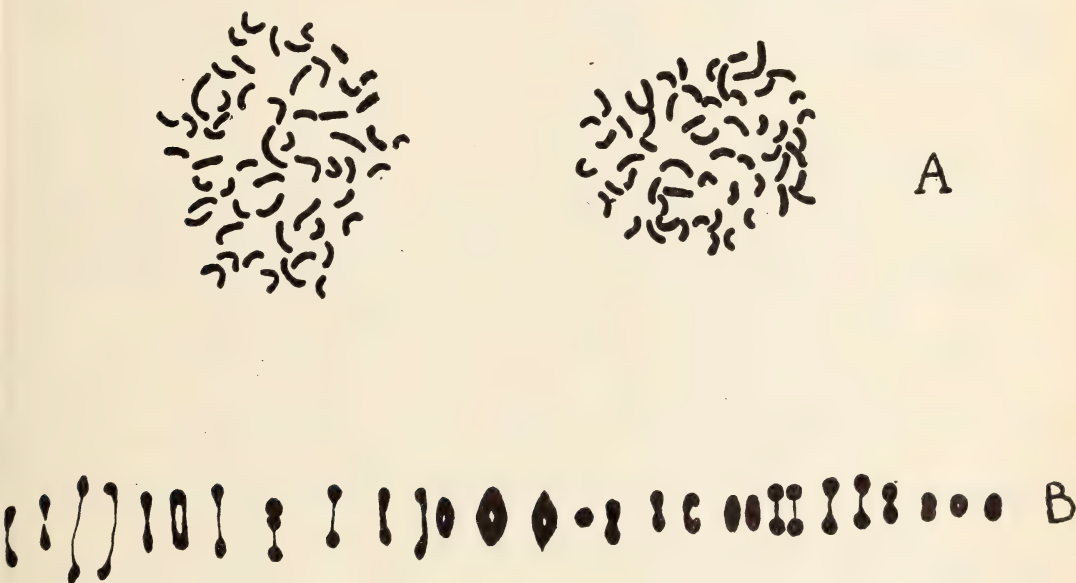


Fig. 2. (a) Somatic chromosomes of $2n = 56$ of a single and semi-double type; (b) Meiotic chromosomes of a $2n = 56$.

This may perhaps be considered as some indication that there is a genetic cause for all types of doubleness. Both sterile doubles and the *Arabis* type occurred without change under varying environmental conditions and were always vegetatively reproduced by the usual leaf buds, but in case of semidoubles, it was noticed that the proliferation occasionally, but not always, disappeared under greenhouse conditions in the following years, and some seeds were produced. It may be suggested that there is a physiological factor controlling the appearance of the semi-double condition.

SUMMARY

- (1) The variability of the species is indicated and a short review of literature on the chromosome number given.
- (2) Three aspects of the British races are discussed, geographical distribution, cytological differences and type of flower.
- (3) No chromosome races except $2n = 30$ and $2n = 56$ were found in the 113 plants examined.

(4) The distribution map supports the conclusion that the $2n = 30$ race is almost restricted to the southern unglaciated part of the country, and thus suggests the superiority of the $2n = 56$ race in invading new territory.

(5) A cytological comparison between the two races indicates that there is not sufficient evidence to determine the type of polyploid relationship between them.

(6) Doubleness of flower in both races is thought to have a genetical cause. In the $2n = 56$ race some unknown physiological factor may render it capable of setting seed. Both the cytological aspect and the subject of the physiological control of semi-doubleness are in need of further investigation.

ACKNOWLEDGMENTS

I am indebted to Professor M. Thomas and Dr. K. B. Blackburn of the Botany Department, King's College, Newcastle-upon-Tyne (University of Durham) for their unfailing interest during the progress of this work and to all those, too many to mention, who have generously supplied me with living material.

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VEGETATIVE REPRODUCTION IN *ARUM MACULUTUM*

By C. T. PRIME

Arum maculatum L. reproduces by seed, but before the corm is large enough to flower, daughters are budded off and these develop more rapidly than seedlings. *A. maculatum* is a gregarious plant growing in clumps or patches and this vegetative method of reproduction readily suggests how some of these may have come about. If the clump is a clone, then the plants would be expected to be identical. On the other hand, a bird or other dispersal agency might well drop several seeds close together. These seeds would most likely be of different genetic constitution, and in due course would give several closely associated plants showing more variation. There is also the third and most likely possibility, namely a combination of the two.

In order to get definite information on these points, certain clumps were dug up and the corms carefully mapped. In one quite typical area there were 233 plants, some in clumps, others more scattered. The general impression gained is that vegetative multiplication is more important than reproduction by seed. In this example about thirty to forty seeds could have accounted for the whole 233 plants. Thus vegetative multiplication is probably about six times as effective as reproduction by seed.

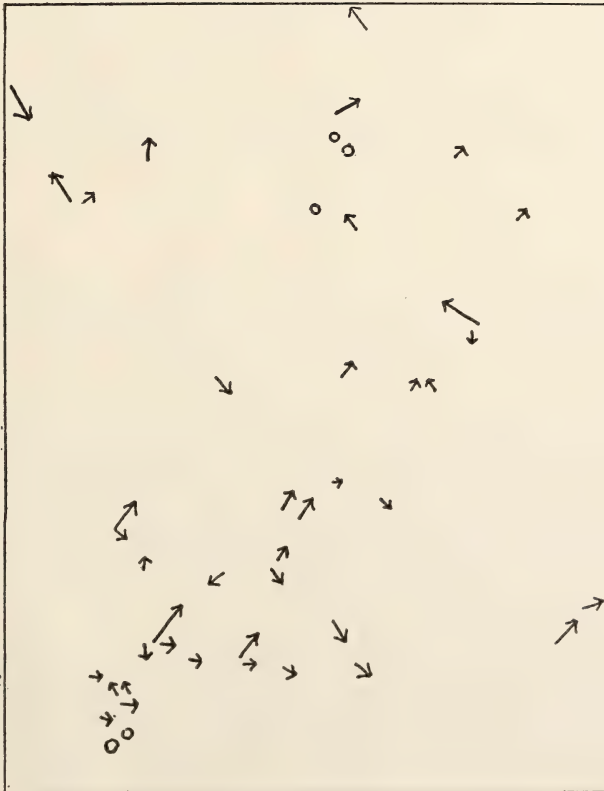


Fig. 1. Map of an *Arum* colony. The arrows indicate the direction of growth and length of corm, the circles indicate corms with a nearly vertical shoot. (Ground scale $\times \frac{1}{4}$; Corm lengths $\times \frac{1}{2}$).

Fig. 1 shows a much smaller area occupied by a group of plants all showing one leaf only. It will be noticed that the corms point in no particular direction and that some are beginning to reproduce vegetatively. It is evident that here the probability is that the great majority are seedlings. On the other hand, a colony is shown (Fig. 2) which was remarkably uniform in appearance. The spotting of the leaves was moderately reddish and it is of interest to note that the only plant which showed a very slight deviation from the rest was a small corm attached to the normal plant. It will be seen from this diagram that the direction of growth of the corms is such as to be completely compatible with vegetative reproduction from one original plant. This was perhaps more convincing in the field than the diagram would suggest. The possibility of some seedlings being present cannot be ruled out but, as these are usually found nearer the surface, the main fact seems clear enough. Further evidence is gained from the leaf measurements of the individuals in a clone. The leaf of *A. maculatum* does not reach full size until the plant is some years old. The measurements taken, therefore, were those from the third leaf of adult flowering plants. The number of mature plants in any one clone is not large but the table below gives the variation in leaf-length for three colonies which gave every appearance of being clones, compared with a similar number of individual leaf lengths chosen at random. The length variation is much less in the clones. This may be a reflection of the more uniform environment of the clone but other evidence, e.g. extreme similarity in the spotting, renders this interpretation the more unlikely.

TABLE 1
Leaf length in clones of *A. maculatum*.

Leaf length cm.	No. of leaves			
	Clone A	Clone B	Clone C	Random choice
8-8.9	1	-	-	1
9-9.9	4	-	-	2
10-10.9	5	1	-	-
11-11.9	1	2	3	1
12-12.9	-	2	4	1
13-13.9	-	4	3	3
14-14.9	-	-	1	-
15-15.9	-	-	-	2
16-16.9	-	-	-	-
17-17.9	-	-	-	1

It is therefore quite possible by studying the clumps in the field in this way to get a fair idea of how they have come into being.

THE MOVEMENT OF CORMS THROUGH THE SOIL

It will be evident from the diagrams that there is actual movement of the corms through the soil. Salisbury (1942) has noted that in heavy soils the resistance to growth may be considerable and says that comparative measurements of rhizome increments in heavier and lighter types of soil show that the annual increment is considerably influenced by this factor.

Attempts were made to measure the movement through the soil by marking the fruiting spike with stiff steel wire and noting the distance between the new shoots and

the wire the following year. Other methods were also used; several corms dug up in the resting period (August) were arranged round a central rod or placed carefully in line, and the positions of their shoots measured in successive years. In experiments involving 87 corms the total distance moved was 99 cm., an average of 1.12 cm per corm. The considerable variation in the individual result is plainly related to many factors. One is the point of origin of the bud giving rise to the next year's shoot, i.e. whether it originates,

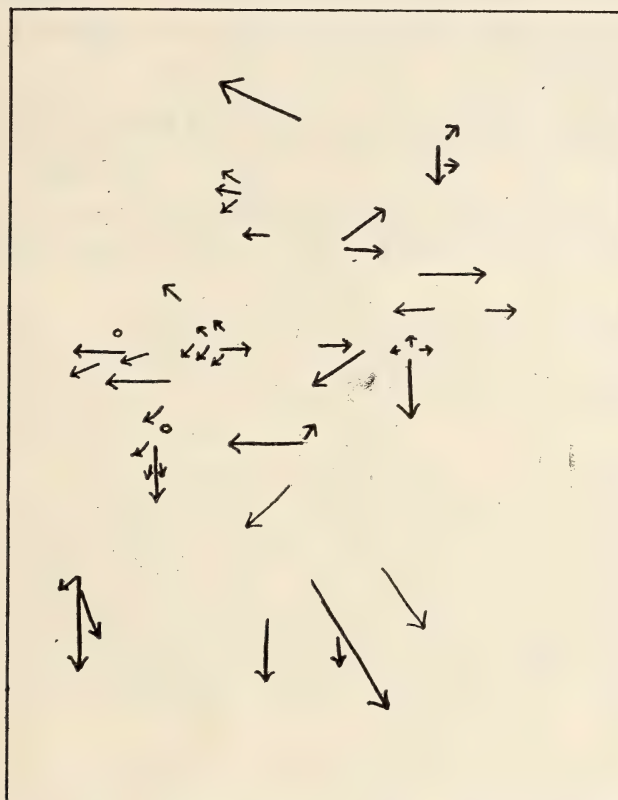


Fig. 2. Map of an *Arum* colony. The arrows indicate the direction and growth of length of corm.
(Ground scale $\times \frac{1}{2}$; Corm lengths $\times \frac{1}{2}$).

with reference to the main axis, behind, to the side of, or in front of the previous year's shoot. Another is the size of the corm itself which will be influenced by the habitat, and another the texture of the soil which will resist the movement.

The clone shown in Fig. 2 measured about 40 cm. across and the only data available suggest that the plant takes seven years to flower from the time of sowing. The first corms are small and in the first seven years it might be said that the corms move about

TABLE 2.
The death rate of *Arum* corms.

Date	Number of corms used	Number of originals lost
1948-49	200	16
1949-50	200	24

3-4 cm. through the soil in growing. Therefore it seems that the age of a colony about 45 cm. in diameter is not less than twenty or thirty years.

A certain number of corms die or are lost in any given year. In some experiments the results given in Table 2 were obtained.

The death of the older corms suggests a factor which limits the size of the clumps. If the older die and are succeeded by daughters, which do not all point in the same directions as the parents and which grow and move more slowly, then a limit will be set to the size, or the clump will break up into smaller parts.

The cause of the death of the older corms is obscure; in the experiment given above there was no evidence of the corms being eaten and in most cases the remains could be found. It was thought possible that flowering and fruiting might cause exhaustion leading to death. This was tested by experiment with negative result. Thus in one experiment the corms that flowered weighed 186.1 gm. in 1950 but 246.4 gm. in 1951. Those which did not flower weighed 264.2 gm. in 1950, and 257.1 gm. in 1951.

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REVIEWS

An Irish Flora. D. A. Webb. 8vo., pp. xxx + 250, 160 line drawings. Dundalgan Press Ltd., Dundalk, second edition 1953; 13/6.

The first edition of Professor Webb's *Irish Flora* was of rather limited appeal to the British botanist since it omitted descriptions of all the rarer plants and was intended as an introduction to a flora which is considerably smaller than our own. The second edition has been enlarged in effect by about 50 pages and now includes at least a brief diagnosis of all Irish plants and a fuller, though still 'introductory,' treatment of critical groups. It should therefore appeal to a wider botanical public, though its usefulness to the complete beginner has been skilfully preserved.

The descriptions of species are concise (they average about 5 lines) but clear, and usually adequate for distinguishing the plants in the field. The number of technical terms employed is small and simple definitions of them, often supplemented by reference to the figures, are given in the glossary.

Vegetative characters are extensively and, as far as can be judged, effectively used, particularly in the keys. The key to the ferns is especially notable in this respect and it will be interesting to test it in the field, though it appears to work well in the herbarium. It would have been an assistance to the user if the genera had been numbered in the keys as they are in the text. In families such as Cruciferae and Compositae one is left, after working through the key to genera, with several pages to search through until (if ever) the arrangement of the genera in these families has been learned by heart.

It will be regretted by many that Professor Webb has continued to give measurements in inches and fractions of inches. These units are much less convenient for the measurement of most parts of plants than centimetres and millimetres, though there is perhaps less risk of errors appearing in the text. It is noteworthy that no dimensions are given for the lemmas and anthers of the species of *Glyceria* section *Fluitantes*, though to anyone using the metric system these provide the easiest means of distinguishing the species.

This is, however, a minor drawback and any botanical visitor to Ireland will find this book very useful and of a convenient size to go in the pocket. It will also prove of great assistance to anyone beginning the study of the British flora, as it provides an easy means of identifying the great majority of our common species.

T. G. TUTIN.

Nordisk Kärleväxtflora I. N. Hylander. xv + 392 pp., 54 figs. and a map. Almquist and Wiksell, Stockholm, 1953; Sw. Kr. 58.

The appearance of the first volume of a new critical Flora of the 'Nordic' countries (Finland, Sweden, Norway, Denmark, Iceland and the Faeroes) is an event of major importance for European systematic botany. It is a tribute to the Linnean tradition in Sweden that such an ambitious project could be planned and executed, and this first volume sets a remarkably high standard in format, style and content.

The ten-page Introduction to the work contains much of interest to taxonomists concerning the scope of the Flora, the policy of admission of non-native species, nomenclatural treatment, and the like. Perhaps the most interesting general remarks concern the treatment of intraspecific variation. A glance at the main body of the Flora reveals the detailed nature of this treatment – *Sparganium erectum* L, for example, is given two pages of text and one of fruit illustrations – and the author's policy has been to concentrate attention on variation consisting of morphologically more or less distinct populations of reasonably wide distribution. In this field, as Dr. Hylander states, there is much that is obscure; and he has not hesitated to point out where knowledge is inadequate or entirely lacking. To risk a free translation (p. xiv): 'most Floras seem to me all too easily to give to the reader the dangerous impression that their treatment of systematic questions is final. A Flora must assuredly give as good a presentation as possible according to present knowledge; but it is almost equally important that it should indicate what we do not know but ought to!'

This first volume contains the Pteridophytes, Gymnosperms and the Monocotyledons, up and including Gramineae, but excluding Cyperaceae. Some idea of the value of the contents can perhaps best be given by selecting a few examples of the treatment of particular species.

Under *Sparganium erectum* L. (p. 83), already quoted, three subspecies are recognized, viz. ssp. *polyedrum* (A. & G.) Sch. & Th., ssp. *microcarpum* (Neum.), and ssp. *neglectum* (Beeby) Sch. & Th.; a detailed note in smaller type discusses the validity of this taxonomic treatment, giving valuable information on the apparent interfertility of the forms in different parts of their range, and accurate diagnostic descriptions, with illustrations, for all three. A purely nomenclatural point of interest is illustrated by this example; 'the author refuses to adopt the 'type subspecies' rule of the Stockholm *International Code* (1952), believing it to be impossible to reconcile with sound systematics.

Phleum pratense L. (p. 336) may be taken as a second example. Here the author has two subspecies' *nodosum* (L.) and *vulgare* (Cel.); he discusses the cytological difference but stresses the difficulty of separating morphologically certain forms of the hexaploid from the diploid *nodosum*. A similar 'conservative' view is shown in *Anthoxanthum* (p. 346), where a careful discussion of Löve's diploid *A. alpinum* (quoting also Tutin 1950) shows the author's inability to find the necessary morphological basis for a division into a southern tetraploid and a northern diploid species.

Other notes on intraspecific variation of particular interest to British botanists include *Pteridium* (p. 24) where the larger, softer southern Swedish form is said to be very probably identical with the British one and rather strikingly different from the common Scandinavian plant; *Ophioglossum* (p. 15), under which there is a discussion of the possible identity of the Icelandic variety (occurring around thermal springs) with the British and Atlantic European ssp. *polyphyllum* (Seub.); and *Sesleria* (p. 229), in which is illustrated the remarkable microscopic difference in leaf epidermis between the British and Swedish subspecies.

The choice of text-figures, the majority of which are reproduced from a wide variety of other works (including a few of the excellent drawings from Hyde and Wade, *Welsh Ferns*), seems on the whole to be a remarkably useful one, although, perhaps inevitably, the treatment of groups is very uneven and certain families, which would have benefited considerably (e.g. *Juncaceae*) are not permitted a single illustration.

The author's very considerably knowledge of the taxonomy and nomenclature of cultivated plants ensures that the treatment given, e.g. to the included non-native *Liliaceae*, *Amaryllidaceae* and *Iridaceae*, is informative and up-to-date, although naturally less space and smaller type is given to garden escapes, casuals, etc. The general policy of inclusion seems to be not unlike that familiar to British botanists in Clapham, Tutin & Warburg's *Flora of the British Isles*.

British botanists will also find refreshingly few points where the nomenclature differs from the new British Flora; there are of course the perennial sources of disagreement such as *Potamogeton pusillus*; and the grass genera *Bromus* and *Agropyron* are very differently circumscribed; but there are very few startling innovations such as *Asplenium scolopendrium* and *Arrhenatherum* including *Helictotrichon*.

There can be no doubt that Dr. Hylander has set himself a gigantic task which few could hope to discharge with anything like his ability. Volume 2, to contain the rest of the Monocotyledons, and the Dicotyledons up to the *Polygonaceae*, is well under preparation, and we can only hope that this great and valuable work can be carried through to a successful conclusion with no undue delay.

S. M. WALTERS.

THE CHANGING FLORA OF BRITAIN

A report of the Conference held in 1952. Edited by J. E. Lousley, pp. 204 + 6 half-tone plates and 25 figures in the text. Bound in buckram. The book contains contributions covering many aspects of the subject, including ecology, palaeo-botany, plant geography, the influx of alien plants, and conservation. The contributors include Dr. Maurice Burton, Prof. A. R. Clapham, Dr. H. Godwin, Canon C. E. Raven, Sir Edward Salisbury, Sir Arthur Tansley, Prof. T. G. Tutin, Dr. S. M. Walters, and Dr. E. F. Warburg. The volume provides much information which is not easily available elsewhere, and some that is new. It should be in the hands of all interested in British field botany. The price of the publication is 15/-, plus 8d. postage, and it is obtainable from E. B. Bangerter, c/o Dept. of Botany, British Museum (Natural History), Cromwell Road, London, S.W.7.

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VARIATION IN *ARUM MACULATUM*

By C. T. PRIME

A study of variation in *Arum maculatum* L. was made as part of an investigation into the general biology of the British species, and the following paper gives a short account of the results.

1. LEAF VARIATION

A. maculatum is slow to germinate; in the first six months the hypocotyl develops a small tuber which by the autumn following (one year after sowing) has developed three or four roots with a small shoot. The first leaf appears above ground in the following spring. This leaf is oval and only after three or four years is the characteristic sagittate shape developed. At maturity the plant usually bears three leaves though the number varies between two and four or even five. The most characteristic shape is shown by the second and third leaves, the first leaf being generally smaller, and borne on a shorter petiole (Table 1).

TABLE 1
Leaf length in *Arum maculatum*

Length of first leaf	8.47 cm. $\pm$.12 (σ = 1.32)
Length of second leaf	10.69 cm. $\pm$.12 (σ = 1.48)
Length of third leaf	11.79 cm. $\pm$.12 (σ = 2.20)

The third leaf may vary in length from 5-19 cm. and from 4-14 cm. in width. Observation and measurement show that any particular leaf form tends to be retained year by year (Table 2).

TABLE 2
The correlation between leaf dimension in successive years in *Arum maculatum*

Petiole length in 1943 and 1944	.58 (P.E. = .09)
Leaf length in 1943 and 1944	.48 (P.E. = .09)
Leaf width in 1943 and 1944	.31 (P.E. = .06)

The distribution of the spotted and unspotted leaf forms (var. *immaculatum*) has been investigated by Pethybridge (1903) who gives the following results.

Sussex :	99% unspotted
Hereford :	5 : 1 unspotted to spotted
Lincoln :	92% unspotted
Northumberland :	90% unspotted
Ireland :	500 : 1 unspotted to spotted

It is not said how these figures were obtained, whether they were visual impressions or otherwise. Bromfield (1856) also says the unspotted form is commoner in the North of England.

A more thorough investigation was undertaken with the assistance of other observers,

whose help is gratefully acknowledged. The results are shown on the map (Fig. 1) which shows clearly that the unspotted form becomes more frequent as one goes further north; there is clear evidence of a cline. The existence of this cline helps to confirm the northern limit of the species. It would be reasonable to regard most of the isolated clumps of spotted plants in northern Scotland (e.g. Aberdeen, Angus) as introduced, a view held by most local observers. Sowter (1949) draws the northern limit of the species between the River Forth and Argyll, and this is supported by the evidence from the cline. Thus there are twelve spotted to four unspotted records north of Sowter's line, but four spotted to fourteen immediately south of the line. If the above explanation is correct, it does not explain why the spotted plant was introduced rather than the unspotted. Possibly, it was considered the more ornamental, or perhaps it was more common at the time of introduction. Moreover the cause of the cline itself remains unexplained.

On the continent, Hock (1934) records a different result, considering the spotted form commoner in North Germany than in the South. All the native plants of Denmark are unspotted, but these belong to a separate chromosome race ($2n = 28$).

In addition to the change in the degree of spotting the size of the plant in this country decreases as one goes further north. The luxuriant growth of the southern plants, which sometimes reach 30 cm., gradually diminishes, 15-20 cm. being the normal height of the Scottish plants.

The leaves of *A. maculatum* contain cyanophoric glucosides. Several hundred tests (Prime 1951) indicated differences in the glucoside content, but these did not appear to be correlated with any other variation.

The stomatal index is not so constant as in other species, and there is no significant difference between plants from different localities, or plants with differing chromosome number. Stomatal index determinations varied from 7.0 to 11.5, the average being 9.28.

2. FLORAL VARIATION

Miller Christy (1914) drew attention to the rolling of the spathe; if it is rolled anti-clock-wise from above he described it as sinistral, if conversely as dextral. In over 1,200

TABLE 3
The numbers of sinistral and dextral spathes

Locality	Sinistral	Dextral	Approximate level of statistical significance	Observer	Date
Essex	645	583	10 %	Miller Christy	1914
Hereford	278	220	10 %	Armitage	1921
Croydon, Surrey	106	91		Prime	1946
Croydon, Surrey	537	463	3 %	Prime	1947
Croydon, Surrey	560	440	1 %	Prime	1948
Northumberland	36	18		Temperley	1949
Aberdeen	11	8		Kerr	1949
Beckenham, Kent	55	45		Sherwood	1949
Culford, Suffolk	10	7		Thompson	1950
Whitby, Yorks.	11	6		Little	1950
Bryanston, Dorset	13	12		Hawkins	1950
Mildenhall, Suffolk	349	314	20 %	Southwell	1950
Stroud, Gloucester	24	35		Hughes	1950
Alton, Hants.	179	140	13 %	Langridge	1950
Swindon, Wilts.	190	157	10 %	Timperley	1950
Bristol, Glos.	22	17		Timperley	1950
Total	3026	2556	1 %		



Fig. 1. The distribution of maculate and immaculate forms of *A. maculatum*. The percentage of spotted leaves is shown as the darkened sector of a circle. The largest circles are based on over 100 counts, the smaller on less than 100. Isolated records of spotted and unspotted forms are shown as the smallest black or white circles. Sower's northern limit for the species is given as a dotted line.

counts he found 10% excess of the sinistral form, a result later confirmed by Armitage (1921). Further results are given in Table 3, and the help of observers is gratefully acknowledged.

The total figures show the differences to be highly significant. It may be noted that there is no evidence of any clinal variation in this character.

In some polyploids there is a relationship between pollen grain size and chromosome number. Pollen from over a hundred samples of *A. maculatum* from over twenty-five localities was measured but it was all of similar size. The pollen of plants from Denmark ($2n = 28$) has the same diameter (41.5 ± 0.024 ; $\sigma = 1.7$) as that of the British plants and so also has the pollen of *A. italicum* Mill. and *A. neglectum* (Townsend) Ridl.

3. FRUIT VARIATION

This has been investigated by Colgan (1911) who compared spotted and unspotted plants, and Salisbury (1942). The following data are based on further counts of several hundred fruits just before ripening. The data may be presented and compared in various ways.

TABLE 4
The average number of fruits in *A. maculatum* and var. *immaculatum*

	Total number of fruits examined	Average number ovules per fruit	Average number ripe seeds per fruit
<i>A. maculatum</i>	1305	1.95 ± 0.39 ($\sigma = 1.40$)	1.36 ± 0.36 ($\sigma = 1.17$)
var. <i>immaculatum</i>	2973	1.73 ± 0.024 ($\sigma = 1.31$)	1.18 ± 0.021 ($\sigma = 1.09$)

The differences shown in Table 4 are statistically significant and further analysis of the figures in Table 5 by the χ^2 test shows that they are due to a tendency for *A. maculatum* to bear a larger number of fruits with a high number of ovules.

TABLE 5
The relation between the number of ovules per fruit and the total number of fruits

	Number of ovules per fruit									
	0	1	2	3	4	5	6	7	8	
<i>A. maculatum</i>	101	463	350	222	135	25	8		1	Data for '35, '40 and '41
var. <i>immaculatum</i>	202	1215	926	473	120	33	3	1		
	Number of ripe seeds per fruit									
	0	1	2	3	4	5				
<i>A. maculatum</i>	163	549	161	148	19	3	Data for '35, '36, '40 and '41			
var. <i>immaculatum</i>	396	1608	638	119	11	—				

The data for Tables 4 and 5 are based on several years' figures, but if data for separate years are analysed, they show that in some years there is no difference between the percentages of ripe ovules per fruit in the two forms. Thus the differences shown in Table 4 are really due to a large difference in one or two years.

Table 6 shows no significant statistical differences in 1936, 1940 and 1941, but

TABLE 6
The number of fruits and ovules in *A. maculatum* and var. *immaculatum* for 1935, '36, '39, '40 and '41.

Year	Number of fruits		Number of ripe seeds	
	<i>maculatum</i>	<i>immaculatum</i>	<i>maculatum</i>	<i>immaculatum</i>
1935	306	600	679	930
1936	143	824	228	1178
1939	376	507	368	598
1940	208	803	212	755
1941	341	473	435	529

significant differences in 1935 and 1939. Further in 1935, the number of ovules in *A. maculatum* was greater than expectation, while in 1939 the reverse was the case.

The average seed output (average number of ripe seeds per fruit $\times$ average number of fruits per spike) of the two forms is shown in Table 7.

TABLE 7
The average seed output of *A. maculatum* and var. *immaculatum*

	Average number fruits per spike	Average number seeds per fruit	Seed output
<i>A. maculatum</i>	26.63 $\pm$.41 (σ = 6.74)	1.36 $\pm$.036 (σ = 1.17)	36.21
var. <i>immaculatum</i>	27.98 $\pm$.34 (σ = 6.77)	1.18 $\pm$.021 (σ = 1.09)	33.01

Thus the significant differences observed between the seed production of the two forms do not account for the preponderance of the var. *immaculatum* and it is unlikely that they have any biological significance. A difference in the rate of vegetative reproduction would account for the greater frequency of var. *immaculatum* but individual forms vary so greatly in this respect that it has not been possible to demonstrate an overall significant difference. Many other factors, besides the reproductive, could operate to produce the observed distribution.

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NOTES ON THE IDENTIFICATION OF SOME BRITISH SPECIES OF *CALLITRICHE*

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Pearsall (1934) and Clapham (1952) point out the difficulty in identifying species of *Callitriche*, with considerable justification. The main reason for difficulty is that the only certain aid to identification is the characters of the mature fruit and often a plant to be identified is in a sterile condition. Identification keys, therefore, are obliged to contain vegetative characters, which here mean chiefly leaf characters. The variability of leaf form in some of the species, however, causes confusion. Again, it is sometimes stated that lower leaves of some species are linear, while upper leaves are oblong. This does not take into account the mode of growth of the plant under different circumstances. It is perfectly possible, as will be shown, for lower leaves to be oblong and upper leaves to be linear, a fact which would cause considerable confusion in identification.

A description follows of the general habit of growth in a species which displays marked variation in leaf form. In view of the importance of fruit form in the identification of species, a description of the fruit is also given. Four species are described: *C. intermedia* Hoffm., *C. obtusangula* Hegelm., *C. stagnalis* Scop., and *C. hermaphroditica* L. (*C. autumnalis* L.)

LEAF FORM IN *C. INTERMEDIA*

When the crown is submerged, linear leaves only are formed. When the crown arrives at the surface, obovate leaves are formed. Between the true obovate leaves and the original linear leaves, however, transitional leaves will appear. Once the crown arrives at the surface it will remain at the surface as long as the water level does not rise. Elongation of the internodes must then result in older leaves being carried down beneath the surface. It is evident then that beneath the surface will be found linear leaves at the base of the shoot, then linear-obovate transitional leaves and finally obovate leaves. In this way typically obovate leaves may be found well beneath the surface. It is therefore misleading to refer obovate leaves to the floating state only. Again, if the level of the water rises and the crown is submerged, then linear leaves will be formed. In this case lower leaves may be obovate and upper leaves linear. It is therefore misleading to refer to lower leaves as though they were necessarily linear, even though, from a consideration of the development of the seedling, growing upwards from the bottom mud of a pool, the sequence of events is certainly linear leaves at the base and then, when the surface is reached, obovate leaves.

FRUIT FORM

The female flower of *Callitriche* consists of a syncarpous ovary, 4-celled by secondary septation (Clapham, 1952), with typically 2 bracteoles. These latter may not be present in some species. The 2 styles are terminal in the young fruit, but, due to developmental changes with maturity, the styles may appear to arise from the sides of the ovary. When

the fruit is viewed from above, 4 lobes are seen, corresponding to the 4 cells. The prominence or otherwise of these lobes and whether they diverge from the point of insertion of the styles or are parallel are of considerable diagnostic importance. Unfortunately, a distinction is made between a less prominent lobe (termed a keel) and a more prominent lobe (or wing), the dividing line between the two states being somewhat obscure. In the present description, the margins of the lobes are described as keels. These are barely discernible in *C. obtusangula* (Fig. 2B 1-4). In *C. hermaphroditica* (Fig. 2D 1-4) a wing is present in addition. In the young fruit the keels may not be easily seen but in the mature fruit, due to the maturation of the seed within the more or less transparent fruit wall, the keels become more prominent. In any case, the young fruits of all 4 species to be described are remarkably similar and should not be used for identification. Where grooves are referred to these relate to the indentations between lobes – in fact between the original 2 carpels, whose positions are indicated by the style origins (Fig. 2C 3).

In this description a distinction will be made between terminal styles (Fig. 2C 1) and lateral styles (Fig. 2A 1). Again, some species have persistent styles and others have styles which fall early. It appears to the writer that the terminal style is associated with persistence and the lateral style with early falling. All styles are initially terminal. In *C. intermedia* for example, the lobes grow over the styles so that these appear lateral. Constriction may result in early fall. In *C. stagnalis*, the lobes grow under the styles keeping them in an erect, terminal position. Here there is no constriction and the styles persist.

METHODS AND MATERIALS

Material of *C. intermedia* (obovate-leaved), *C. obtusangula*, and *C. stagnalis* was obtained from a drainage ditch at Tanybwllch near Aberystwyth, Cardiganshire. Linear-leaved material of *C. intermedia* was obtained from the river Rheidol near Aberystwyth. The floral characters of the linear-leaved form agreed with that of the obovate-leaved form. These forms were also shown to be identical by means of transplant experiments (these are described elsewhere – Jones, 1955). *C. hermaphroditica* was gathered from the outflow of Llyn Maeiog in Anglesey, probably its southernmost locality in Britain.

In order to arrive at a 'typical' fruit form, ten fruits from each species were drawn silhouetted in face view with the aid of a camera lucida. The fruits were mature and in the case of each species were from several shoots. The average length and breadth of the ten fruits were calculated and a 'typical' fruit constructed diagrammatically to these dimensions, taking into consideration the general form shown by the ten fruits. Side views and views from above were constructed with a binocular microscope, a camera lucida being used initially to find the correct proportions. The views from above may not, in all cases, show the full thickness of the fruit as this had to be cut transversely and the top part placed on a slide. Otherwise it was found difficult to maintain the fruit absolutely upright.

Lengths of styles (mean of 10 styles from 5 fruits) were recorded where the fruit was mature and where the style was evidently entire. At later stages of fruit development, the distal portions of styles were commonly broken off. Filament lengths were taken from stamens with mature anthers. The length quoted is an average of 10 filament lengths, except in *C. hermaphroditica* where stamens were scarce. Here only 2 stamens were found with dehiscent anthers and where it could be assumed that the filaments were of maximum length. Bracteoles were found to be very variable in size and the bracteoles, illustrated in Fig. 2, 5 and 6, represent the largest recorded. Chromosome numbers were estimated from root-tip squashes.

Leaves were fixed in formalin-acetic-alcohol, and were sufficiently transparent after

a few days for details of venation to be clearly seen. For subsequent examination, leaves were transferred through a range of alcohols to water and mounted between glass in the negative carrier of a photographic enlarger. Photographic negatives were then made by projecting the image of the leaf on to a lantern plate, a millimetre grid being also projected on to the same plate to give the scale. The projected image from these negatives was then traced at suitable magnifications.

Aid in identification of the species was derived from : Hegelmaier (1864), Samuelsson (1925), Pearsall (1934), Butcher and Strudwick (1946) and Clapham (1952). Nomenclature follows that of the last quoted.* I should like also to acknowledge gratefully the facilities afforded me to examine the *Callitriche* species in the Welsh National Herbarium at the National Museum of Wales, Cardiff.

Since this account was written, a paper has appeared on the section *Eucallitriche* Hegelm. in the Netherlands, containing an account of the distribution and morphology (including chromosome morphology) (Schotsman 1954). In general (where the same morphological features are referred to) there is close agreement between the description of the first three of four species which follows and Schotsman's description of these species, if allowance is made for Schotsman's retention of the name *C. hamulata* Koch (with cogent reasons given for this) while in the present paper *C. intermedia* G. F. Hoffm. is used.

In the following description, where comparative statements are made, these refer only to the four species of *Callitriche* described.

A. *CALLITRICHE INTERMEDIA*

Leaf form (Fig. 1A 1-5)

The greatest range in leaf form is shown here. The extreme linear leaf is up to 4 cm. long by 1 mm. broad and has a pincer-like tip. While an emarginate tip may be seen on leaves in still water, the exaggerated pincer tip is displayed by leaves of plants found in running water. This may be connected with the maintenance of shoots in a horizontal or inclined plane by the water current since shoots submerged in still water in a horizontal plane produce leaves with pincer tips. The extreme obovate leaf is up to 2 cm. long by some 5 mm. broad. The tip of the leaf is emarginate, as indeed are all leaves of all four species described. The outline of the obovate leaf is of little use in separating *C. intermedia* from *C. obtusangula*. Figs. 1A 3 and 5 show how the tip of the leaf may be rounded or more or less pointed. The leaves 3, 4 and 5 are all from the same shoot, being separated from each other by 3 nodes. Leaf 3 was formed when the crown was at the surface. The level of the water then rose and leaf 4 is the result of submergence on the development of a leaf which had attained a certain stage under aerial conditions. The influence of submergence is greater on the basal part of the leaf since in *C. intermedia* this part develops last. Accordingly this leaf has a rounded tip and is attenuated basally. The crown subsequently arrived at the surface once more. Leaf 5 shows a somewhat pointed tip while basally it is broader than leaf 3. Leaf 5 reflects the influence of submergence in early development through its pointed tip while the later conditions of floating existence have resulted in the broader base. While, in the other 3 species considered, it appears that the range of leaf form is less marked, at the same time the writer considers that leaf shape cannot be relied upon in identification, unless the history of the shoot with regard to submergence or emergence is known.

In the obovate leaf 3 veins are present with possibly branching from the 2 lateral veins. In the linear leaf a single vein occurs. It appears that leaf shape and venation are controlled by separate factors. In the transition from obovate leaf to linear, it is

* Except for *C. autumnalis* which, according to Mr. J. E. Dandy, is an illegitimate substitute for the earlier *C. hermaphroditica* L.

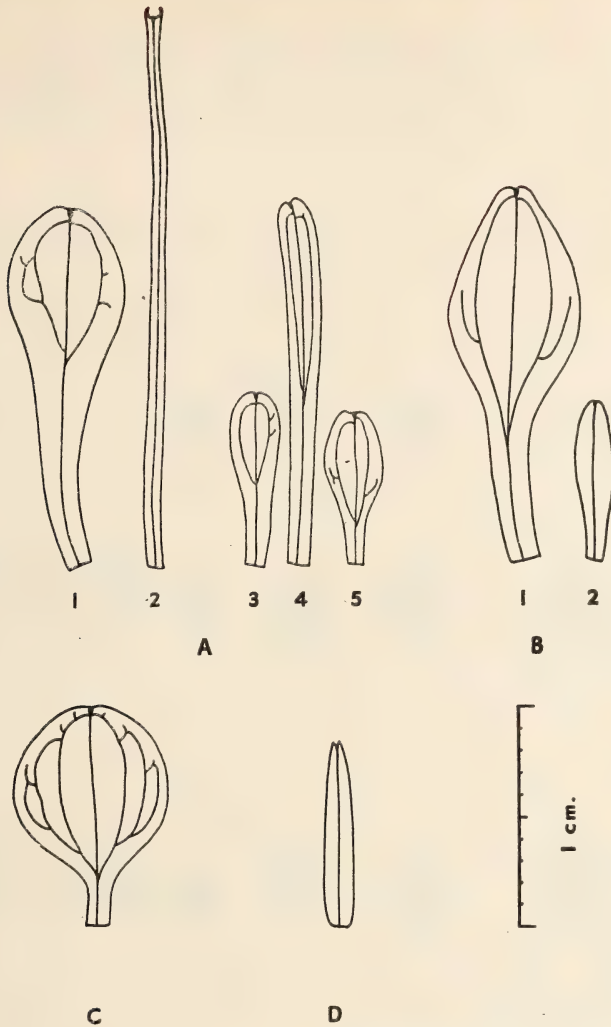


Fig. 1. Leaves of four species of *Callitriche*.

A. *C. intermedia*. 1 and 2 represent extremes of leaf form, 1 from a floating crown in still water and 2 from a submerged crown in running water. 3, 4 and 5 are leaves from the same shoot, there being three nodes between each leaf. Leaf 3 formed in a floating crown. The crown was then submerged and leaf 4 is the result of early development under floating conditions and later development under submerged conditions. The crown later arrived at the surface again and leaf 5 shows the influence of early development under submerged conditions and later development under floating conditions. B. *C. obtusangula*. 1. Leaf from floating crown. 2. Leaf from submerged axillary shoot. C. *C. stagnalis*. Leaf from floating crown. D. *C. hermaphroditica*. Leaf from submerged crown.

possible to have a leaf which is linear in outline with 3 veins. The converse is not true, however. As soon as an obovate leaf becomes discernible, the 3-veined condition occurs.

Fruit form and styles (Fig. 2A 1-4)

Fruits 1.3 mm. long by 1.4 mm. broad. In face view the fruits are not narrowed towards the base. Grooves and keels of medium development, the keels being parallel. Styles are lateral, between 1 and 2 mm. long and fall early. All fruits which have been observed in the Aberystwyth district over a period of some 9 years have been sessile. On

this latter character and by the possession (at least at times) of linear leaves with widened and deeply emarginate apices, the present description would appear to apply to subsp. *hamulata* (Koch) Clapham. Schotsman (1954) refers to stalked and non-stalked fruits, sometimes on the same plant, a character suggesting subsp. *pedunculata* (DC.) Clapham.

Bracteoles (Fig. 2A 6)

Those of the male flower small and falcate. Bracteoles of the female flower rare but of the form of the male bracteoles where present.

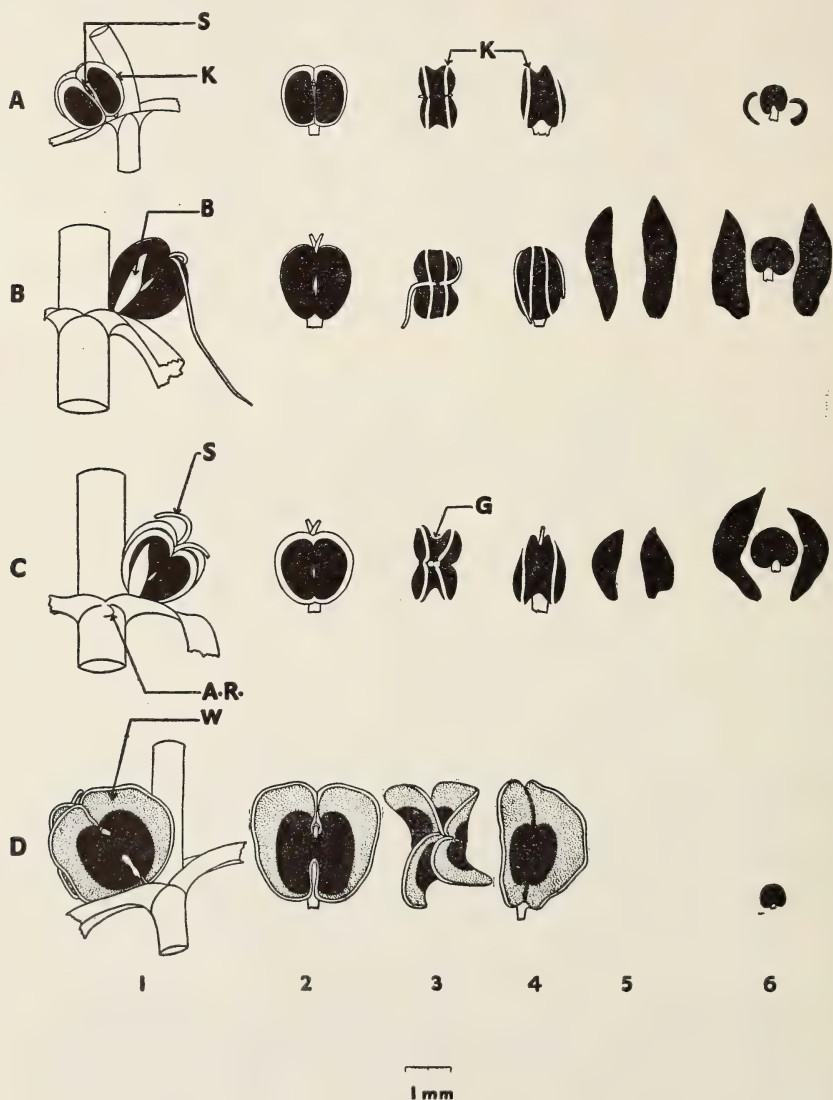


Fig. 2.

A. *C. intermedia*. B. *C. obtusangula*. C. *C. stagnalis*. D. *C. hermaphrodita*. 1. General habit of fruit at node. 2. Face view of typical fruit (diagrammatic). 3. Fruit viewed from above. 4. Fruit in side view. 5. Bracteoles of female flower. 6. Male flower (full length of stamen filament not shown). S - Style. K - Keel. B - Bracteole. G - Groove. A.R. - Adventitious root. W - Wing.

Stamens (Fig. 2A 6)

Filaments between 1 and 2 mm. and anthers small.

Chromosome number

$2n = 38$.

B. *CALLITRICHE OBTUSANGULA**Leaf form* (Fig. 1B 1 and 2)

Under conditions of still or slowly running water where the plant is usually encountered, obovate leaves about 1.5 cm. long by about 5 mm. broad are produced in the floating crowns. 3 veins are present with possibly secondary branches. The surface of the leaf bears raised ribs corresponding to the veins. More or less linear leaves are produced on submerged axillary shoots. These leaves are 1-veined, up to about 1 cm. long and 1 to 2 mm. broad. Under conditions of submergence in running water (under experimental conditions - Jones, 1955) linear leaves approximating more to those of *Callitriche intermedia* have been produced but without the pincer tip.

Fruit form and styles (Fig. 2B 1-4)

Fruits 1.6 mm. long by 1.5 mm. broad. In face view the fruits are narrowed slightly towards the base. Grooves and keels are poorly developed, characters which readily separate this species from the others described. Keels parallel. Styles terminal, about 4 mm. long and persistent.

Bracteoles (Fig. 2B 5 and 6)

Bracteoles of male and female flowers large and straight.

Stamens (Fig. 2B 6)

Filaments about 8 mm. and anthers large.

Chromosome number

$2n = 10$.

C. *CALLITRICHE STAGNALIS**Leaf form* (Fig. 1C)

In its typical form the leaf enables the species to be readily identified, the typical leaf being short (about 1 cm. long) and very broad (about 7 mm.). At least 5 veins are usually present. Leaves of submerged axillary shoots are also obovate in form. The first few leaves of the seedling are linear and 1-veined (Jones, 1955). While no seedlings have been grown by the writer beyond the 3 or 4 leaf stage, all seedlings of *C. stagnalis* which have been seen under natural conditions have linear initial leaves which then grade into very large multi-veined leaves, some 2.5 cm. long and 1 cm. broad (somewhat of the form figured for *C. obtusangula* in Fig. 1B 1). Subsequent leaves while still large - some 2 cm. long by about 1.3 cm. broad - are of the 'typical' rounded form. The large leaved form has always been found in the sterile condition and is probably a juvenile form. The chromosome number of the large form is $2n = 10$.

Fruit form and styles (Fig. 2C 1-4)

Fruits 1.6 mm. long by 1.7 mm. broad. In face view the fruits are narrowed slightly towards the base. Grooves and keels are well developed, the keels diverging noticeably

from the point of insertion of the styles. Styles are terminal, about 3 mm. long and persistent.

Bracteoles (Fig. 2C 5 and 6)

Bracteoles large, those of the female being straight and those of the male slightly falcate.

Stamens (Fig. 2C 6)

Filaments 4.5 mm. long, anthers large.

Chromosome number

$2n = 10$.

D. *CALLITRICHE HERMAPHRODITICA*

Leaf form (Fig. 1D)

Linear leaves only are described (this plant having been found by the writer always submerged). The leaf is about 1 cm. long and about 1.5 mm. broad. The leaf is broader at the base than at the tip and is characteristically curved downwards towards the base of the shoot. Leaf 1-veined.

Fruit form and styles (Fig. 2D 1-4)

Fruits 2.7 mm. long by 2.8 mm. broad. The size of the fruit alone is sufficient to identify this species. In face view the fruit is narrowed slightly towards the base. Grooves are very conspicuous, the lobes being produced into well-marked wings with sinuate margins. Wings are divergent. Styles are lateral, about 2 mm. long and fall early.

Bracteoles

Bracteoles are absent.

Stamens (Fig. 2D 6)

Filaments are short (1.2 mm.) and anthers are small.

Chromosome number

$2n = 6$.

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*CYTOGENETIC STUDIES
IN THE *DRYOPTERIS SPINULOSA* COMPLEX - I

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ABSTRACT

The inter-relationships of species within the *Dryopteris spinulosa* complex have been studied by investigating chromosome pairing during meiosis in wild and synthesised hybrids.

The three tetraploid species *D. cristata*, *D. spinulosa* and *D. dilatata* are shown to be allopolyploids requiring at least four ancestral diploids to account for their origin. Experimental hybridisations indicate that one of these ancestral genomes is now represented by two distinct diploid forms.

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(1) INTRODUCTION

A cytogenetic and taxonomic investigation of the *Dryopteris spinulosa* complex, as found in Europe and North America, is helping to elucidate the relationships between members of this circumboreal group of ferns. This paper is devoted entirely to the *D. spinulosa* complex in Europe. A report on the complex in N. America is being prepared, whilst further work, inter-relating species on both sides of the Atlantic, is in progress.

The *D. spinulosa* complex has long been a source of confusion for taxonomists. In modern Floras it is represented by three distinct species and the hybrids between them. The nomenclature varies somewhat but following Christensen (1905, 1913) they may be listed :

- (i) *Dryopteris cristata* (L.) A. Gray,
- (ii) *Dryopteris spinulosa* (O. F. Muell.) Watt,
- (iii) *Dryopteris dilatata* (Hoffm.) A. Gray,
- (iv) Hybrid, *D. × uliginosa* (Newm.) Druce (= *D. cristata* × *spinulosa*),
- (v) Hybrid, *D. dilatata* × *spinulosa*.

* Part of a thesis approved for the degree of Ph.D. by the University of Leeds.

D. cristata was first named by Linnaeus in 1753 as *Polypodium cristatum*. *D. spinulosa* was not recognised as a separate species until described as *Polypodium spinulosum* by Müller in 1767 and *D. dilatata* was not considered distinct from *P. spinulosum* until 1795 when it was named *Polypodium dilatatum* by Hoffmann.

Since these dates of separate recognition the generic conception has changed and the plants have been placed under *Aspidium*, *Nephrodium*, *Lastrea*, *Thelypteris* and *Dryopteris*. It is more significant, however, that some authors have referred to the three species merely as subspecies or even varieties of a single species (Newman, 1844, 1865; Druery, 1912). The specific epithet *dilatata* has been replaced in the new *Flora of the British Isles* (Warburg, 1952) by *austriaca*, following the continental nomenclature, and *D. cristata*, *D. spinulosa* and *D. austriaca* (Jacq.) Woytnar, 1915, are recognised as distinct species.

The use of the name *D. austriaca* raises problems of its own, however. Christensen (1913-16) states that "*D. austriaca* = *D. spinulosa*" and this was at a time when Christensen considered *D. spinulosa* and *D. dilatata* as separate species. The original name *Polypodium austriacum* was given to a fern collected by Jacquin (1764) but the type specimen is unavailable, even if one exists. Herbarium sheets from Jacquin's herbarium at the British Museum and labelled "*P. austriacum*", but not by Jacquin, are a mixed collection of genuine *D. spinulosa* and *D. dilatata*. Without returning to the type locality, a decision regarding the identity of *D. austriaca* cannot be reached and for this reason the writer prefers the retention of the name *D. dilatata*.

(2) MATERIALS

A number of collectors have helped to supply the material for the investigation, all of which has been checked for identification and cytological behaviour. Representative plants of all the specimens collected (except one) have been maintained in culture and herbarium specimens kept by the writer. A duplicate set of herbarium specimens is to be deposited with the British Museum (Natural History), London.

The material of *D. cristata* was collected and supplied originally from Surrey, England by its discoverer in that locality (Payne, 1939) and is now in cultivation at the Royal Botanic Gardens, Kew. From this specimen a number of plants have been raised and are now in cultivation at Liverpool. *D. spinulosa* has been sampled from England, France, Germany and Sweden. *D. dilatata* is known to include two cytological forms, one diploid and the other tetraploid (Manton, 1950). The tetraploid has been collected from France, Germany, Sweden, Ireland and many localities in England, and the diploid from Norway, Sweden, Switzerland, Scotland and also the island of Madeira (consideration of this plant is included here although it is from outside Europe).

Only one plant of the hybrid *D. × uliginosa* has been available owing to its relative rarity; this is maintained in cultivation at Leeds and was used also by Manton (1950) for cytological study. A number of specimens of the hybrid between *D. spinulosa* and *D. dilatata* have been collected from two Yorkshire (England) localities and a single specimen from Ireland, the latter having been found by Dr. R. L. Praeger.

(3) METHODS

Prothallial cultures were grown in 3 in. pots containing a sterilised compost comprising peat, loam and sand in the ratio of 3 : 2 : 1 respectively. The pots were protected from stray spores by clock glass covers and watered only from below, thus preventing access to free surface water and minimising the chances of fertilisation within parent cultures. The young prothalli could be maintained in a more juvenile state for a longer period if grown at temperatures of 70° to 80°F; in these conditions they were found to



Fig. 1. Silhouettes of specimen fronds from the tetraploid species and hybrid. ($\frac{1}{4}$ natural size).



(a) "*D. dilatata*" (2n-Scotland). (b) Hybrid (3n) "*D. dilatata*" (2n-Scotland) $\times$ *D. dilatata* (4n). (c) Hybrid (3n) "*D. dilatata*" (2n-Scotland) $\times$ *D. spinulosa*.

Fig. 2. Silhouettes of specimen fronds, as labelled (quarter natural size).



(a) "*D. dilatata*" (2n-Madeira). (b) Hybrid (3n) "*D. dilatata*" (2n-Madeira) $\times$ *D. dilatata* (4n). (c) Hybrid (3n) "*D. dilatata*" (2n-Madeira) $\times$ *D. spinulosa*.

Fig. 3. Silhouettes of specimen fronds, as labelled (quarter natural size).

produce large numbers of antheridia. Prothalli required as females were pricked out into pots at an early stage so that each prothallus was separated from its neighbour by about $\frac{3}{4}$ in.; this almost precludes fertilisation within the cultures before hybridisation.

Somatic chromosome counts have been made mainly by embedding and sectioning root tips and using iron haematoxylin stain, though some aceto-carmine root-tip squashes have also been made after hydroxyquinoline pretreatment (Tjio and Levan, 1950; Meyer, 1952). Hybrids became fertile approximately 12-18 months after fertilisation and detailed analyses of meiotic chromosome pairing have been made, using the aceto-carmine squash technique (Manton, 1950). Photographic evidence is supported by explanatory diagrams where necessary. In most cases the analyses have been made from several plants of the same hybrid combination.

(4) SURVEY OF THE PREVIOUS WORK

The taxonomic history has been outlined very briefly above. The three recognised species of the complex, *D. cristata*, *D. spinulosa* and *D. dilatata*, have a circumpolar distribution in the Northern Hemisphere, particularly within the Temperate Zone, and can be separated by their morphology and type of habitat (Warburg, 1952; Hyde & Wade, 1948). *D. cristata* is distinguished more readily from the other two species than these two are from one another. Consequently the exact distribution of *D. spinulosa* and *D. dilatata* is incompletely known as the two species have not always been treated as distinct.

The hybrids *D. × uliginosa* and *D. dilatata × spinulosa* can be found in habitats which will support both parents; *D. × uliginosa* is therefore restricted to very wet situations whereas *D. dilatata × spinulosa* abounds in marshy woods which are gradually drying out. Both hybrids exhibit morphological characters intermediate between those of their parents and produce abortive spores. The differences in frond shape and degree of pinnation in the species and species hybrids are illustrated by Fig. 1.

D. cristata, *D. spinulosa* and *D. dilatata* occur as tetraploids (Manton, 1950), each with regular chromosome pairing at meiosis and a gametic count of $n = 82$ (see Plate 15, fig. (a)). Manton also gave cytological evidence of hybridity for *D. × uliginosa* and the suspected hybrid between *D. spinulosa* and *D. dilatata*; both are tetraploid and show a number of paired and unpaired chromosomes during meiosis.

In 1948 a diploid form of *D. dilatata* was found on the continent and collected from Trondheim in Norway, Storlien in Sweden and Arolla in Switzerland (Manton, 1950). All show typical *D. dilatata* features but possess a more finely cut pinnation. This character was mentioned by Moore (1863) in his description of *D. dilatata* var. *alpina*. In 1949 a specimen agreeing with the characters of var. *alpina* was collected from the upper regions of Ben Lawers in Perthshire, Scotland (this was the location of the type specimen in Moore's herbarium) by Mr. A. H. G. Alston of the British Museum. This specimen is diploid and Ben Lawers is, as yet, the only confirmed locality in the British Isles where it can be found.

Another form of *D. dilatata* was collected from the island of Madeira in 1948 and is also diploid (Manton, unpublished). This is a very elegant form with an even more finely cut lamina and is quite distinct from the European diploids as illustrated by Figs. 2 (a) and 3 (a). All these diploids exhibit 41 bivalents during meiosis as seen in Plate 16, figs. (a) and (b).

(5) EXPERIMENTAL

(A) Hybrids of wild origin

The extent to which hybridisation occurs in the wild is relatively unknown in

Europe. Apart from *D. × uliginosa* and *D. dilatata × spinulosa*, only one other hybrid plant has been located which represents a cross between the diploid and tetraploid forms of *D. dilatata*. This plant was collected in 1951 by Mr. Alston near the Huberspitze in Bavaria. At the time of collection it was not recognised as a hybrid. It agrees morphologically with *D. dilatata* but differs cytologically in being triploid with $2n = 123$. A systematic search for more hybrids is yet to be made; probably the most reliable guide to hybridity in the field will be the production of abortive spores.

Cytological investigation of the wild hybrids is outlined below :

(1) *D. × uliginosa* (Newm.) Druce - Many squash preparations were sufficiently good to indicate that the number of univalents outnumbered that of the bivalents by approximately 2 : 1 but only four were available for complete meiotic analysis. Three of these contain 39 paired and 86 unpaired chromosomes and the remaining cell has 38 and 88 respectively. One plate showing the former arrangement is illustrated by Fig. 4 corresponding to the cell photographed in Plate 15 fig. (b).



Fig. 4. Explanatory diagram of Plate 15 fig. (b) showing meiosis in the tetraploid hybrid *D. × uliginosa*. $n = 39 \text{ pairs} + 86 \text{ singles}$ ($\times 1500$).

(2) *D. dilatata × spinulosa* - Three plants, each from a different locality, have been used in the study of meiosis in this hybrid. Ten cells have been analysed in which the numbers of bivalents vary from 32 to 35 and those of univalents from 100 to 94 correspondingly. An example of one plate showing the more constant number of 33 pairs and 98 singles can be seen on Plate 15, fig. (c), and explained by Fig. 5.

(3) Hybrid "*D. dilatata*" - This was not examined cytologically until the Spring of 1953 by which time a number of similar hybrids had been synthesised. Seven cells in 1st division meiosis were analysable; six show 38 bivalents and 47 univalents, as seen in Plate 15, fig. (d), and explained by Fig. 6 and the other has 39 bivalents and 45 univalents.



Fig. 5. Explanatory diagram of Plate 15, fig. (c) showing meiosis in the tetraploid hybrid *D. dilatata* $\times$ *D. spinulosa*. $n = 33$ pairs + 98 singles ($\times 1500$).

(B) Synthesised hybrids

The programme of hybridisation is conveniently summarised by Table 1, in which is indicated the number of attempts made at any one hybrid combination and the relative amounts of success achieved. Further information is given below.

(1) *D. cristata* $\times$ *D. spinulosa* – This attempt to synthesise *D. uliginosa* has so far been unsuccessful but more trials are being made.

(2) *D. dilatata* $\times$ *D. spinulosa* (4n) – Using *D. spinulosa* from France as the female and a British *D. dilatata* as male, it is probable that this wild hybrid has been synthesised; cytological proof, however, is wanting. Two plants out of four potential hybrids were normal *D. spinulosa*. The other two plants, however, exhibit glands on the rhachis and rhacheolae and possess an almost erect rhizome; these are now 3 years old but have never developed beyond a juvenile stage with fronds of 2 in. to 3 in. high. A reason for this lack of development is not evident. They have not produced fertile fronds and an investigation of the somatic chromosome number would not give confirmation of hybridity since both parents are tetraploid and the hybrid would be also.

(3) *D. cristata* $\times$ *D. dilatata* (4n) – The few attempts to cross these species have

TABLE 1

Hybridisation		No. of prothalli used	Fertilised Prothalli		Confirmed Selves		Confirmed Hybrids		Unconfirmed	
♀	♂		No.	%	No.	%	No.	%	No.	%
<i>D. cristata</i>	<i>D. spinulosa</i>	12	—	—	—	—	—	—	—	—
<i>D. spinulosa</i>	<i>D. dilatata</i> (4n)	12	4	33	2	50	—	—	2	50
<i>D. cristata</i>	<i>D. dilatata</i> (4n)	12	—	—	—	—	—	—	—	—
" <i>D. dilatata</i> " (2n-Scotland)	<i>D. dilatata</i> (4n)	36	30	83	2	7	28	93	—	—
<i>D. dilatata</i> (4n)	" <i>D. dilatata</i> " (2n-Scotland)	8	3	38	—	—	3	100	—	—
" <i>D. dilatata</i> " (2n-Norway)	<i>D. dilatata</i> (4n)	16	2	13	—	—	2	100	—	—
<i>D. dilatata</i> (4n)	" <i>D. dilatata</i> " (2n-Norway)	24	2	8	1	50	1	50	—	—
" <i>D. dilatata</i> " (2n-Switzerland)	<i>D. dilatata</i> (4n)	24	21	88	1	5	19	90	1	5
" <i>D. dilatata</i> " (2n-Madeira)	<i>D. dilatata</i> (4n)	34	15	44	2	13	13	87	—	—
<i>D. dilatata</i> (4n)	" <i>D. dilatata</i> " (2n-Madeira)	18	2	11	1	50	1	50	—	—
" <i>D. dilatata</i> " (2n-Scotland)	<i>D. spinulosa</i>	12	7	58	6	86	1	14	—	—
<i>D. spinulosa</i>	" <i>D. dilatata</i> " (2n-Scotland)	12	9	75	6	67	3	33	—	—
" <i>D. dilatata</i> " (2n-Madeira)	<i>D. spinulosa</i>	24	6	25	—	—	6	100	—	—
<i>D. spinulosa</i>	" <i>D. dilatata</i> " (2n-Madeira)	18	4	22	3	75	1	25	—	—
<i>D. cristata</i>	" <i>D. dilatata</i> " (2n-Scotland)	36	—	—	—	—	—	—	—	—
<i>D. cristata</i>	" <i>D. dilatata</i> " (2n-Madeira)	36	2	6	2	100	—	—	—	—



Fig. 6. Explanatory diagram of Plate 15, fig. (d) showing meiosis in the triploid hybrid "*D. dilatata*" (Bavaria).
 $n = 38 \text{ pairs} + 47 \text{ singles}$ ($\times 1500$).

been unsuccessful. The two species are ecologically separated in the wild and, so far, a wild hybrid is unknown.

(4) *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$ -Scotland) – A frond from a 3 years old plant of this combination is illustrated by Fig. 2 (b). In this particular plant the tetraploid had been used as the female parent. The morphology of the hybrid tends to be intermediate between that of its parents but likeness with the diploid is most evident. Tetraploids of different origin have been used with similar success and the reciprocal cross has also been made. Six chromosome analyses of meiosis in one cross and eight of the reciprocal show, in the majority of cases, 39 bivalents and 45 univalents. This can be seen in the photographed cell, Plate 16, fig. (c) and explained by Fig. 7. In two cases the number of bivalents formed was 38 and in another was 40.

(5) *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$ -Norway) – Spores collected from a plant in Trondheim, Norway were used as the source of the diploid in this hybrid. The original diploid plant was not maintained in culture but was examined cytologically by Manton (1950) and a herbarium specimen kept. Reciprocal crosses have been made. Altogether nine cells have been analysed at meiosis, seven of which show 39 paired and 45 unpaired chromosomes. The other two show 38 bivalents and 47 univalents.

(6) *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$ -Switzerland) – Using the diploid as female, 19 hybrids have, so far, been confirmed. The reciprocal cross has not been attempted. Only three cells have been completely analysed for chromosome pairing and, as in the previous hybrids involving European diploid and tetraploid forms of *D. dilatata*, 39 pairs and 45 singles can be recognised.



Fig. 7. Explanatory diagram of Plate 16, fig. (c) showing meiosis in the triploid hybrid *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$ -Scotland). $n = 39$ pairs + 45 singles ($\times 1500$).

(7) *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$ -Madeira) – A frond from a 3 year old hybrid plant in which the female parent was diploid is illustrated by Fig. 3 (b). Comparison of this with Fig. 2 (b) shows clearly the morphological differences found in triploid "*D. dilatata*" when the European or Madeiran diploid forms are used. Eleven analyses of meiotic chromosome pairing in one cross and four analyses from the reciprocal cross have been made. In all cells except one the number of bivalents ranges from 34 to 37 together with the corresponding 55 to 49 univalents; nine cells show 36 pairs and 51 singles. In one cell, however, as illustrated by Plate 16, fig. (d) and explanatory Fig. 8 one quadrivalent and one trivalent were found. One or two cells in anaphase have also suggested multivalent formation but the percentage is small. Small segmental interchanges between chromosomes otherwise non-homologous are probably the cause of multivalents in this case.

(8) "*D. dilatata*" ($2n$ -Scotland) $\times$ *D. spinulosa* – Fig. 2 (c) shows the outline of a frond from a hybrid plant when 18 months old. Intermediate characters between the parents such as pinnation, non-prostrate rhizome and two-coloured scales are evident in living specimens. Reciprocal crosses have been made and, in all, eight cells analysed during meiosis; 38 paired and 47 single chromosomes can be seen as in Plate 16, fig. (e) and explained by Fig. 9. Variations of $\pm$ one bivalent have been found in three of the plates examined.

(9) "*D. dilatata*" ($2n$ -Madeira) $\times$ *D. spinulosa* – Again reciprocal crosses have been made and Fig. 3 (c) shows a frond from a hybrid, when 18 months old. Cytological investigation of meiosis has shown 35 bivalents and 53 univalents in 7 analysed cells and 34 bivalents with 55 univalents in two other cells. An example of the former arrangement can be seen on Plate 16, fig. (f) and explanatory Fig. 10.

(10) *D. cristata* $\times$ "*D. dilatata*" ($2n$) – No hybrids have been formed when attempting to cross *D. cristata* with either of the diploid forms of *D. dilatata* from Scotland

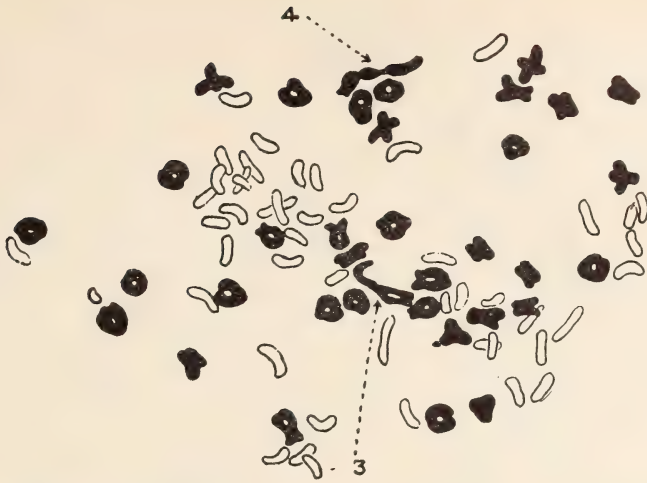


Fig. 8. Explanatory diagram of Plate 16, fig. (d) showing meiosis in the triploid hybrid *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$ -Madeira). $n = 1$ quadrivalent + 1 trivalent + 34 pairs + 48 singles ($\times 1500$).



Fig. 9. Explanatory diagram of Plate 16, fig. (e) showing meiosis in the triploid hybrid *D. spinulosa* $\times$ "*D. dilatata*" ($2n$ -Scotland). $n = 38$ pairs + 47 singles ($\times 1500$).

or Madeira. Two young plants which did develop were found to be normal *D. cristata* which had been used as the female parent and probably selfed at the time of attempted hybridisation.

Attempts to synthesise any hybrid utilising *D. cristata* as one parent have not been successful. The prothallial cultures of this species have never produced sex organs in quantity; the numbers of swimming spermatozooids have been relatively small and mature archegonia few at any one time. This may be attributed to the present cultural conditions

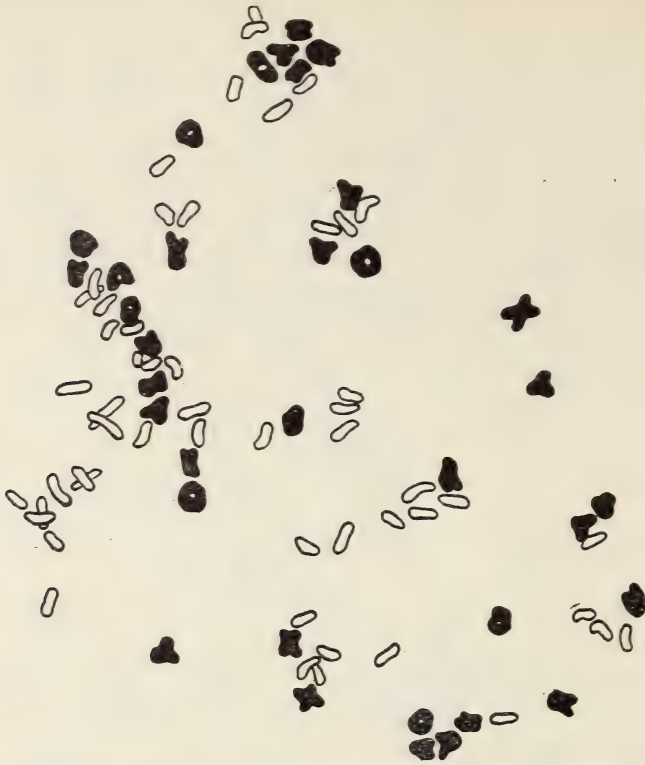


Fig. 10. Explanatory diagram of Plate 16, fig. (f) showing meiosis in the triploid hybrid *D. spinulosa* $\times$ "*D. dilatata*" (2n-Madeira). $n = 35$ pairs + 53 singles ($\times 1500$).

which, though satisfactory for other species, may have to be varied for a species like *D. cristata* which normally inhabits acid bogs and swampy places. The need for preventing access to free water within cultures may be disadvantageous for the normal growth and sex organ development in prothalli of *D. cristata*.

(6) DISCUSSION

Hybridisation within the *D. spinulosa* complex and the corresponding cytological evidence given above is represented by Fig. 11. Reciprocal hybrids have been studied in all the synthesised lines but no cytological differences found. Chromosome counts of the species and wild or synthesised hybrids so far investigated are summarised in Table 2.

In the genus *Dryopteris* the basic haploid chromosome number is $x = 41$ (Manton, 1950). The presence of 39 bivalents during meiosis in *D. $\times$ uliginosa* and of 33 in the hybrid *D. dilatata* $\times$ *spinulosa* is therefore highly significant since these numbers are not far removed from 41. Either autopolyploidy exists in one or more of the tetraploid species *D. cristata*, *D. spinulosa* and *D. dilatata*, in which case the bivalents could be formed from the gametic chromosome set of the autopolyploid parent, or there is evidence of allopolyploidy with common ancestral diploids, one between *D. cristata* and *D. spinulosa* and another between *D. spinulosa* and *D. dilatata*.

Not one of the three parent tetraploids exhibit multivalent formation during meiosis, which would indicate duplicated sets of chromosomes common to autopolyploids, but this ability may have been lost and yet the tendency for homologous pairing to occur in the

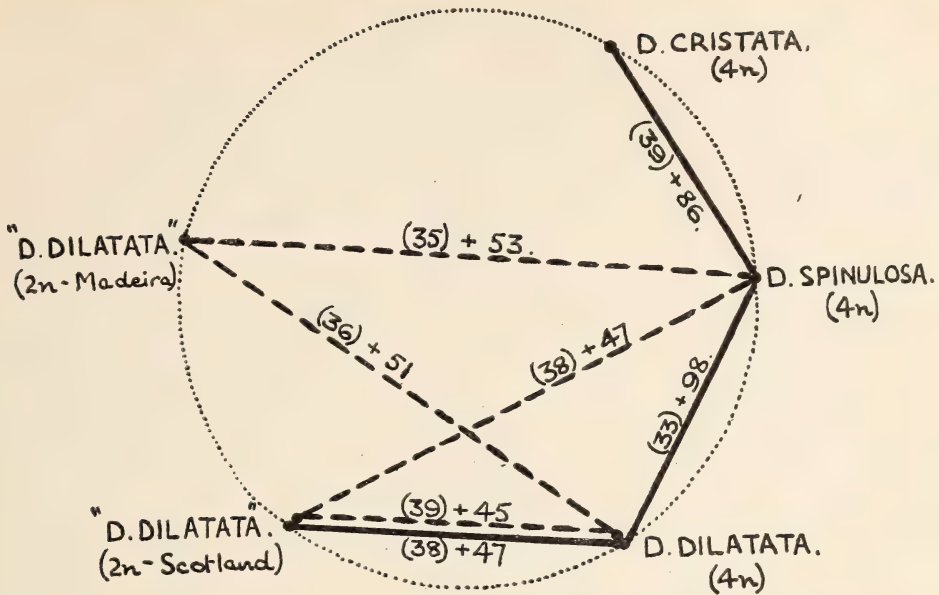


Fig. 11. Hybridisation within the complex. Continuous lines show wild hybrids and broken lines those synthesised. Numbers of bivalents formed during meiosis are shown in brackets; other numbers represent the univalents formed.

gametic chromosome set present in a species-hybrid still remain. The available evidence, however, suggests that *D. cristata*, *D. spinulosa* and *D. dilatata* are in fact allotetraploids.

In Eastern North America and Canada *D. cristata* is involved in a number of hybrids which have been cytologically examined (Manton & Walker, 1953; Walker, unpublished). Two of these are triploid and show complete failure of pairing at meiosis but another is tetraploid with pairs and univalents; bivalents are not formed therefore where there is a lack of chromosome homology between the parent species and this excludes autopolyploidy in *D. cristata*.

Evidence against autopolyploidy in *D. dilatata* has been provided by an investigation of induced apogamy in this species (Manton & Walker, 1954). An apogamous sporophyte with a somatic complement of 82 (normal sexually reproduced sporophytes have $2n=164$) shows complete failure of pairing between these chromosomes during meiotic division.

For *D. spinulosa* the evidence is less complete. This species does not, so far as is known, form hybrids, which show complete failure of meiotic chromosome pairing, nor has the formation of an apogamous plant yet been induced. Reference to Fig. 11 however, will indicate the variation in the number of bivalents (33 to 39) formed in hybrids involving *D. spinulosa*. If this species were an autotetraploid, the number of bivalents, arising from homologous pairs within the gametic chromosome set, should remain more constant in the different hybrids.

The *D. spinulosa* complex includes, on available evidence, three allotetraploid species inter-related by common diploid ancestors. If the genomes of the ancestral diploids are represented by letters, the genetic constitution of the three allotetraploids can be illustrated as below :

<i>D. cristata</i>	..	A + B
<i>D. spinulosa</i>	..	B + C
<i>D. dilatata</i>	..	C + D (or B + D, or C + A)

TABLE 2

Species or Hybrid	Source	2n (Roots)	n (bivalents in brackets)	Ploidy
<i>D. cristata</i> (L.) A. Gray	England	c. 160	(82)	Tetraploid
<i>D. spinulosa</i> (Müll.) Watt	England	—	(82)	Tetraploid
	France	c. 160	(82)	Tetraploid
	Germany	—	(82)	Tetraploid
	Sweden	—	(82)	Tetraploid
<i>D. dilatata</i> (Hoffm.) A. Gray	England	c. 160	(82)	Tetraploid
	France	—	(82)	Tetraploid
	Germany	—	(82)	Tetraploid
	Ireland	—	(82)	Tetraploid
	Shetlands	—	(82)	Tetraploid
	Sweden	—	(82)	Tetraploid
" <i>D. dilatata</i> "	Madeira	82	(41)	Diploid
	Norway	—	(41)*	Diploid
	Scotland	82	(41)	Diploid
	Sweden	82	(41)	Diploid
	Switzerland	—	(41)	Diploid
" <i>D. dilatata</i> "	Bavaria	—	(38) + 47	Triploid
<i>D. × uliginosa</i> (Newm.) Druce	Continent	c. 160	(39) + 86	Tetraploid
<i>D. dilatata × spinulosa</i>	England	—	(33) + 98	Tetraploid
	Ireland	c. 160	(34) + 96	Tetraploid
<i>D. dilatata</i> (induced apogamy)	England	82	82	Diploid
<i>D. dilatata</i> (4n) × " <i>D. dilatata</i> " (2n-Britain)	Synthetic	c. 120	(39) + 45	Triploid
<i>D. dilatata</i> (4n) × " <i>D. dilatata</i> " (2n-Norway)	Synthetic	c. 120	(39) + 45	Triploid
<i>D. dilatata</i> (4n) × " <i>D. dilatata</i> " (2n-Switzerland)	Synthetic	c. 120	(39) + 45	Triploid
<i>D. dilatata</i> (4n) × " <i>D. dilatata</i> " (2n-Madeira)	Synthetic	c. 120	(36) + 51	Triploid
" <i>D. dilatata</i> " (2n-Britain) × <i>D. spinulosa</i>	Synthetic	c. 120	(38) + 47	Triploid
" <i>D. dilatata</i> " (2n-Madeira) × <i>D. spinulosa</i>	Synthetic	c. 120	(35) + 53	Triploid

* (Manton, 1950)

The ancestral genome B is common to *D. cristata* and *D. spinulosa*, whilst C is common to *D. spinulosa* and *D. dilatata*. That genome B cannot be common to all three species is evident from hybrids known in N. America and those synthesised between European and American species of the complex (Walker, unpublished); this excludes the alternative B + D combination for *D. dilatata* as above. The combination C + A can also be excluded since genome A must carry the factors responsible for simple pinnation in *D. cristata* and the suggested genome D will be responsible for the erect rhizome habit and scale colour in *D. dilatata*.

The three tetraploid species within the complex can have been formed therefore only as a result of hybridisation amongst at least four ancestral diploids, and as the present-day distribution of *D. cristata*, *D. spinulosa* and *D. dilatata* is wide so is the field of search for ancient diploids.

Hybrids which have been synthesised between the diploids from Europe and Madeira and tetraploid *D. dilatata* or *D. spinulosa* are all triploid and show an approximation to equal numbers of bivalents and univalents during meiosis (Table 2). This suggests that the ancestral diploid common to *D. dilatata* and *D. spinulosa* is now represented by diploid forms of "*D. dilatata*" in Europe and Madeira. The diploids from Britain, Norway, Sweden and Switzerland are similar in their morphology and cytological behaviour; hybrids between any one of them and tetraploid *D. dilatata* show the same number of bivalents when analysed during meiosis. The diploid from Madeira, however, is distinct in its morphology, being more finely cut than the European diploids and also producing spores smaller in size, which average $42\ \mu$ in length as against an average of $55\ \mu$. It differs cytologically when involved in triploid hybrids; the number of bivalents formed in hybrids with the Madeiran form is constantly lower than in triploids involving the European form; in those with the European form there are 38 to 39 pairs and with the Madeira form 35 to 36 pairs with a possibility of multivalent formation to a very small degree.

These differences between the diploid forms are significant but nevertheless insufficient to suggest that the diploids represent other than the same ancestral genome from which they evolved separately; their separation may well have taken place even before the origin of the tetraploid species. That the two diploid forms represent the same ancestral genome can be confirmed by hybridisation between them. This is now in progress. If the two forms are closely related, as seems to be the case from experimental hybrids, chromosome pairing should be high in the hybrid with a possibility of a few univalents or one or two multivalents.

Separation of the Madeiran form from the normal tetraploid *D. dilatata* is simple on the type of pinnation alone, although spore size differences apply also as in the separation of the Madeiran and European diploids. It is more difficult to distinguish the European diploid from the tetraploid, particularly in the field. The problem is enhanced by the wide range of form exhibited by the tetraploid itself which may vary in mature size and shape even in the same locality. The most reliable macroscopic characters in the diploid are the marked unevenly deltoid basal pinnae and the greater tendency to tripinnation. However, microscopic characters are more useful and recently Crane (1955) has shown that the spores of the tetraploid and diploid *D. dilatata* differ in their ornamentation, though not in their size. Other characters are being studied.

The diploids from Europe and Madeira differ from tetraploid *D. dilatata* both cytologically and in their morphology. Triploid hybrids, wild and synthesised, are sterile with abortive spores. On this evidence the diploids represent a distinct species and should be separated from *D. dilatata*. Further, the European and Madeiran forms of the diploid can be separated from one another by their morphology and slight chromosomal differences exhibited in the synthesised hybrids; they are worthy of subspecific recognition. The final details of nomenclature and taxonomic descriptions of the diploids will be considered in a later paper when the inter-relationships of species in Europe and N. America have been made known.

The *D. spinulosa* complex in Europe now consists of four recognisable species, three tetraploid and one diploid, with hybrids between them, both tetraploid and triploid. To what extent, if any, the hybrids are able to back-cross is unknown, though the appearance of mixed populations of *D. dilatata* and *D. spinulosa* suggests there may be slight fertility

in the hybrids. Spore sowings have not confirmed this and the apparent intergrading is probably not a result of introgression but arises from the polymorphism present in *D. dilatata*. A detailed cytological survey of mixed populations could give further information. An alternative explanation of the appearance of mixed populations may simply be the effect of matrocliny; Chandler (1948) working on the morphology of *Dryopteris* hybrids in N. America does suggest that this may occur in the wild. In the experimental hybridisation between species of the *D. spinulosa* complex reciprocal crosses have been made without any evidence of matrocliny; in almost every synthesised triploid there has been evidence of the diploid involved, irrespective of whether the diploid was the male or female parent. This could be explained by gene dosage, each triploid possessing twice the genome of the diploid present, and would not discount matrocliny as a possibility in tetraploid hybrids.

(7) SUMMARY

Cytological observations have been made on the species and species-hybrids, both wild and synthesised, in the *Dryopteris spinulosa* complex as represented in Europe (see Table 2 and Fig. 11).

There are three tetraploid species in the complex, namely *D. cristata*, *D. spinulosa* and *D. dilatata*, all of which are allopolyploids. At least four ancestral diploid species would be required to account for the origin of these triploids. One of the ancestral genomes is common to *D. cristata* and *D. spinulosa*, and another is common to *D. spinulosa* and *D. dilatata*.

Chromosome pairing in synthesised hybrids suggests that the common ancestor of *D. spinulosa* and *D. dilatata* is now represented by two distinct diploid forms of "*D. dilatata*"; one is found in Britain and on the continent of Europe and the other on the island of Madeira. It is suggested that these forms should be recognised as subspecies of a single diploid species which is additional to the polyploid complex. The nomenclature and taxonomic description must be left for discussion in a later paper. These diploids differ slightly in their cytological behaviour when hybridised with the tetraploid species *D. spinulosa* or *D. dilatata*, indicating that there is differentiation within the diploid genome resulting in a loss of chromosome homology.

Reciprocal crosses between species in different grades of ploidy have been made without difficulty or evidence of matrocliny.

(8) ACKNOWLEDGMENTS

I am indebted to Professor I. Manton for her supervision of this work, the supply of material and criticism of the manuscript. Thanks for material and discussion on the taxonomy of the complex are due also to Mr. A. H. G. Alston and for further suggestions to my colleagues at Liverpool.

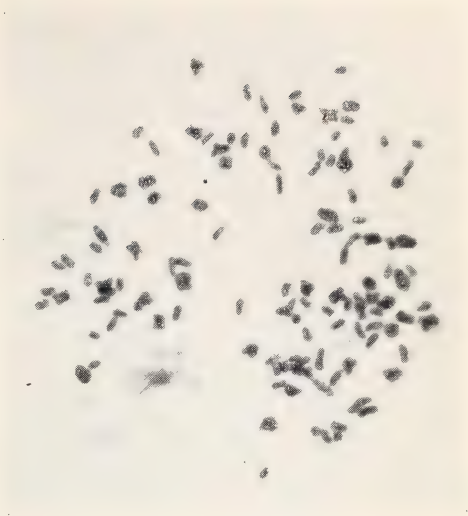
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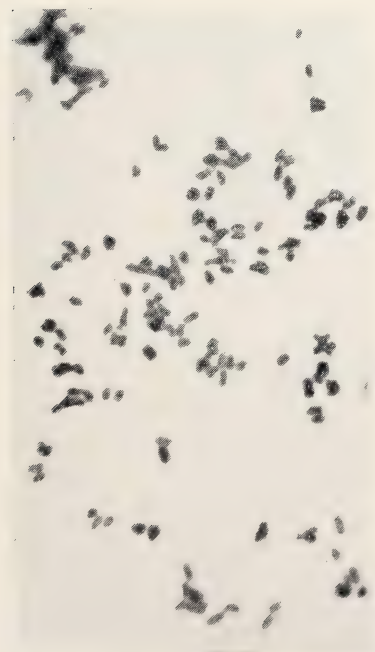
PLATE 15



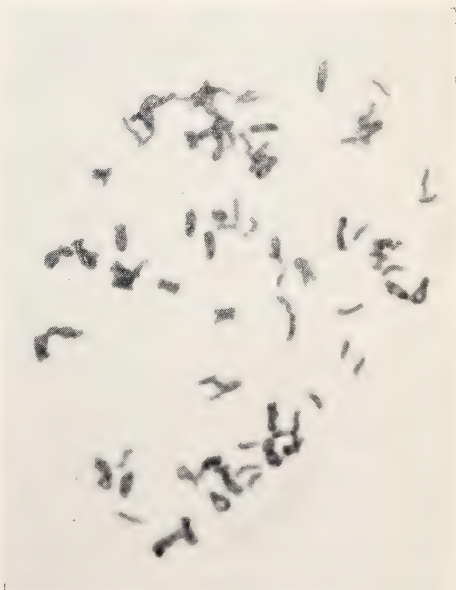
(a)



(b)



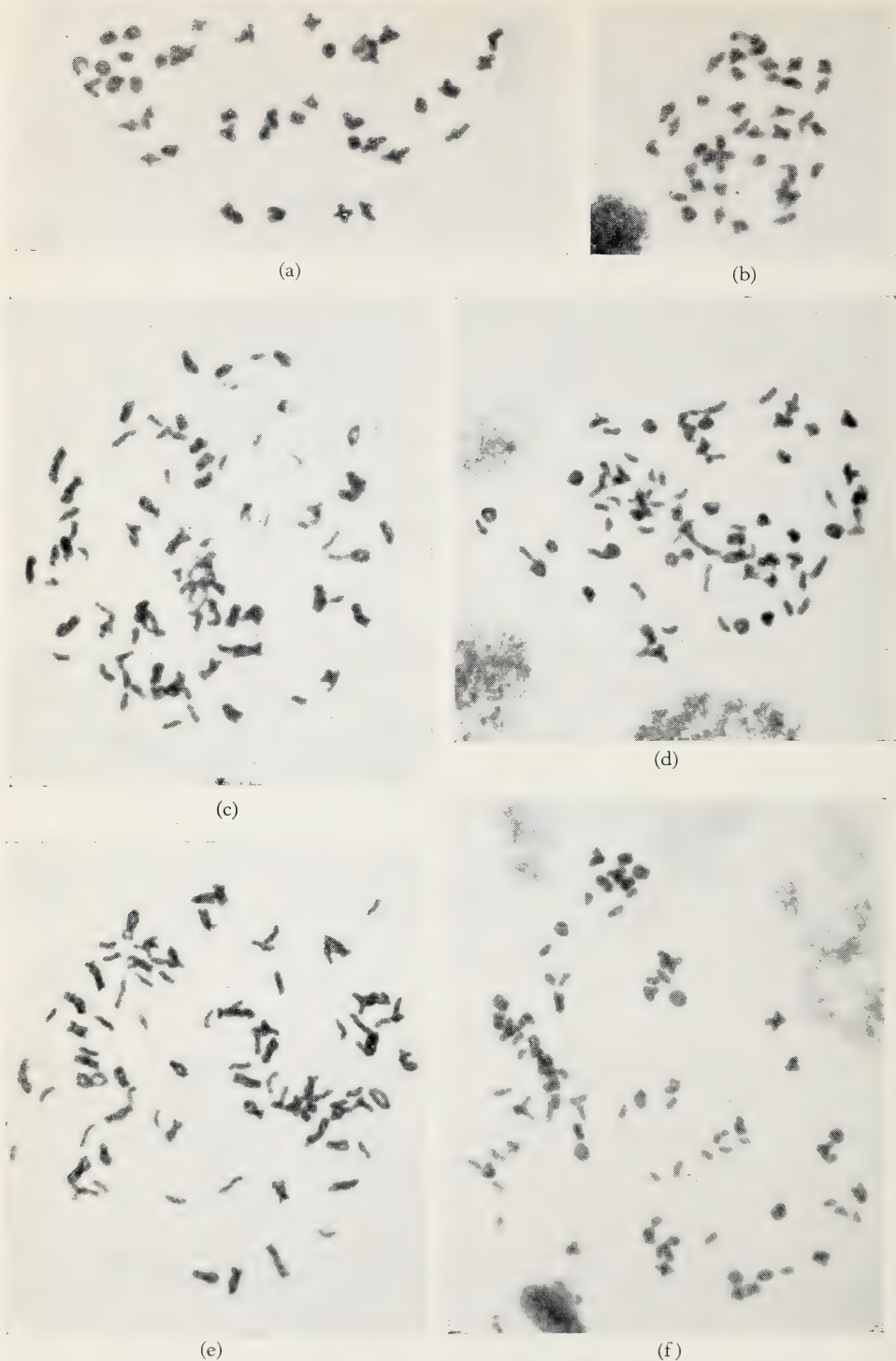
(c)



(d)

Shows meiosis in the following :

- (a) *D. cristata*. 1st diakinesis. $n = 82$ pairs ($\times 1,000$).
- (b) *D. x uliginosa*. 1st metaphase. $n = 39$ pairs + 86 singles ($\times 1,000$). See explanatory Fig. 4.
- (c) Hybrid *D. dilatata* $\times$ *spinulosa*. 1st metaphase. $n = 33$ pairs + 98 singles. ($\times 1,000$). See explanatory Fig. 5.
- (d) Hybrid "*D. dilatata*" (Bavaria). 1st diakinesis, early. $n = 38$ pairs + 47 singles ($\times 1,000$). See explanatory Fig. 6.



Shows meiosis in the following :

- (a) "*D. dilatata*" (Scotland). 1st diakinesis. $n = 41$ pairs ($\times 1,000$).
- (b) "*D. dilatata*" (Madeira). 1st diakinesis. $n = 41$ pairs ($\times 1,000$).
- (c) Hybrid *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$, Scotland). 1st diakinesis, early. $n = 39$ pairs + 45 singles ($\times 1,000$). See explanatory Fig. 7.
- (d) Hybrid *D. dilatata* ($4n$) $\times$ "*D. dilatata*" ($2n$, Madeira). 1st diakinesis. $n = 1$ quadrivalent + 1 trivalent + 34 pairs + 48 singles ($\times 1,000$). See explanatory Fig. 8.
- (e) Hybrid "*D. dilatata*" ($2n$, Scotland) $\times$ *D. spinulosa*. 1st diakinesis, early. $n = 38$ pairs + 47 singles ($\times 1,000$). See explanatory Fig. 9.
- (f) Hybrid "*D. dilatata*" ($2n$, Madeira) $\times$ *D. spinulosa*. 1st diakinesis. $n = 35$ pairs + 53 singles ($\times 1,000$). See explanatory Fig. 10.

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TRAGOPOGON PRATENSIS IN THE CENTRAL COTSWOLDS

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Three subspecies of *Tragopogon pratensis* L. are listed by Clapham (1952) but in the *Flora of Gloucestershire* (Riddelsdell, Hedley & Price, 1948) two of these subspecies are recorded as distinct species, namely, *T. minor* Mill. and *T. pratensis* L., and it is stated that the records do not distinguish clearly between them, it being thought that the great majority of the plants belong to *T. minor*. Thus a study of the distribution and cytology of *T. pratensis* and its subspecies was made in the Cirencester area, embracing much of the central Cotswolds and coinciding with botanical districts 6 and 7b of Gloucestershire which are parts of vice-counties 33 and 34.

In the Central Cotswolds *T. pratensis* is exceptionally common on road verges, a fact which greatly facilitated the sampling, and is also found in waste places such as old quarries and gravel pits. The species is common on permanent grasslands, being most abundant on rough pastures subjected to little interference by man. The soils colonised in the area were chiefly over the Oolitic limestones with a pH of approximately 7.2, though other soils were the Fullers earth, pH 6.2, Alluvial soils, pH 7.0, and Corn-brash, pH 7.0, determined by pH meter. The main characteristics of the subspecies were studied by the individual examination of 2,450 plants from a wide variety of habitats and all have been found to be *T. pratensis* subsp. *minor*. The observations were made when capitula were open, for reasons discussed below. Further and more detailed data within a single population at Deer Park, Cirencester, were obtained from a limited number of specimens.

TABLE 1
Plant characters of *T. pratensis* subsp. *minor* from Deer Park, Cirencester

Character	Sample size	Mean
1. Number of basal branches	45	5.6 $\pm$ 0.62
2. Number of capitula per plant	100	17.2 $\pm$ 0.91
3. Number of florets per capitulum	100	55.35 $\pm$ 1.07
4. Number of ligules per capitulum	100	8.39 $\pm$ 0.11
5. Number of achenes per capitulum	50	34.94 $\pm$ 2.02
6. Number of fruiting heads per plant	50	16.86 $\pm$ 1.31

As the identification of the subspecies depends chiefly upon floral characters, the structure and behaviour of the capitula were closely investigated. The apical capitula open first and do so during the morning between 7.0 a.m. and 2.10 p.m. B.S.T. at Cirencester. The outer florets of the capitulum open first and are about or just over half the length of the bracts. The corolla is bright yellow, and the anthers are purple to brown above and yellow below. A pale yellow, bifid stigma leads to an inferior ovary, there being a pappus of hairs. Observations showed that the closed stigma emerges through the fused anthers which split along their inner walls thus dusting the outer

sides of the stigma. The stigma opens before it has fully emerged above the anthers and pollen readily finds its way on to it. This introrse dehiscence has been found on marked capitula before the involucre has opened, and thus a cleistogamous behaviour may be common in the outer and older florets of any head.

After fertilisation, ovary development is rapid, so that the tips of the outer florets may be lifted above the involucre even though the central florets may be undeveloped. These fertilised florets soon show a browning with orange-tinging of the corolla and browning of anthers and stigma. When all florets are fertilised, the capitulum remains closed; thus closed and open capitula are to be found on the same plant. As the ovaries increase in length, the withering floral parts are eventually ejected past the tips of the involucre and the pappus becomes visible. When ripe, the achene-bearing capitula open during fine weather and do so well into the evening. The development of capitula is uneven and so all stages from flowering to ripe achenes may be found on single plants.

The effect of ovary elongation is important in relationship to the identification of the subspecies and records should only be made in the morning when flowering capitula will be open and fertilised heads closed. Partially fertilised heads show florets of variable length and only the true flowering heads should be used for classification.

The extreme unevenness of emergence and ripening of capitula prevented assessment of the number of achenes produced by individual plants. Thus mature heads were taken at random during the season and the mean number of achenes per capitulum calculated. The mean number of fruiting heads per plant was then calculated in late August and the multiple of these gave an approximate output of 589 achenes per plant.

The seed gave an 85 per cent germination so that the effective reproductive capacity was 480.65 per plant. The achene weight was calculated by weighing three samples of 100 achenes from which the long beaks had been removed. The achene weight was 0.00744 grams.

Basal branching from the lowest axillary buds is a characteristic feature of the species and a mean number of 5.6 ± 0.62 main branches per plant was obtained by late August sampling.

The number of ligules per capitulum was 8.39 ± 0.11 and indicates a variability which is considerable even within single plants.

The number of florets per capitulum was 55.35 ± 1.07 and it is interesting to compare this with the number of achenes per capitulum. It is seen that there is considerable difference, probably due to competition in the capitulum, since empty achenes are invariably in the centre of the head. The latter cannot be taken as a means of calculating fertility.

T. pratensis has a chromosome number of $2n = 12$ (Winge, 1938), and Ownbey (1950) has given the same number for North American material morphologically identical with subsp. *pratensis*. Clapham (1952) gives two chromosome numbers, $2n = 12$ for subsp. *minor* and $2n = 14$ for subsp. *pratensis*. In the present work, meiosis in anthers has been studied in detail and observations on root tips and other somatic tissue, such as the corolla, have been made. In all approximately 200 plants have been counted by the Feulgen squash and aceto-carmin squash techniques and permanent preparations have been made (Darlington & La Cour, 1947). The plants were selected from a wide variety of habitats and distribution and in all cases $2n = 12$. P.M.C. meiosis has regularly shown six bivalents. At diakinesis the shorter chromosomes normally form ringlike structures having two chiasmata, usually terminal in position. The one long bivalent usually shows three chiasmata. One feature, common at anaphase and telophase, is the lagging in the separation of the long bivalent so that a chain-like appearance results. This is probably the same as the bridge-like structure described from one plant by Ownbey

(1950). Separation is eventually normal. The absence of subsp. *pratensis* has not permitted any work on the different numbers reported by Clapham (1952) and Ownbey (1950).

Two fungous parasites have been of widespread occurrence namely *Cystopus cubicus* (Strauss ex Unger) Lév. and *Puccinia hysteriorum* (Strauss) Röhling. The former causes white blistering on all parts of the plant and when severe has prevented flowering. *P. hysteriorum* is easily detected by its orange coloured sori; infection is invariably severe. The attacked plants develop a sickly yellow colour and the capitula are often severely torn so that they become blind.

From the notes above, it will be seen that in the identification of the subspecies the making of field observations during the morning is of critical importance. Some difficulty was encountered in the early observations, but this was resolved when variable floret-length within capitula of single plants was seen to result from ovary elongation following fertilisation. It is possible that the ambiguity which might arise from this fact has been responsible for the large number of previous records for subsp. *pratensis* in Gloucestershire and in the area of survey. No specimens of subsp. *pratensis* have been found in the present field work and whilst this cannot be complete enough to be absolute it is obvious that subsp. *minor* is the prevalent type.

Detailed examination has shown floral morphology of remarkable uniformity and the main characters in the central Cotswold plants may be summarized as follows :

Subsp:	Florets	Bracts	Anthers	Achene	Chromosome
					No.
<i>minor</i>	Bright, sometimes pale yellow; approx. half length of bracts	Red or pink bordered	Dark purple to brown above, yellow below	Outer scaly muricate ridges, tuberculate in between	12

In conclusion I should like to thank Mr. J. Stevens for his ready aid and Dr. I. G. Thorpe for his interest in the fungi, also to Principal Botflower for facilities.

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TAXONOMIC STUDIES IN THE GENUS *CERASTIUM*

1. *C. ATROVIRENS*, *C. PUMILUM*, *C. SEMIDECANDRUM*

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The treatment of 'critical groups' is today the subject of much discussion amongst systematists. Usually, these groups are those where the variation of morphological characters between the groups overlap to such an extent that it is not possible to find good correlation of these characters nor definite bimodality of the distribution of their variation. Further confusion has been caused by the use of indefinite adjectives in descriptions such as "long," "short," "large," "small," etc.; this leads to a very subjective classification whose value it is difficult to test or assess. Appropriate biometric and statistical methods can reduce the subjective element in classification, and some of these together with their merits are described by Whitehead (1954).

The annual species (section *Viscosa*) of the genus *Cerastium* are an example of taxa which have given difficulty to taxonomists although the reason for such difficulty may not be immediately apparent. Of these species the following are the subject of the present investigations: *C. atrovirens* Bab. (*C. tetrandrum* Curt.), *C. semidecandrum* L., *C. pumilum* Curt., *C. subtetrandrum* (Lange) Murb. and *C. glutinosum* Fr.

A close examination of these taxa shows that there is considerable variation and on the basis of any one character complete separation is not possible. In this investigation an attempt has been made to find characters relatively unaffected by growth conditions and the following were chosen for use in the biometrical treatment which follows:

1. *Seed size* – that is to say, the length of the seed multiplied by its breadth. Length was taken as being the distance between the funicle and the centre of the opposite arc. Breadth was taken as being the greatest distance at right angles to the length.

2. *Pollen size*. The pollen grains were found to be spherical if undamaged. The dimension used was that of the diameter of the grain.

3. *Sepal/Petal ratio*. This was the average length of the sepals divided by the average length of the petals. Sepal length was measured from the inner point of attachment on the receptacle to the end of the scarious tip, if present, not including hair bases. Petal length was measured from the inner point of attachment on the receptacle to the extreme point of the longest of the two, three or four divisions of the petal.

4. *Bract/Scarious tip ratio*. This ratio was that between the total length of the bract divided by the length of the scarious tip. The bract was taken as being the top-most bracteole subtending a developed bud or flower. The length was measured from the inner point of attachment on the stem to the extreme point, not including enlarged hair bases. The scarious tip was measured from the point at which, in the centre of the bract, the cells ceased to contain chlorophyll, to the extreme point of the bract, not including hair bases.

5. *Petal/Cleft ratio*. This ratio was that between the length of the petal and the length of the cleft. Petal length was measured as in determining the sepal/petal ratio.

The cleft was measured from the deepest point of the cleft to the extreme point of the longest of the petal divisions.

6. *Petal Length/Breadth ratio*. This ratio was that of the total length of the petal to its breadth. Length was measured as described above and breadth was measured at widest point at right angles to a line joining the lowest point of the cleft to the centre of the petal base.

THE CHARACTER SEED SIZE

This character was examined in detail because Scandinavian taxonomists have attached much importance to it. A good example of its use is to be found in Lindman (1918). It is used, in this flora, to distinguish between *C. atrovirens* and *C. subtetrandrum* and between *C. pumilum* and *C. glutinosum*; the seed sizes being given as 0.7 mm and 0.5 mm, respectively. No seed size is given for *C. semidecandrum*. It is obviously necessary to know to what extent this character varies from plant to plant in the same population and from cloned plant to cloned plant under different conditions.

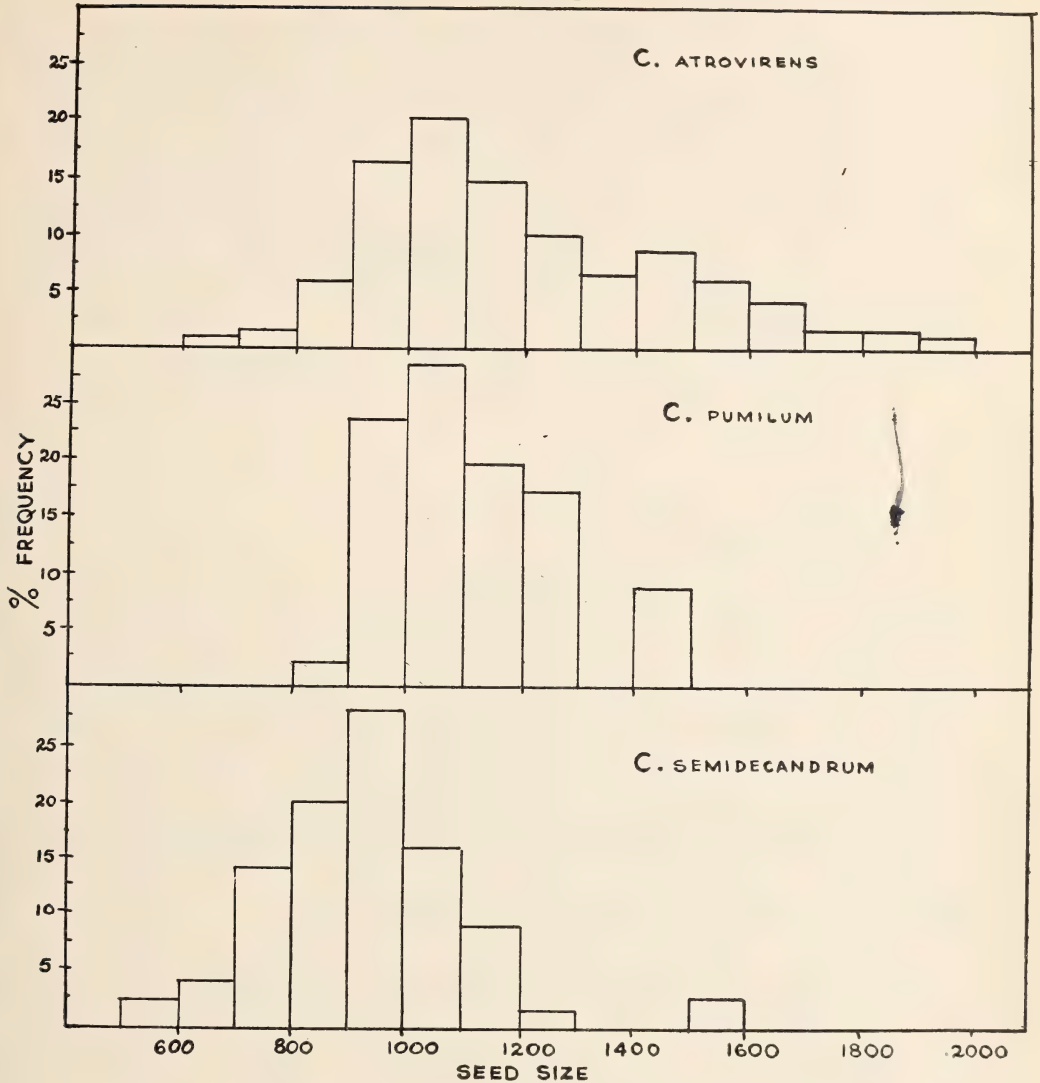
The variation within the populations studied is shown in the histogram (Fig. 1). The variation in response to growth conditions and between cloned plants under similar conditions was investigated by the following experiment.

Four plants grown from seed coming from one wild population were grown under similar conditions. The seeds were collected and measured and the data are shown in the histogram (Fig. 2) as Group 1. This group can be regarded as indicating the variation between individuals in a single population. Eight rooted cuttings of a single plant from the same population were treated as follows: four of these plants were grown in sand, watered with tap water, and kept as dry as was possible without damaging the plants. The variation in their seed size is shown as Group 2 in Fig. 2. This group may be considered as showing the variation in seed size of a single genotype under one set of extreme conditions. The other four were grown in a 50 per cent John Innes potting compost - 50 per cent sand mixture - with an ample water supply. Group 3 of Fig. 2 shows the variation in the size of seeds produced by these plants and represents the variation in seed size of the same genotype as Group 2 but grown under very different conditions. From histogram 2 it can be seen that, although there is quite a wide range of variation for each group, the range and distribution of this character is little affected by differences of conditions of growth. It follows that this character is also fairly constant in the population used, and a fairly small number of seeds can be used to sample the variation in a wild population.

It was found that the mean seed size differed for the three primary groups consisting of specimens of *C. atrovirens* (Group A), *C. pumilum* (Group B) and *C. semidecandrum* (Group C) as can be seen from the histogram (Fig. 1). It can also be seen that there is considerable overlap of the variation of this character in the three primary groups, there being a large area in the centre of the histogram where all three groups overlap. Nevertheless, it appeared that the means of the primary groups might be significantly different. Since N is large for each group the significance of the difference of the means was determined by calculating the standard error of the difference between the means. If the means are $\bar{z} A$ and $\bar{z} B$, their standard deviations σ_1 and σ_2 and the numbers in the samples N_1 and N_2 respectively, then the standard error of the difference between the means is given by the formula

$$\text{S.e. of difference} = \sqrt{\frac{\sigma_1^2}{N_1} + \frac{\sigma_2^2}{N_2}} \quad . \quad . \quad . \quad . \quad (1)$$

FIG. 1



If the difference between the two means is greater than twice its standard error then the means are significantly different.

In groups A and B the standard error of the difference between the means for this character was found to be 2.3 and the actual difference between the means 9.65; since this is greater than twice the standard error the two means are significantly different. Similarly, the standard error of the difference between the means of groups A and C was 2.46 and the difference between the means 20.09 whilst the standard error of the difference between means of groups B and C was 2.4 and the actual difference 10.5. In all these groups, then, there is a significant difference in the means for this character.

It is of interest to note that seed size varies within each capsule according to the position of the seed in the capsule. Distally the seeds tend to be larger than at the proximal end of the capsule. The average of seed size for each capsule shows less variation.

THE CHARACTER POLLEN SIZE

This character does not appear to have been used previously for differentiating between the *Cerastium* taxa. It appears, however, to be of considerable diagnostic value, especially in distinguishing between *C. atrovirens* and *C. subtetrandrum*. As with the character seed size, it would appear that cultural conditions do not materially affect its constancy. This was shown by the experiment already described above.

Examination of the three groups showed that, as with seed size, there is a considerable overlap of the variation in each primary group, together with a central range of variation common to all groups. Although the means are significantly different it is not possible to use this character by itself for distinguishing between the groups. The actual figures obtained were as follows :

Groups	Standard error of difference between means	Actual difference between means
A and B	7.84	21.01
B and C	0.30	28.37
A and C	0.86	7.36

THE CHARACTER SEPAL/PETAL RATIO

This character is referred to in many floras. Lid (1944) states that in *C. atrovirens* and *C. semidecandrum* the calyx is larger than the petals. Lindman (1918) states that *C. pumilum* and *C. glutinosum* have petals as long as the calyx, whilst by implication *C. atrovirens*, *C. semidecandrum* and *C. subtetrandrum* have petals shorter than the calyx. It is further stated that *C. subtetrandrum* has long, acutely-pointed sepals. Schinz & Keller (1909) state that the petals are as long as the calyx in *C. pumilum* and shorter in *C. semidecandrum*. Coste (1901) makes similar statements about these species. No details are given, however, of the precise value of the ratio sepal length/petal length. It was considered that this character might be of importance in distinguishing between the three groups.

The data for the means for this character are shown below :

Groups	Standard error of difference between means	Actual differences between means
A and B	1.17	16.87
B and C	2.58	17.81
A and C	2.54	1.04

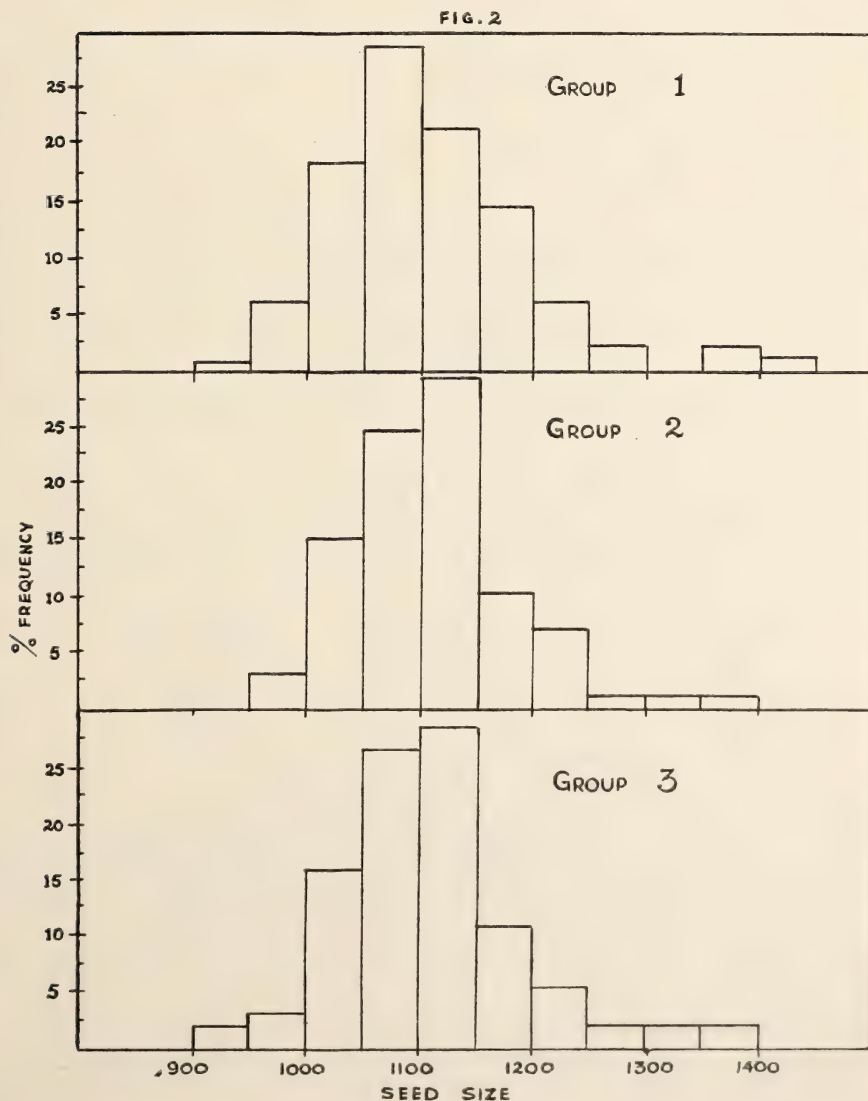
It can be seen that, although the means for this character show significant differences between groups B and C and B and A, the difference between the means of A and C is not significant. The variation of this character was examined in the experimental plants and although no significant differences resulted from the different treatments, there was greater variation throughout than with the two previous characters.

THE CHARACTER OF BRACT LENGTH/SCARIOUS TIP

This character is one of the most frequently mentioned as being of importance diagnostically and the importance attached to it is fully justified by its high discriminant value in the analysis described later. In the experimental treatment of plants, since it was *C. atrovirens* that was grown and, indeed, a population characterised by the herbaceousness of its bracts, little or no difference could be found between the bracts of the different plants.

The floras, however, state that the bracts of *C. atrovirens* are always completely herbaceous. This was found to be incorrect. When the bracts were examined under the microscope, in every case there was at least one row of colourless cells at the tip of the bract and in some cases there was a scarious tip almost as large as the usual *C. pumilum* tip. In a few cases the bract tips of *C. atrovirens* are more scarious than the least scarious-tipped *C. pumilum*. This character, as with the previous characters, is not an absolute criterion but it does more nearly approach absoluteness than any of the other characters. It was found that the means for groups A, B and C were all significantly different as may be seen from the data below.

Group	Standard difference between means	Actual difference between means
A and B	2.0	27.80
B and C	1.7	3.62
A and C	1.9	31.42



It should be noted that in considering this character comparable bracts or bracteoles must be used. In the present investigation the uppermost bract, i.e., the uppermost bract subtending a developed bud or flower, has been used.

THE CHARACTER PETAL LENGTH/PETAL CLEFT

This character is seldom, if ever, mentioned in the usual floras. It is implied in Coste (1901) since, although not mentioned in the text, it is clearly shown in illustrations that the petals of *C. pumilum* are more deeply cleft than those of *C. semidecandrum*. Ascherson & Graebner (1919) give more details than the other floras including some idea of the range of size of the depth of the cleft in terms of petal length.

The measurement of this character is complicated by the occurrence of petals divided into more than two segments. This tendency for the petals to be tri- or quadrifid appears to be much more common than previously noted, and is most marked in *C. semidecandrum*.

The occurrence of quadrifid petals in other *Cerastium* species is mentioned in the literature.

In the herbarium specimens examined tri- or quadrifidy occurred in approximately 5 per cent of the *C. semidecandrum* samples, in approximately 1 per cent of *C. atrovirens* samples and only in about 0.1 per cent of the *C. pumilum* samples. If the character of petal/cleft ratio is to be employed it is important to know how representative a sample was contained in the herbarium material. This is especially important when the idiosyncrasies of the collector are known.

Large amounts of material were collected from Newborough Warren, Anglesey, of *C. semidecandrum* and *C. atrovirens*, which were then examined for the occurrence of abnormal petals. Seven hundred and fifty-five flowers of *C. semidecandrum* were examined and quadrifid petals were observed in thirty-four examples, giving an occurrence of 4.5 per cent. Two hundred and twelve flowers of *C. atrovirens* were examined and two had trifid petals, that is 0.94 per cent of the total examined.

Although only one population has been examined it would appear probable that the distribution of this character in nature differs little from that of the herbarium material used.

The differences between the means of the groups were found to be significantly different as may be seen from the data below. The constancy of this character was tested by comparing its range and distribution in the experimental plants, no significant difference being found.

Groups	Standard error of difference between means	Actual difference between means
A and B	1.93	12.60
B and C	2.66	24.70
A and C	2.51	12.10

THE CHARACTER PETAL LENGTH/PETAL BREADTH RATIO

This character is not normally mentioned as being diagnostic. Although it has not been used in the analysis it shows significant though small differences for the primary groups A, B and C. However, this character proved to be of importance in differentiating between *C. atrovirens* and *C. subtetrandrum* and will be discussed more fully in a later paper relating to the analysis of these two taxa.

THE CHARACTER "PLANT PHYSIOGNOMY"

To express a concept such as the physiognomy of a plant in mathematical terms obviously presents difficulties. Although this character has not been used in this analysis

it is thought that the points raised in its consideration are of such importance that they should be mentioned.

An examination of many plants showed that there was considerable variation in the angle formed by the outer branches of the dichasium. Correlated with this character was a variation in the angle made with the ground by the vegetative branches and the lower parts (i.e. below the first dichasium) of the flowering branches.

Investigation showed that these two sets of characters can be taken as expressing the characteristic physiognomy of the plant. It was found that there appear to be differences between the means of the primary groups for the character dichasial angle.

Observations made in the field, however, gave the impression that the plants with large dichasial angles were well-grown plants growing apart from other plants. On the other hand, plants with small dichasial angles were always growing amongst longish grass or closely surrounded with other *Cerastium* plants. It appeared from these observations that the dichasial angle might be varying more or less completely in response to environment and its use as a taxonomic or diagnostic character would be open to considerable doubt. Since a number of varietal names have been given to taxa distinguished by this type of character it was considered of importance to ascertain its reliability. A preliminary investigation of the relationship of these characters to environment (Whitehead 1955) showed that they were not suitable for use in discriminating between these groups.

It remains to account for the observed differences of dichasial angles in the field and herbarium material. If the usual habitats of the three taxa are considered, the observed differences are not so surprising. *C. atrovirens* is a plant of sand-dunes and cliff turf, usually very short, and is only occasionally found inland, growing among taller vegetation. Tall plants with smaller dichasial angles are often found at the entrances to rabbit burrows but the majority of plants are from habitats fully exposed. Even where there is great mutual competition the plants are usually short and do not shade each other to the extent that they would if their growth were more luxuriant.

To some extent these remarks apply to *C. semidecandrum*, but it is more frequently found inland than *C. atrovirens*, where it can be found, sometimes, as a fairly large plant up to 30 cm. high growing amongst tall vegetation; nevertheless, it is more often found growing on rather exposed patches of soil and forming part of the ephemeral element of vernal annuals. It is also found associated with *C. atrovirens* on sand-dunes and, as far as physiognomy is concerned, is then identical with it.

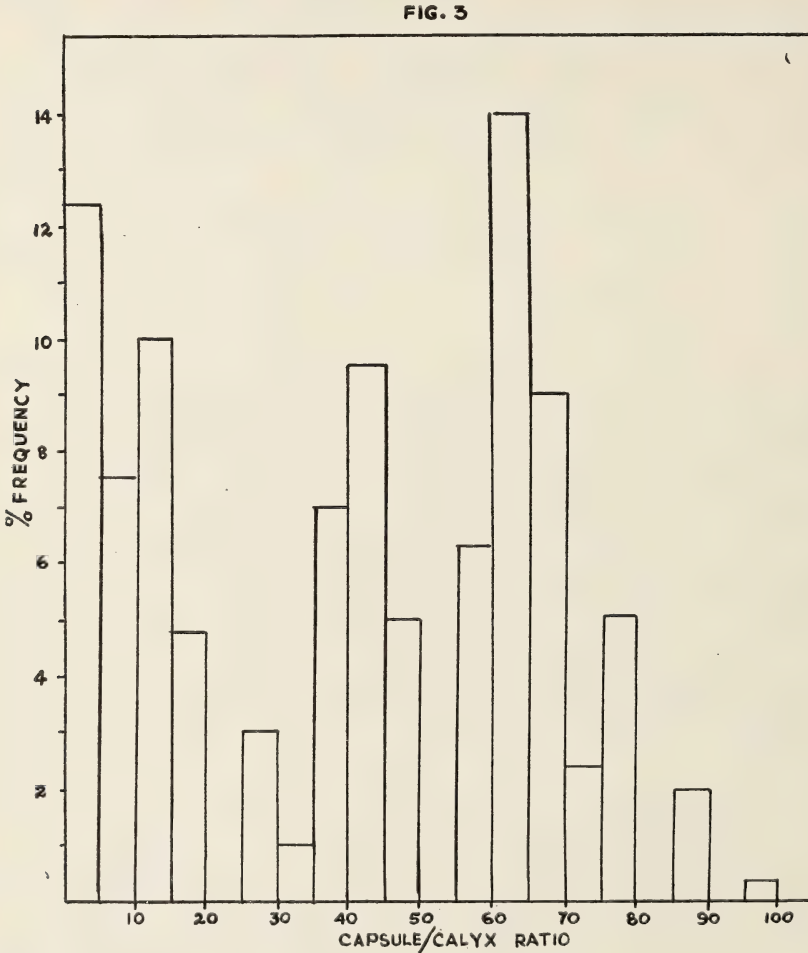
C. pumilum, however, despite its occurrence in grazed turf and amongst limestone detritus in some localities, is much more often found growing among rather taller vegetation. From its original description the impression is obtained that it is a very dwarf *Cerastium* but an examination of the range of this taxon shows it to be quite as tall as the other taxa and with a greater frequency of taller plants.

It can be seen that *C. pumilum* is the taxon most frequently found in competition with the taller vegetation and it was found to have rather narrower dichasial angles than the other taxa, *C. atrovirens* having the larger dichasial angles and being more restricted to exposed habitats. *C. semidecandrum*, which has the widest range of dichasial angle, is also the taxon with the greatest range of habitats.

THE CHARACTER CALYX LENGTH/CAPSULE LENGTH

This character has long been used diagnostically and it was hoped that it might be used in this analysis. One limitation of the statistical treatment which follows is that a value for each character for each specimen is absolutely necessary. It was found that

the variation of this character was considerable, the standard errors large, and the distribution not normal. A graphical representation of the measurements of 136 samples of *C. pumilum* is shown in the histogram (Fig. 3). The distribution of this character approximates to bimodality, except that one half of one mode is not represented. It was difficult at first to account for this type of distribution but further examination of the specimens showed that two uncorrelated variables were in fact being measured. Because of the difficulty of determination there appears to be a tendency to collect *C. pumilum*



in a young state so that many specimens have only immature capsules. These are shorter than the fully mature capsules, and in any collection of these plants there will tend to be a greater proportion of capsule/calyx ratios approaching unity than would be found if all the specimens had fully mature capsules. The measurements in fact give an estimate not only of the range in size of the mature capsule/calyx ratio but also the range of maturity of the samples. Since many of the specimens being used were so young that fully mature capsules were lacking, it was not possible to use this character further.

Of the characters discussed above, the following were selected for use in the discriminant analysis which appeared to be the most suitable method for use in separating these taxa :

- | | | |
|-----|--------------------------------|-----|
| (1) | seed size | x |
| (2) | pollen size | y |
| (3) | sepal/petal ratio | z |
| (4) | bract/scarious tip ratio | u |
| (5) | petal length/petal cleft ratio | v |

As described in Whitehead (1954) it is first necessary to construct tables of critical values; that is, the total range of variation for each character is divided into 100 parts. These critical values are shown in Tables 1 to 5.

The results of the discriminant analysis between groups A, B and C, whose working in full is given in Whitehead (1948 thesis), were as follows :

$$\begin{array}{lll} \lambda_1 = -42 & \lambda_3 = -7 & \lambda_4 = -90 \\ \lambda_2 = -20 & & \lambda_5 = +29 \end{array}$$

TABLE 1
Critical values of pollen size (diameter in μ)

Class No.	Diam. μ	Class No.	Diam. μ	Class No.	Diam. μ
01	19.695	35	26.325	69	32.955
02	19.890	36	26.520	70	33.150
03	20.085	37	26.715	71	33.345
04	20.280	38	26.910	72	33.540
05	20.475	39	27.105	73	33.735
06	20.670	40	27.300	74	33.930
07	20.865	41	27.495	75	34.125
08	21.060	42	27.690	76	34.320
09	21.255	43	27.885	77	34.515
10	21.450	44	28.080	78	34.710
11	21.645	45	28.275	79	34.905
12	21.840	46	28.470	80	35.100
13	22.035	47	28.665	81	35.295
14	22.230	48	28.860	82	35.490
15	22.425	49	29.055	83	35.685
16	22.620	50	29.250	84	35.880
17	22.815	51	29.445	85	36.075
18	23.010	52	29.640	86	36.270
19	23.205	53	29.835	87	36.465
20	23.400	54	30.030	88	36.660
21	23.595	55	30.225	89	36.855
22	23.790	56	30.420	90	37.050
23	23.985	57	30.615	91	37.245
24	24.180	58	30.810	92	37.440
25	24.375	59	31.005	93	37.635
26	24.570	60	31.200	94	37.830
27	24.765	61	31.395	95	38.025
28	24.960	62	31.590	96	38.220
29	25.155	63	31.785	97	38.415
30	25.350	64	31.980	98	38.610
31	25.545	65	32.175	99	38.805
32	25.740	66	32.370	100	39.000
33	25.935	67	32.565		
34	26.130	68	32.760		

These values of λ are multipliers; the actual value of a character taken from the tables of critical values is multiplied by the appropriate value of λ , i.e. the value for seed size (x) being multiplied by λ_1 ; the value for pollen size (y) by λ_2 , etc. The quantities thus obtained are added together to give the discriminant function (F) for that specimen. F (the discriminant function) is the best linear function of the characters seed size (x), pollen size (y), sepal/petal ratio (z), bract/scarious tip ratio (u) and petal length/petal cleft ratio (v) to discriminate between the groups A, B and C.

If the actual mean values, $\bar{x}$, $\bar{y}$, $\bar{z}$, $\bar{u}$, and $\bar{v}$, for one of the groups A, B or C are substituted in the equation,

$$F = \lambda_1 x + \lambda_2 y + \lambda_3 u + \lambda_4 v + \lambda_5 z$$

then a value of F can be obtained which will be a mean value for that group. But F is a linear function so that the mid-points between the mean values of F for the groups will be the point at which probability in classification changes. In other words, if the value of F obtained for an unclassified specimen is nearer the mean value of F for one group

TABLE 2
Critical values of seed size (length in $\mu \times$ breadth in μ)

Class No.	$l \times b$	Class No.	$l \times b$	Class No.	$l \times b$
01	1542	35	2738	69	3935
02	1577	36	2774	70	3970
03	1612	37	2809	71	4006
04	1647	38	2844	72	4041
05	1683	39	2879	73	4076
06	1718	40	2914	74	4111
07	1753	41	2950	75	4146
08	1788	42	2985	76	4182
09	1824	43	3020	77	4217
10	1859	44	3055	78	4252
11	1894	45	3090	79	4287
12	1929	46	3126	80	4322
13	1964	47	3161	81	4358
14	1999	48	3196	82	4393
15	2034	49	3231	83	4428
16	2070	50	3266	84	4463
17	2105	51	3302	85	4498
18	2140	52	3337	86	4534
19	2175	53	3372	87	4569
20	2210	54	3407	88	4604
21	2246	55	3442	89	4639
22	2281	56	3478	90	4674
23	2316	57	3513	91	4710
24	2351	58	3548	92	4745
25	2386	59	3583	93	4780
26	2422	60	3618	94	4815
27	2457	61	3654	95	4850
28	2492	62	3689	96	4886
29	2527	63	3724	97	4921
30	2562	64	3759	98	4956
31	2598	65	3794	99	4991
32	2633	66	3830	100	5026
33	2668	67	3865		
34	2703	68	3900		

than of another then the probabilities are that it should be assigned to the first group. These values for the groups A, B and C are shown below.

$\bar{F}$ Group A.	<i>C. atrovirens</i> =	— 4770
$\bar{F}$ Group B.	<i>C. pumilum</i> =	— 2459
$\bar{F}$ Group C.	<i>C. semidecandrum</i> =	— 1590

Since, as before stated, the function is linear and the mid-point between the mean values of F is the point of delineation between groups, a value of F of more than — 3614 shows that it most probably should be classified as *C. atrovirens*; if it has a value of F of less than — 2024 it should be classified as belonging to *C. semidecandrum*; if it has an intermediate value of F it should be classified as *C. pumilum*.

It will be found, however, that complete and unequivocal separation is not achieved by this analysis of the three groups although it gives better results than any arbitrary weighting of characters. Those specimens which are difficult to allocate using this analysis are those which would prove to be difficult using any system of determination. The

TABLE 3
Critical values of bract/scarious tip ratio

Class No.	Ratio	Class No.	Ratio	Class No.	Ratio
01	2.95	34	67.30	67	131.65
02	4.90	35	69.25	68	133.60
03	6.85	36	71.20	69	135.55
04	8.80	37	73.15	70	137.50
05	10.75	38	75.10	71	139.45
06	12.70	39	77.05	72	141.40
07	14.65	40	79.00	73	143.35
08	16.60	41	80.95	74	145.30
09	18.55	42	82.90	75	147.25
10	20.50	43	84.85	76	149.20
11	22.45	44	86.80	77	151.15
12	24.40	45	88.75	78	153.10
13	26.35	46	90.70	79	155.05
14	28.30	47	92.65	80	157.00
15	30.25	48	94.60	81	158.95
16	32.20	49	96.55	82	160.90
17	34.15	50	98.50	83	162.85
18	36.10	51	100.45	84	164.80
19	38.05	52	102.40	85	166.75
20	40.00	53	104.35	86	168.70
21	41.95	54	106.30	87	170.65
22	43.90	55	108.25	88	172.60
23	45.85	56	110.20	89	174.55
24	47.80	57	112.15	90	176.50
25	49.75	58	114.10	91	178.45
26	51.70	59	116.05	92	180.40
27	53.65	60	118.00	93	182.35
28	55.60	61	119.95	94	184.30
29	57.55	62	121.90	95	186.25
30	59.50	63	123.85	96	188.20
31	61.45	64	125.80	97	190.15
32	63.40	65	127.75	98	192.10
33	65.35	66	129.70	99	194.05
				100	196.00

lack of precision in the first analysis arises from the fact that all three groups have been treated at the same time. If, however, we use this analysis to decide to which two groups, out of the three, these specimens belong, it is possible to use another analysis, based on the two groups only, to determine to which group they should be allocated. Since these latter analyses are based on two groups only, they are correspondingly more sensitive and determination is the more sure. The values of λ and of $\bar{F}$ for these discriminant analyses are shown below :

Between Groups A and B (*C. atrovirens* and *C. pumilum*)

$\lambda_1 = + 4$
 $\lambda_2 = - 17$

$\lambda_3 = + 11$
 $\lambda_4 = + 5$

$\lambda_5 = + 16$

$\bar{F}$ Group A. *C. atrovirens* = + 634

$\bar{F}$ Group B. *C. pumilum* = - 345

So that specimens with values of F above + 145 should be placed in *C. atrovirens* and those with values of F below + 145 in *C. pumilum*.

TABLE 4
Critical values of the ratio sepal/petal

Class No.	Ratio	Class No.	Ratio	Class No.	Ratio
01	0.9235	35	1.7225	69	2.5215
02	0.9470	36	1.7460	70	2.5450
03	0.9705	37	1.7695	71	2.5685
04	0.9940	38	1.7930	72	2.5920
05	1.0175	39	1.8165	73	2.6155
06	1.0410	40	1.8400	74	2.6390
07	1.0645	41	1.8635	75	2.6625
08	1.0880	42	1.8870	76	2.6860
09	1.1115	43	1.9105	77	2.7095
10	1.1350	44	1.9340	78	2.7330
11	1.1585	45	1.9575	79	2.7565
12	1.1820	46	1.9810	80	2.7800
13	1.2055	47	2.0045	81	2.8035
14	1.2290	48	2.0280	82	2.8270
15	1.2525	49	2.0515	83	2.8505
16	1.2760	50	2.0750	84	2.8740
17	1.2995	51	2.0985	85	2.8975
18	1.3230	52	2.1220	86	2.9210
19	1.3465	53	2.1455	87	2.9445
20	1.3700	54	2.1690	88	2.9680
21	1.3935	55	2.1925	89	2.9915
22	1.4170	56	2.2160	90	3.0150
23	1.4405	57	2.2395	91	3.0385
24	1.4640	58	2.2630	92	3.0620
25	1.4875	59	2.2865	93	3.0855
26	1.5110	60	2.3100	94	3.1090
27	1.5345	61	2.3335	95	3.1325
28	1.5580	62	2.3570	96	3.1560
29	1.5815	63	2.3805	97	3.1795
30	1.6050	64	2.4040	98	3.2030
31	1.6285	65	2.4275	99	3.2265
32	1.6520	66	2.4510	100	3.2500
33	1.6755	67	2.4745		
34	1.6990	68	2.4980		

Between Groups B and C (*C. pumilum* and *C. semidecandrum*).

$$\begin{array}{lll} \lambda_1 = + 88 & \lambda_3 = + 291 & \lambda_4 = + 62 \\ \lambda_2 = + 97 & & \lambda_5 = + 58 \end{array}$$

$$\bar{F} \text{ Group B. } C. \text{ pumilum} = + 10464$$

$$\bar{F} \text{ Group C. } C. \text{ semidecandrum} = + 7889$$

Specimens with values of F above + 9177 should be placed an *C. pumilum* and those with values of F below + 9177 in *C. semidecandrum*.

Although it will not normally be necessary to use an analysis between Groups A and C, the results of such an analysis are given below.

Between Groups A and C (*C. atrovirens* and *C. semidecandrum*).

$$\begin{array}{lll} \lambda_1 = + 23 & \lambda_3 = + 44 & \lambda_4 = - 17 \\ \lambda_2 = + 23 & & \lambda_5 = - 16 \end{array}$$

TABLE 5
Critical values of the ratio petal/cleft

Class No.	Ratio	Class No.	Ratio	Class No.	Ratio
01	2.368	35	6.550	69	10.731
02	2.491	36	6.673	70	10.854
03	2.614	37	6.796	71	10.977
04	2.737	38	6.919	72	11.100
05	2.860	39	7.041	73	11.223
06	2.983	40	7.164	74	11.346
07	3.106	41	7.287	75	11.469
08	3.229	42	7.410	76	11.592
09	3.352	43	7.533	77	11.715
10	3.475	44	7.656	78	11.838
11	3.598	45	7.779	79	11.961
12	3.721	46	7.902	80	12.084
13	3.844	47	8.025	81	12.207
14	3.967	48	8.148	82	12.330
15	4.090	49	8.271	83	12.453
16	4.213	50	8.394	84	12.576
17	4.336	51	8.517	85	12.699
18	4.459	52	8.640	86	12.822
19	4.582	53	8.763	87	12.945
20	4.705	54	8.886	88	13.068
21	4.828	55	9.009	89	13.191
22	4.951	56	9.132	90	13.314
23	5.074	57	9.255	91	13.437
24	5.197	58	9.378	92	13.460
25	5.320	59	9.501	93	13.683
26	5.443	60	9.624	94	13.806
27	5.566	61	9.747	95	13.929
28	5.689	62	9.870	96	14.052
29	5.812	63	9.993	97	14.175
30	5.935	64	10.116	98	14.298
31	6.058	65	10.239	99	14.421
32	6.181	66	10.362	100	14.544
33	6.304	67	10.485		
34	6.427	68	10.608		

$$\begin{array}{lll} \bar{F} \text{ Group A. } C. \textit{atrovirens} = & + & 2336 \\ \bar{F} \text{ Group C. } C. \textit{semidecandrum} = & - & 194 \end{array}$$

Specimens with values of F above + 1071 should be placed in *C. atrovirens* and those with values of F below + 1071 in *C. semidecandrum*.

The results of these analyses can, for convenience, be made into a "key" as follows:

1. Specimens with values of F above - 5270 (Groups A and B) 2.
 Specimens with values of F below - 5270 (Groups B and C) 3.
 WHERE $\lambda_1 = -42$, $\lambda_2 = -20$, $\lambda_3 = -7$, $\lambda_4 = -90$, $\lambda_5 = +29$
2. Groups A and B
 Specimens with values of F above + 145 Group A. *C. atrovirens*.
 Specimens with values of F below + 145 Group B. *C. pumilum*.
 WHERE $\lambda_1 = +4$, $\lambda_2 = -17$, $\lambda_3 = +11$, $\lambda_4 = +5$, $\lambda_5 = +16$.
3. Groups B and C.
 Specimens with values of F above + 9177 Group B. *C. pumilum*.
 Specimens with values of F below + 9177 Group C. *C. semidecandrum*.
 WHERE $\lambda_1 = +88$, $\lambda_2 = +97$, $\lambda_3 = +291$, $\lambda_4 = +62$, $\lambda_5 = +58$.

To use this key is comparatively simple. The values of the characters, seed size, pollen size, etc. must first be determined. These are converted to the coded values given in the tables of critical values shown in Tables 1 to 5.

These coded values are multiplied by the appropriate factor; the value of seed size by λ_1 and so on. Note that the appropriate value of λ must be used for the different analyses, these values being shown under the appropriate portions of the key. The value of F obtained indicates which of the two more sensitive analyses should now be used. No further measurements are necessary and the same coded values are used but the appropriate values of λ are used to obtain the value of F for that specimen.

However, it must be borne in mind that any such method as that adopted here has very definite limitations. Briefly, these are: (1) only the characters used in the analysis are used in the determination and this must always be a poor substitute for the "eye" of the born taxonomist who, although often using a larger number of characters subconsciously in his determination, is seldom able to describe these characters adequately. (2) That a number of measurements must be made before the key can be used. This precludes its use in the field. However, where field characters can be used, the need for such analyses does not arise.

Nevertheless, the method has certain very definite advantages which may more than outweigh the disadvantages mentioned above. For instance, it is possible to calculate the probability of correct classification by the use of appropriate statistical tables. The extent that a specimen approximates to another can also be calculated and this may be of great use in separating back-crosses from parents or 1st generation hybrids, etc. To those not gifted with taxonomic "sense," the method furnishes a means of correctly determining specimens which otherwise would have to be sent to a specialist. Finally, although the method depends in the first place on the subjective decision regarding the choice of groups and samples to represent those groups, these subjective decisions are subsequently tested objectively and the allocation of further unclassified specimens is also objective.

By means of this treatment of the data it is possible to obtain a clear separation of these three taxa. Taking into account the differences which exist in distribution, ecology, etc., it appears that the recognition of these three taxa as species is fully justified.

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A NEW BRITISH SPECIES OF *SENECIO*

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In September 1953 specimens of a large, radiate groundsel were received from Mr. H. E. Green, who had seen similar plants, growing by a roadside in Flintshire, since 1948. They could not be assigned to any described European species of *Senecio* and though they bore some resemblance to the hybrid *S. × baxteri* Druce (*S. squalidus* L. $\times$ *S. vulgaris* L.) were more robust, with larger heads and a high percentage of fertile fruits.

When, in 1954, a chromosome count was made from root tips of plants grown from the Flintshire seed they were found to have the chromosome number $2n = 60$; in the same year Professor S. C. Harland and Miss A. Haygarth Jackson produced a similar plant by colchicine treatment of the synthetic hybrid *S. squalidus* $\times$ *vulgaris* ($2n = 30$). This evidence confirmed us in the view that the plant should be described as a new species. A description follows.

***Senecio cambrensis* Rosser, sp. nov.**

Herba (annua vel) perennis, ad 50 cm. altitudine. Caulis erectus, basi sublignosus saepe parte media dense ramosa et foliosa. Folia inferiora petiolata, superiora sessilia, auriculata; omnia alte et irregulariter pinnatifida, cum lobis distantibus, majoribus liguliformibus, minoribus lanceolatis, marginibus dentatis vel quandoque lobulatis; folia iuvenescencia tomentosa praesertim subtus, glabrescentia, cum axillis foliorum maturorum lanuginosis. Inflorescentia foliosa, imprimis dense corymbosa postea ramis florentibus longioribus, pedunculis tempore fructescendi longius extensis. Capitula imprimis late cylindracea (ca. 10.0×6.0 mm.) tempore florendi flosculorum radii nonnihil campanulata (ca. 12.0 mm. tota diametro); periclinii squamae exteriores minus quam dimidium longitudinis interiorum, omnes apicibus nigris; flosculi radii (8)-13-(15), corollis flavis, ligulatis latis et curtioribus quam periclinio (ca. 4.8 mm. longitudine et 2.0 mm. latitudine) mox revolutis (saepe ante anthesin flosculorum meiorum disci). Grana pollinis a visu polari (32.8)-33.2-(36.9) μ maxime expansa, pleraque foraminibus quattuor. Cypselae 3.0-3.5 mm. longitudine. leviter sulcatae, costis glabris et sulcis hirtellis; pappus albus, sericeus, a fructu facile se disjungens.

Typus. Roadside near Ffrith, Flintshire, North Wales, 2-10-1954, with *Senecio vulgaris* L. No. 54102/2 L. W. Frost and E. M. Rosser in Herb. Musei Mancuniensis.

Isotypi. Herb. Musei Mancuniensis; Herb. Musei Cambrensis; Herb. J. E. Lousley.

An (annual or) perennial herb, up to 50 cm. high. Stem erect with base somewhat woody, often with the central portion densely branched and leafy. Lower leaves petiolate, upper sessile, auriculate; all deeply and irregularly pinnatifid, with lobes distant, the larger lobes strap-shaped, the smaller lanceolate, with margins of leaves dentate or sometimes lobulate; young, growing leaves tomentose, especially below, becoming glabrous, with tufts of cottony hairs in the axils of fully grown leaves. Inflorescence leafy, at first

a dense corymb, later with longer flowering branches and with peduncles elongated further when fruiting. Heads at first broadly cylindrical (ca. 10.0×6.0 mm.), somewhat campanulate when the ray florets open (total diameter then about 12.0 mm.); outer involucre bracts less than half the length of the inner ones, all with black tips; ray florets (8)-13-(15), bright yellow, with ligules broad and shorter than the involucre (ca. 4.8 mm.



Fig. 1. *Senecio cambrensis* Rosser. Habit. A plant which was collected at Ffrith, showing the horizontal stem base characteristic of the plants growing in stony soil and in the crevices of the wall but otherwise typical of the species. ($\times \frac{1}{2}$).

long $\times$ 2.0 mm. broad) soon becoming revolute (often before the opening of the central florets of the disc). Pollen grains in polar view $(32.8)-33.2-(36.9) \mu$ when fully expanded, mostly four-pored. Cypselae 3.0-3.5 mm. long, shallowly grooved, with ribs glabrous and grooves hirtellous; pappus white, silky, readily becoming detached from the fruit. Fl. 5-10 (+ ?). $2n = 60$.

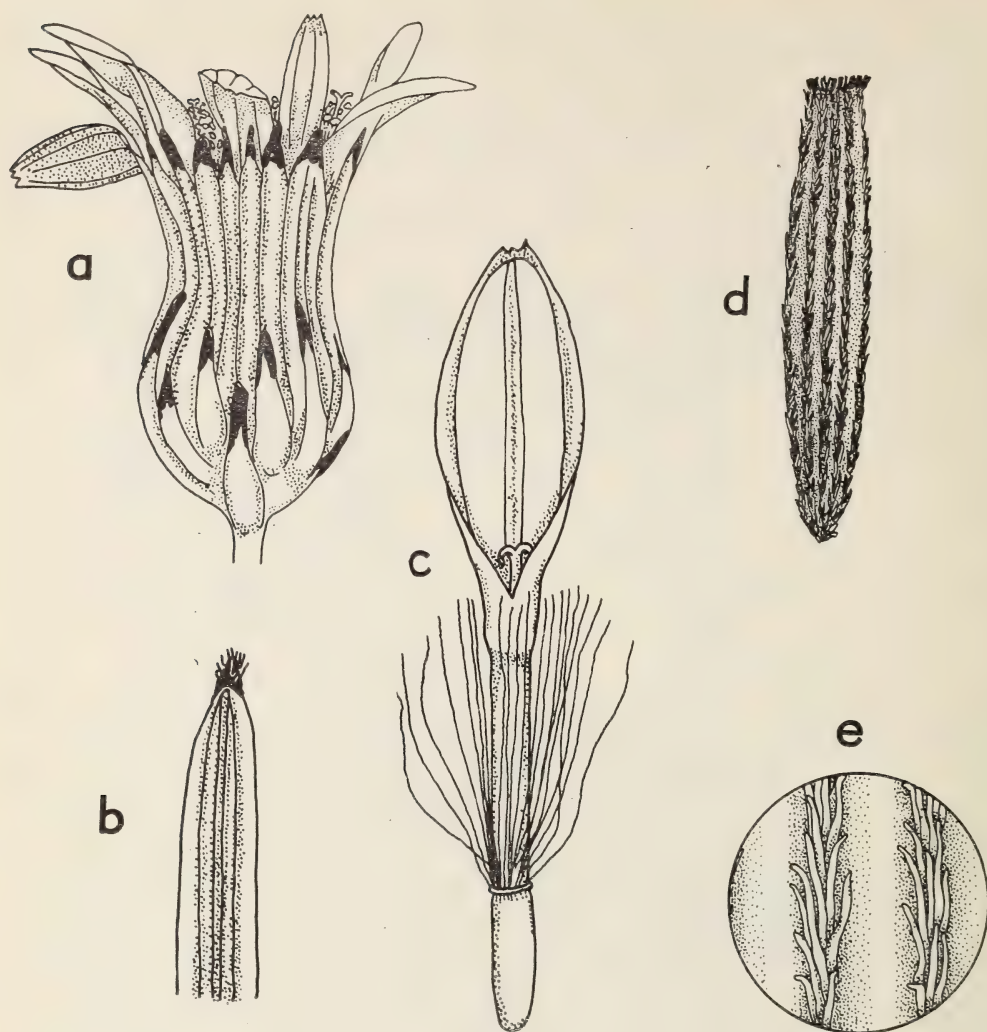


Fig. 2. *Senecio cambrensis* Rosser. (a) Capitulum at time when ray florets are fully expanded ($\times 5$); (b) a single involucre bract ($\times 10$); (c) ray floret ($\times 10$); (d) cypsela ($\times 20$); and (e) the surface of the cypsela ($\times 160$).

First Record

Near Cefn-y-bedd, 15-8-1948, *H. E. Green* in Herb. MANCH.

Reference has already been made to the experimental evidence provided by Professor Harland and Miss Jackson, whose synthesis of *S. cambrensis* has shown that it is an allopolyploid which appears to have originated at Ffrith very recently by hybridisation between *S. squalidus* and *S. vulgaris*, followed by doubling of the chromosomes. Both the naturally-occurring and synthetic plants were exhibited at the Exhibition Meeting of the Botanical Society in November, 1954, already reported (Lousley, 1955).

The present population at the type locality includes some plants of *S. vulgaris* (non-radiate) and though the hybrid *S. × baxteri* Druce could not be found in the vicinity *S. squalidus* was collected a few miles away. The wild plant shows little variation; plants grown in the greenhouse from seed collected at Ffrith differ from those in the wild

population only in their greater luxuriance. Mr. Green reports that the species has spread slowly in the area since it first appeared; since it seems probable that it will eventually spread to other areas some notes on the distinction between *S. cambrensis* and radiate forms of *S. vulgaris*, *S. squalidus* and *S. × baxteri* are given below.

(1) Radiate forms of *S. vulgaris* L.

S. cambrensis may be distinguished in the field from all these forms by its more robust habit, broader, generally more numerous ligules of the ray florets, and the longer, more sparsely pubescent but longer-haired cypselae shown in Fig. 2 (d) and (e) (cypselae < 2.5 mm. in *S. vulgaris*); older plants of the polyploid may be distinguished also by the woody base of the stem. Comparison of the pollen grains (three-pored and $20-25\ \mu$ in diameter in *S. vulgaris*) may also be used in determination of herbarium material or fresh material in the laboratory.

(2) *S. squalidus* L.

The more prominent auricles of the upper cauline leaves, the smaller, less broadly campanulate involucre, short, ovate ligules, and the larger, long-haired cypselae distinguish the polyploid from all forms of *S. squalidus* (cypselae < 2.5 mm.). As in *S. vulgaris*, pollen grains of *S. squalidus* are smaller and only three-pored ($20-25\ \mu$ in diameter).

(3) *S. × baxteri* Druce.

Discrimination between this hybrid and *S. cambrensis* in the field may be more difficult; the high percentage of abortive fruits in the hybrid is likely to prove the best guide. At the end of the season, however, when, as Mr. Green has also observed, the capitula of *S. cambrensis* become successively smaller, the polyploid itself, like other *Senecio* species (e.g. *S. sylvaticus* and *S. viscosus*), may produce a high proportion of abortive fruits and confusion between the hybrid and the polyploid is probable. Where fruits are available, those of the hybrid (judging by the small quantity of undoubted hybrid seed which has been available for examination) can be distinguished by their smaller size (< 2.5 mm.) and by the very short, scattered hairs with which the grooves are lined. Though the pollen may contain some four-pored grains the majority of those examined were three-pored (ca. $25\ \mu$ in diameter), compared with a high proportion of four-pored grains in *S. cambrensis*.

Discussion of leaf characters in general seems unlikely to prove of any value, in view of the variability in leaf dissection exhibited by *S. squalidus* and *S. vulgaris*, though the deeply dissected, highly tomentose developing leaves of *S. cambrensis* may be used to discriminate between its seedlings and those of the parent species.

Since *S. vernalis* Waldst. & Kit., a European annual having the chromosome number $n = 10$ (Afzelius, 1929),¹ has been reported from Britain on a number of occasions (though probably always erroneously) it may perhaps be usefully stated here that although young plants of *S. vernalis* bear a superficial resemblance to those of the polyploid *S. cambrensis* they may easily be distinguished from the latter by their relatively longer ligules, smaller cypselae and normal small-grained pollen. Fruit characters and pollen grain size and morphology also serve to distinguish the polyploid from such closely related European species as *S. leucanthemifolius* Poir. ($n = 10$, Afzelius, 1949), and *S. rupestris* Waldst. & Kit. ($n = 10$, Afzelius, 1924 as *S. nebrodensis* L.). *S. abrotanifolius* L. var. *tyrolensis* A. Kerner ($2n = 60$, Tischler, 1950), recorded only from the Tyrol, and other 12-ploid species, are sufficiently distinct from *S. cambrensis* to require no detailed consideration here.

It is a pleasure to record my thanks to Mr. H. E. Green both for material and information, to Professor S. C. Harland for permission to make use of experimental evidence, to Mr. J. Ellis for the chromosome count of *S. cambrensis* and to Mr. G. B. Kerferd who kindly revised the grammar of my Latin diagnosis.

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NOTES ON BRITISH *HIERACIA* - I

By P. D. SELL and C. WEST

This paper makes valid the new names and combinations to be used in the Society's revised British Plant List. We are grateful to Mr. N. Y. Sandwith for his help in preparing the Latin descriptions.

***Hieracium hartii* (F. J. Hanb.) Sell & West, sp. nov.**

H. cerinthiforme var. *hartii* F. J. Hanbury (1892), *J. Bot.*, **30**, 169; in Babington (1904), 240. *H. anglicum* var. *hartii* (F. J. Hanb.) F. N. Williams (1902), 95; Pugsley (1948), 69. *H. anglicum* var. *cerinthiforme* f. *hartii* (F. J. Hanb.) W. R. Linton (1905), 11. *H. mougeotii* subsp. *anglicum* var. *cerinthiforme* f. *hartii* (F. J. Hanb.) Zahn (1921), 186.

***Hieracium saxorum* (F. J. Hanb.) Sell & West, sp. nov.**

H. hypochaeroides var. *saxorum* F. J. Hanbury (1892), *J. Bot.*, **30**, 209; in Babington (1904), 250; Williams (1902), 117; W. R. Linton (1905), 29; Pugsley (1948), 112. *H. wiesbaurianum* subsp. *hypochaeroides* var. *saxorum* (F. J. Hanb.) Zahn (1921), 264. *Lectotype*: Rhaiadr Falls, Montgomery, A. Ley, 1891, in Herb. Hanbury (Herb. Mus. Brit.).

***Hieracium dicella* Sell & West, nom. nov.**

H. furcelliferum Dahlstedt (1934), *Rep. Bot. Soc. and Ex. Cl. Brit. Isles*, **10**, 475; non *H. furcelliferum* Omang (1927), *Skr. Vid-Akad. Oslo, Mat.-Nat.*, No. 4, 63.

***Hieracium subbritannicum* (A. Ley) Sell & West, sp. nov.**

H. stenolepis var. *subbritannicum* A. Ley (1909), *J. Bot.*, **47**, 12. *H. britannicum* var. *subbritannicum* (A. Ley) Pugsley (1948), 114.

Lectotype: Craig Cille, Brecon, A. Ley, 1894, in Herb. A. Ley (Herb. Univ. Birmingham).

***Hieracium stenolepiforme* (Pugsley) Sell & West, sp. nov.**

H. britannicum var. *stenolepiforme* Pugsley (1948), 114.

Holotype: Cheddar, Somerset, E. F. Linton, 1890, in Herb. Mus. Brit.

***Hieracium uistense* (Pugsley) Sell & West, sp. nov.**

H. clovense var. *uistense* Pugsley (1948), 117.

Holotype: Ben Eaval, N. Uist, Shoolbred, 1894, in Herb. Hanbury (Herb. Mus. Brit.).

***Hieracium camptopetalum* (F. J. Hanb.) Sell & West, sp. nov.**

H. murorum var. *camptopetalum* F. J. Hanbury (1894), *J. Bot.*, **32**, 228; in Babington, (1904), 253. *H. duriceps* var. *camptopetalum* (F. J. Hanb.) Pugsley (1948), 137.

Holotype: Allt-na Caillich, Sutherland, Hanbury, 1888, in Herb. Hanbury (Herb. Mus. Brit.).

***Hieracium asteridiophyllum* Sell & West, sp. nov.**

H. pellucidum var. *lucidulum* sensu Pugsley (1948), 141; non *H. lucidulum* (A. Ley) Roffey (1925).

Ab *H. pellucido* Laestad. foliis coriaceis floccosis, capitulis majoribus squamis involucri paulum pilosis differt.

Caulis ad 55 cm. altus, robustus, striatus, plerumque basi purpurascens, ubique paulum floccosus atque pilosus, sursum glanduloso-pilosus. *Folia* coriacea, opaca, saturate viridia, plerumque praecipue infra purpurascentia; radicalia plerumque numerosa; primordialia subrotunda, rotundato-obtusa mucronulata, integra vel denticulis paucis minutis praedita, basi truncata, breviter petiolata; prima late ovalia usque ad ovata, rotundato-obtusa mucronulata, regulariter denticulata vel saepius dentibus brevibus acutis horizontalibus basin versus praedita, dentibus duobus basalibus saepius longioribus atque retrorsis, basi truncata; posteriora ovata usque ad ovato-lanceolata, subacuta acuta vel rarius acuminata, sursum denticulata, basin versus dentata dentibus brevibus horizontalibus acutis vel mammiformibus, basalibus nonnunquam retrorsis rarius pinnulas in petiolis satis brevibus praebentibus, basi truncata; caulina 1-2, inferiora ovata usque ad ovato-lanceolata, subacuta vel acuta, denticulata vel rarius inferne breviter dentata, basi truncata vel raro cuneata, petiolata, superiora si adsunt bracteiformia; omnia supra epilosa vel pilis paucis sparsis praedita, infra plus minusve pilosa, supra saepe infra plerumque floccosa, marginibus ciliatis, petiolis pilosis. *Inflorescentia* paniculato-corymbosa, 3-15-cephala, ramis gracilibus erectis acladium satis breve superantibus; pedunculi floccosi, pilis glandulosis brevibus obscuris numerosis necnon aliis simplicibus raris obscuris praediti. *Involucra* mediocria, basi rotundata. *Squamae* in gemmis incumbentes, nigrescenti-virides, lineari-lanceolatae, acutae, plus minusve floccosae, subsenescentes, pilis glandulosis obscuris multis necnon aliis simplicibus paucis longis obscuris praeditae. *Ligulae* apice glabrae. *Styli* lividi. *Alveoli receptaculi* marginibus breviter dentatis. *Achaenia* nigrescentia, 3 mm. longa.

Stem up to 55cm. high, robust, striate, usually purplish at the base, slightly floccose and pilose throughout, becoming glandular upwards. Leaves coriaceous, dull, dark green, usually suffused with purple beneath and less so above; the radical usually numerous; the primordial subrotund, rounded-obtuse-mucronulate, entire or with a few minute denticulations, truncate-based, shortly petioled; the earlier broadly oval to ovate, rounded-obtuse-mucronate, uniformly denticulate or more frequently with shallow, horizontal, sharp teeth towards the base, the two basal often longer and retrorse, base truncate; the later ovate to ovate-lanceolate, subacute to acute or occasionally acuminate, denticulate above becoming dentate below, the teeth shallow, horizontal and sharp, or mammiform, the basal sometimes retrorse, in extreme cases occurring as pinnae on the rather short petioles, truncate-based; cauline leaves 1-2, the lower ovate to ovate-lanceolate, subacute to acute, denticulate or occasionally shallowly dentate below, truncate-or rarely cuneate-based, petiolate, the upper when present bractlike; all epilose or with a few scattered pili above, $\pm$ pilose beneath, often floccose above, usually $\pm$ floccose beneath, the margins ciliate, petioles pilose. Inflorescence paniculate-corymbose, 3-15-headed, with slender, erect branches exceeding the rather short acladium, the peduncles floccose, with numerous short, dark glands and occasional dark hairs. Heads medium, rounded at the base. Phyllaries incumbent in bud, blackish-green, linear-lanceolate, acute, $\pm$ floccose, slightly senescent, with many dark glands and a few long dark hairs. Ligules glabrous-tipped. Styles livid. Margins of the receptacle pits shortly dentate. Achenes blackish, 3 mm. long. *Holotype*: Daren Cilau (Craig Cille), Brecon, C. West, 1952, in Herb. Univ. Cantab.

Hieracium glevense (Pugsley) Sell & West sp. nov.

H. exotericum var. *glevense* Pugsley (1948), 144.

Holotype: Chalford, Gloucester, Riddelsdell, 1920, in Herb. Mus. Brit.

Hieracium snowdoniense Sell & West sp. nov.

H. pulcherrimum sensu Pugsley (1948), 147; non (F. J. Hanb.) Roffey (1925).

Ab *H. duricipiti* F. J. Hanb. squamis involucris pilosis ligulis glabris, ab *H. pellucido* Laestad. forma indumentoque foliorum differt.

Caulis ad 40 cm. altus, striatus, basi parce pilosus, plus minusve floccosus, superne sparse glanduloso-pilosus. *Folia* pallide viridia, saepe praecipue infra purpureo-suffusa, radicalia patentia; primordialia parva, rotundata, mucronata, remote denticulata, basi truncata; posteriora obovata, ovata vel ovato-elliptica, obtusa mucronata usque ad acuta, plerumque ab omni parte denticulata, nonnunquam vix alte sinuata vel basin versus cuneatam vel raro subtruncatam acute atque alte dentata; caulina 1-3, inferiora elliptico-ovata, acuta, similiter dentata, basi cuneata vel subtruncata, petiolata usque ad subsessilia, superiora plerumque parva bracteiformia; omnia utrinque plus minusve pilosa, pilis paginae superioris brevibus subsetiformibus, marginibus valde ciliatis, petiolis breviusculis villosis. *Inflorescentia* paniculato-corymbosa, compacta, ad 20-cephala, acladio brevi ramis brevibus erectis; pedunculi floccosi, pilis rigidis inaequalibus nigris glandulosis dense induti. *Involucra* satis parva, inferne rotundata. *Squamae* in gemmis incumbentes, nigrescenti-virides, intimae pallidiores, lineari-lanceolatae, acutae, marginibus floccosis, subsenescentes, pilis glandulosis densis inaequalibus nigris indutae, pilis simplicibus nullis. *Ligulae* aureae, apice glabrae. *Styli* lividi. *Alveoli* receptaculi marginibus inciso-dentatis. *Achaenia* nigrescentia, 2.5-3 mm. longa.

Stem up to 40 cm. high, striate, sparingly pilose at the base, $\pm$ floccose, sparsely glandular above. Leaves light green, often suffused with purple, especially beneath; the radical spreading; the primordial small, rotundate, mucronulate, remotely denticulate, truncate based; the later obovate, ovate, or ovate-elliptic, obtuse-mucronate to acute, mostly denticulate throughout, sometimes shallowly sinuate or sharply and deeply dentate towards the cuneate or occasionally subtruncate base; the cauline 1-3, the lower elliptic-ovate, acute, toothed like the radical leaves, cuneate-or subtruncate-based, petiolate to subsessile, the upper usually small and bractlike; all $\pm$ pilose on both surfaces, the hairs on the upper surface short and subsetiform, the margins strongly ciliate, the petioles rather short, villous. Inflorescence paniculate-corymbose, compact, up to 20-headed, with short acladium and short, erect branches; peduncles floccose and densely clad with strong, unequal, black, glandular hairs. Heads rather small, rounded below. Phyllaries incumbent in bud, blackish green, the innermost paler, linear-lanceolate, acute, floccose on the edges, slightly senescent, with dense, unequal, black glandular hairs. Ligules golden yellow, glabrous-tipped. Styles livid. Margins of the receptacle pits incise-dentate. Achenes blackish, 2.5-3 mm. long.

Holotype: Ysolion Duon, Caernarvon, Griffith, 1893, in Herb. A. Ley (Herb. Univ. Birmingham).

***Hieracium angustatiforme* Sell & West, sp. nov.**

Ab *H. angustato* Lindeb. ac *H. rhomboide* (Stenstr.) Johannis. squamis involucris pedunculisque minus glanduloso-pilosis, foliorum marginibus valde ciliatis differt, praeterea ab *H. cacuminum* (A. Ley) A. Ley foliis aequaliter serratis distinguitur.

Caulis ad 40 cm. altus, gracilis, striatus, inferne vel nonnunquam per totam longitudinem purpurascens, glabrescens. *Folia* obscure viridia; radicalia numerosa atque patentia, ovato-elliptica, elliptico-lanceolata vel lanceolata, obtusa mucronata usque ad acuta, tenuiter aequaliter acute serrata, basi cuneata; caulina 0-2, inferiora lanceolata usque ad lineari-lanceolata, acuta, tenuiter serrata vel denticulata, petiolata vel sessilia; omnia supra glabra infra plus minusve pilosa, marginibus longe ciliatis, petiolis longe pilosis. *Inflorescentia* furcato-corymbosa, 1-4-cephala, ramis sublongis gracilibus suberectis acladium longum superantibus; pedunculi paulum floccosi atque pilosi. *Involucra*

mediocria, inferne plus minusve rotundata. *Squamae* in gemmis incumbentes, saturate virides, interiores pallidiores, lanceolato-subulatae, plerumque subacutae, inferne paulum floccosae, pilis simplicibus obscuris inaequalibus necnon aliis glandulosis paucis minutis praeditae. *Ligulae* apice glabrae. *Styli* lutei. *Alveoli receptaculi* marginibus breviter dentatis. *Achaenia* nigrescentia, 3-3.5 mm. longa.

Stem up to 40 cm. high, slender, striate, purplish below, sometimes throughout, glabrescent. Leaves dull green; the radical numerous and spreading, ovate-elliptic, elliptic-lanceolate or lanceolate, obtuse-mucronate to acute, sharply, finely and regularly serrate, cuneate-based; the cauline 0-2, the lower lanceolate to linear-lanceolate, acute, finely serrate or denticulate, petiolate or sessile; all glabrous above and $\pm$ pilose beneath, with long ciliate margins, petioles long-pilose. Inflorescence furcate-corymbose, 1-4-headed, with $\pm$ long, slender, suberect branches exceeding the long acaulium; peduncles slightly floccose and pilose. Heads medium, $\pm$ rounded below. Phyllaries incumbent in bud, dark green, inner paler, lanceolate-subulate, mostly subacute, slightly floccose below, with dark, unequal hairs, and occasionally with a few minute glands. Ligules glabrous-tipped. Styles yellow. Margins of the receptacle pits shortly dentate. Achenes blackish, 3-3.5 mm. long.

Holotype : Craig Cerrig-glesiad, Brecon, Sell (no. 53/116), 1953, in Herb. Univ. Cantab.

Hieracium radyrense (Pugsley) Sell & West, sp. nov.

H. lachenalii var. *radyrense* Pugsley (1948), 216.

Holotype : Radyr, Glamorgan, Riddelsdell, 1910, in Herb. Mus. Brit.

Hieracium gratum Sell & West, nom. nov.

H. demissum var. *pulchelliforme* W. R. Linton (1905), 73. *H. demissum* subsp. *demissum* var. *pulchelliforme* (W. R. Linton) Zahn (1921), 885. *H. pulchelliforme* (W. R. Linton) Pugsley (1946), *J. Ecol.*, **33**, 346; (1948), 221; non *H. pulchelliforme* Dahlstedt ex Omang (1944), *Nytt. Mag. Naturvidensk. Oslo*, **84**, 151.

Hieracium vinicaule Sell & West, nom. nov.

H. crocatum var. *vinaceum* Beeby (1908), *Ann. Scot. Nat. Hist.* 115. *H. vinaceum* (Beeby) Pugsley (1946), *J. Ecol.*, **33**, 346; (1948), 227; non *H. vinaceum* Johansson et Samuelsson (1923), *Dalarnes Hier. Silvat.* 90.

Lectotype : Roeness Voe, Northmaven, Shetlands, Beeby (no. 1087), 1891, in Herb. Mus. Brit.

Hieracium acamptum Sell & West, sp. nov.

H. cantianum var. *subrigidum* E. F. Linton ex Hanbury (1904), in Babington 263; W. R. Linton (1905), 80; Pugsley (1948), 265.

Hieracium salticola (Sudre) Sell & West, sp. nov.

H. virgultorum microg. *dispatulum* var. *salticolum* Sudre (1902), *Hier. Cent. France*, 24.

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PAPERS

are invited both from members of the Society and others. They should have a bearing on the taxonomy or distribution of British Vascular Plants or Charophytes. Papers should be typed. They should be double-spaced and typed on one side of the paper only. The form adopted in this part should be used for citations and references. Full references should be put at the end, except where special reasons exist (e.g., the citation of place of publication of a plant name) or in very short papers. Illustrations, which may take the form of line drawings or photographs will be considered for publication, but photographs should only be used where essential. Papers should begin with a short abstract. Twenty-five separates of each paper are given free to the author, and further copies may be obtained on payment; requests for extra copies should be made when proofs are returned. Papers should be sent to the Editor, Dr. E. F. Warburg, University Department of Botany, South Parks Road, Oxford.

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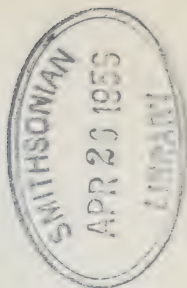
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RUBUS ARCTICUS L. IN BRITAIN

By R. M. HARLEY

In the past few months a number of herbarium sheets of reputedly British *Rubus arcticus* L. have come to light as a result of investigation prompted by the discovery of a specimen in J. Cosmo Melvill's herbarium in the Butler Museum at Harrow School.

There are two specimens in the British Museum (Natural History), one being from Ben Lomond, v.c. 86 (ex herb. J. Forbes Young), and the other from Ben-y-Ghloe, v.c. 89 (ex herb. J. Sowerby). This last is mentioned by Smith (1806, 1585): "Mr. Sowerby has been favoured by Richard Cotton, Esq., with a dry wild specimen from the high regions of Ben-y-glo, Blair, in Scotland . . ." The specimen at Harrow dated 1837 is reputedly from Ben Lawers. There are four other records, apparently unsubstantiated by any dried material, mentioned by Druce (1920, 755). One of these is said to have been gathered by "the late Rev. Dr. Walker, Professor of Natural History at Edinburgh . . . in rocky mountainous parts of the isle of Mull," in 1782. There is also mentioned "a specimen too imperfect to decide . . . from head of Glen Tilt" in 1841. Syme (1864, 260) states: "Ben More, in the Isle of Mull, and on Ben-y-Gloe, Perthshire; but recent search has failed to discover it. Mr. Watson had a specimen sent him which was said to have been gathered on a moor in Yorkshire, but he had reason to believe that the specimen was of garden origin. It appeared in the garden of the late Mr. J. Irvine Boswell, Kingcausie, near Aberdeen, on a bank of peat mould brought from the neighbourhood in preparation for a rhododendron bed; but careful search failed to detect it growing on the spot whence the mould was brought, and after a few years the plant died out in the garden. It is not an unlikely plant to occur; the most probable place for it is the district near the Sow of Atholl . . ." Also there are at Edinburgh two separate unlocalised specimens, apparently British, but these I have not seen.

Discounting probable horticultural introductions, there remain three or four records which constitute a claim for the consideration of the species as British. It has been mentioned by Polunin (1953, 34) as a plant likely to occur in this country.

Rubus arcticus L. is an unarmed plant with a creeping rootstock from which arise annual stems 4-8 in. high. The trifoliolate leaves consist of bluntly serrate leaflets. From the few sheets examined, the serration appears to be considerably blunter in the so-called British material than in the Scandinavian. There is usually a single terminal flower with notched or entire petals of the same purple hue as the styles and stamens. The fruit is dark purple, of a few large drupelets, with a strong flavour.

The plant is found in parts of North Russia, Finland, Norway, Sweden and, rarely, in what was formerly Estonia. In Finland it sets seed only north of the 62nd parallel, though the plant, presumably distributed by birds, occurs south of this line. Characteristically it is a plant of damp pastures and damp, open woodlands at fairly low altitudes.

The scattered reputed distribution in Britain suggests either that it was a relic from times when conditions were more favourable when it had a wider distribution, or that it has been introduced naturally or otherwise, each locality representing a single introduction.

Two points seem to bear on this problem. Firstly, it has never been refound in any of its localities in spite of evidence of searching, and secondly, Finnish records suggest that it might prove sterile in Britain, which lies mainly south of the 59th parallel. It would, however, be worth while cultivating the plant under natural conditions to see if



Rubus arcticus L. ($\times \frac{3}{2}$) drawn from the specimen at Harrow

this is so. It is perhaps unlikely that the plant would linger more than a few years reproducing vegetatively and thus, if sterile, its occurrences in this country would have to be attributed to adventives. It seems likely that seeds may have been brought over by winter migrants from Scandinavia, such as the fieldfare, which migrates direct to Scotland. The fact that these migrants to England come via Scotland or Europe perhaps explains why no plants have been seen in the south of England. In Scandinavia, fieldfares appear to inhabit ground suitable for *Rubus arcticus*, that is birch, pine or spruce woods, commonly near damp meadows. Feeding is said to reach a peak before migration; and it seems at least possible that some seeds might reach the British Isles by their agency. Even so, it is hard to imagine that this would explain the presence of the plant in all its recorded localities, especially in view of its apparent absence in Britain today.

It is greatly to be hoped that more recent specimens will soon be found to shed some light on the problem.

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A NEW SUBSPECIES OF *PEDICULARIS SYLVATICA* L.

By D. A. WEBB

Trinity College, Dublin

PEDICULARIS SYLVATICA subsp. *HIBERNICA*, subsp. nov. A typo (subsp. *sylvatica*) *discedit calycibus pedicellisque ubique pilis albis crispis longiusculis indutis*. A subspecies *lusitanica* (Hoffmanns. & Link) *Fic. discedit calyce tota superficie, non solum secus angulos, villosa, et habitu minore, cum caule centrali infra spicam brevissimo*.

Differs from the type (subsp. *sylvatica*) in the calyx and pedicels, which are uniformly clothed with rather long white curled hairs. Differs from subsp. *lusitanica* (Hoffmanns. & Link) *Fic.* in that the calyx is hairy all over and not merely on the angles, and in its lower stature, with the main stem almost entirely occupied by the terminal spike.

Type in Herb. British Museum : Ireland, Kerry, among heather on Mt. Carrantuohill, August 22, 1883, H. N. Ridley.

In every European flora which I have been able to consult, except those of Portugal, the calyx of *Pedicularis sylvatica* is described as glabrous, and frequently this is used as a key character to separate the species from *P. palustris*. This is, indeed, very natural, for the curiously smooth and polished surface of the accrescent fruiting calyx is one of the most conspicuous and characteristic features of normal *P. sylvatica*. In 1952 I noticed, however, first in Kerry and later in Donegal, that a large proportion of the plants in these regions stand out equally conspicuously (especially after mist or rain) by virtue of a loose but fairly abundant indumentum of curled white hairs, which covers the calyx, the pedicels, and indeed much of the upper part of the plant.

A difference of this kind, confined apparently to a single character, would scarcely be worth taxonomic recognition (any more than, say, albinism, which is not uncommon in this species), were it not for the fact that the hairy forms occur only in a well-defined geographical area. A search through the material at Kew, the British Museum, Oxford, Cambridge, Dublin, Brussels and Madrid, showed that plants with a hairy calyx are confined to the British Isles, Portugal, S. Spain, Morocco and Algeria. All hairy specimens from the last four countries are, however, referable to *P. lusitanica* Hoffmanns. & Link,* which is usually regarded now by Portuguese authors as a variety or subspecies of *P. sylvatica*. In this plant the hairs on the calyx are confined to the angles, and there are few or none on the pedicels; moreover it is taller, with an erect main stem usually 15-25 cm. high with several more or less elongated internodes below the inflorescence. Nothing like this has been seen in the British Isles.

Within the British Isles, it would appear that the hairy form is very nearly confined to those areas of western Ireland in which blanket-bog is a prominent feature of the landscape. In Kerry and West Cork, in Connemara and West Mayo, and in West Donegal it is common and ubiquitous, and it occurs also, though over less extensive areas, on the bogs or moorlands of Clare, Sligo and Fermanagh. The pattern of distribution, shown on the accompanying map, is certainly incomplete, for only Co. Galway has been at all systematically searched : it is almost certain that most of the gaps in Kerry, West Cork, northwest Mayo and West Donegal can be filled, and it is probable that there are a few stations still to be found further east – in mid Cork, E. Clare, Tyrone and perhaps Derry and Antrim. Still, the general pattern is clear, and there is no doubt

* A beautiful plate accompanies the original description in the *Flore Portugaise*.



Fig. 1.

Distribution of *Pedicularis sylvatica* subsp. *hibernica* D. A. Webb, in Ireland and (inset) in the Hebrides. Each circle is centred in the 10 km. square from which a record has been obtained. Open circles indicate that only slightly hairy plants, transitional to subsp. *sylvatica*, have been seen from this square.



that the plant is very common in most of the West of Ireland and distinctly rare in the East and Centre.

The few outlying stations, somewhat cut off from the main areas of distribution, are as follows :

- Co. WATERFORD : Exposed moorland at 550 ft. between Ardmore and Dungarvan, 02/1149, D. A. Webb and W. A. Watts, Sept. 1954.
 Co. WICKLOW : Calary Bog, R. L. Praeger, 1895 (Herb. Nat. Mus. Ireland).
 Kilbride Camp, R. L. Praeger, 1904 (Herb. Nat. Mus. Ireland).
 Co. SLIGO : Bog near Cliffony, E. J. Archer, July 1950 (Herb. T.C.D.).
 Co. TYRONE : Near Omagh, M. C. Knowles, 1896 (Herb. Nat. Mus. Ireland).
 Co. FERMANAGH : Tappaghan Mt., N. of Lack, 05/43, R. D. Meikle, May 1955.

It will be noticed that in three of these stations the plant is of an intermediate type – i.e. only slightly hairy.

Outside Ireland this subspecies is known with certainty only from a single locality in the Hebrides – the islet of Scalpay which lies off the east coast of Harris. Two separate gatherings from this station, both in the British Museum, are exactly similar to plants from the West of Ireland; one was collected by J. W. Campbell, the other by A. J. Wilmott, M. S. Campbell and E. B. Bangerter. There are, in the same herbarium, fourteen other gatherings from the Outer Hebrides (Scalpay, Barra, Benbecula, Harris, Lewis), and they are all typical subsp. *sylvatica*. There is one other Scottish plant apparently of subsp. *hibernica* in the British Museum herbarium, collected by Pugsley in Glen Callater, Aberdeenshire, on 30 July, 1923. But as it is labelled “*fl. albis*” and the specimen has indubitably pink flowers, it would appear that a transposition of labels may have taken place, and it cannot be accepted as it stands. But the occurrence of the subspecies in a few localities in the Highlands is by no means improbable.

On a vice-comital basis its distribution as at present known is : 110; H 1, 2, 3, 6, 8, 9, 16, 20, 27, 28, 33, 35, 36.

In almost all localities in the West of Ireland in which hairy plants are found it is possible to find normal glabrous ones as well. The ratio of hairy to glabrous is roughly proportional to the longitude : in the extreme west it rises to something like 20 to 1, and as one approaches the eastern boundary of the continuous distribution of subsp. *hibernica* it falls to unity or less. Plants of an intermediate (only slightly hairy) character are not very common, and they seem to occur chiefly near the eastern limit of subsp. *hibernica*.

This hairy form seems, therefore, undoubtedly to deserve subspecific rank; it is morphologically discriminable although intermediates exist, and it has a well-defined geographical area, with a fairly narrow zone of overlap. I should be grateful for any reports of its occurrence in regions other than those which are here set out in the map.

Three possible hypotheses as to its history can be entertained. (1) It could be endemic to the British Isles, dating from interglacial or pre-glacial times, and have survived one or more glaciations in refuges on the western seaboard, more successfully in Ireland than in Scotland. (2) It could be of post-glacial origin in Ireland, and have spread to Scotland by a chance of long-range dispersal. (3) It could have survived the last glaciation in south-west England or western France, spread to Ireland and Scotland early in the post-glacial, and subsequently undergone fragmentation, including extinction in all its original territory. None of the hypotheses seems thoroughly plausible; on the whole I prefer the first. It must be remembered, however, that typical *P. sylvatica* seems less hardy than one might imagine : it is not found north of 64°N. in Scandinavia, nor above 1,110 m. in the Alps.

SOME NEW CHROMOSOME NUMBERS IN THE CYPERACEAE*

By ELIZABETH W. DAVIES

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A number of chromosome counts have recently been made on some genera of the *Cyperaceae*, including a number of several different species of *Carex*. These have all been made on material of known origin, collected mostly from the British Isles, and other parts of northern Europe, or grown in the Botanic Garden at the University College of Leicester. Although the cytogenetics of this family and more especially the genus *Carex* will be described elsewhere, it seemed worth recording the results here.

A list of haploid chromosome numbers follows.

Genus	Species	Haploid chromosome number	Locality
I. <i>Eriophorum</i>	<i>E. angustifolium</i> Honck.	29	Teesdale, Durham
II. <i>Eleocharis</i>	<i>E. quinqueflora</i> (F. X. Hartm.) Schwarz		
	(<i>E. pauciflora</i> (Lightf.) Link)	10	Wicken Fen, Cambs.
	<i>E. multicaulis</i> (Sm.) Sm.	10	Derby Fen, Norfolk
	<i>E. uniglumis</i> (Link) Schult.	20	Holmsley Bog, Hants.
III. <i>Isolepis</i>	<i>I. setacea</i> (L.) R. Br. (<i>Scirpus setaceus</i> L.)	13	Derby Fen, Norfolk
IV. <i>Schoenus</i>	<i>S. nigricans</i> L.	22	Wittering Marsh, Northants.
V. <i>Carex</i>			
Subgenus I. <i>Carex</i>			
Section			
1. <i>Elateae</i> Kükenth.	<i>C. laevigata</i> Sm.	36	Windermere, Westmorland
2. <i>Distantes</i> Lang.	<i>C. hostiana</i> DC.	28	Wittering Marsh, Northants.
		28	Ben Lawers, Mid Perth
		28	Ryvoan Pass, Inverness
		28	Waulk Mill Bay, Orkney
	<i>C. punctata</i> Gaud.	34	Rhosneigr, Anglesey
	<i>C. distans</i> L.	37	St. Nectaire, France
		37	Ireland
	<i>C. binervis</i> Sm.	37	Teesdale, Durham
3. <i>Extensae</i> Fr.	<i>C. flava</i> L.	30	see <i>Watsonia</i> , vol. 3, pt. 3, 1955
	<i>C. extensa</i> Good.	30	Rhosneigr, Anglesey
	<i>C. lepidocarpa</i> Tausch	34	see <i>Watsonia</i> , vol. 3, pt. 3, 1955
	<i>C. mairii</i> Coss. & Germ.	34	see <i>Watsonia</i> , vol. 3, pt. 3, 1955
	<i>C. demissa</i> Hornem.	35	see <i>Watsonia</i> , vol. 3, pt. 3, 1955
	<i>C. serotina</i> Mérat	35	see <i>Watsonia</i> , vol. 3, pt. 3, 1955
	<i>C. scandinavica</i> E. W. Davies	35	see <i>Watsonia</i> , vol. 3, pt. 3, 1955
4. <i>Longirostres</i> Kükenth.	<i>C. sylvatica</i> Huds.	29	Leigh Woods, Somerset
5. <i>Rhomboidales</i> Kükenth.	<i>C. depauperata</i> With.	22	Axbridge, Somerset
6. <i>Gracillimae</i> Carey	<i>C. strigosa</i> Huds.	33	Loddington Wood, Leics.
7. <i>Pachystylae</i> Kükenth.	<i>C. pallescens</i> L.	32	Leigh Woods, Somerset
	<i>C. filiformis</i> L. (<i>C. tomentosa</i> auct.)	24	Leigh Woods, Somerset
8. <i>Paniceae</i> Tuckerm.	<i>C. panicea</i> L.	16	Teesdale, Durham
		16	Shapwick, Somerset
		16	Abisko, Sweden

* Part of a thesis approved for the degree of Ph.D. by the University of London.

Section	Species	Haploid chromosome number	Locality
9. Trachychlaenae Drej.	<i>C. flacca</i> Schreb.	38	Pickworth Wood, Leics.
		38	Knighton, Leics.
		38	Teesdale, Durham
		38	Shapwick, Somerset
10. Hirtae Tuckerm.	<i>C. hirta</i> L.	56	Shapwick, Somerset
		56	Wittering Marsh, Northants.
11. Montanae Fr.	<i>C. pilulifera</i> L.	9	Dingley Moor, Yorkshire
		9	Teesdale, Durham
		9	Roudsea Wood, Lancs.
	<i>C. ericetorum</i> Poll.	15	Markland Grips, Derbyshire
	<i>C. montana</i> L.	19	Gotland, Sweden
		19	Roudsea, Haverthwaite, Lancs.
	<i>C. caryophyllea</i> Latourr.	32	Markland Grips, Derbyshire
		33	Ingleborough, Yorkshire
		34	Cressbrook Dale, Derbyshire
12. Digitatae Fr.	<i>C. humilis</i> Leyss.	18	St. Vincent's Rocks, Bristol
		18	Blandford, Dorset
	<i>C. digitata</i> L.	24	Markland Grips, Derbyshire
		25	Roudsea Wood, Lancs.
		26	Skåne, Sweden
13. Atratae Kunth	<i>C. pediformis</i> C. A. Mey.	35	Cult. Botanic Garden
	<i>C. atrata</i> L.	27	Craig-na-Caillich, Mid Perth
14. Fuliginosae Tuckerm.	<i>C. frigida</i> All.	28	Albula Pass, Switzerland
15. Acutae Fr.	<i>C. elata</i> All.	37	Askham Bog, Yorkshire
	<i>C. aquatilis</i> Wahlenb.	38	Windermere, Westmorland
	<i>C. caespitosa</i> L.	40	Denmark
	<i>C. nigra</i> (L.) Reichard	42	Strines Moor, Derbyshire
16. Bicolores Tuckerm.	<i>C. bicolor</i> All.	25	Albula Pass, Switzerland
Subgenus II. <i>Vignea</i> (Beauv.) Nees			
17. Arenariae Kunth	<i>C. disticha</i> Huds.	31	Shapwick, Somerset
18. Muhlenbergianae Tuckerm.	<i>C. divulsa</i> Stokes	29	Leigh Woods, Somerset
19. Elongatae Kunth	<i>C. remota</i> L.	31	Leigh Woods, Somerset
20. Canescentes Fr.	<i>C. lachenalii</i> Schkuhr	29	Abisko, Sweden
21. Ouales Kunth	<i>C. ovalis</i> Good.	32	Shapwick, Somerset
Subgenus III. <i>Primocarex</i> Kükenth.			
22. Pulicares Tuckerm.	<i>C. peregrina</i> Link	31	Grand Curral, Madeira
23. Dioicae Tuckerm.	<i>C. dioica</i> L.	26	Teesdale, Durham

THE CHROMOSOME NUMBERS OF THE BRITISH MENTHAE

By J. K. MORTON

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The mints provide an excellent basis for cytological study. The taxonomic position of many is uncertain, minor variation is abundant, putative hybrids frequently occur, and many polyploids exist. An investigation into the chromosome numbers of this group was undertaken in the hope that they would help to clarify the taxonomic position, the main objects of the work being, (a) to ascertain the extent of polyploidy, (b) to determine whether the chromosome numbers support the suggested hybrid origin and parentage of many mints, (c) to provide the basis for an investigation into the association between polyploidy, hybridity and speciation.

The material for this work was collected from many parts of Great Britain and cultivated in the Botanic Gardens of King's College in the University of Durham. Also continental material of several British mints was obtained for purposes of comparison. Chromosome counts were made from root-tip preparations using a section technique. The roots were prefixed in a saturated aqueous solution of paradichlorobenzene for a period of one and a half hours. The chromosomes of most mints are short, but their large number, small size, and close proximity in the metaphase plate make counting difficult. Prefixation in paradichlorobenzene solution reduces them to a length little greater than their breadth and thus facilitates counting. Fixation was in Langlet's Modification of Navaschin's Fluid; sections were cut at 8 to 10 μ and staining was by Newton's Gentian Violet Method. The illustrations are camera-lucida drawings from such preparations.

Herbarium material of all the plants which have been used in this work is, for the time being, housed in the writer's own collections. Additional specimens of many of these plants are also in the herbarium of Mr. R. A. Graham.

Chromosome counts for several of the British species of *Mentha* have been published (see Darlington & Janaki, 1945; A. & D. Löve, 1948; Maude, 1939; Tischler, 1938). These counts were, however, based on non-British material. The diploid numbers are summarised below:

<i>Species</i>	<i>2n</i>	<i>Authority</i>
<i>M. aquatica</i>	96	Ruttle
	36	Schürhoff
	c. 96	Junell
<i>M. arvensis</i>	72	Ruttle, Schürhoff, Lietz
	12, 60-62, 72	Junell
	64, c. 90, 92	Nagao
<i>M. longifolia</i>	18	Heimans, Schürhoff
	24	Ruttle
	48	Nagao
<i>M. × niliaca</i>	24, 56	Ruttle
<i>M. × piperita</i>	36	Schürhoff, Wolf
	66, 68, 70	Ruttle
	36, 64 (128*)	Glotov

* Experimentally produced.

Species	2n	Authority
var. <i>officinalis</i>	72, 84	Nagao
var. <i>vulgaris</i>	68, 72	Nagao
<i>M. rotundifolia</i>	18	Heimans
	24	Ruttle, Nagao
	c. 54	Schürhoff
<i>M. × verticillata</i>	54	Schürhoff
	96, c. 120	Junell
<i>M. spicata</i>	36	Junell, Schürhoff
	48	Junell, Ruttle
	36, 48, 84	Nagao
(<i>M. canadensis</i>)	54	Schürhoff, Wolf
<i>M. pulegium</i>	20, 40	Ruttle

The variation of chromosome number within the species as shown by this list is probably exaggerated. The genus shows greater morphological variation on the Continent, but the affinities of some of these variants are imperfectly known, hence unrelated plants may have been grouped together. It is difficult to draw any conclusions from this list without material of the actual plants from which these chromosome numbers were obtained. My own results suggest a greater uniformity in the chromosome numbers of each species, and material from Continental sources has rarely differed in this respect.

THE CHROMOSOME NUMBERS OF PLANTS FROM BRITISH SOURCES

(a) *The Species and their Varieties*

M. aquatica L. A wide range of this very variable mint, collected in the following vice-counties, has been examined: v.cs. 13, 17 (4), 20, 21 (3), 65 (2), 66 (15), 67 (2), 70, 80, 102 and 104 (4). All thirty-five plants had a diploid number of 96: They included plants referable to vars. *major* Sole, *lobeliana* Becker (in the sense of Briquet and Fraser), and *hirsuta* (Huds.) besides other variations in leaf shape and dentation, pubescence, pigmentation, number of inflorescences, position of the stamens (whether included or exerted), habit, etc. Hence it is clear that the considerable variation of this species cannot be attributed to numerical chromosomal differences. The behaviour under cultivation, of the above and many other plants, showed that the trend of variation originally noted in the field was usually still recognisable, but much less pronounced. Far more noticeable was the "levelling out" effect produced by the cultivation of transplanted material under relatively uniform conditions. Hence I am of the opinion that the commonly occurring varieties of *M. aquatica* are the result of the complementary inter-reaction of minor genetical variation and the environment.

M. crispa L. This mint has been considered both as a variety of *M. aquatica* and as a hybrid between this species and *M. spicata* or between *M. spicata* and *M. rotundifolia*. Material from the Gardens of the Royal Horticultural Society at Wisley had a diploid number of 96, hence the suggestion that this plant is a variety of *M. aquatica* appears to be the most probable.

M. arvensis L. All seven plants examined from the following vice-counties had a diploid number of 72: v.cs. 13, 17 (2), 21 (2), 66, 102. This included both annual and perennial forms. Continental material from Essen Botanic Gardens also had the same chromosome number.

M. longifolia (L.) Huds. There is some difficulty in separating this species from its hybrid *M. × nemorosa*. However, it appears certain that at least two cytotypes exist

in Britain with diploid numbers of 36 and 48. No morphological differences between these two cytotypes have been noted. In addition, a plant from Amsterdam Botanic Gardens had a diploid number of 24, but was not identical with British material.

M. rotundifolia (L.) Huds. Material of this species from nine sources all had a diploid number of 24. Three of these sources were British (v.cs. 17 and 66 (2)), and the remainder Continental (Paris, Nantes, Lund, Brussels, Sacarvem and Liège Botanic Gardens).

M. spicata L. Two different chromosome numbers occur in this species, $2n = 36$ and 48. Plants with 36 chromosomes were obtained from v.cs. 21 (2), 66 (6) and 70. Also a plant referable to var. *ciliata* Druce from v.c. 66 and another referable to var. "*lacerata*" from the Gardens of the Royal Horticultural Society at Wisley had this chromosome number. Plants with 48 chromosomes were obtained from v.cs. 21 (3) and 66 and from the Gardens of the Royal Horticultural Society at Wisley (a very hairy plant). In addition Continental material with $2n = 36$ was supplied by Liège, Geneva (2) and Warsaw (2) Botanic Gardens, and with $2n = 48$ by Paris, Lund, Copenhagen, Warsaw, Amsterdam (2) and Geneva Botanic Gardens. This material was received under a variety of names - i.e. *M. sativa*, *M. piperita*, *M. gentilis*, *M. longifolia*, *M. arvensis*, *M. canadensis*, *M. lacerata* and *M. crispata*, but it all grew into plants identical with, or very closely related to, British forms of *M. spicata*.

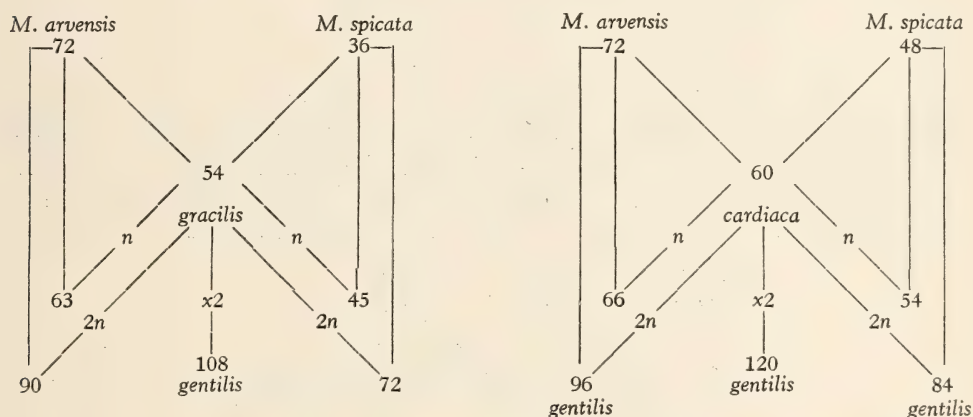
M. pulegium L. Efforts to obtain living material of this now rare mint from British sources were unsuccessful. However, material was obtained from several Continental sources and this proved to have a euploid series with a base number of 5. The diploid numbers obtained were, 10 (Liège Botanical Gardens), 20 (Geneva and Nantes Botanical Gardens), 30 (Liège Botanical Gardens), 40 (Sacarvem Botanical Gardens). In addition material belonging to the related *M. gattefossii* Maire was received from Mainz Botanic Gardens and had $2n = 40$. Both taxonomic and cytological characters indicate that *M. pulegium* belongs to a different section of the genus from all the other British species.

(b) *The Hybrids*

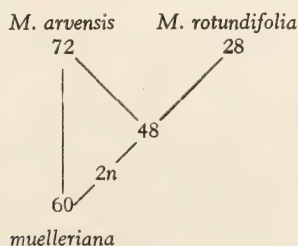
M. × alopecuroides Hull is usually considered as a hybrid involving *M. rotundifolia* and *M. longifolia*. If this is the case the diploid chromosome number of 36, in the three plants examined from v.cs. 17 (2) and 31, indicates that this mint is probably the F_1 hybrid between these two species. The marked stability of this mint suggests that it may be a completely sterile hybrid. The suggested parentage is difficult to reconcile with the existence of another, and different looking, hybrid (*M. × nemorosa*) of the same parentage and chromosome number, and showing the greater range of variation so frequently associated with hybridity. Further evidence on seed production and fertility etc. is required before any conclusions can be reached on the status or origin of *M. × alopecuroides*.

M. × gentilis L. (including *M. × cardiaca* (Gray) Baker and *M. × gracilis* Sole). This range of hybrids forms one of the most interesting and complex in the genus. A consideration of their chromosome numbers provides an explanation of their origin and parentage. The two species involved are *M. arvensis* and *M. spicata*. Diploid numbers of 54, 60, 84, 96, 108 and 120 were found in the eighteen plants which were examined. The vice-county distribution of these plants was : $2n = 54$ from v.c. 21; $2n = 60$ from

v.c. 17; $2n = 84$ from v.cs. 17, 65, 66 (4) and 67; $2n = 96$ from v.cs. 66 and 67 (2); $2n = 108$ from v.cs. 67 and 104; $2n = 120$ from v.cs. 40, 67, 70, and 77. The plant with a diploid number of 54 was referable to *M. × gracilis* and the one with a diploid number of 60 was referable to *M. × cardiaca*. Further material of both these is required in order to determine whether these numbers are constant. The diagram below indicates the main hybrid combinations and recombinations which are theoretically possible between *M. arvensis* and both cytotypes of *M. spicata*. It is noteworthy that both forms of *M. spicata* can take part in the formation of the *M. × gentilis* complex, though it appears that the one with $2n = 48$ is most frequently involved. *M. × gentilis* with $2n = 84$ is known to set fertile seed on occasions, and young plants have been raised from such seed, but these had not flowered up to the time of writing. Hybrid swarms are frequently encountered and the ones examined have been combinations of *M. × gentilis* ($2n = 84$) and *M. arvensis*. The plants in such swarms show every intermediate between *M. × gentilis* and *M. arvensis* and frequently set well-formed seed.

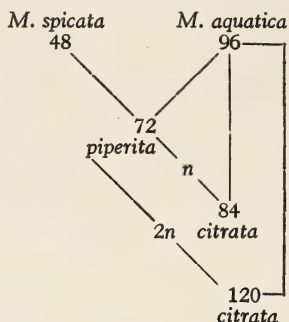


M. × muelleriana F. W. Schultz. Material of this very rare mint, from its original Devon locality, was found to have a diploid chromosome number of 60. *M. arvensis* and *M. rotundifolia* are obviously the parents involved in this hybrid, and the above chromosome number indicates a back-cross of the F_1 hybrid with the *M. arvensis* parent.

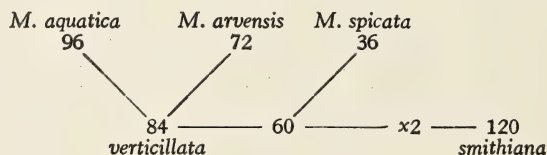


M. × nemorosa Willd. Morphological characters suggest a *M. longifolia* × *M. rotundifolia* parentage for this mint. Plants belonging to this hybrid frequently so closely resemble the former parent that so far I have been unable to separate them. A diploid number of 36 was obtained in material from v.c. 91 which is definitely referable to this hybrid. The presence of at least two cytotypes ($2n = 36$ and 48) in *M. longifolia*, one of which ($2n = 36$) is the same as would be expected to occur in *M. × nemorosa*, prevents the separation of the species from its hybrids on a cytological basis. As already mentioned

M. × alopecuroides is generally believed to have the same parents as *M. × nemorosa* but is a very different plant in its appearance. A possible explanation may lie in the way in which these hybrids have arisen, *M. × alopecuroides* being produced when *M. rotundifolia* is the female parent and *M. × nemorosa* when *M. longifolia* is the female parent. Additional material of both *M. × nemorosa* and *M. longifolia* is required from as many sources as possible for further study.



M. × piperita L. (including *M. × citrata* Ehrh.). The *M. aquatica* × *M. spicata* parentage of this mint would be expected to produce F_1 hybrids with two different chromosome numbers (i.e. $2n = 66$ and 72) depending on which cytotype of *M. spicata* is involved. Eleven plants of *M. × piperita* have been examined and ten of these had $2n = 72$ (from v.c.s. 17 (2), 21, 66 (4), 90 and 91 (2)) and one had $2n = 66$ (from v.c.



81). Those with $2n = 72$ were referable to var. *vulgaris* Sole, var. *officinalis* Sole, and *f. hirsuta* (J. Fraser) R. A. Graham. Two plants of *M. × citrata* were examined and these had $2n = 84$ (v.c. 21) and $2n = 120$ (v.c. 62). These two numbers indicate back-crosses of *M. × piperita* with the *M. aquatica* parent, in the first case a normal gamete of *M. × piperita* being involved, and in the latter an unreduced gamete.



Fig. 1

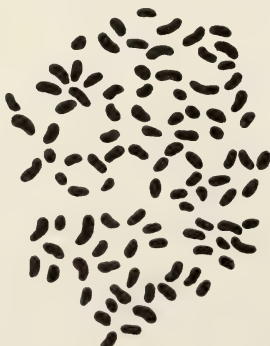


Fig. 2

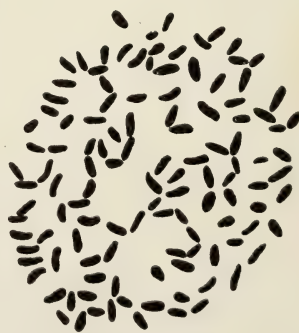


Fig. 3

Fig. 1. Root-tip metaphase plate in *Mentha rotundifolia* (L.) Huds. × 3750. ($2n = 24$).

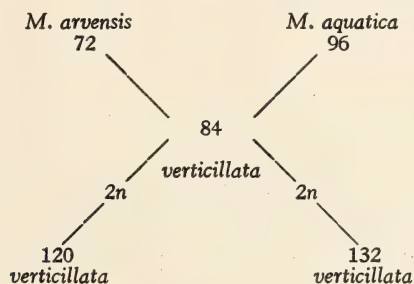
Fig. 2. Root-tip metaphase plate in *Mentha aquatica* L. × 3750. ($2n = 96$).

Fig. 3. Root-tip metaphase plate in amphidiploid *Mentha × gentilis* L. × 3750 (as in Fig. 1). ($2n = 120$).

M. × smithiana R. A. Graham. The triple parentage of this mint is supported by its chromosome number. Two plants (from v.cs. 17 and 21) were examined and both had $2n = 120$. This number can only be satisfactorily accounted for on the basis of an amphidiploid hybrid involving *M. × verticillata* and *M. spicata*.

The gametes of *M. × verticillata* are shown to be fertile from the occurrence of both back-crosses and fertile seed in this hybrid. Amphidiploidy is of frequent occurrence in hybrid plants and is a common means by which stability and fertility are attained. Whether *M. × smithiana* produces fertile seed is not known, and field and experimental observations on this point are needed. The plant is, however, very stable and shows little variation when considered in the strict sense. It is probable that some plants referable to *M. × gentilis* with $2n = 120$ have been included under *M. × smithiana* in the past. They show a similar long tubular calyx but this is smaller than that of *M. × smithiana* and the plants have not the distinct habit associated with this latter mint.

M. × verticillata L. The hybrids included under this name all have a *M. aquatica* × *M. arvensis* parentage. *M. × verticillata* is very variable and several different chromosome numbers have been found in the plants examined. These are: $2n = 42$ from v.c. 66; $2n = 84$ from v.cs. 17 (5), 21 (3), 65 (2) and 66 (4); $2n = 120$ from v.cs. 65 and 66 (3); and $2n = 132$ from v.c. 66. These numbers are derived from the F_1 hybrid and its unreduced gametes back-crossed with either parent.



The plant with a diploid number of 42 is of interest because it contains only half the normal chromosome complement and presumably must have developed from an unfertilized gamete.

The various hybrids appear to be correlated with several named varieties. The normal plant, and also var. *paludosa* (Sole) Druce (which rarely retains its characters under cultivation) have $2n = 84$. The back-cross with *M. arvensis* very closely resembles this parent and is referable to *M. arvensis* var. *densifoliata* Briq. The back-cross with *M. aquatica* has the verticils concentrated in the upper nodes and the bracts much smaller. It is subglabrous and has the narrower leaves associated with var. *acutifolia* (Sm.) Fraser. *M. × verticillata* with $2n = 84$ is frequently sterile but on occasions it has been observed to produce a varying amount of seed. Whether this is fertile is not known. The plants with $2n = 120$ have produced a full crop of seed, some at least of which was fertile.

M. × villosanervata Opiz. A plant which appears to belong to this hybrid between *M. longifolia* and *M. spicata* was found to have a diploid number of 48. It was discovered growing with the parents on waste land at Sherburn Hill (v.c. 66). The inflorescence is very poorly developed and few flowered. The flowers have included stamens and open several weeks later than those of either parent. All those examined died without setting seed.

British Mints - Their chromosome numbers, polyploidy and status or parentage

Name	2n	2x	4x	6x	7x	8x	9x	10x	11x	12x	14x	16x	18x	20x	22x	Status or Parentage
<i>M. aquatica</i>	96											x				Species
var. <i>crispa</i>	96											x				Species
<i>M. arvensis</i>	72			x						x						Species
<i>M. longifolia</i>	36					x										Species
	48															Species
<i>M. rotundifolia</i>	24															Species
<i>M. spicata</i>	36		x													Species
	48			x		x										Species
var. <i>ciliata</i>	36			x												Species
var. <i>lacerata</i>	36			x												Species
<i>M. pulegium</i>	10															Species
(from non-British material)	20	x														Species
	30			x												Species
	40					x										Species
<i>M. x alopecuroides</i>	36													x		Probably ♀ <i>rotundifolia</i> × ♂ <i>longifolia</i>
<i>M. x gentilis</i>	120															Amphidiploid <i>arvensis</i> × <i>spicata</i> (48)
	108												x			Amphidiploid <i>arvensis</i> × <i>spicata</i> (36)
	96										x					(<i>arvensis</i> × <i>spicata</i> 48) unreduced × <i>arvensis</i>
	84															(<i>arvensis</i> × <i>spicata</i> 48) unreduced × <i>spicata</i> (48)
var. <i>cardiaca</i>	60							x								<i>arvensis</i> × <i>spicata</i> (48)
var. <i>gracilis</i>	54						x									<i>arvensis</i> × <i>spicata</i> (36)
<i>M. x muelleriana</i>	60							x								(<i>arvensis</i> × <i>rotundifolia</i>) unreduced × <i>arvensis</i>
<i>M. x nemorosa</i>	36															Probably ♀ <i>longifolia</i> × ♂ <i>rotundifolia</i>
<i>M. x piperita</i>	66				x											<i>aquatica</i> × <i>spicata</i> (36)
	72								x							<i>aquatica</i> × <i>spicata</i> (48)
var. <i>citrata</i>	84										x					<i>piperita</i> (reduced) × <i>aquatica</i>
	120													x		<i>piperita</i> (unreduced) × <i>aquatica</i>
<i>M. x smithiana</i>	120													x		<i>piperita</i> (unreduced) × <i>aquatica</i>
<i>M. x verticillata</i>	84															Amphidiploid, <i>verticillata</i> × <i>spicata</i> (36)
	84										x					<i>aquatica</i> × <i>arvensis</i>
(<i>M. arvensis</i> var. <i>densifoliata</i>)	42															Haploid <i>verticillata</i>
var. <i>acutifolia</i>	120													x		<i>verticillata</i> (unreduced) × <i>arvensis</i>
	132															<i>verticillata</i> (unreduced) × <i>aquatica</i>
<i>M. x villosa-nervata</i>	48														x	<i>longifolia</i> × <i>spicata</i>

DISCUSSION

The above account of the chromosome numbers of the various species and hybrids clearly indicates the importance of polyploidy in the genus *Mentha*. There are two distinct polyploid series: the section *Pulegium* with a base number of 5, and the section *Mentha* with a base number of 6. The former provides a complete euploid series from 10 to 40, and the latter from 24 to 132. These chromosome numbers are apparently the result of both autopolyploid and allopolyploid changes in the genus.

(a) Autopolyploidy

Only three British species were found to have more than one chromosome number, namely *M. pulegium*, *M. longifolia* and *M. spicata*. *M. pulegium* has four different numbers, but no correlation between these and any morphological characters, or annual and perennial habit, could be found in the available material. In *M. spicata* the two cytotypes are probably separable by distinct though minor taxonomic characters. Further attention is being devoted to them in order to determine the reliability of these characters. The two cytotypes appear to be genetically isolated for no plants with an intermediate number of chromosomes have been encountered even though both forms frequently grow in close proximity. The occurrence of cytotypes with 36 and 48 chromosomes in both *M. spicata* and *M. longifolia* suggests that ancestral types with a diploid number of 24 may occur in both species. Ruttle (in Darlington & Janaki, 1945) has reported the existence of such a plant in *M. longifolia*. As far as is known no similar plant has been encountered in *M. spicata* but further work may well lead to its discovery.

(b) Allopolyploidy

In the type section, *Mentha*, of this genus the main cause of variation in chromosome number is the frequent occurrence of hybrids. The position is further complicated by amphidiploidy, the production of diploid gametes, and the occurrence, in one case, of a haploid plant. The existence of amphidiploid plants has already been noted in the *M. × gentilis* complex and in *M. × smithiana*. These amphidiploid mints are noticeably more stable than most of the other hybrids in the genus. However stability in this case is probably due to sexual sterility and reproduction by vegetative means rather than to the attainment of a normal fertility and seed production. Neither of the two amphidiploid forms of *M. × gentilis* has set seed in the plants under observation but further observations are required to confirm this point. *M. × smithiana* has been observed in the wild state to produce a varying amount of seed, but this is not always well formed and no information on its fertility is available.

The production of functional diploid gametes has clearly been of importance in the formation of several hybrid mints. In *M. × muelleriana* and the *M. × gentilis* and *M. × verticillata* complexes only back-crosses produced from the unreduced hybrid gametes are known. In *M. × piperita* both types of gamete must, on occasions, be fertile because *M. × citrata* can arise from either type. The three remaining hybrid mints which have been investigated are apparently F_1 hybrids. *M. × alopecuroides* and *M. × villosa* are probably highly sterile. Little is known about the third hybrid, *M. × nemorosa*, but its greater variability suggests that it may be partially fertile and back-cross with the parents.

An important feature in this genus is the part played by vegetative reproduction in the propagation of the species and their hybrids. By this means the effects of disorders in sexual reproduction, which may cause varying degrees of sterility, have been overcome. Thus hybrids, even when formed very infrequently, are maintained and dispersed, and somatic variation in the sexually reproducing species is perpetuated.

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SUMMARY

The chromosome numbers of British species and hybrids of the genus *Mentha* have been determined from root-tip preparations and are summarised in the accompanying table. In addition material from several Continental sources has been examined. The status of these mints and the parentage of the hybrids are discussed.

The mints contain two euploid series, the section *Pulegium* having diploid numbers of from 10 to 40 and a base number of 5, and the section *Mentha* with diploid numbers of from 24 to 132 and a base number of 6. Many of these numbers have arisen by allopolyploidy, but autopolyploid races occur in several of the species. The production of functional diploid gametes and the occurrence of amphidiploidy in several of the hybrids are noted. Vegetative reproduction plays an important part in the propagation both of the species and of the hybrids in this genus.

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HYBRIDISATION BETWEEN DIPLOID AND TETRAPLOID SPECIES OF *EUPHRASIA*

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The chromosome numbers of the British species of *Euphrasia* have been tabulated in a previous paper (Yeo, 1954). Five species are diploid with $n = 11$. They are *E. rostkoviana* Hayne, *E. montana* Jord., *E. rivularis* Pugsl., *E. anglica* Pugsl. and *E. hirtella* Jord. These constitute the series *Hirtellae*, characterized by the possession of long glandular hairs, which in Britain only occur exceptionally outside the *Hirtellae*. In other groups, only the tetraploid number, $n = 22$, has been found, and it is probable that this is the chromosome number of all the other British species.

Warburg (1952) lists four hybrids whose parents are now known to be diploid and tetraploid respectively. Such hybrids would be expected to be sterile triploids and to occur only as occasional isolated individuals. However, in at least some cases, they are fertile and form populations of more or less numerous plants. Several populations of this type, representing various forms, have now been investigated. Observations made at Withypool, S. Somerset, will be reported first.

Diploid-Tetraploid Hybrids at Withypool

The plants concerned were found on a heath at 1200 feet elevation near Withypool, Exmoor (grid. ref. 21/826367), in August, 1952.

Four forms of *Euphrasia* were present; their characters and habitats are given in Table 1, and herbarium specimens are shown in plate 17, fig. 1.

The flower measurements for *E. anglica* given in the table represent a population (E.180) about a mile nearer Withypool than that (E.187B) which accompanied the hybrids. The specimens in the photograph were also taken from this population since the plants of E.187B show slight traces of the hybrid influence which is present in E.187A. Owing to their occurring in grazed turf, it is difficult to find intact plants of *E. anglica* late in the season, and neither of the two plants in the photograph is intact; that on the left has been drawn up by long grass but has been included because it shows the leaves relatively well.

It will be seen from Table 1 and Plate 17, fig. 1, that there were two species present, *E. anglica* and *E. micrantha* Rchb., which are widely different morphologically, and which differ in habitat. The dwarf habit of *E. anglica* is correlated with its short-turf habitat, while the tall *E. micrantha* is found in the immediate vicinity of *Calluna vulgaris* and *Erica cinerea*. In addition there was a single triploid hybrid, very like *E. micrantha* but with a slightly larger flower, and some stalked glands, which, together with the chromosome number, indicate *E. anglica* as the other parent. Finally, there was a population of a diploid form which is rather variable, but which possesses some of the characters of *E. anglica* and some of *E. micrantha*. In the characters listed in Table 1 it resembles *E. anglica* in four, *E. micrantha* in four, and is intermediate in three. It also differs from *E. anglica* in growing in taller grass. In its extreme form (No. 3 in Plate 17, fig. 1) it is very similar to the triploid. The morphological distinctness of this form would qualify

* The work reported in this paper was carried out during the tenure of a Research Scholarship at the University College of Leicester.

TABLE 1.
Characters of the *Euphrasias* at Withypool

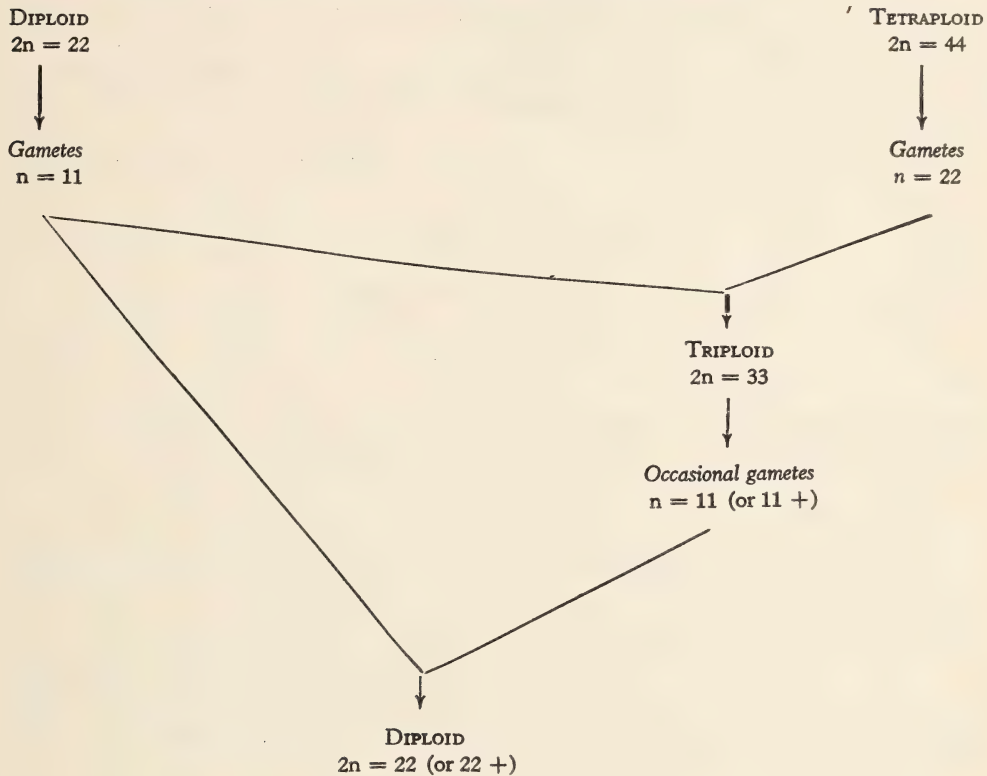
Name Collector's Number	<i>E. anglica</i> E 187B	E 187A	<i>E. anglica</i> × <i>micrantha</i> E 185C	<i>E. micrantha</i> E 185A
Internodes	Short	Long	Long	Long
Position and length of branches	Basal, not much exceeded by main stem	Central, much exceeded by main stem	Central, much exceeded by main stem	Central, much exceeded by main stem
Leaf shape	Broad	Narrow	Narrow	Narrow
Anthocyanin in (a) Leaves	None	Upper surface in some plants	Upper surface	Upper surface
(b) Stems	Little	Much	Much	Much
Foliar glands	Long, dense	Long, dense	Shorter, sparse	None
Corolla length	6.5-8 mm.	6.5-7 mm.	Smaller than E187A	5-6.5 mm.
Corolla-lip breadth	5.5-6.5 mm. (E 180, cult.)	4.5-5 mm. (cult.)	—	3.5-4.5 mm.
Corolla colour	White, upper lip sometimes lilac	White, upper lip sometimes lilac	Faint lilac	White, with magenta upper lip, or medium lilac, or intense red-purple
Capsules	Large, broad	Large, broad	None	Small, narrow
Normal-looking pollen	98 per cent.	98 per cent.	3 per cent.	95 per cent.
Chromosomes at meiosis	Not counted, but 11 bivalents in this sp. at several other localities	n = 11 (Plate 18, fig. 2)	Approximately 11 bivalents and 11 univalents	About 22 bivalents
Habitat	Closely grazed turf and paths	Longer grass around bushes of <i>Calluna</i> , <i>Erica cinerea</i> , <i>Rubus</i> and <i>Ulex</i>	One plant only, with E 185A	Periphery of <i>Calluna</i> and <i>Erica cinerea</i> bushes.

it for specific recognition. This is ruled out, however, on account of its distribution as at present known.

Interpretation of the Situation at Withypool

The observations show that it is possible for triploid hybrids between diploid and tetraploid species to occur. They also show strong evidence of the occurrence of plants of similar parentage which are fertile and have the diploid chromosome number. Meiosis in these plants is usually, at least, quite normal, as can be seen in plate 18, fig. 2, where at the end of the second meiotic division there are four groups of eleven chromosomes. The

occurrence of these diploids can be accounted for by supposing that triploids have occurred and have produced haploid gametes with eleven (or slightly more) chromosomes, which, by back-crossing with the diploid, have produced a fertile diploid of hybrid origin, containing germ-plasm derived from the tetraploid. This process is represented in the accompanying diagram; it will now be considered in more detail.



The production of gametes with a viable set of eleven chromosomes is only likely to happen, if, at meiosis in the triploid, eleven univalents and eleven bivalents are formed. For then the twenty-two chromosomes forming the eleven bivalents will separate regularly, while the others will either be scattered at random, or form a separate nucleus. In the former case, haploid (or slightly more than haploid) nuclei will occasionally be formed in accordance with the chance distribution of the unpaired chromosomes; in the latter, the other two haploid nuclei will produce four haploid pollen grains. In the Withypool triploid approximately eleven bivalents and eleven univalents were formed, and the univalents appear to be distributed at random (Yeo, 1954).

The eleven chromosomes coming from the triploid could be partly derived from the diploid parent, and partly from the tetraploid. In addition they would be affected by crossing over at meiosis in the triploid so that probably every one of them would contain some genes from the tetraploid parent. The sorting of the chromosomes and the positions of crossing-over in them would determine which genes were represented in the first diploid back-crossed individual. Since these factors operate more or less at random, the genetic constitution of this plant is unpredictable and could vary greatly between one occurrence of the process and another. The diploid back-crossed individual is likely to develop in the presence of the pure diploid, so that further back-crossing is possible. Owing to the heterozygosity of the first back-crossed generation, its progeny, whether

produced by self- or cross-fertilisation, will be highly variable. Thus a great source of variation in the diploid becomes available.

For this process to result in the production of a distinct form such as E.187A, there must be close at hand a plant community not occupied by a diploid species, to which the progeny of the back-crossed individual can gain access. This community must be one to which these progeny are adapted or can become adapted, by selection from their especially great variation. The genes derived from the tetraploid would thus enable their possessors to evade the parental diploid and grow in ecological isolation, and so obtain sufficient genetical isolation to remain distinct. The habitat of relatively long grass at Withypool fulfils this requirement.

Some additional possibilities can now be stated. One is that the diploid may result from a triploid fertilising itself by producing both male and female spores that are viable. There arise various other considerations which do not essentially alter the picture. The process of hybridisation between diploid and tetraploid, followed by back-crossing to the diploid, is presumably happening all the time with some low frequency. The process may also occur directly between the tetraploid and the new diploid. By both these means, the new form will be able to draw into itself other genes as they become available, provided they are favoured by selection. One would expect that ultimately, when the new form had "sampled" all the genes the tetraploid had to offer, an equilibrium would be reached. Selection after the original cross, and after later ones, would reduce variation, but could result in some variation persisting in response to minor habitat variation.

It is thus possible to explain the occurrence of a fertile diploid whose parents are diploid and tetraploid respectively, and to account for its existence as a morphologically distinct population. The hypothesis would appear still more probable if the suggested sequence of hybridisations could be made to occur experimentally. So far efforts in this direction have not even resulted in the production of a triploid. Finally it may be mentioned that *E. confusa* Pugsley also grew on the heath at Withypool and approached quite near to the colony of the hybrid. Some individuals of the hybrid show suggestions of *E. confusa* in their branching, and it is conceivable that this species has contributed to its origin by the same process as suggested for *E. micrantha*.

EUPHRASIA VIGURSII DAVEY

This is the commonest and best known of the reported hybrids whose parents are respectively diploid and tetraploid. It was described as a species by F. H. Davey (1907), and was said to occur at Porth Towan and Perranzabuloe, both in v.c. 1, W. Cornwall, and at Roborough Down, v.c. 3, S. Devon. It is now well represented in herbaria, by specimens not only from the original localities, but from several others in Devon and Cornwall. Pugsley (1930) regarded it as a hybrid between *E. anglica* and *E. micrantha*. From the morphological point of view, this seems plausible, and Pugsley pointed out that in some gatherings a proportion of the capsules are malformed, though such capsules are not necessarily completely barren.

Observations on *E. vigursii* at Roborough Down

The following observations were made at Roborough Down, which is a tract of heathland extending along, and on both sides of, the Plymouth-Tavistock road, for a distance of about six miles. The area investigated extended for about three-quarters of a mile from the southern end, and was mostly to the west of the main road (grid ref. 20/5063-20/5064).

The *Euphrasiae* present were *E. confusa* (of which three very small colonies were found), *E. anglica*, *E. vigursii*, and a form which will be referred to as *E. nemorosa*, though,

since it is far from typical of that species, and to some extent resembles *E. micrantha*, the name will be used in quotation marks. It might conceivably be a hybrid between *E. micrantha* and *E. confusa* or *E. nemorosa* (Pers.) Mart., but it appeared quite uniform. *E. confusa* is not considered important and will not be mentioned further; the other three forms occurred in large quantity. Their characters are shown in Table 2, and photographs of *E. "nemorosa"* and *E. vigursii* are given in plate 17, fig. 2, numbers 1 and 2.

Of the characters listed in Table 2, *E. vigursii* resembles *E. anglica* exactly in only one (chromosome number), *E. "nemorosa"* in two, and is intermediate in three, being nearer *E. anglica* in two of these. In addition, it is outside the range of these two species in the four floral characters listed. It will be noted that the characters in which *E. vigursii* resembles *E. "nemorosa"* are those of habit.

TABLE 2.
Characters of the Euphrasias at Roborough Down

Name Collector's Number	<i>E. anglica</i> E198	<i>E. vigursii</i> E 197A	<i>E. "nemorosa"</i> E 196
Internodes	Short	Long	Long
Position and length of branches	Basal, not much exceeded by main stem	Central, much exceeded by main stem	Central, much exceeded by main stem
Leaf shape	Broad	Intermediate, rather broad	Narrow
Anthocyanin in leaves	Probably a trace	Less than in " <i>nemorosa</i> "	Usually present
Foliar glands	Dense, long	Dense, long, often less dense than in <i>E. anglica</i>	Occasional short stalked glands present
Corolla length	6.7.5 mm.*	7.8.5 mm.	5.5-6.5 mm.*
Corolla-lip breadth	5.5.5 mm.*	6.5-8 mm.	4.4.5 mm.*
Shape of lobes of lip	Nearly parallel-sided	Considerably dilated	Narrow, little dilated apically
Corolla colour	White, with upper lip lilac, or finally faint lilac throughout	Purplish red to pale lilac, sometimes white with upper lip lilac	Upper lip lilac, lower usually lilac, sometimes white
Capsules	Normal	Occasionally with reduced numbers of seeds, down to one	Normal
Normal looking pollen	93 per cent.	c. 64 per cent. but results inconsistent	100 per cent.
Chromosome Number (2n)	Not counted, but 22 in this sp. at several other localities	22 (Plate 18, fig. 1)	Over 22 (44 in its nearest relatives)

* These measurements (especially the lip-breadths) may be underestimated through being taken two days after collection

No clear chromosome count of *E. "nemorosa"* could be obtained, but it is very likely that the number is $2n = 44$ as in true *E. nemorosa* and *E. micrantha*. Meiosis in *E. vigursii* was seen at early anaphase of the first division (Plate 18, fig. 1), and metaphase of the second division, and appeared normal.

The three forms concerned were differentiated ecologically, as well as morphologically. Lists of species occurring with *E. anglica* and *E. vigursii* at Roborough are given in Table 3. *E. anglica* occupied its characteristic habitat of short turf. *E. "nemorosa"* was usually found in longer grass than *E. anglica*, round bushes of *Rubus fruticosus* agg. and *Ulex europaeus*, but it was also present in quite short grass by the roadside in places. *E. vigursii*, also a tall plant, grew in still taller vegetation. This was characteristically a heathy community consisting of *Agrostis setacea*, *Calluna vulgaris*, *Erica cinerea*, and *Ulex gallii*. It also grew in a grassy community with rather long grass, mostly *Agrostis setacea*, and more or less scattered fronds of *Pteridium aquilinum*. The first of these two communities occupied the greater part of the heath and *E. vigursii* is probably commoner than either of the other species.

The habitat differences keep the greater part of the populations of the forms apart. Occasionally, however, *E. anglica* and *E. "nemorosa"* were more or less intermixed. At such places no intermediate could be found. *E. vigursii* mixes less with these two than they do with one another, but in some places it met *E. anglica*, and, in intermediate habitats on the embankment of a side-road, plants intermediate between the two were found.

Interpretation of the Situation at Roborough Down

E. vigursii occurs at Roborough in company with diploid and tetraploid forms between which it might, on morphological grounds, be interpreted as a hybrid. It is a fertile diploid, differentiated in habitat from its presumed diploid parent. This situation appears to be analogous to that at Withypool, and the same hypothesis can be used to explain it.

There are, however, some differences between the Withypool and Roborough situations. At Roborough, *E. vigursii* is not so clearly intermediate between the two supposed parents as E.187A is. This can be explained by the complex series of crosses involved, causing the removal of genes from the tetraploid into a new genetic environment in which they may have a modified action.

E. vigursii is morphologically distinct from the fertile hybrid at Withypool. But, at least at localities other than Roborough, it appears to have *E. micrantha* as its tetraploid parent. The morphological difference between the two forms could be attributed to the transmission of different sets of genes from the tetraploid. Another possibility is that, as already suggested, *E. confusa* has been involved in giving rise to the hybrid at Withypool, as well as *E. micrantha*.

Though the tetraploid accompanying *E. vigursii* at Roborough is not true *E. micrantha*, the latter might nevertheless have been its original parent there, since *E. vigursii*, being fertile, can persist in the absence of its parents. *E. micrantha* may have subsequently died out on the heath, or it may still occur somewhere on the large part of the heath not explored.

The habitat which *E. vigursii* occupies at Roborough is different from that of E.187A, and is more clearly distinct from the habitat of *E. anglica*. In addition, *E. vigursii* forms an abundant population spread over a wide area. The importance of the ecological conditions in enabling the diploid population to become split into two different forms is again evident.

Further Examples of E. vigursii Populations

Some other populations of *E. vigursii* at more westerly localities will now be described. Species lists for the first four dealt with are given in Table 3. The habitats were similar to that of *E. vigursii* at Roborough but poorer in species, probably because of burning.

E. micrantha and *E. vigursii* were found at Pensilva, on the slopes of Caradon Hill, E. Cornwall, v.c. 2 (grid ref. 20/279695-283696). They are shown in Plate 17, figs. 2 Nos. 3 and 4 respectively. The profuse branching of the specimen of *E. micrantha* shown is due to its being luxuriant. The *E. vigursii* here was similar to that at Roborough. The greater part of the heath had been burnt over and *Ulex gallii* had not yet regenerated over the area as a whole, so that the vegetation consisted mainly of *Agrostis setacea* and *Molinia caerulea*. *E. micrantha* formed a small colony in a place where *Erica cinerea* and *Calluna vulgaris* were present (grid. ref. 20/282696). *E. anglica* was fairly common in the district but it was not found nearer the *E. vigursii* population than about a quarter of a mile.

The remaining populations to be described were in W. Cornwall, v.c. 1, in the neighbourhood of Perranzabuloe. At Zela Hill (grid. ref. 10/821529) *E. vigursii* much resembled that at Roborough and Pensilva. The vegetation had been recently burnt here also; the dominants were *Agrostis setacea* and *Erica cinerea*. The only other species of *Euphrasia* present was *E. confusa*, but this did not occur on the same ground as *E. vigursii*.

At Polgoda Down (grid ref. 10/792525) *E. vigursii* grew mostly in parts of the heath where the vegetation was relatively thin with *Agrostis setacea* and *Erica cinerea* codominant. At this locality, *E. vigursii* was of an extreme form (Plate 18, fig. 3), with small elliptic cauline leaves with rounded teeth, strongly suggestive of *E. micrantha*. It was also rather small, and the anthocyanin pigmentation was strongly developed in the vegetative parts. It had the usual large purplish-red flowers. Growing with the glandular *E. vigursii* were eglandular plants which were not distinguishable except by this character, though on the average the plants were slightly less vigorous and had smaller leaves. Their flowers were identical with those of the glandular plant. The chromosome number of the eglandular plant is $n = 11$. The eglandular form must therefore be regarded as a form of *E. vigursii*. Apparently introgression of *E. micrantha* genes has gone so far that, in a proportion of the population, suppression of gland development has resulted. There was no gradation in the density of the glands between the strongly glandular and the eglandular types. The only other *Euphrasia* present at Polgoda Down was *E. confusa*.

A similar situation was found on a piece of heath-land about half-way between Zela Hill and Carland (grid ref. 20/837536), on the edge of Newlyn Downs. The *Euphrasias* occurred by paths and in other places where the vegetation was relatively thin. *E. micrantha* was present and in places grew with *E. vigursii*. A few plants of the eglandular form of *E. vigursii* were found growing with the normal form.

The eglandular *E. vigursii* is the only eglandular *Euphrasia* known to me which has the diploid chromosome number.

The observations on these four populations are considered to support the idea that *E. vigursii* is a hybrid, one of whose parents is *E. micrantha*, since in two of them *E. micrantha* was present, and, at Polgoda and Newlyn, the *E. vigursii* was an extreme form, showing a pronounced resemblance to *E. micrantha* in leaf-shape, indumentum (in a proportion of the plants), and habit.

A rather distinct form of *E. vigursii* was found on heathy slopes above the cliffs to the south-west of Perranporth. Here the dominant plant of the heathy ground is *Erica cinerea*. *Calluna vulgaris*, *Ulex* sp. (? *europaeus*), and *Molinia caerulea* were also present. *Euphrasia vigursii* grew in the grassier parts of the heathy area. It had the usual rather large reddish-purple flowers, and taller habit than *E. anglica*, but in its somewhat fleshy leaves, in the shape of these leaves, and in the formation of a dense flowering spike, it resembled *E. occidentalis* Wettst., a species which was very common in the short turf adjacent to the heath.

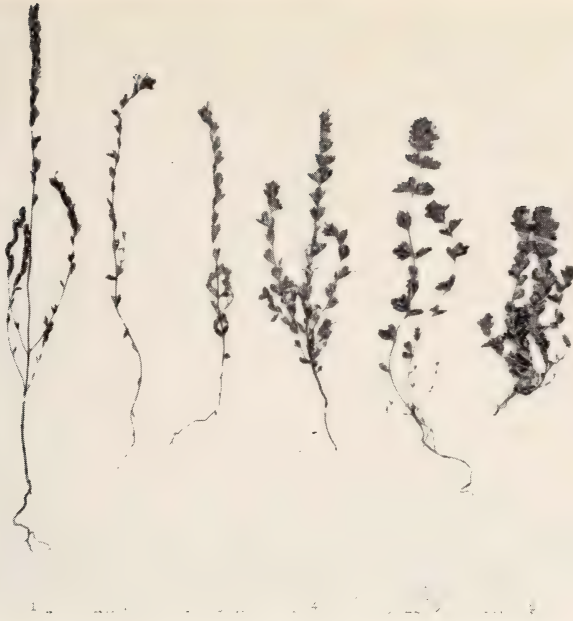


Fig. 1. Plants from Withypool : 1, *E. micrantha* (E185A); 2, *E. anglica* $\times$ *micrantha* sterile triploid (E185C); 3 and 4, *E. anglica* $\times$ *micrantha* fertile diploid (not *E. vigursii*) (E187A); 5 and 6, *E. anglica* (E180). In 2 note that calyces (teeth conspicuous) at nodes 1, 2 and 5 below lowest flower contain no capsules (compare corresponding nodes in 3).



Fig. 2. 1, *E. "nemorosa"* (E196) Roborough Down; 2, *E. vigursii* (E197A) Roborough Down; 3, *E. micrantha* (E375) Pensilva; 4, *E. vigursii* (E374) Pensilva; 5, *E. nemorosa* (E334) Lane End Common; 6, *E. anglica* $\times$ *nemorosa* (E335C) Lane End Common.

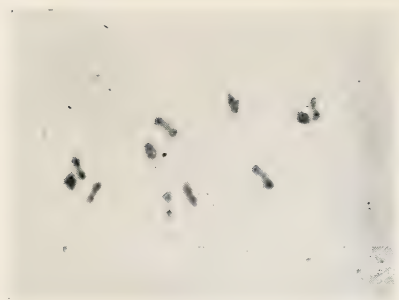


Fig. 1. *E. vigursii* from Roborough Down (E197A) : metaphase of first division, pollen mother cell meiosis ($\times 1000$).

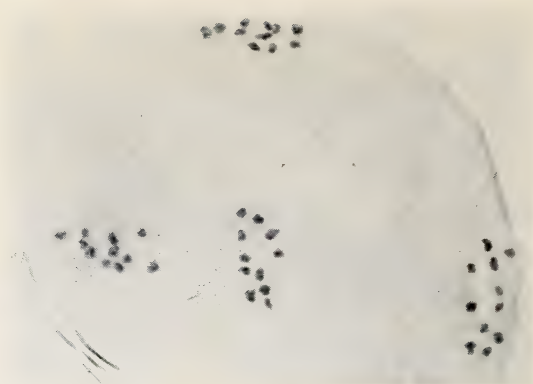


Fig. 2. E187A (see fig. 1) : anaphase of second division, pollen mother cell meiosis ($\times 1000$).



Fig. 3. *E. vigursii* (E348) extreme form, Polgoda Down, W. Cornwall.
Other species seen are *Agrostis setacea*, *Erica cinerea* and *Ulex gallii*.

This suggests either that the plant is a hybrid whose parents are *E. anglica* and *E. occidentalis*, or that *E. vigursii* arose from *E. anglica* and *E. micrantha* in the usual way, and that subsequently, by the same process, there has been introgression into it by *E. occidentalis*. The first alternative would not account for the purple flowers. The second gets some support from the presence of *E. micrantha* in the cliff-top heath, though this was found only at a point about one and a half miles from Perranporth, and was not adjacent to the *E. vigursii* population.

With the glandular *E. vigursii* form here, an eglandular plant with purple flowers was found; in one example a very few glands were present. In addition a small isolated colony consisting entirely of dwarf eglandular plants with fairly large purple flowers was found near the cliff-top. These may both be analogous to the eglandular *E. vigursii* at Polgoda Down.

At one of Davey's original *E. vigursii* localities, Porth Towan, the form present is markedly different from that at other places in its short internodes and broad rounded leaves. Davey first considered that the two forms should be distinguished as varieties. Since Porth Towan is a coastal locality it seems possible that this form has been introgressed by *E. occidentalis*, as suggested for the Perranporth form.

Distribution and Status of Euphrasia vigursii

A list of localities from which *E. vigursii* has been recorded is given in the appendix. At several of these *E. micrantha* is recorded, and, at a few, *E. anglica* has been found.* Its association with these two species supports the strong morphological evidence that it is a hybrid between them. Therefore, as regards the origin of *E. vigursii*, I accept Pugsley's view. A knowledge of the chromosome numbers of the three forms has, however, necessitated a special hypothesis to explain this origin.

The appendix shows that *E. vigursii* occurs in 7 of the 8 floristic divisions of Cornwall (see Davey, 1909), and that it thus occurs widely in the two vice-counties of Cornwall, as well as in part of a third (v.c. 3, S. Devon). Though in some places it is found with *E. micrantha* or *E. anglica*, it can exist independently of either. I did not see *E. anglica* at all in the Perranporth-Perranzabuloe district, and according to Rilstone (1923) it† is rare in this part of Cornwall, being unknown in District 8 (Land's End) and very rare in District 5 (North Coast), the district which includes Perranzabuloe. (There is, however, in the Cambridge herbarium, a gathering made by Curnow and Ralfs at Tregarrest, Penzance, in District 8). *E. vigursii* has a distinct habitat, namely heath with *Agrostis setacea*, and some or all of the following: *Calluna vulgaris*, *Erica cinerea*, *Molinia caerulea*, *Ulex gallii*. The only other *Euphrasia* found with it in this habitat is *E. micrantha*, from which it differs in chromosome number. It is morphologically very distinct and easily recognisable. It thus has the appearance of being a species. Davey's description of it as a species was based on his and Vigurs' knowledge of it in the field. Vigurs (1908) noted the constancy of its habitat, saying: "All the known localities but one . . . are heathy and furzy downs and crofts." In order, therefore, to signify its species-like status, I have adopted Davey's name, rather than Pugsley's hybrid formula.

E. vigursii may have had either a multiple or a single origin. If one supposes that it is of fairly recent origin, it is easier to imagine that it arose repeatedly in various localities, than to imagine its having migrated from one spot to the various areas of moorland which

* At localities not visited by me the absence of records or specimens of the presumed parents does not necessarily mean that they are absent.

† Rilstone used the name *E. rostkoviana* Hayne. The southern English plant known by this name was distinguished as *E. anglica* by Pugsley in 1930.

it now inhabits. If this is so, one must assume that in some areas *E. anglica* was once present and has now become extinct, probably owing to the elimination of its habitat.

Diploid-Tetraploid Hybridisation as a Source of New Species

E. vigursii is in effect a new species, assuming the hypothesis offered to account for its origin is correct. This suggests that other species may have been formed in the same way. The two forms most likely to have arisen in this way would appear to be *E. brevipila* Burnat & Gremli var. *notata* Pugsl. and var. *reayensis* Pugsl., since they combine characters typical of tetraploid species with the long-glandular indumentum of the diploids. The former occurs in central Scotland and is best known around Loch Tay. Here there also occurs a diploid species, *E. hirtella*. *E. brevipila* var. *reayensis* occurs along part of the north coast of Scotland, in Caithness and West Sutherland. No diploid species has, however, been reported north of the Loch Tay area. These two varieties of *E. brevipila* were investigated in 1953 and both were found to be tetraploid, as already reported (Yeo, 1954).

It is conceivable that *E. rivularis* may have arisen from *E. rostkoviana* and *E. curta* (Fr.) Wettst. var. *rupestris* Pugsl.

There are several other cases of apparent hybrids between diploid and tetraploid species, and these will be considered in the next two sections.

Further forms analogous to E. vigursii

Under this heading hybrids in which the habit of the diploid is modified will be dealt with. When these have been seen in the field the habitat has also been found to be modified. When they have not it is nevertheless to be expected that in fact the habitat is modified. All such forms are thus thought to be strictly analogous to *E. vigursii*.

(1) *E. anglica* × *nemorosa*

Pugsley (1930) described a form from Piltdown Common, E. Sussex, v.c. 14, as *E. anglica* × *pseudokernerii* Pugsl. A modified form of *E. anglica* has also been collected at Lane End Common, two and a half miles west of Piltdown (Milne-Redhead & Summerhayes, No. 1085, 1937, in Herb. Kew). The herbarium specimens from both these places are long-glandular, like *E. anglica*, but rather tall and large-flowered, and differing from *E. anglica* in leaf shape.

On visiting these two places, I was unable to find pure *E. anglica*, but at Piltdown (grid ref. 51/444224-446226) two forms of the glandular plant were found. One was only slightly modified; it had green leaves as in *E. anglica*, but the leaves were narrower and the internodes longer. It grew in grass of moderate length. The other form was much more modified, being taller and stouter-stemmed, and having a good deal of anthocyanin in the vegetative parts. It looked much like the Roborough form of *E. vigursii*, but the flowers were white with the upper lip lilac. This form grew in a grass-heath community, and with it was found a small colony of a form of *E. nemorosa*. This form was rather small-leaved and usually had lilac flowers; it is possibly var. *transiens* Pugsl. The same form was found at Lane End Common and a specimen from there is shown in Plate 17, fig. 2, No. 5.

At Lane End Common (grid ref. c. 51/404223), *E. nemorosa* (Plate 17, fig. 2, No. 5) was much commoner than at Piltdown, growing in short turf along the edges of the paths. The apparent hybrid showed variation according to habitat, tending towards *E. anglica*

on the one hand and *E. nemorosa* on the other (Plate 17, fig. 2 No. 6). Its commonest form, however, was intermediate between the extremes, being tall but with little anthocyanin, and very distinctive in appearance. It grew in long grass where *Pteridium aquilinum* was present, with the fronds well spaced out. The variation of the apparent hybrid might be due either to selection in response to habitat variation, or to phenotypic responses to different conditions. Probably both causes operate.

The glandular plant from Lane End Common has the diploid chromosome number, and at meiosis two of the larger chromosomes quite frequently occur as univalents, instead of as one bivalent.

The glandular plant at these two localities is presumably derived from *E. anglica*, by crossing with the form of *E. nemorosa* present, since it distinctly resembles the latter in its more extreme modifications. *E. anglica* is presumed to be the diploid parent because it is the only diploid species known in southern England. The modification of *E. anglica* is comparable in extent to that which *E. vigursii* shows, and it enables the glandular plant to grow in communities in which normal *E. anglica* would not be expected to occur. The hybrid populations are thus closely analogous to *E. vigursii*.

Like *E. vigursii*, the Sussex plant has rather large flowers, and this evidently led Pugsley to regard it as a hybrid between *E. anglica* and *E. pseudokernerii*. The nearest place to Piltdown where the latter is likely to occur is the South Downs, six miles away. *E. pseudokernerii* is therefore much less likely to be the parent than *E. nemorosa*. Owing to the unpredictable results of the process of crossing involved, the parentage of these fertile hybrid-populations should be inferred from the species associated with them, and not from the hybrids' morphology alone.

(2) *E. anglica* × *brevipila*

At Street Heath, N. Somerset, v.c. 6, two forms were found (grid ref. 31/396461). One is *Euphrasia brevipila*, a plant with long internodes, rather few branches, short-stalked glands on the leaves, and medium-sized flowers (6-7.5 mm. across the lower lip). The other is a long-glandular plant, similar in habit to *E. brevipila*, and attaining a very large size and having very large flowers, 7-11 mm. across the lower lip. The plants were found in moderately long grass, in two separate clearings, about 50 yards apart, in the fen carr which occupies most of Street Heath. *E. brevipila* was found by a peat cutting, the other plant in a relatively acid spot, with *Myrica gale*, *Erica tetralix* and *Calluna vulgaris*. The long-glandular plant is similar to *E. rostkoviana* Hayne, but the fine leaf- and calyx-teeth of some plants suggest that it is a hybrid.

Mr. C. C. Townsend has kindly sent me specimens of a plant collected at Street Heath and reported as *E. anglica* in *Proc. B.S.B.I.*, 1, 59 (1954). These plants resemble *E. anglica* in habit and flower size, but appear somewhat modified in habit, and more distinctly so in the fine teeth of the leaves and calyx. These plants tend to confirm that the very tall and large-flowered plant is in fact *E. anglica* × *brevipila*.

The hybrid parallels *E. vigursii* in having larger flowers than either parent, and in having a modified habit and habitat, as compared with *E. anglica*.

Two records of this hybrid from the Somerset peat moors have been obtained from herbaria. They are : (1) Sharpham, near Street, with *E. brevipila*, in low peaty pasture, V. S. Summerhayes, 19/7/1928 (Herb. Kew); (2) "Carex evoluta enclosure," Turfmoor, with *E. brevipila* and more or less normal *E. anglica*, H. S. Thompson, 1922 (Herb. Univ. Cantab. and Herb. N. D. Simpson). These two gatherings are probably both from the same place, which is probably the Sharpham Reserve of the Society for the Promotion of Nature Reserves.

(3) *E. confusa* × *rostkoviana*

This hybrid is one of those listed by Warburg (1952). The specimens to be described were collected in a "damp pasture near Whinlatter road, bottom of Hobcarton Gill, v.c. 70," Cumberland, by S. M. Walters.

E. rostkoviana is a tall plant of hayfields, with rather few branches and large flowers. It was not collected at this locality. *E. confusa* is a dwarf plant with flexuous branches, rather narrow, finely toothed leaves, and small flowers. The plants collected (No. 53/76) represent a rather sparingly branched form. The apparent hybrid (No. 53/77) was growing with it. It is long-glandular and has large flowers, 8-10 mm. long, like *E. rostkoviana*, but has numerous slender flexuous branches and is dwarf in habit. The capsules are longer and narrower than in *E. rostkoviana*, the leaves are smaller and narrower, and the teeth of the bracts and calyces are finer. In all these characters it approaches *E. confusa*.

Here, the tall hayfield species, *E. rostkoviana*, has been modified in such a way as to enable it to grow in a grazed pasture, that is, to become like *E. anglica*. The situation is therefore the converse of that at Street. *E. rostkoviana* is absent from Somerset, and *E. anglica* is absent from Cumberland.

(4) *E. rostkoviana* × *salisburgensis*

Specimens in Herb. Kew from fields near Innsbruck, collected by A. Kerner, show clear indications of the modification of *E. rostkoviana*, or an allied species, by a small form of *E. salisburgensis* Hoppe. Of the six plants on the sheet one is correctly determined by Pugsley as *E. salisburgensis*. The others resemble this plant in their relatively short, thin, wiry stems and branches and their long narrow leaves, deeply cut and with the teeth directed towards the apex, but are large-flowered and long-glandular plants.

The occurrence of this hybrid is interesting since *E. salisburgensis* is not closely related to the other tetraploids mentioned in this paper.

Diploid-Tetraploid Hybridisation Resulting Only in Introgression

Where a diploid and a tetraploid hybridise in the manner suggested for *E. vigursii* but without change of habit in the diploid, the process can be regarded simply as the introgression of genes from the tetraploid into the diploid. The absence of habit modification may be either because the diploid and the tetraploid are the same in habit, or, if they are not the same, because there is no habitat not occupied by the diploid parent to which it could become adapted by acquisition of genes from the tetraploid. However, even in the absence of habit modification, there might be physiological changes which would alter the diploid's tolerance with respect to environmental factors other than tallness of vegetation. The forms to be described now are, therefore, those in which there has been introgression of ecologically neutral characters, and possibly also of characters significant with respect to habitat factors not easily observed with the eye.

The first of these to be described was found at Friday Street, Surrey. This is the locality of another plant determined by Pugsley (1933) as *E. anglica* × *pseudokernerii*. The specimens of this were originally collected by Salmon in 1899. They have short internodes, and since both *E. anglica* and *E. pseudokernerii* have short internodes they are more plausibly regarded as *E. anglica* × *pseudokernerii* than the tall Piltdown plant. Salmon's plant is very like *E. pseudokernerii* in habit and foliage, and its flowers are very large, larger, in fact, than is usual in *E. pseudokernerii*. In 1953 I found what may be the locality of Salmon's plant (grid ref. 51/132461). The only *Euphrasia* present apart from the

supposed hybrid was *E. nemorosa*, which was abundant. No pure *E. anglica* was found at Friday Street, though it is common in Surrey. The apparent hybrid was found to occupy only a few square yards of ground, over which it occurred quite densely in short grass. It differed from *E. anglica* primarily in its small, narrow, ovate leaves. The corolla lobes were unusually narrow for *E. anglica*; this might have resulted from hybridisation but it was not a character of the *E. nemorosa* population here. The colony was visited in July and late September, and on neither occasion were the flowers large. The difference between my specimens and Salmon's in this respect may be attributed either to the evolution of a smaller flower-size in the last fifty-five years, or to my not having found the same population as Salmon.

Friday Street is on acid sandy soil, unsuitable for *E. pseudokernerii*, which is not likely to occur less than two miles away, on the North Downs, so that it seems as if the tetraploid parent must be *E. nemorosa*.

E. anglica × *confusa* occurs quite frequently. These two species are both dwarf in habit, so that hybridisation results in no change in stature. *E. anglica* affected by introgression from *E. confusa* tends to show the flexuous branches of the latter, but the main indication of hybridity is seen in the leaf shape. The occurrences of this hybrid known to me are:

V.c. 5, S. Somerset: round Withypool, visited in 1952, *E. anglica* was almost invariably accompanied by *E. confusa*, and in some populations it appeared to be modified by introgression from that species. At Elworthy in 1951 Mr. M. C. F. Proctor collected, as well as more or less normal *E. anglica*, plants that were strongly modified, especially in leaf shape. *E. confusa* was collected at the same place.

V.c. 6, N. Somerset: at Gorsey Bigbury, N.E. of Cheddar (grid ref. 31/479559), *E. anglica* and *E. confusa* were found growing together, and the former showed definite characters of the latter. Herbarium specimens collected by Turrill (in Herb. Kew) from Mendip Moors, near Cheddar, 1930, appear to represent this hybrid, as do those of Bucknall from "boggy ground, in thick spongy turf on Mendips, near Rowberrow," as "*E. rechingeri*, with the parents," 1916. The parents of *E. × rechingeri* Wettst. are *E. kernerii* Wettst. and *E. rostkoviana*, and Bucknall (1917), citing earlier gatherings from here, said it occurred with these two species. His description of "*E. kernerii*" suggests that it was *E. confusa*, and *E. anglica* was usually called *E. rostkoviana* at that period. Pugsley (1930, 540) regards the Rowberrow plant as abnormal *E. anglica*.

V.c. 39, Stafford, and v.c. 57, Derby: at Stanshope, near Wetton (v.c. 39) (grid ref. 43/126544) and at Thorpe (v.c. 57) (grid ref. 43/151506), populations of *E. anglica* were found which showed, in their habit and foliage, indications of introgression from *E. confusa*, which was growing with it in both places.

E. anglica is a very variable species, in spite of its nearly always being easily identified, and part of this variation is probably due to introgression from various tetraploid species.

In the British Isles, the diploid *E. rostkoviana* is usually accompanied by the tetraploid *E. brevipila*, and some of its variation may be due to introgression from that species. A probable indication of this is the variation in capsule shape, which is typically short and broad but is sometimes longer and narrower. The two species are similar in habit, both being tall.

Much Continental material of *E. rostkoviana* shows characters recalling those of tetraploids, but field observation is needed to assess the significance of this.

DISCUSSION

The main conclusion drawn from the observations described in this paper is that genes can pass from tetraploid species of *Euphrasia* into diploid species. A hypothesis

is offered to account for the achievement of fertility, in the diploid state, of forms whose ancestry includes both diploid and tetraploid forms. Such a result has not been achieved experimentally and it is therefore of interest to enquire whether a comparable process is known in any other group.

Anderson & Hubricht (1938) demonstrated, by morphological investigation, introgression from the tetraploid *Tradescantia canaliculata* into the diploid *T. bracteata*. This state of affairs is comparable with that described in some *Euphrasia* populations. Unfortunately, the chromosome numbers of the forms in the population investigated were not stated. The authors add that the case needs further investigation, since *T. bracteata* presents the most complicated pattern of intraspecific variation yet encountered among American *Tradescantias*.

The second example is also provided by wild plants and is more fully investigated than the first. It concerns hybrids between *Polystichum lonchitis* and *P. lobatum*, described by Manton (1950). These two species are diploid and tetraploid respectively. Plants of the putative hybrid, *P. illyricum*, from a locality where the other two species grow together, formed an almost continuous series of morphological intermediates between *P. lonchitis* and *P. lobatum*. Cytological investigation showed that some plants of *P. illyricum* were triploid, but one, which resembled *P. lobatum* more closely, was tetraploid, and one, which resembled *P. lonchitis* more closely, was diploid or nearly so. The behaviour of the chromosomes at meiosis in the triploid showed that *P. lobatum* is an allotetraploid, one of whose parents is *P. lonchitis*. The diploid plants, referred to *P. illyricum*, thus appear to have originated in the way suggested for the *Euphrasia* hybrids discussed in this paper. Manton says: "That some signs of hybridity still persist in such progeny would merely seem to imply that some extra chromosomes belonging to one or other species are still present or that a measure of gene exchange can occur between the chromosomes of the two species." It is not clear whether the second alternative concerns the sets which pair at meiosis in the triploid or those that usually do not. However, one can assume that the sets which pair in the triploid, while being cytologically homologous, are not genetically identical. In that case, since there will have been crossing-over between the chromosomes that paired in the triploid, characters found in the tetraploid will be expected to appear in the back-crossed diploid.

Müntzing (1937) obtained a partially fertile diploid in *Dactylis* by crossing the tetraploid *D. glomerata* with the diploid *D. polygama* (*D. aschersoniana*) and back-crossing the resulting triploid with the diploid parent. In this case *D. glomerata* itself forms quadrivalents frequently at meiosis and the triploid forms a high proportion of trivalents. Pollen fertility in the triploids was between 4 and 10 per cent. This indicates a closer relationship between the haploid set in the diploid with both sets in the tetraploid than is the case in *Euphrasia*.

The cross *Viola reichenbachiana* $\times$ *riviniana* provides a final example. Valentine (1950) crossed these two species, the first of which is a tetraploid with $2n = 40$ and the second a diploid with $2n = 20$, and thereby produced a triploid.

The commonest arrangement of the chromosomes at meiosis consisted of ten bivalents and ten univalents. The triploid was highly sterile, but most of its few offspring had a diploid chromosome number between 18 and 21. These varied from weak and non-flowering, through flowering but sterile, to slightly fertile. They were produced cleistogamously, so that the process involved differs from that suggested for *Euphrasia* (p. 255), but the selfing of the triploid is an alternative possibility for *Euphrasia* that has been mentioned (p. 256). The fertility of the diploid is very low, but might increase in later generations. It is interesting to note that Valentine, in his discussion, considers the possible achievement of fertility in hybrids between species differing in chromosome

number. He envisages repeated back-crossing leading to fertility, resulting in introgression by which one or other of the original species may be progressively modified. It would seem, however, that introgression into the diploid, by this process, is of rare occurrence.

No definite indications of introgression from diploid into tetraploid have yet been encountered in *Euphrasia*.

The conclusions drawn with regard to hybridisation mean that gene exchange is possible between two groups which would be expected to be genetically isolated on account of polyploidy. In Turesson's terminology of experimental taxonomy, forms that would be expected to belong to two coenospecies belong to the same one. A difference of chromosome number may in some cases mark the separation of two coenospecies, while in others, such as that of *Euphrasia*, it will not. It is therefore perhaps preferable to use the new terminology of Gilmour & Heslop Harrison (1954), which in its general definitions is explicitly elastic, but which is made precise in any particular case by the qualifications introduced by the user. According to this terminology *E. anglica* and *E. micrantha* may be said to constitute two different hologamodemes (within which all individuals are able to interbreed with a high level of freedom), which are not completely discontinuous and therefore belong to one coenogamodeme. Gene exchange between the two hologamodemes is at present only known to go in one direction. In a particular population *E. anglica* and *E. micrantha* form two gamodemes which are largely, but not completely, isolated genetically, while the diploid hybrid forms another gamodeme genetically isolated from *E. micrantha* (which may be called a cytogamodeme) and ecologically isolated from *E. anglica* (which may be called an ecogamodeme). Though the frequency of transfer of genes from the tetraploid to the diploid population is low, individuals showing intermediate characters may be very numerous. In spite of the abundance of intermediate individuals and the possibility of their closely resembling the tetraploid parent, the two gamodemes will be able to persist as largely discontinuous breeding units because of the difference in their chromosome numbers, which cannot be bridged by intermediates as the morphological differences can.

Finally, attention is drawn to the occurrence of hybrid forms with flowers larger than those of either parent. This is so frequent as to suggest that such forms may be selected for some reason.

SUMMARY

The parents of some reported hybrids are now known to be diploid and tetraploid respectively. The hybrids, however, are fertile and numerous.

Such a hybrid is described from Withypool, Exmoor. It looked intermediate between *E. anglica* and *E. micrantha* which accompanied it, and it grew in longer grass than the dwarf diploid *E. anglica*. It was diploid. A single triploid individual was also found, evidently a hybrid between *E. anglica* and *E. micrantha*.

Probably the diploid hybrid arose through the back-crossing of a triploid to the parental diploid by means of a haploid gamete. If this hybrid possesses characters derived from the tetraploid which enable it to grow in a habitat not occupied by the parental diploid, it may form an independent population of a new diploid type with distinct morphology and habitat.

The plant described as *E. vigursii*, and regarded as *E. anglica* $\times$ *micrantha* by Pugsley, was investigated, and presented an analogous situation, but no triploid was found. *E. vigursii*, though morphologically different from the Withypool plant, appears to have the parentage suggested by Pugsley. *E. vigursii* occurs in three vice-counties, is distinct in morphology and habitat, and resembles a species.

At one locality *E. vigursii* itself appears to have been modified by introgression from another tetraploid species.

Four other hybrids analogous to *E. vigursii* are described. In addition, there occur hybrids of similar origin, but in which there is merely introgression of characters with no apparent ecological significance, and no isolation of hybrids from the diploid parent.

Reported cases are mentioned of diploids in four other genera whose immediate ancestry includes a diploid and a tetraploid; in two cases the occurrence was natural.

In spite of the abundance of intermediate individuals derived from the kind of hybridisation described, the two original populations cannot merge into one, owing to the difference of chromosome number.

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APPENDIX : Localities for *E. vigursii*

Cornish records are grouped according to the floristic divisions of Davey (1909). The following abbreviations are used to indicate the sources of records : BM, the British Museum (Nat. Hist.) Herbarium; CGE, Cambridge University Herbarium; DF, Davey's (1909) *Flora of Cornwall*; K, the Kew Herbarium; PM, Pugsley's (1930) monograph; S, Mr. N. D. Simpson's herbarium.

All specimens collected by me are in my herbarium, and most gatherings are also in the herbaria of the University College of Leicester and Cambridge University.

Records of *E. anglica* and *E. micrantha* from localities for *E. vigursii* are also included.

V.c. 1. W. CORNWALL

District 7 : Lizard Downs, Salmon, 1926 (BM).

District 6 : edge of Newlyn Downs between Carland and Zela Hill, Yeo, 1953 (locality for *E. micrantha*, Yeo, 1953).

District 5 : Perranzabuloe, Babington, 1839 (CGE), (locality for *E. micrantha*, Babington, 1839 (CGE)); Reen Common, Perranzabuloe, Vigurs, 1907 (CGE), (locality for *E. micrantha*, Vigurs, 1907, (CGE)); Ventongimps, Perranzabuloe, Rilstone, 1918 (K); Goonhavern, Davey, 1906 (CGE), Tresidder, 1909 (CGE), (locality for *E. micrantha*, Tresidder, (DF), Rilstone, 1922 (PM)); Mill Down, Goonhavern, Thurston, 1916 (K); Polgoda Downs, Lousley, 1936, (K), Yeo, 1953; Newlyn Downs, Thurston, 1916 (K); Shepherds, Druce, 1917 (BM); Zela Hill, Yeo, 1953; Droskyn Point, Perranporth, Thurston, 1916 (K), Yeo, 1953; downs near Perranporth, Rilstone, 1918 (CGE); Quintrell Downs, near Newquay, Vigurs, 1907 (K), (locality for *E. micrantha*, Vigurs, (DF), Hume (PM)); Connor Downs, (DF); Porth Towan, Davey, 1905 (CGE).

District 4 : St. Issey Downs, near Padstow, Riley, 1906 (K), (locality for *E. micrantha*, Riley, 1906 (K)).

V.c. 2. E. CORNWALL

District 3 : Helman Tor, Rilstone, 1923 (? *E. vigursii*); Cheesewring Down, Minions, Rilstone, 1920 (BM); opposite Duchy Terrace, Minions, Thurston, 1923 (K), (Minions is a locality for *E. micrantha*, Thurston, 1923, (K), Yeo, 1953, and for *E. anglica*, Yeo, 1953); slopes of Caradon Hill, Rilstone, 1920 (BM) and Yeo, (Pensilva), 1953, (locality for *E. micrantha*, Yeo, 1953); Herod Down, near Pillaton, Jenkins (DF).

District 2 : Kit Hill, Callington, *Rilstone*, 1917 (K), *Rilstone & Thurston*, 1923 (K), (locality for *E. anglica* (as *E. rostkoviana*), *Hammond* (DF)).

District 1 : Kittows Moor, near Treneglos, *Little*, 1924 (BM, CGE, PM), (locality for *E. micrantha*, *Little*, 1924 (CGE, K, PM)); Wilsey Down, near Treneglos, *Little*, 1924 (C); Laneast Downs, *Marsden-Jones*, 1929 (K).

V.c. 3. S. DEVON.

Roborough Down, *Vigurs*, 1906 (CGE), *Sara*, 1907 (CGE), *Simpson*, 1939 (S), *Yeo*, 1953 (locality for *E. cf. micrantha* (*E. "nemorosa"* in this paper); *Simpson*, 1939 (S), *Yeo*, 1952, and for *E. anglica*, *Yeo*, 1952); Horrabridge, Roborough Down (N. end), *Stephenson*, 1937 (BM); Yelverton, *Williams*, 1925 (CGE, K, S); Yannadon Down, Yelverton, *Hume*, 1902 (BM), (locality for *E. micrantha*, *Hume*, (PM)); near Hand Tor, Dartmoor, *Stephenson*, 1937 (S); Lydford, Dartmoor, *Martin* (BM).

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GERANIUM PURPUREUM VILL. AND G. ROBERTIANUM L.
IN THE BRITISH FLORA

II. GERANIUM ROBERTIANUM

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Geranium robertianum L. is a commoner and more variable species in the British flora than *G. purpureum* which was dealt with in the previous paper of this series (Baker, 1955). Experiments, which will be described elsewhere, have demonstrated that some of this variability is the direct result of the influence of environmental factors while the remainder, some of which is important taxonomically, is genetically determined. Although populations of the species are often relatively uniform, there may be striking differences between populations. Part of the intra-population uniformity can be related to the prevailing self-pollination in this species (as in *G. purpureum*) (Baker, 1952).

This classification, which relates genetically determined morphological and ecological character-differences to each other, cuts right across the groupings made simply on the basis of the hairiness of the various plant parts even though such characters remain constant in cultivation. To take a single example—Druce's varietal name *hispidum* (Druce, 1917) was applied by its author to maritime material from Berry Head, South Devon and to hillside plants growing near Buxton in Derbyshire (Druce, 1924). On the other hand, glabrous plants grow on the shingle at Shoreham, Sussex and at several inland stations on Carboniferous Limestone, corresponding with those where the hirsute Derbyshire plants grow. Between these extremes a complete series may be made out in maritime and woodland populations.

The subdivision of British material of *Geranium robertianum* into varieties was attempted by Wilmott (1921) and three taxa with this status are listed by Warburg (1952) as "the more distinct forms" in a variable species "which is probably divisible into several ssp." In the present paper the division is made into subspecies in accordance with the principles of Clausen, Keck and Hiesey (1939).

The type subspecies is a race inhabiting woodlands, hedgebanks and patches of soil among rocks as well as on moist walls. Maritime material, usually found growing in relatively stable beach shingle, belongs to the subsp. *maritimum*, while subsp. *celticum* represents an ecoclimatic race apparently restricted to unshaded limestone rocks in the west. This last subspecies appears to be endemic to the British Isles.

GERANIUM ROBERTIANUM L. (1753), *Sp. Pl.*, 955

G. ROBERTIANUM subsp. ROBERTIANUM

G. robertianum var. *incisum* St. Hil. (1825), *Fl. Bras. mer.*, **1**, 82.

G. robertianum var. *alpinum* Gaud. & var. *flore albo* Gaud. (1829), *Fl. Helvet.*, **4**, 417.

G. robertianum var. *mosquense* Ledeb. (1842), *Fl. Ross.*, **1**, 474.

G. robertianum var. *genuinum* Gren. et Godr. (1848), *Fl. France*, **1**, 306.

G. robertianum L. sec. Jord. ex Boreau (1851), *Fl. Cent. France*, ed. 3, **2**, 131.

G. robertianum f. *subglabrum* Grognot (1861 ?), *Pl. vasc. Saône et Loire*, 139.

- G. robertianum* var. *genuinum* Syme (1864), *Eng. Bot.*, ed. 3, **2**, t. 305, 203.
G. robertianum var. *graniticarum* Martr. Don. (1864), *Florule du Tarn*, 126.
G. robertianum var. *leucanthemum* Dum. & var. *laciniatum* Beckh. ex Wilms. & Beckhaus (1879), *7 Jahresber. Westfal. Prov.-Ver.*, 1878, 178.
G. robertianum var. *typicum* Fiori & Paoletti (1896-1908), *Fl. anal. d'Italia*.
G. robertianum var. *crassicaule* Rouy (1897), *Fl. France*, **4**, 95.
G. robertianum var. *umbraticum* Westerlund (1904), *Bot. Notis.*, **1904**, 14.
G. robertianum subsp. *eu-robertianum* Briq. ex Knuth (1912), *Pflanzenr.*, **4**, **129**, 64-5.
Gams in Hegi (1924), *Fl. Mittel-Eur.*, **4** (3), 1714.
G. robertianum var. *trilobatum* Takeda (1916), *Rep. Bot. Soc. & E. C.*, **4**, 191.
G. robertianum L. var. *robertianum* sec. Warburg in Clapham, Tutin & Warburg (1952), *Fl. Br. Is.*, 390.

This subspecies is distributed throughout the British Isles, being commonest in partial shade in areas of base-rich soils at elevations up to 2,300 ft., well above the tree-line. It develops an ascending habit, at least in cultivation, where most plants behave as biennials. In their first season, the rosette of leaves is rather dense and mound-forming with long petioles. Stems and petioles are generally of a dull but deep red colour and bear eglandular hairs especially near the base and glandular hairs in the inflorescence and especially on the sepals. Leaflet-segments are rather broad. Petals are at least twice as long as the sepals (with flowers usually between 1.2 and 1.7 cms. in diameter). Anthers vary in colour from orange to dark purple while the fruits are more or less hairy with a pattern of well-spaced ridges and reticulations on the back (Fig. 1).



Fig. 1. Dorsal view of fruit of *G. robertianum* L. subsp. *robertianum* from Cheddar Gorge, N. Som. ($\times 20$).

A great many varieties, forms, etc. have been described by those who have only observed the plants in the wild. As a result of the cultivation experiments it has been decided that, of those listed above in synonymy, even the forms breeding true have no separate ecological significance and they are, consequently, retained within the subspecies. There is an interesting contrast between Wilmott's (1921) belief in a significant correlation between glabrousness and growth on limestone in Britain and the observations of French

workers (vide Rouy, 1897) who believe that the equally glabrous plants which they call *graniticarum* are restricted to siliceous soils.

The partial albino (f. *leucanthemum* Dum.) has rather yellow-green foliage but otherwise differs from the type only in having white petals. It occurs quite commonly. On the other hand, the *complete* albino (which lacks anthocyanin anywhere in the plant) is very rare in Britain and appears to have been found only once; as a true-breeding weed at Newport, Isle of Wight (Long, 1936).

In some Carboniferous limestone areas of the south-west (e.g. in the Cheddar Gorge and around Pontsticill, Breconshire) plants show less than the usual amount of anthocyanin in stems and petioles and the leaves are of a lighter green. The flowers may show white stigmata. In these characters they show a transition towards the subspecies *celticum*. The interpretation of this transition is not clear and there are alternative possibilities of introgression and parallel differentiation.

Similarly, in the vicinity of the River Camel, in Cornwall, many of the plants of *G. robertianum* have lemon-yellow anthers instead of the normal orange-red and they breed true for this character which is likely to have been obtained by introgression from *G. purpureum* which is common in the same hedgebanks.

Of the ecads (the forms which are the results of direct environmental modification), the shade-form is often seen (f. *umbraticum* Westerl.) This has broad leaflet-segments, relatively little vegetative anthocyanin and a rather upright habit due to the prolonged development of the leading shoot from the rootstock.

Contrasting with this is the exposed form. In inland rocky regions *Geranium robertianum* may be found growing in the open, sprawling over the rocks. It is often reddened where it is exposed to wind and sun (and such plants have often been called var. *rubricaula* by British botanists). This coloration develops particularly in plants growing on walls. The plants are usually dwarfed.

At the end of the summer, plants may be found bearing small flowers with dull yellow anthers. These have been mistaken by some observers for hybrids with *Geranium purpureum* or even with *G. lucidum*. Nevertheless, fruits from these plants produce perfectly normal plants in cultivation. In unusually cold weather a laciniated-leaved condition is produced, just as it is (more easily) in *Geranium purpureum*, and this form has been reported quite frequently by naturalists. It seems, however, that morphologically similar but genetically determined forms also exist (e.g., Stephenson, 1920; Druce, 1927, etc.).

G. ROBERTIANUM subsp. *MARITIMUM* (Babington) comb. nov.

G. robertianum L. var. *purpureum* sec. Pauquy (1831), *Fl. Somme*, 76.

G. purpureum Vill. sec. Bouch. (1833), *Fl. d'Abbeville*, 61; non Vill.

G. robertianum L. var. *rubricaula* Hornem. (1837), *Dansk. Oec. Pl.*, **2**, 226; sec.

Willk. & Lange (1878), *Prodr. Fl. Hisp.*, **3**, 531 (at least in part).

Robertianum vulgare var. *purpureum* sec. Picard (1838), *Ét. Geran.*, 42.

G. robertianum L. var. *maritimum* Babington (1851), *Man. Brit. Bot.*, ed. 3, 62.

G. robertianum L. var. *purpureum* sec. Syme (1864), *Eng. Bot.*, ed. 3, **2**, t. 307, 204.

G. purpureum Vill. var. *littorale* Rouy (1897), *Fl. France*, **4**, 98.

G. robertianum L. var. *hispidum* Druce (1917), *Rep. Bot. Soc. & E. C.*, **5**, 406 (partim).

G. robertianum var. *intermedium* Willmott (1921), *J. Bot.*, **59**, 99 (including the "Kingsdown form").

Type locality : Shingle beach, Shoreham, Sussex, England.

It is necessary to explain why Hornemann's varietal name has not been used in constructing the subspecific epithet. It has already been rejected by Wilmott (1921) on the grounds that it is impossible to refer this name to any shingle form in particular. Although, with the more widely cast boundaries of the subspecies used here, this objection no longer applies, it is true that from Hornemann's original description it is not certain that he had only shingle-beach plants in mind and, indeed, most subsequent authors have used the name *rubricaula* for any conspicuously reddened plants irrespective of their habitat. Unfortunately Hornemann left no herbarium specimen which could serve as a type.

There is no ambiguity, however, concerning Babington's appropriately named variety *maritimum*. Contrary to Wilmott's (1921) suggestion, there is no evidence that Babington intended to restrict his seashore variety to the almost completely glabrous plant found at Shoreham. In any case, the Shoreham plant merely represents the extreme form in a long series (or cline) in which the hairiness increases (through Wilmott's var. *intermedium*) to the extremely hirsute plants which grow on the Chesil Beach, on such islands as Steep Holm and Flat Holm and on the cliffs at Berry Head in South Devon (var. *hispidum* of Druce). Therefore it seems justifiable to raise Babington's variety to the status of a subspecies and to include within it all the inherently prostrate maritime plants.

One character of these maritime plants to which Wilmott (1921) has drawn particular attention is their prevailingly glabrous fruits. This is certainly a useful adjunct to the identification of fragmentary and ill-labelled herbarium material in which the habit of the original plant is often indistinguishable, but it is incorrect to assume, as does Wilmott, that material of this subspecies may never have hairy fruits. Thus his exclusion of some of the plants which grow on the shingle at Kingsdown (East Kent), for this reason, is unnatural, especially as the cultivation of similar material from Three Cliffs Bay (Glam.) has shown that its behaviour and habit are exactly the same as in glabrous-fruited maritime plants.

This, then, is the "*var. purpureum*" of most authors of local floras and it is largely to them that the confusion between this subspecies and *G. purpureum* itself has been due (vide Baker, 1955). The characters which distinguish the subspecies from typical *G. robertianum* are often not well preserved in herbarium material and, in critical cases, cultivation from seed may be necessary for certainty in determination. Nevertheless there are strong physiological and ecological differences and some distinctive morphological features, so that subspecific recognition is quite justified.

Very few plants of subsp. *maritimum* flower in their first season, during which they normally produce a prostrate, open rosette in which all petioles are much of the same length. The leaves have characteristically narrower leaflet-segments and shorter petioles than those of subsp. *robertianum*. There is a tendency for plants to rot at the crown in moist garden soil and the rosette-leaves decay more easily than those of the type subspecies. In cultivation subsp. *maritimum* tends to flower rather later and, in the flowering condition, the stems lie prostrate or ascend arcuately from the crown. The flowers are slightly smaller than those of subsp. *robertianum* (usually 1.3-1.4 cm. in diameter) and the fruits are usually nearly or completely glabrous.

It is found on stable shingle, particularly at the rear of fringing beaches, around the coasts of the British Isles and, less frequently, on cliffs and seaside walls. It is unlikely that a real climatic preference is to be seen in the greater frequency of this subspecies in south-eastern England, where its abundance is surely related to the large number of suitable beaches. Bøcher (1947) has pointed out that, in its European distribution, this subspecies may reach from Madeira to Norway and the Baltic, although there are many

gaps in the range. He, however, compares it with other "southern continental" plants and suspects that its absence from many of the shingle beaches of Jutland may be due to climatic factors.

The distribution list and the map which is given in Fig. 2 are both incomplete because the appropriate characters are often difficult to discern in herbarium specimens of *G. robertianum* and there is still much collecting to be done in all coastal areas except south-eastern England. This is particularly so in Ireland.

CHANNEL ISLES :

GUERNSEY : La Rochelle, 1939, *Dovaston* (K).

- V.c. 1. W. CORNW. : Coverack, 1910, *Fox* (Ox.) (Cam.), 1911 (Cam.); Padstow, 1904, *Barratt* (Cam.); Kynance Cove, 1926, *Salmon* (B.M.).
2. E. CORNW. : Par, 1920, *Thurston* (K), 1929, *Medlin* (K).
3. S. DEVON : Berry Head, 1916, *Druce* (Ox.) (WNH) (Cam.) (B.M.), 1916, *Hiern* (Ex. Hiern), 1918, *Larter & Crabbes* (Ex. Hiern), 1920, *Druce* (B.M.), 1927, *Druce* (Ox.), 1931, *C. I. & N. Y. Sandwith* (K); Paignton, 1945, *Robinson* (B.M.); Torquay, 1850, *Parker* (B.M. Bosw.), 1877, *Lomax* (Cam.); Seaton, 1909, *Hiern* (Ex. Hiern), 1920, *Larter* (Ex. Hiern); Axmouth, 1910, *Hiern* (Ex. Hiern); Beer Ferrers, 1876, *Briggs* (Cam.); Caldown Quarries, 1837, *Johns* (Cam.). Several of the stations given by Martin & Fraser (1939) for *G. purpureum* probably refer to this subspecies.
4. N. DEVON : Trentishoe, 1843, *Griffiths* (Cam.) (B.M.); Woody Bay, 1920, *Fox* (Ox.); Instow Burrows, 1882, *Ley* (Cam.) (B.M.); Lynton Foreland, 1917, *Barton* (B.M.). Records in Martin & Fraser (1939) for Landkey and West Buckland probably refers to this subspecies.
5. S. SOM. : Minehead, 1908, *Marshall* (Cam.) (WNH) (B.M.), 1942, *Lousley* (B.M.); Porlock, 1907, *Marshall* (B.M.) (Cam.), 1905, *Riley* (K); Bossington, 1942, *Lousley* (B.M.). It is probably this subspecies which is referred to by Marshall (1914) as growing between Stolford and Steart.
6. N. SOM. : Steep Holm, 1913, *Druce* (Ox.), 1914, *Roper* (L.Rop.), 1923, *Hyde* (WNH); betw. Worle & Kewstoke, 1907, *Marshall* (B.M.) (Cam.).
9. DORSET : Chesil Beach - many stations from the Neck of Portland to Abbotsbury. Winspit, 1936, *Ridley* (K); Lodmore, 1916, *Smith* (Ex. Hiern). Recorded from Fordington by Good (1948).
10. ISLE OF WIGHT : Whitecliffe Bay, 1877, *Stratton* (Ox.); no local., 1901, *Palmer* (Ox.). Records for St. Laurence, Culver and Steephill in Townsend (1904) probably refer to this subspecies, as does that from Totland in Rayner (1929).
11. S. HANTS. : Hayling Isl., 1919, *Druce* (Ox.). Records from Christchurch, Lepe and Hook in Townsend (1904) probably refer to this subspecies.
13. W. SUSSEX : Cockburn Common, 1833, *G. E. Smith* (Cam.); Selsey, n.d., *Tyacke* (Ox.), 1849, *Babington* (Cam.); Pagham, Bognor, 1913, *Little* (Cam.); Lancing, 1872, *Joad* (K); Shoreham, including Type specimen (Cam.); Southwick, n.d., *Hilton* (B.M.) (probably same station as Shoreham). Wolley-Dod (1937) records material from Bosham and Clymping.
14. E. SUSSEX : Many stations from Beachy Head to the Kent border.
15. E. KENT : Dungeness; Folkestone, 1869, *Syme* (B.M. Bosw.), 1891, *Marshall* (Cam.), 1930, *Albrecht* (B.M.); Walmer, 1888, *Marshall* (Cam.), 1903, *Druce* (Ox.), 1907, *Foord-Kelsey* (Cam.); Kingsdown, 1901, *J. & A. Bennett* (B.M.), 1907, *Foord-Kelsey* (Ox.), 1915, *Fox* (Ox.). Probably correctly recorded (as "*purpureum* auct. angl.") by Hanbury & Marshall (1899) from near Hythe on the authority of Mr. Duthie.
25. E. SUFFOLK : Felixstowe, 1888, *Hind* (Cam.), 1885, 1909, *Gray* (Cam.). Also (as *G. purpureum* Forst.) probably correctly recorded in Hind (1889) as collected by F. K. Eagle at Aldeburgh.
28. W. NORFOLK : Wolferton, 1946, *Hubbard* (K).
30. E. GLOS. : Sapperton, 1911, *Druce* (Cam.).
41. GLAM. : Flat Holm, 1922, *Hyde* (WNH); Sully, 1937, *Wade* (B.M.) (K); Barry, 1920, *Wade* (WNH) (K) (L.Rop.) (Cam.) (B.M.), 1946, *Baker* (Bak.); Porthkerry, 1906, *Riddelsdell* (B.M.); Mumbles, 1854, *Purchas* (B.M.); Langland Bay, 1913, *Shepherd* (B.M.); Three Cliffs Bay, 1946, *Baker* (Bak.); Port Eynon, 1903, *Groves* (B.M.) (WNH); Paviland, 1910, *Riddelsdell* (B.M.); The Leys, 1904, *Riddelsdell* (WNH) (B.M.).
45. PEMB. : Giltar Beach, n.d., *Trimen* (B.M.).
46. CARD. : $\frac{1}{2}$ mi. from mouth of R. Ystwyth, 1930, *Montfort, Turrill & Carter* (K); Aberystwyth, 1849(?), *Forster* (B.M.).



Fig. 2. Distribution of *G. robertianum* L. subsp. *maritimum* (Bab.) H. G. Baker in the British Isles.
● Stations verified by examination of herbarium specimens ; ○ records from the literature.

48. MER. : Betw. Barmouth & Llanaber, 1926, Britton (K); Barmouth, n.d., Bowman (Cam.).
50. DENB. : Plants probably referable to this subspecies grow between Pensarn and Llandulas according to a record by Dallman (1911).
58. CHESHIRE : Stations will certainly be found in this county where Lord de Tabley (1899) mentions the occurrence of the species on maritime shingle.
60. MID LANCs. : Wheldon and Wilson (1907) record *G.r.* var. *purpureum* (Forster) " as having been found on the north shore of Bare by F. A. Lees.
69. WESTMORL. : Slack Head, 1919, Adamson (B.M.).
74. WIGTOWN. : Stranraer, 1883, Druce (B.M.) (Ox.); nr. Drummore, 1909, Druce (B.M.) (Ox.); Marrock Bay, 1909, Smith (Ex. Hiern).
100. CLYDE ISLES : Whiting Bay, Arran, 1883, Ley (B.M.) (WNH) (Cam.); Glen Catacol, Arran, 1947, Cuany (Cam.).
107. E. SUTHERL. : Probably on shingle near Dunrobin (see Wilmott, 1921).
111. ORKNEY : no details, Gillies (B.M.); St. Ola, Mainland, 1922, Johnston (K) (B.M.).
112. ZETLAND : Boddam, 1924, Druce (Ox.).
- H. 2. N. KERRY : Records from Rossbehy, Cromane & Castlemaine Harbour for *G.r.* var. *purpureum* in Scully (1916) probably refer to this subspecies.
 4. MID CORK : Carrabinny, 1890, Dixon (B.M.).
 9. CLARE : Ballyvaughan, 1948, Baker (Bak.). Probably also in the Aran Isles (see Praeger, 1909).
 16. W. GALWAY : var. *purpureum* Forst. is recorded from Inishbofin by Praeger (1909) and is probably this subspecies.
 39. ANTRIM : Giant's Causeway, 1890, Dixon (B.M.).

It is unfortunate that the population at the type locality on Shoreham Beach is now very small, but although plants have been collected there by a horde of botanists during a complete century, it is most likely to be the disturbance of the habitat during the second world war which is responsible for the decline in the numbers of plants. A similar interference has operated along the whole length of these south-eastern beaches and increasing urbanisation is taking a further toll.

G. ROBERTIANUM subsp. *CELTICUM* Ostenfeld (1920), *Rep. Bot. Soc. & E. C.*, **5**, 551-2.
G. robertianum var. *celticum* (Ostenf.), Druce (1928), *British Plant List*, ed. 2, 21.

Type locality : Calcareous cliffs near Ballyvaughan, Co. Clare, Ireland.

This subspecies was described by Ostenfeld nine years after he collected fruits on the limestone of the Burren, near Ballyvaughan in western Ireland, during the International Phytogeographical Excursion in 1911. He grew four generations in Copenhagen and found it to be constant in its characters. Seeds were collected at the same time by Druce who then cultivated the plant in Oxford.

The most striking morphological feature of the subspecies is its colour. Vegetative anthocyanin is restricted to the region of the nodes on the stems and to the bases of the petioles. The laminae of the leaves have a clear green colour and the rather short petioles have a coppery green tinge. The rather large flowers are paler than in the subsp. *robertianum* due to a widening of the white streaks on the dorsal surface of the petals while the anthers, which are usually rather darkly red or purple, show up conspicuously. In material from the Burren the stigmata are pink but in plants from the Glamorgan population the stigmata are white. The fruits are hairy and relatively large (a feature which is correlated with stout fruiting calyces and shorter, stouter beaks). Most of the plants (which are decidedly intolerant of frost) flower as annuals and appear to favour a more humid atmosphere than that tolerable to the other subspecies.

An interesting difference between Welsh cliff-top material and plants from the Burren is that the former are prostrate in cultivation while some at least of the latter have an ascending habit. As one might expect there are differences in hairiness between the populations, the Welsh material being strongly hairy, the Irish much less so.

Subsp. *celticum* has not yet been recognised on the continent of Europe but it is likely that its distribution, even in the British Isles, is imperfectly known. It appears to be intolerant of shade, growing in crevices amongst limestone rocks in the south-west of the British Isles where the humidity may be high in sheltered places. Its distribution is mapped in Fig. 3.

V.c. 41. GLAM. : Cliffs above Three Cliffs Bay, Gower, 1946, *Baker* (Bak.).

42. BRECON : Erwood, 1926, *Mrs. M. S. Wedgwood* (Ox.).

44. CARM. : Reported by Hamer from Llyn-Llech Owen in *Rep. Bot. Soc. & E. C.*, 7, 564 (1925). This has been misquoted as a Glamorgan locality by Vachell (in *Glam. Co. Hist.*) following a misprint in *Rep. Bot. Soc. & E. C.*, 6, 831 (1923).

H. 9. CLARE : Rocks above Ballyvaughan, 1911, *Ostenfeld* (B.M.) (K) (Ox.) (Camb.) (WNH) (L. Rop.); 1911, *Druce* (Ox.) (Cam.) (WNH) (L. Cry.) (L. Rop.) (B.M.) (K) (specimens cultivated from seed in Copenhagen and Oxford respectively); 1948, *Baker* (Bak.).

16. W. GALWAY : Galway (? exact locality), 1920, *Mrs. Evans* (Ox.) (also see *Praeger* (1934)).

The record from Galway is not satisfactory as it is possible that the specimen was collected in the limestone of the Burren near to Galway City (but still in Clare). In the Burren the subspecies is common (along with subsp. *robertianum*) in the crevices of the limestone pavement and amongst the rocks at least as far south as Poulsallagh. It reaches the rear of the shingle beach at Ballyvaughan but is replaced nearer the sea by subsp. *maritimum*.

In addition to these records of undoubted subsp. *celticum* there are herbarium specimens from other western limestone regions which suggest this subspecies very strongly and fresh material from these areas would undoubtedly extend its known range. For example, many of the North Wales collections, some of the Somerset plants collected by E. S. Marshall and the specimen from Pen Moyle (W. Glos.) collected by W. A. Shoolbred in 1892 (WNH) are very close to *celticum*. J. A. Wheldon collected plants at Silverdale, W. Lancs., and cultivated them, noting their approximation to this subspecies (Wheldon, 1922). My own observations on Breconshire and Cheddar plants have already been quoted (p. 272).

There remains only one more curious form of *G. robertianum* to be described. This distinctive form is well-known in cultivation and is erroneously known to the horticultural trade as "var. *celticum*." It is a very neat, prostrate, small-leaved and rather small flowered form completely lacking anthocyanin. Consequently, the stems and leaves are a pale, clear green while the petals and stigmata are white and the anthers are lemon yellow. Almost every plant flowers in the first season and the plants are quite susceptible to frost-damage. At Kew, where it grows in the Students' Garden, it is believed to have come from Messrs. Ingwersen, who, in turn, believe it to have originated in Connemara. This is supported by the label on a specimen in the British Museum (Natural History) which was prepared by F. Dukes from a plant grown in Birmingham, labelled "var. *celticum* Ostenf." and "origin ? Connemara." Another specimen from the beds at Kew was collected jointly by A. J. Wilmott and J. S. L. Gilmour in 1936 (B.M.). Mr. Gilmour later suggested (according to the label) that this was the variety "*creticum*." I have not been able to find any more information about such a variety and Mr. Gilmour now has no reference to it. A most likely reference to this plant is given in the *Gardeners' Chronicle*, 1926, i, p. 188, where it is described. Noting this description, Druce (1927) says, "It came from Sir Charles Isham's garden at Menai Bridge, to which most of the plants were brought from western Ireland. Possibly this is a white-flowered form of Ostenfeld's *G. celticum*." While there is no real evidence to support this postulated ancestry, it seems that this is where the horticultural trade name was picked up and there is very good reason for searching for this interesting plant in western Ireland, particularly in Connemara.



Fig. 3. Distribution of *G. robertianum* L. subsp. *celticum* Ostenf. in the British Isles.

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THE GENUS *SYMPHYTUM* IN BRITAIN

By T. G. TUTIN

University College of Leicester

The identification of *S. peregrinum* has caused much trouble to British botanists but a re-examination of the *S. officinale-peregrinum-asperum* complex suggests that there are in fact only two species and a hybrid swarm involved.

The main morphological differences between the three taxa which have been commonly recognised are set out in Table 1.

TABLE 1.

	<i>S. officinale</i>	' <i>S. peregrinum</i> '	<i>S. asperum</i>
Flower colour	Yellow-white (rarely purple)	Purple	Blue
Calyx-teeth	linear-subulate	variable	triangular
Calyx	not accrescent	± accrescent	strongly accrescent
Leaf base	strongly decurrent	± decurrent	not decurrent
Hairs	stiff	variable	almost prickly
Anthers	longer than filaments	equalling filaments	shorter than filaments

S. officinale L. is a rather local plant of river banks and wet ditches occurring in most of Europe, except the arctic, eastwards to the Caucasus, W. Siberia and Central Asia. In W. Europe it most commonly has yellowish-white flowers, but purple-flowered forms were recorded by Ray in the 17th Century and still earlier by Gerarde. It is interesting to note that Popov (1953) does not mention the yellowish-white form at all as a Russian or Asiatic plant.

S. asperum Lepechin (*S. asperrimum* Donn) is native in the Caucasus but is now widely naturalised in Europe though very rare in Britain. It appears to have been introduced about the beginning of the 19th Century and to have been described from the gatherings of M. Bieberstein, for which no precise locality was given. Donn records it as having first been cultivated in the Cambridge Botanic Garden in 1801 (not 1811; see *English Botany*) and it was grown extensively as fodder a few years later. It is presumably from this introduction that the hybrids arose, some of which have gone under the name of '*S. peregrinum*'; the whole hybrid swarm should in fact be known as *S. × uplandicum* Nyman. *S. × uplandicum* Nyman was first described as *S. patens* E. M. Fries (non *S. patens* Sibth.) in 1839 from the province of Uppland in Sweden, where it must have resulted from the crossing of native *S. officinale* with introduced *S. asperum*. This invalid name was later replaced by the name *S. uplandicum* Nyman. It should be noted that the original, and presumably correct, spelling of the name is *uplandicum* in spite of the fact that the province after which it is named is called Uppland. The hybrid is also well known from the Caucasus, where the geographical areas of the parents appear to overlap.

The range of variation in the hybrid is great and plants may be found showing all combinations of the characters of the parents. The fact that the parents maintain their distinctness would appear to be due mainly to their ecological isolation; *S. asperum* is a

plant of dry places, while *S. officinale*, as has already been pointed out, occurs only by water. Further investigation may show, nevertheless, that these two taxa should be regarded as subspecies in order to emphasise what appears to be their close genetical similarity.

On the scanty evidence available about the distribution of the two colour forms of *S. officinale* it is perhaps unwise to draw conclusions, but it is tempting to suggest that the purple-flowered form may be due to introgression between *S. officinale* and *S. asperum*.

S. × uplandicum is probably the commonest *Symphytum* in this country, being frequent in hedgebanks, beside roads and sometimes in open places in woods. It seems to be better suited to conditions in Britain than *S. asperum* which, though widely distributed, is rare.

S. tuberosum L. is the only other native species. It is a local woodland plant found chiefly in N. England and in Scotland. It is not known to hybridise with any other species and is easily recognised by its little-branched stems, tuberous stock and by having the middle stem leaves larger than the basal ones.

S. orientale L. is locally naturalised. It may be recognised by its early flowering (April-May), soft hairs, broad leaves and short calyx-teeth, which are about half as long as the tube.

S. grandiflorum DC. is another early-flowering species which is often grown in gardens and has become naturalised in woods and hedgebanks. It is sometimes confused with *S. tuberosum* but may be readily distinguished by its spring flowering (with often a second crop of flowers in October and November), and by the long creeping sterile shoots which root at intervals.

Two other introduced species are recorded as established locally :

S. caucasicum M. Bieb., which is like *S. orientale* but has clear blue flowers and sessile, shortly decurrent upper leaves; and *S. tauricum* Willd. which differs from *S. orientale* in having bullate leaves with undulate margins and lanceolate acute calyx-teeth. Three other species have been recorded, but according to Mr. A. E. Wade, their identity is open to great doubt.

The genus *Symphytum* in Britain is therefore represented by the following :—

Native species :	<i>S. officinale</i> L., <i>S. tuberosum</i> L.
Naturalised species :	<i>S. asperum</i> Lepechin, <i>S. orientale</i> L., <i>S. grandiflorum</i> DC., <i>S. caucasicum</i> M. Bieb., <i>S. tauricum</i> Willd.
Hybrid swarm :	<i>S. × uplandicum</i> Nyman.

ACKNOWLEDGMENTS

I am most grateful to Dr. A. Melderis for translating the relevant portions of Flora U.R.S.S. and thus providing some information essential for the understanding of *Symphytum* in Britain, and to Mr. A. E. Wade for information about some of the introduced species, and a few other points.

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REVIEWS

Drawings of British Plants : Part VII - Leguminosae. Stella Ross-Craig. 76 plates. G. Bell & Sons, Ltd., London, 1954; 12s.

The family dealt with in the seventh part of Miss Ross-Craig's series of drawings is one which is, in its British representation at least, remarkably free from current taxonomic problems. Thus the claim of a species to inclusion must be settled, not on its validity as a species, but on its right to be considered a British plant. This can be just as personal a question as the other, with finality equally unattainable; in her solution Miss Ross-Craig selects seventy-six of the eighty-seven species numbered in the *Flora of the British Isles*.

A few of the omissions have little real claim to inclusion; these are plants of recent or deliberate introduction, casuals and escapes from cultivation. There is more to be said for five of the excluded species; these are *Trifolium aureum*, *T. incarnatum*, *Vicia sativa*, *Ornithopus pinnatus* and *Lathyrus niger*. The two *Trifoliums*, having reached the stage in recognition of being assigned a vice-comital number, may justly feel that they have been rather long in the British list to be thrown out now, while *Vicia sativa* has been recorded, though perhaps not continuously, from every British and Irish vice-county. I should have favoured the inclusion of these species, and should have pressed even more strongly the claims of the *Ornithopus* and the *Lathyrus*. Presumably these have been excluded on the grounds that the former is not known to occur on the mainland of Britain, while the latter has not been recorded within living memory. That *Lathyrus niger* was among the first illustrations I looked for when I opened the book was perhaps wishful thinking; I am reluctant to give this species up as lost.

The nomenclature followed is, in almost every case, that favoured by the *Flora*. There are minor changes; thus *Medicago hispida* Gaertn. becomes *M. denticulata* Willd., without synonym, and *M. arabica* (L.) All. is attributed to "(L.) Huds." *Trigonella* has returned to *Trifolium*; it is also, I think, worth noting that the mystery which has so long enveloped the identity of Shamrock is a mystery no longer.

It is difficult to fault the drawings themselves; the high standard set in the previous parts is well maintained. To deal adequately with the soft pubescence of such plants as *Trifolium arvense* and *Lotus hispidus* must be a heart-breaking task for both illustrator and reproducer. There are full dissections of the flower on every plate; in these the broken line is sometimes used without its significance being either obvious or explained. I felt less satisfied than usual with the plate of *Trifolium medium* (25); the flowers are less spreading, and so the inflorescence is more compact-looking, than I think should be. Nor is there any indication of the aptness of the British name of "Zigzag Trefoil." The plate of *Lotus corniculatus* (43) does not show flower-buds, and so an important diagnostic difference between this species and *L. uliginosus* - direction of calyx teeth in flower-bud - is missed. The appearance of the "false septum" in the fruits of *Oxytropis* (52G, 53J) scarcely tallies with the descriptions published in the *Flora*; I feel that this may be due to an over-simplification in the text of the latter.

As I looked at these drawings, I had a growing conviction that I recognise rare plants from black and white drawings more readily than I do common ones. I suppose the explanation is that I only see the rare ones as black and white drawings; the common ones I see often enough in the field, and colour must play an important part in recognition. Miss Ross-Craig has done what she could to make good this deficiency; there are very full descriptions of flower colour throughout. Indeed, some of these are almost lyrical, though I feel she has done rather less than justice to the colour-range in the flowers of *Trifolium molinerii* (28) and *T. repens* (37).

I have only detected one typographical error in this excellent work - *glycyphyllos* is mis-spelt both in the text and the index.

R. MACKECHNIE.

Vascular Plants of Illinois. George Neville Jones and George Damon Fuller. 4to, pp. xii + 593, vegetation map and 1,375 small outline maps. University of Illinois Press, Urbana, and Illinois State Museum, Springfield (Museum Scientific Series, vol. vi), 1955; \$10.00.

What does a British botanist know of the State of Illinois? That one of the world's greatest cities, Chicago, is at its north-east corner on the shore of Lake Michigan, while the whole of its western border

is the Mississippi River? Certainly, the vegetation cannot concern him much, being mainly of southern American affinities. The boreal element is extremely small, but a few familiar plants like *Milium effusum* and *Liparis loeselii* are native in the northern counties. Of the 2,450 odd species recorded from this State some 25 per cent are introductions, mostly from Europe. Only three endemics have survived the rapid destruction of the natural prairie and forests: the cornfields and cows have triumphed, and over a large part of the area "there is scarcely a foot of waste land."

This book is a scholarly and scientific enumeration, without descriptions and keys, which will interest those who are working on bibliography, distribution maps and county floras because there has been nothing quite like it here. The accent is on bibliography, on the concise and complete presentation of all the references to each species in published works relating to the area since the days of Michaux (died 1802). The method has, of course, required a good deal of synonymy, both nomenclatural and taxonomic, and the book sometimes looks rather like a cross between a monograph and a county flora. In the very numerous outline maps at the head of pages distribution is shown by various symbols placed in the counties of Illinois. A novel feature is the quotation of the type locality of each species when that was designated. There is hardly ever a paragraph of criticism or comment, and no appeal whatever to the imagination after the four-page introductory sketch of the area and its vegetation. It seems a model and admirable book of reference, but such formal perfection is lifeless and one returns with relief to the more old-fashioned, rambling style of an English county flora.

N. Y. SANDWICH.

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NEW SPECIES AND COMBINATIONS IN THE GENUS RUBUS L.

By W. C. R. WATSON

(The following descriptions of new *Rubus* species, etc. are taken verbatim from the manuscript of a monograph on the genus in Britain by the late W. Watson, which is to be published by the Cambridge University Press. The Publishers have kindly consented to this separate publication, in order that the Watson nomenclature might be used in the forthcoming British Plant List, which should then agree, both in content and order, with the Monograph. The opportunity has also been taken to publish a number of combinations, and to cite fully the synonymy).

P. D. Sell

S. M. Walters.

RUBUS CAESIUS L.

var. **grandis** W. Wats., var. nov.

Robustus. Differt foliolis magnis rugosis subtus dense pubescentibus, petalis sepalisque latis ovatis. Anglia.

Holotype: Turpington Lane, Bickley, W. Kent, 4/8/1952, W. Watson, in Herb. W. Watson.

var. **denticulatus** W. Wats., var. nov.

Gracilis. Differt foliolis regulariter denticulatis. Surreia.

Holotype: Gravel Road, Addington, Surrey, W. Watson, in Herb. W. Watson.

var. **pinnensis** W. Wats., var. nov.

Robustus. Differt foliolis argute profunde serratis, sublobatis, subcordatis, acuminatis. Middlesexia.

Holotype: Near the Pinn Brook, near Swakeleys, Uxbridge, Middlesex, W. Watson, in Herb. W. Watson.

RUBUS BERTRAMII G. Braun ex Focke

var. **minor** (Boul.) W. Wats., comb. nov.

R. biformis var. *minor* Boul., 1900, in Rouy, *Fl. France*, 6, 40.

Rubus arrheniiformis W. Wats., sp. nov.

Radix repens propagulifera. *Turio* primo erectus demum arcuatus, parum ramosus, angulatus rufus nitidus subglaber; aculei tenues recti vel falcatis flavescentes. *Folia* parvula 5-foliolata; petiolus leviter sulcatus, aculeis parvis armatus; foliola remota, supra glabrescentia, subtus pubescentia, subaequaliter serrata, terminale ovatum lanceolatum deorsum contractum. *Panicula* $\pm$ longa subracemosa, ramuli ejus numero ad 20 longi tenues, singuli 1-12 aculeis falcatis armati. *Flores* c. 1.75 cm. lati. *Sepala* acuminata pubescentia virescentia, margine alba, post anthesin ascendunt. *Petala* obovata apice modo *Rubi arrhenii* lata rotundata, roseola, numero saepe ad 12. *Stamina* alba stylos virescentes fere vel quidem aequantia. *Germina* semper fere glabra. Folio, panicula, flore *R. arrhenii* referens.

Holotype: Buxted Park, near Uckfield, E. Sussex, 24/7/1936, W. Watson, in Herb. W. Watson.

Rubus ooliticus W. Wats., sp. nov.

R. corylifolius var. *calcareus* Rogers ex Riddelsd., 1920, *J. Bot.*, **58**, 104.

Rubus eboracensis W. Wats., sp. nov.

Eglandulosus, tomentosus. *Turio* acutangulus glaber ; aculei recti breves. *Foliola* profunde obtuse $\pm$ duplicato-serrata, subtus albo-tomentosa pubescenti-velutina ; foliolum terminale subcordatum ovato-rhomboideum, breviter acuminatum ; foliola infima majuscula sessilia imbricata. *Paniculae* floriferae pyramidales ; ramuli plerumque fasciculati ; folia inferiora saepe 4-5-foliolata, foliolo terminale anguste rhomboideo. *Petala* lata ovata roseola. *Stamina* alba stylos virescentes aequantia. *Carpella* pilosa.

Holotype : Sowerby, Yorks., 27/7/1937, W. Watson, in Herb. W. Watson.

Rubus halsteadensis W. Wats., sp. nov.

R. dumetorum var. *raduliformis* A. Ley, 1904, *J. Bot.*, **42**, 120 ; non *R. raduliformis* Sudre, 1910, *Bull. Soc. Bot. Belg.*, **47**, 206.

Rubus ludensis W. Wats., sp. nov.

R. sciaphilus sensu W. Wats., 1929, *Rep. Bot. Soc. & E. C.*, **8**, 782 ; non Lange, 1886-88, *Dan. Fl.*, 781, no. 1288.

Robustus. *Turio* angulatus, fusco-viridis, pilosus, glaucescens, glandulis sparsis ; aculei reclinati, falcati, basi lati, atque pauci, parvi, apice glanduliformes. *Folia* magna, 5-foliolata, subdigitata ; foliola subtus pilosa griseo-viridia, inaequaliter crenato-serrata dentibus parum profundis ; foliolum terminale cordato-ovatum sensim acuminatum. *Panícula* magna, pyramidalis, basi foliosa, superne cum bracteis lanceolatis ; ramulorum mediorum pedunculi longi obliqui 3-7-flori ; superiores 1-3-flori ; rhachis pilosa, glandulosa, turioni similiter armata. *Flores* 2.5-3 cm. lati. *Sepala* viridia, glandulosa, aculeolata, ovato-lanceolata, appendiculata, mox erecta. *Petala* sepalaque 5-7. *Filamenta* alba ; antherae glabrae. *Carpella* glabra ; styli flavescentes. *Fructus* ovoideo-oblongatus, satis magnus.

Holotype : Whitcliffe, Ludlow, Shropshire, 8/7/1953, W. Watson, in Herb. W. Watson.

Rubus crespignyanus W. Wats., sp. nov.

R. similatus sensu W. Wats., 1938, *Rep. Bot. Soc. & E.C.*, **11**, 444 ; non P. J. Muell., 1859, *Pollichia*, 114.

Turio procerus obtusus parce pilosus, aculeis parviusculis rectis falcatisve munitus. *Foliola* serrata-dentata, utrinque glabrescentia, tandem convexa rugosa ; terminale subrotundum ovatum vel ellipticum acuminatum. *Ramus* longus pilosus, aculeis parvis curvatis defensus. *Paniculae* ramuli medii saepe profunde partiti. *Calyx* basi discoideus ; sepala aliquanto rubrantia, attenuata, tenuiter glandulosa, aculeata, post anthesin patula. *Petala* leviter rosea, elliptica, apice incisa. *Styli* rubri. *Anglia*.

Holotype : Addington Hills, Surrey, 6/8/1926, W. Watson, in Herb. W. Watson.

Rubus cambrensis W. Wats., sp. nov.

R. nemoralis var. *glabratus* sensu Rogers, 1900, *Handb. Brit. Rub.*, 31 ; non Bab., 1846 ; nec *R. glabratus* Kunth, 1823. *R. cambrensis* W. Wats., 1937, *J. Bot.*, **75**, 196, et 1946, *J. Ecol.*, **33**, 338 (nom. nud.).

Turio gracilis ; aculei breves, subulati, basi rubra. *Folia* 5-foliolata, digitata ; aculei retrorsi, falcati ; foliola superne glabrescentia, subtus pubescentia vel griseo-tomentosa, crenata vel leviter duplicato-serrata ; foliolium terminale emarginatum, rotundum, cuspidato-acuminatum. *Panicula* aequalis, longa, subracemosa, foliis 1-6 rotundo-ovatis serrulatis ; pedunculi longi, aculeis brevibus rectis armati ; rhachis pubescens tomentosaque. *Flores* c. 2 cm. lati. *Sepala* tomentosa, glanduloso-punctata, aciculata. *Petala* late obovata, unguiculata. *Stamina* stylis aequalia. *Carpella* glabra. *Receptaculum* pilosum.

Holotype : Athelstane's Wood, Herefordshire, July 1893, A. Ley & E. F. Linton, in Herb. Kew.

RUBUS MUENTERI MARSS.

var. *robii* W. Wats., var. nov.

A planta typica nihilo differt nisi parvitate omnium partium.

Holotype : Yearsley Moor, N.E. Yorks, 29/7/1937, W. Watson, in Herb. W. Watson.

Rubus obesifolius W. Wats., sp. nov.

R. grabowskii sensu Bab., 1847, *Ann. & Mag. Nat. Hist.*, **19**, 83 ; Bloxam in Kirby, 1850, *Fl. Leicester*, 46 ; non Wimmer & Grab., *Fl. Siles.*, **2**, 32.

Turio humilis, purpureus, angulatus, hirsutus ; aculei numerosi, longi, validi, ad angulos turionis saepe biseriati, patentes. *Folia* parvula, pedata ; petiolus persulcatus, aculeis curvatis armati ; foliola 3-5, subtus griseo-tomentosa pilosaque ; foliolium terminale cordatum, reniforme, breviter lateque acutum, crenato-dentatum. *Panicula* longa, aequalis, superne densa, folio uno tomentoso ovato, hirsuta, glandulis sparsis, aculeis confertis curvatis validis ; ramuli medii et superni 3-flori. *Flores* c. 2.5 cm. lati. *Sepala* tomentosa, aculeolata, glandulosa, mox erecta. *Petala* ovata vel obovata. *Filamenta* alba, stylos subvirides parum superantia ; antherae pilosae. *Carpella* glabra. *Receptaculum* hirsutum, pilis inter carpella et sub eisdem prominentibus. *Fructus* perfectus, ovoideus.

Holotype : Between Belmont and Cheddleton, Staffs., 22/7/1950, W. Watson, in Herb. W. Watson.

Rubus poliodes W. Wats., sp. nov.

Dumus persistens vigorosus ramosus pubescens eglandulosus. *Turio* crassus, e basi sulcata arcuatus ramosus glaucescens, pube brevi divergente indutus ; aculei breves vel brevissimi, multo declinati. *Folia* magna 5-foliolata, supra strigosa, subtus pubescentia, saepe cinerea ; foliola lata, omnia conspicue petiolulata, tandem convexa, depresso vel argute serrato-crenata, dentibus principalibus patulis ; terminale subrotundum, subquadratum vel obovatum, breviter cuspidatum. *Panicula* inferne pubescens, superne tomentosa, lata laxa composita, ramulis mediis 3- ad 7-floris sat longis, foliorum simplicium ex axillis ortis ; aculei pauci tenues patentes vel declinati. *Flores* latitudine 2.5 ad 3 cm. *Sepala* cinerea tomentosa inermia, breviter acuminata, patula apicibus ascendentibus. *Petala* ovata vel obovata deorsum contracta, dilute roseola. *Stamina* alba longa. *Styli* virescentes ; germina pilosiuscula vel glabra. *Receptaculum* hirsutum. *Fructus* magnus ovoideus, atosanguineus deinde niger. Facie *R. londinensem* referens. Anglia.

Holotype : Boars Hill, Berks., 6/7/1936, W. Watson, in Herb. W. Watson.

Rubus rubritinctus W. Wats., nom. nov.

R. cryptadenes Sudre, 1904, *Bull. Soc. Etudes Sci. Angers*, 31 ; non *R. cryptadenus* Dumort., 1863, *Bull. Soc. Roy. Bot. Belg.*, **2**, 230.

Rubus septicola (Sudre) W. Wats., sp. nov.

R. alterniflorus subsp. *septicolus* Sudre, 1909, *Rubi Europae*, 65.

Rubus chloocladus W. Wats., nom. nov.

R. pubescens Weihe ex Boenn., 1824, *Prod. Fl. Monast.*, 152 ; non Raf., 1811, *Med. Repos. N. York*, Ser. 3, 2, 333 ; nec Vest ex Tratt., 1828, *Ros.*, 3, 4.

Rubus ahenifolius W. Wats., sp. nov.

R. dentatifolius sensu W. Wats., 1931 (for 1930), *Lond. Nat.*, 73 ; non *R. borrieri* var. *dentatifolius* Briggs, 1880. *R. ahenifolius* W. Wats., 1946, *J. Ecol.*, 33, 341 (nom. nud.).

Folia surculorum immaturorum aenea. *Truio* obtusus, sulcatus, leviter pilosus ; aculei numerosi, flavi, basi robusti, breves vel leviter longi, declives vel falcati. *Folia* 5-foliolata, digitata ; aculei parvi adunci ; foliola longa, angusta, superne glabra, subtus glabrescentia, crasse serrata vel subtiliter subduplicato-dentato-serrata, breviter petiolulata ; foliolium terminale ellipticum, longe acutum. *Panicula* aequalis, angusta ; ramuli medii alte dividui turioni similiter armati. *Sepala* aciculata, patentia vel amplexa, apice lineari. *Petala* obovata spatulata vel oblanceolata, margine glabra, dilute rosea. *Filamenta* longa ; antherae pilosae. *Carpella* pilosa. *Fructus* parvus.

Holotype : Farley Heath, near Guildford, Surrey, July, 1930, W. Watson, in Herb. W. Watson.

RUBUS DISCERPTUS P. J. Muell.

var. *microphyllus* (Blox.) W. Wats., comb. nov.

R. rudis var. *microphyllus* Blox. in Kirby, 1850, *Fl. Leicester*, 41.

Rubus malacotrichus (Sudre) W. Wats., sp. nov.

R. apiculatus microg. *malacotrichus* Sudre, 1906, *Diagn.*, 36.

Rubus pseudadenanthus W. Wats., sp. nov.

R. adenanthus sensu Rogers, 1900, *Handb. Brit. Rub.*, 53 ; non Boul. & Gill., 1881, *Assoc. Rub. Ann.*, no. 429.

Surculi immaturi aenei. *Turio* sulcatus, pilosus, $\pm$ fuscus, glaucescens ; aculei inaequales nonnulli longi subulati. *Foliola* 3-5, $\pm$ convexa, superne glabrescentia, duplicato-serrata undulata dentibus nonnullis patentibus ; foliolium terminale breviter petiolulatum, rhombeo-ovato-ellipticum vel obovatum subcuneatum, basi integrum ; petioluli foliorum infimorum 1-3 mm. *Panicula* longe pyramidalis ; ramuli medii cymoso-partiti, pedicellis satis longis ; rhachis villosa, turioni similiter armata cum aciculis longis in parte inferiore. *Flores* mediocres. *Sepala* laxa reflexa vel patula. *Petala* anguste elliptica, dilute rosea vel alba. *Styli* interdum basi rubri. *Carpella* glabra. *Fructus* suboblongus.

Holotype : Roscarrock Hill, Port Isaac, E. Cornwall, 16/8/1952, W. Watson, in Herb. W. Watson.

Rubus subtercanens W. Wats., nom. nov.

R. thyrsiflorus P. J. Muell., 1858, *Flora*, 41, 165 ; non *R. thyrsiflorus* Weihe ap. Bluff & Fing., 1825, *Comp. Fl. Germ.*, 1, 684.

Rubus trichodes W. Wats., sp. nov.

Folia floresque parvula. *Turio* ruber pilosus, glandulis aciculis aliquantum brevibus aculeisque longis rectis inaequalibus munitus. *Folia* (3-4)-5-foliolata, pedata; foliola supra strigosa, subtus viridia ad venas molliter pilosa, inaequaliter crenata serrata, terminale suborbiculatum cordato-ovatum vel obovato-oblongum, breviter acuminatum. *Panicula* pilosa longa, leviter angustata, valde foliosa; ramuli patuli (1-3)-5-flori, pedicellis longis tomentosis aculeatis. *Flores* circiter 1.5 cm lati. *Sepala* viridia albo-marginata, florum imprimis terminalium foliaceo-appendiculata, ejusdem floris parte reflexa parte patula vel erecta. *Petala* 5-6 dilute rosea, obovata longe unguiculata apice emarginato vel retuso vel apiculato, margine glabra. *Filamenta* alba stylos pallidos vel rubentes parum superantia. *Carpella* barbata. *Fructus* haud magnus, subglobosus. Per Angliam meridiionalem dispersus.

Holotype: Wareham Hill, Witley, Surrey, 9/7/1937, W. Watson, in Herb. W. Watson.

Rubus putnei W. Wats., sp. nov.

Robustus. *Turio* humilis obtusus pruinosis primo pilosus, glandulis rubris plerumque brevibus, aciculis, aculeisque declinatis confertis obsitus. *Folia* majuscula virentia; foliola glabrescentia, irregulariter crenato-serrata, terminale suborbiculatum vel obovatum cuneatum, cuspidatum. *Panicula* ad summum subracemosa inferius ramulis paniculatis, pubescentia tomentosa, glandulis aculeisque brevissimis necnon aculeis tenuibus recurvis creberrime munita; folia simplicia cinerascens; foliola terminalia obovata cuneata. *Flores* magnitudine 2-3 cm. *Petala* angusta remota, dilute rosea, margine glabra. *Sepala* viridia angusta attenuata appendiculata, patula. *Filamenta* alba stylos saepe roseolos parum superantia. *Carpella* glabra. *Fructus* subovoideus. Anglia meridionalis.

Holotype: Putney Heath, Surrey, 12/7/1943, W. Watson, in Herb. W. Watson.

Rubus sprengelii (Sudre) W. Wats., sp. nov.

R. erraticus subsp. *sprengelii* Sudre, 1906, *Diagn.*, 41.

Rubus obscuriformis (Sudre) W. Wats., sp. nov.

R. obscurus microp. *obscuriformis* Sudre, 1907, *Fl. Toul.*, 75.

RUBUS INSERICATUS P. J. Muell.

subsp. *newbouldianus* (Rilst.) W. Wats., subsp. nov.

R. newbouldianus Rilst., 1950, *J. Linn. Soc. Lond. Bot.*, 53, 417.

Rubus pseudoplinthostylus W. Wats., sp. nov.

R. plinthostylus sensu Rogers, 1900, *Handb. Brit. Rub.*, 83; non Genev., 1868, *Mem. Soc. Acad. Maine-et-Loire*, 24, 108.

Turio acute angulatus, glaber, glandulis aciculisque sparsis brevibus; aculei subulati basi brevi. *Folia* magna, pedata; aculei petiolo obliqui retrorso-falcati; stipulae filiformes; foliola 3-5, supra glabra, subtus pubescentia vel tomentosa, inaequaliter serrata vel serrato-dentata, basi integra; foliolium terminale breviter petiolulatum, ellipticum longe acutum, basi subcuneatum. *Panicula* valde longa, laxa subpyramidalis; ramuli superiores patuli 1-3-flori, inferiores valde ascendentes; rhachis tomentosa pubescens, aculeis aciculisque numerosis brevibus, glandulisque paucis; pedicelli tomentosi glandulis tenuibus. *Flores* 1.5-2 cm. lati. *Sepala* laxa reflexa vel patula. *Petala* anguste obovata, rosea. *Filamenta* alba. *Carpella* pilosa; styli dilute rosei. *Receptaculum* pilosum. *Fructus* parvus.

Holotype: Foxholes Wood, Bailey Gate, Dorset, 17/9/1931, W. Watson, in Herb. W. Watson.

Rubus breconensis W. Wats., sp. nov.

R. lejeunei sensu Rogers, 1900, *Handb. Brit. Rub.*, 70 ; non Weihe & Nees, 1825.
R. breconensis W. Wats., 1946, *Journ. Ecol.*, **33**, 341 (nom. nud.).

Turio fuscus, gracilis, sulcatus, pilosus, glandulis numerosis, aculeolis aciculisque numerosis brevibus ; aculei flavi inaequales parvi graciles. *Folia* 3-5-foliolata, pedata ; foliola longa, angusta, subtus breviter et molliter pilosa, tenuiter acute serrata ; foliolium terminale ellipticum acuminatum apice et basi angustum ; foliola intermedia basaliaque breviter petiolulata. *Panicula* inferne lata, ramulis basalibus mediisque patulis 3-6-floris pedunculis longis, sursum angusta, apice acute racemosa ; rhachis flexuosa, villosa, aculeis infirmis plerumque falcatis ; unum e foliis paniculae plerumque simplex, cetera 3-foliolata, foliolium terminale angustum longe cuneatum. *Flores* 1-1.5 cm. lati. *Sepala* angusto-ovato-attenuata, villosa, aculeata. *Petala* obovata basi attenuata, rosea. *Filamenta* longa, rosea. *Receptaculum* glabrum. *Fructus* parvus.

Holotype : Mill Lane, Brynau, Glamorgan, 11/8/1941, J. A. Webb, in Herb. W. Watson.

Rubus lapeyrousianus (Sudre) W. Wats., sp. nov.

R. koehleri subsp. *lapeyrousianus* Sudre, 1900, *Rub. Pyr.*, 79.

Rubus graciliflorens (Sudre) W. Wats., sp. nov.

R. tereticaulis microg. *graciliflorens* Sudre, 1901, *Rub. Pyr.*, 175. *R. schleicheri* microg. *graciliflorens* Sudre, 1913, *Rubi Europae*, 206.

A BIOSYSTEMATIC STUDY OF SOME GLYCERIA SPECIES IN BRITAIN*

1. TAXONOMY

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INTRODUCTION

The genus *Glyceria*, a critical taxonomic group, has been the subject of several recent papers. The wider aspects of its classification and cytology have been dealt with by Church (1949). The taxonomy of the British species has been studied by Hubbard (1942, 1954), Lambert (1949) and Jungblut (1953), whilst the cytology has been investigated by Maude (1939) and Fitzpatrick (1946). The diploid species *G. declinata* has formed the subject of papers by Walters (1948) and Störmer (1951).

It is generally agreed that in Britain the following three species of section *Glyceria*‡ and one hybrid occur :

- | | |
|--|---------|
| 1. <i>G. fluitans</i> (L.) R. Br. | 2n = 40 |
| 2. <i>G. plicata</i> Fr. | 2n = 40 |
| 3. <i>G. declinata</i> Bréb. | 2n = 20 |
| 4. <i>G. × pedicellata</i> Towns. (<i>G. fluitans</i> × <i>G. plicata</i>) | 2n = 40 |

During the course of biosystematic studies to be described in subsequent papers, it was found that a proportion of the specimens could not be classified with complete confidence. The taxonomy of the group was therefore investigated in an attempt to resolve this difficulty, and the results are given here.

THE HOMOGENEITY OF THE SPECIES

The variability of the species suggested the presence of intraspecific chromosomal races. Such races usually have detectable morphological differences (Muntzing 1936), and in order to study phenotypic variation from this point of view numerous herbarium specimens were examined, measurements being made of lemma length, anther length, and pollen diameter.

The specimens were selected in order to include plants from diverse geographical localities and types of habitat. In each species, the frequency distribution of these taxonomic characters approximated to a normal curve, as illustrated for anther length in *G. fluitans* in Fig. 1 and for pollen diameter in all three species in Fig. 2; they therefore belonged to a single population in the statistical sense, showing that widespread intra-specific chromosomal races are absent.

CRITICAL TAXONOMY

General Remarks

Floristic characters show wide and overlapping ranges of variation as can be seen in Table 1. Vegetatively, and in growth habit, the species intergrade so extensively

* Part of a thesis for the degree of Ph.D. of the University of London.

† The experimental work for this investigation was carried out in the Botany Department of the University College of Leicester.

‡ The sectional name *Glyceria* replaces the name *Euglyceria* proposed by Grisebach in 1853, in accordance with the new rule that : "the subgenus or section containing the type species of a generic name must bear that name unaltered."

that features such as leaf-shape are of limited use in identification. For instance, an abruptly contracted, mucronate leaf-apex is a characteristic, though inconstant, feature of *G. declinata*. This morphological intergrading could be explained by the formation of interspecific hybrids, especially if associated with hybrid swarms produced by back-crossing. Church (1949) noted a large range of variation in lemma shape and length in the North American *G. septentrionalis* (from 4 mm. long with truncate apices, to 5.5 mm. with acute apices) and drew attention to the possibility of hybridisation with *G. fluitans*, followed by back-crossing.

An equally large range of variation in lemma length occurs in both the British tetraploids (Table 1). However, any suggestion that forms of *G. fluitans* with short lemmas are due to the introduction of genes from *G. plicata* following hybridisation, can be ruled out, since the naturally occurring hybrid between *G. fluitans* and *G. plicata* (*G. × pedicellata*) is very highly pollen-sterile, and the anthers are in any case non-dehiscent. In addition, the existence of naturally occurring triploid hybrids between *G. declinata* and *G. plicata* or *G. fluitans* has not been confirmed cytologically. These three species would therefore appear to be free from confusion due to hybridisation. The most useful morphological criteria for the identification of British species of section *Glyceria* are shown in Table 1, from which it appears that *G. declinata* and *G. plicata* are similar in many respects such as lemma and anther length. The toothing of the lemma apex in *G. declinata* is not by itself a satisfactory character, since this intergrades into the markedly three-lobed condition seen in some specimens of *G. plicata*.

Epidermal Characters

The species can be clearly separated by using the epidermal characteristics of the sheath nerves towards the blade, and the type of grain, oblong-elliptic in *G. declinata* and obovate in *G. plicata*. Such qualitative epidermal characters can be diagnostic for taxa when they are mutually exclusive; for instance Church (1949) was able to distinguish between *Glyceria* with smooth-walled cells, and *Puccinellia* and *Torreyochloa* with ripple-walled cells.

The structure of the epidermal cells of the nerve of the leaf-sheath is completely different in each species of the *G. fluitans* complex.

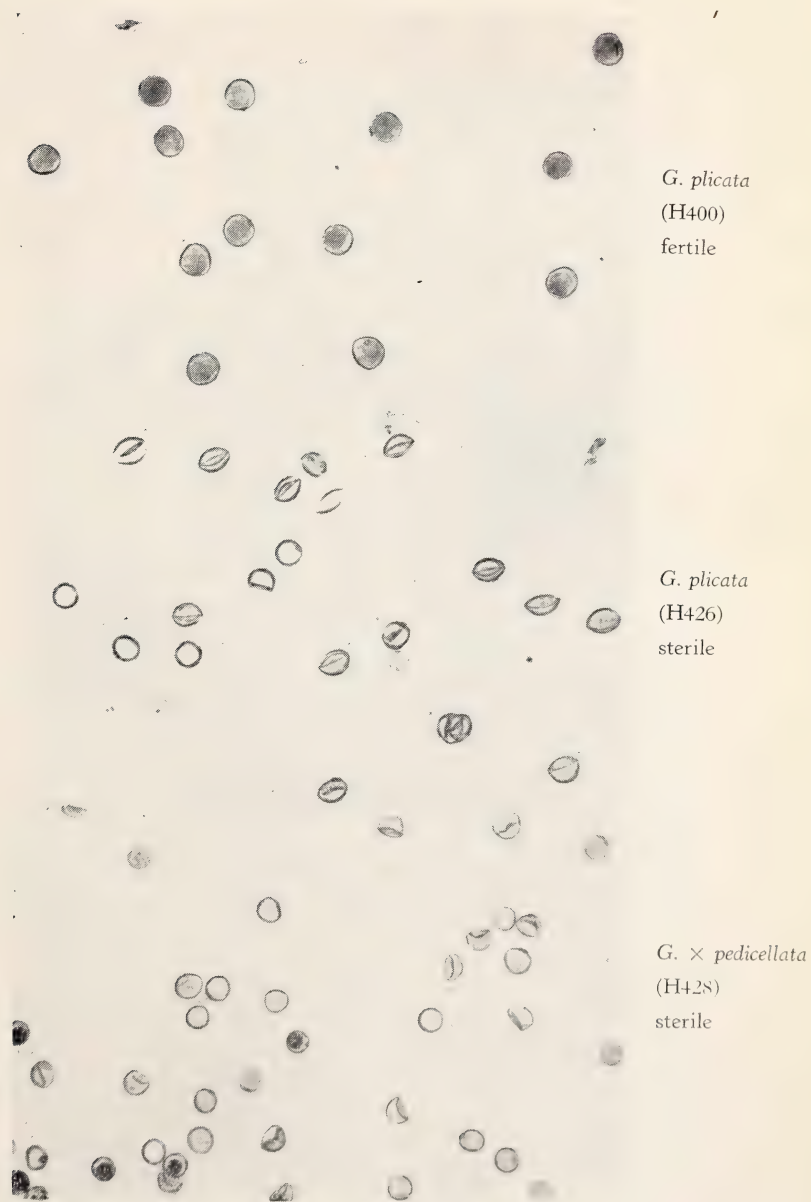
These cells are characteristically swollen in *G. declinata* and each cell, at the end towards the blade, bears a very small lateral tooth. By contrast, in *G. plicata* many of the cells bear a conspicuous lateral tooth; these render the surface distinctly scabrid. These types are quite distinct in appearance, and in *G. plicata* the sheaths are rough to the touch, the teeth being visible under a $\times 10$ hand lens. *G. fluitans* has sheaths with rounded smooth cells. The sheaths of both *G. declinata* and *G. fluitans* are smooth to the touch, and a low-power binocular microscope of about $\times 50$ is required in order to distinguish clearly between these types.

Pollen

Pollen diameter is sometimes useful in discriminating between species with otherwise similar phenotypes (Goodspeed and Bradley, 1942). Measurements of pollen size and counts of good pollen were therefore made using a modification of the cotton-blue staining technique described by Stebbins & Valencia (1946). Only darkly stained grains were counted as fertile.

Three mature, undehiscent anthers were taken from a basal floret of each gathering. In order to avoid selecting particular grains all those present in three eyepiece-fields were measured. No data were obtained for pollen diameter in *G. × pedicellata* since this pollen is mostly shrunken and irregular in shape (See Plate 19).

PLATE 19.



Pollen fertility in *Glyceria*
(photographed to scale).

PLATE 20



G. filiformis
(H490)
race N*

G. × padicellata
(H428)

Herb. Babington
(Sheet 407)

Herb. Babington
(Sheet 106)

G. plicata (sterile)
(H426)

G. plicata
(H400)
race F*

G. declinata
(H506)
race E*

Spikelets of *Glyceria* species and hybrid
(scale in millimetres).

*These races will be described in Paper 3

TABLE 1.
Diagnostic Characters of British *Glycerias* (see Plates 1 and 2)

Character*	<i>G. declinata</i>	<i>G. plicata</i>	<i>G. × pedicellata</i>	<i>G. fluitans</i>
Lemma length (mm.)	3.5-5.25	3.5-5.2	4.4-6.6	5.5-7.4
Lemma apex	3-toothed, sometimes only 3-lobed.	Rounded-truncate or obscurely lobed, sometimes markedly 3-lobed.	Variable, sometimes slightly lobed and subobtuse, to smooth and more or less acute.	Acute to subobtuse
Lemma surface and nerves	Both highly scaberulous	Scaberulous on nerves, rarely slightly on general surface.	Variably scaberulous	Both highly scaberulous
Palea apex	Sometimes exceeds lemma. Apex with acuminate, deeply bifid prominent teeth.	More or less equals lemma. Apex obtuse with indistinct teeth.	More or less equals lemma. Apex variable, acuminate to obtuse with 2 short teeth.	Sometimes greatly exceeds lemma. Apex with 2 short teeth.
Caryopsis length (mm.)	1.75-2.25, oblong - elliptic, light brown	1.5-2.5, obovate, dark brown	Does not develop, stigmas weak.	2.5-3.0, oblong-elliptic, mid-brown
Mature undehiscent anthers (mm.)	0.75-1.25, purple, rarely yellow.	0.8-1.25, yellow, rarely purple.	1.0-1.8, X-shaped sterile, shrunken, yellow.	1.75-3.0, purple, rarely yellow.
Pollen diam. (μ)	41	48	—	42
Fertility	Good	Good	Sterile	Good
Spikelet length (mm.)	Short, 10-20	Short, 10-20.	Variable, lax, often long, 10-40.	Long, 15-30(-35)
Epidermal cells of sheath nerves towards blade	Cells swollen, each with a small lateral tooth at the end towards the blade.	Highly scabrid, about 1 cell in ten with a prominent lateral tooth	Variable, smooth to highly scabrid.	Smooth, cells rounded not toothed.
Ligule (length)	Ovate, acute, about 1.5 times width of blade.	Ovate, acute, about equalling width of blade.	Variable	Lanceolate, about twice width of blade.
Fruiting panicle	Branches adpressed, spikelets breaking up.	Branches divergent, or deflexed, spikelets breaking up.	Variable, adpressed or divergent, spikelets persistent.	Branches often adpressed, sometimes divergent or deflexed, spikelets breaking up.

*—Spikelet characters measured on the terminal spikelet of the major pedicel at each node.

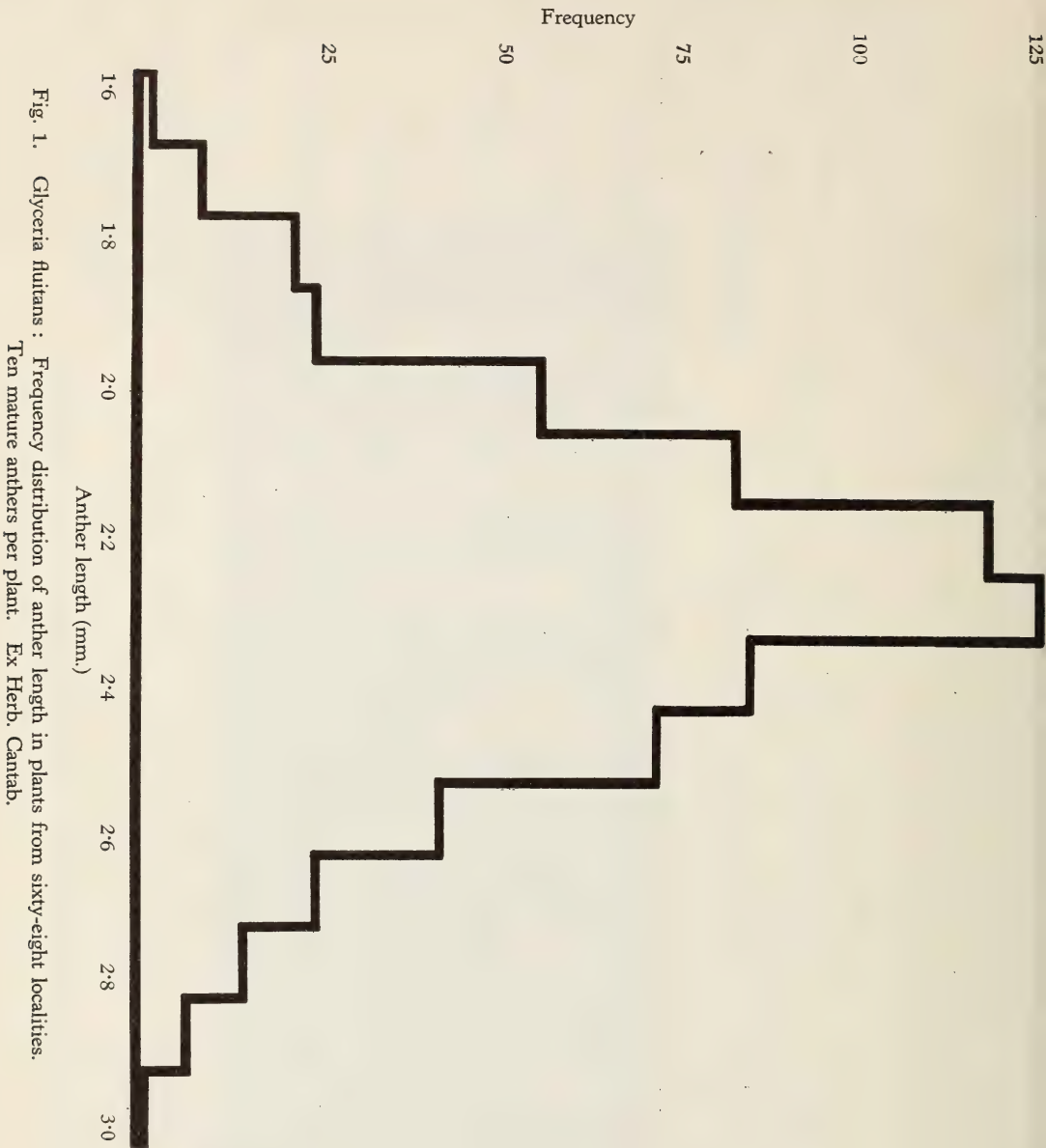


Fig. 1. *Glyceria fluitans* : Frequency distribution of anther length in plants from sixty-eight localities. Ten mature anthers per plant. Ex Herb. Cantab.

The results are given below :

Mean Pollen Diameter

Species	No. of gatherings	No. of grains	Mean Diam. (μ)	Difference	Fitzpatrick (1946)	
					No. of grains	Mean Diam. (μ)
<i>G. declinata</i>	41	766	41.1	1.0 6.2*	20	38.9
<i>G. fluitans</i>	47	1004	42.1		20	45.1
<i>G. plicata</i>	43	752	48.3		20	47.0

* = significant at $P = 0.05$

From these data it is clear that the *G. plicata* grains are, on average, larger than those of the other two species. A "t" test shows that this difference is significant at $P = 0.05$. The frequency distribution of pollen grain size is shown in Fig. 2, where histograms of the three species are superimposed, those for *G. declinata* and *G. fluitans* being more or less coincident. In each case there is a fairly good approximation to a normal curve. Because of the overlapping ranges of variation, a statistical test would be required in order to separate *G. plicata* by means of pollen size. Fitzpatrick (1946), whose results are given above for comparison, found that both the tetraploid species had significantly larger pollen grains than those of the diploid, but only 20 of the largest and fullest grains were measured, which suggests that this result may not be reliable.

Pollen fertility, determined whilst making the foregoing measurements, was good in all three species.

The hybrid G. × pedicellata

G. fluitans and *G. plicata* can easily be distinguished morphologically, but their hybrid shows a wide range of intermediate forms, some of which resemble one or other parent very closely, and are usually recognised by the fact that they are completely sterile with persistent spikelets on the mature culms.

Much taxonomic confusion has been caused by the existence of this hybrid, which has not been given adequate treatment by previous authors, and will therefore be discussed here.

The hybrid was first recognised by Townsend (1850, 1853) (see also 1904) who, in a paper read before the Botanical Society of Edinburgh, in 1846 suggested for it the name *G. hybrida*. Subsequently Townsend (1850) decided on the name *G. × pedicellata* and as such read an account of the plant before the Botanical Society of Edinburgh on 13 December 1849, which was published in 1853. The species was cited from several places in Cambridgeshire (v.c. 29), and at Dovedale, near Blockley (v.c. 57). The following is a description of a specimen in Herb. Babington at Cambridge written by Townsend.

"Perennial, with a stout, creeping rhizome. Culm ascending, stout, darkened at the nodes, smooth, leaf-sheaths with cross-nerves, striate, glabrous and smooth; ligule membranous, whitish, up to 10 mm. long; blades up to 15 cm. or more long, up to 9 mm. wide, obtuse or more often acute, nerved on the upper surface, with the nerves minutely scaberulous, smooth beneath.

Panicle loose, ovate to pyramidal, up to 30 cm. long; axis smooth; branches 4 to 2 nate, filiform, gradually decreasing in length upwards, the longer at the base up to 11 cm. long and this branched with the longer branchlets bearing 2-3 spikelets, the other basal branches unequal in length, simple and from 4 to 1 spiculate, branches spreading, the lower horizontally; pedicels 5-10 mm., spikelets more or less adpressed to the branches and branchlets, linear-oblong 15 to 20 mm. long, 9 to 13 flowered, pale green.

Glumes scarious, one nerved, obtuse; lower about 2 mm. long; upper 3 to 3.5 mm. Lemmas at first imbricate, at length unrolled and exceeding the rachilla, thinly coriaceous (dry) except for the hyaline tip, prominently 7-nerved and depressed between the nerves when dry, broadly elliptic oblong and very obtuse when flattened 4 to 5 mm. long, minutely scaberulous on the nerves and smooth or nearly smooth between them (*Italics mine, M.B.*).

"Paleas very slightly shorter than the lemmas, oblanceolate-elliptic minutely 2-toothed, keels relatively broad-winged up to the apex, wings widest above the middle. Anthers 1-1.2 mm., with imperfect pollen."

Townsend's herbarium was presented to the South London Botanical Institute, but the type specimen of *G. × pedicellata* is not there. Several of Townsend's specimens

are in Babington's Herbarium at Cambridge including a duplicate of the type. The following morphological notes were made from specimens of Townsend's which have been examined.

Morphological Notes :— Townsends' specimens of *G. × pedicellata* in Herb. Babington at Cambridge.

Fulbourn Ditch, Cambs. May, 1846
— as (MS) *Glyceria hybrida*. F.T.
Sheet 106 (Sheet 108 Duplicate).

Anthers 1.0–2.20 mm., *completely sterile*. Sub-basal lemmas 4.5–5.0 mm., scaberulous on nerves and to some extent on general surface. Lemma apices lobed and rather truncate, as in *G. plicata*. Leaf sheaths slightly scabrid on ribs towards blade.

There is a specimen of *G. plicata* on this sheet, lemmas 4.0–4.3 mm., anthers 1.0–1.3 mm. Fertile.

Wood Ditton, Cambs. 27/5/1848.
— as (MS) *G. hybrida* Towns. Sheet
407.

Anthers 1.5–1.75 mm., *completely sterile*. Sub-basal lemmas 5.0–5.75 mm., highly scabrid on nerves and on general surface. Lemma apices obtuse. Leaf sheaths highly scabrid on nerves and approaching *plicata* type.

The specimens on sheets 106 and 407 in Herb. Babington are so different that the range of variation in lemma and anther length does not appreciably overlap. Townsend's description refers to the form with short lemmas. The epidermal character of the lemmas is of the *G. plicata* type, this is made clear by the passage italicised by me in Townsend's description. It is nevertheless apparent that Townsend recognised the great variability of the hybrid and included in his collections specimens varying in intermediacy between the parents.

Some specimens named *G. × pedicellata* are met with, which are indistinguishable from *G. plicata* except that they are pollen-sterile. Amongst these one may include the duplicate of Townsend's type specimen in Herb. Babington, the description and morphology of which would equally well fit *G. plicata*. Similar specimens have been seen in Herb. Kew (CEH 12744) and in Herb. British Museum.

The range of variation exhibited by *G. × pedicellata* overlaps that of the parent species to an extent which suggests that the hybrid is polytopic in origin, involving infrequent crosses between plants from different parts of the variable populations of the parental species.

Sterile G. plicata

Sterile plants morphologically indistinguishable from *G. plicata* are not often met with in the field; however, after much searching, a clone was discovered at Empingham Marsh, v.c. 55 (H.426*). The diagnostic features of this plant are :—

Lemmas short, 3.75 to 4.75 mm., apices rounded, scabrid on the nerves only; anthers 0.9 to 1.15 mm., indehiscent, pollen sterile; no seed produced, spikelets persistent. Nerves of leaf-sheath towards blade highly scabrid, of *plicata* type (Table 1. q.v.). The results of cytological studies (to be given in a second paper) strongly suggest that this plant is a form of *G. plicata*. The morphology of typical spikelets of species of the section *Glyceria* is illustrated in Plate 20, enabling a comparison to be made between H.426 (sterile *G. plicata*), Townsend's short and long lemma forms, "typical" *G. × pedicellata*, and the fertile

* Specimen citation given in the following abbreviated form : H.426 = specimen No. 54426 in Herb. University College Leicester.

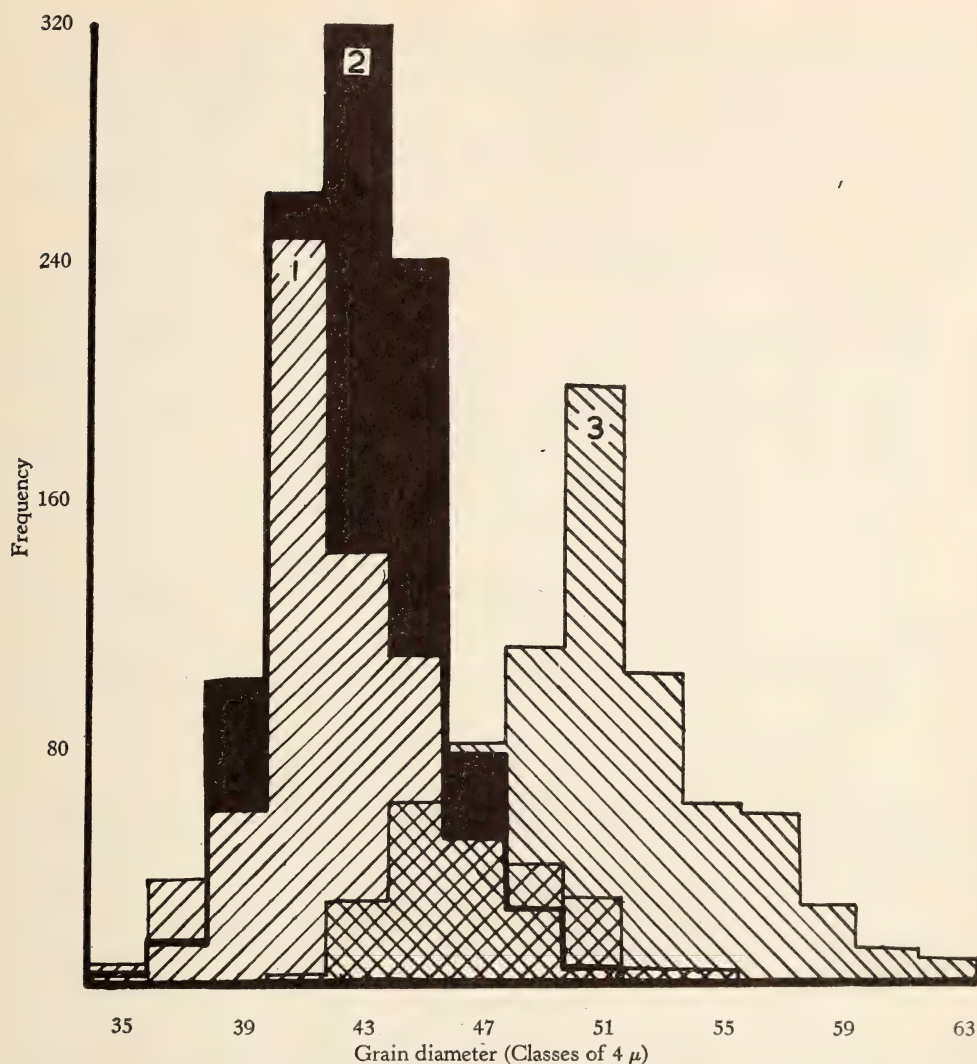


Fig. 2. Pollen diameter in three species of *Glyceria*. Grain diameter (classes of $4\ \mu$). Means : 1. *G. declinata* $41.1\ \mu$. 2. *G. fluitans* $42.1\ \mu$. 3. *G. plicata* $48.3\ \mu$. Difference between 1 and 3 significant at $P = 0.05$.

species. Plate 19 shows pollen of H.426, *G. × pedicellata*, and for comparison of fertility. *G. plicata* also. The pollen of *G. declinata*, *G. plicata* and *G. fluitans* is highly fertile. That of *G. × pedicellata* and H.426 is highly sterile.

CONCLUSION

It is apparent that, in the absence of cytological evidence, some sterile specimens of section *Glyceria* will be difficult to identify, involving a chance of error. This applies to the particular plant described by Townsend, which may in fact be a form of *G. plicata*.

Difficulties in identification are due to :—

1. The intrinsic variability of the species, which results in overlapping ranges of variation in quantitative and qualitative morphological characters.
2. The presence of the very variable hybrid between *G. fluitans* and *G. plicata*.
3. The occasional occurrence of sterile clones of *G. plicata*.

For many specimens the diagnostic key given by Tutin (1952), taken in relation to the general habit, vegetative and floral characters of the plant, will be found satisfactory. The following key has been devised taking into account the extreme variants found in this group. To identify *G. × pedicellata* the culms should be young enough to contain anthers, or old enough for the persistent nature of the spikelets to become apparent. In the other species the diagnostic value of the epidermal cell character deserves emphasis.

Identification Key for Critical Specimens of Section Glyceria.

1. Plants sterile, anthers shrunken and x-shaped, pollen empty; or empty, persistent spikelets on mature culms. 2
Plants fertile, anthers normal, pollen full, or seed present and spikelets breaking up on mature culms 4
2. Lemmas mostly exceeding 5.0 mm, anthers mostly over 1.2 mm *G. × pedicellata*
Lemmas 4.5 to 5.0 mm., anthers less than 1.2 mm. 3
3. Irregular pairing at meiosis, many univalents present *G. × pedicellata*
Complete pairing at meiosis, sometimes multivalents present *G. plicata* forma
4. Lemmas 5.25 to 7.25 mm., with apices acute or obtuse, anthers 1.75 to 2.75 mm.; nerves of sheath towards blade smooth, caryopses oblong-elliptic 2.5–3.0 mm. *G. fluitans*
Lemmas 3.5 to 5.25 mm., with apices rounded, lobed, or 3- to 5-toothed 5
5. Lemma apex 3- to 5-toothed, sometimes obscurely or markedly three-lobed, nerves and surface minutely scaberulous; sheath nerves towards blade with inflated cells, these each having a minute lateral tooth, caryopses oblong-elliptic, 1.5–2.0 mm. *G. declinata*
Lemma apex rounded, or obscurely, rarely markedly, three-lobed, surface scabrid on nerves only; sheath nerves towards blade very scabrid, with numerous minute rough points; caryopses obovate, 1.5–2.5 mm. *G. plicata*.

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A BIOSYSTEMATIC STUDY OF SOME GLYCERIA SPECIES IN BRITAIN†

2. CYTOLOGY

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INTRODUCTION

An investigation of chromosome pairing at meiosis in the British species of Section *Glyceria* was undertaken in order to study the relationships of the species.

Previous cytological studies in this group were confined to somatic chromosome counts in the root-tips, and the findings of these authors are summarised in the section of this paper dealing with chromosome numbers. *G. × pedicellata* has been counted only once before, by Fitzpatrick in 1946.

MATERIAL

In the species of Section *Glyceria* many small local populations occur, often distinguished by minor morphological characteristics, and fixations were made from some of these in order to see whether they were chromosomal races. The sources of these populations are listed in Table 1; herbarium specimens of representative plants were prepared and citations are given in the following abbreviated form:— e.g. H.403 = specimen No. 54403 in the Herbarium at the University College of Leicester. The race references in the table indicate that the population concerned was sampled for seed, and subsequently compared in an experimental garden trial, the results of which will form part of a further paper.

TABLE 1.
Source of plants used for chromosome counts.

Herb. No.	Race	Plants counted	Location	Vice-county	Habitat
<i>G. declinata</i>					
403		5	Botcheston Pond	Leicester	Shallow water in mud
413	C	8	Ulverscroft	Leicester	Gravel bed of stream
427	D	4	Cadgwith	West Cornwall	Quarry pond at cliff top
436		3	Grimley Pond	Worcester	Water-logged mud
443		1	Narborough 'bog'	Leicester	Trampled mud
446		3	Ashtead Woods	Surrey*	
448		5	Roeccliffe	Leicester	Swampy place in field
450		1	Roeccliffe	Leicester	Stony stream bed
458		2	Malham	Mid West York	Tarnside near Gt. Close Mire
464	B	7	Malham	Mid West York	Foot of limestone cliff
468	A	4	Malham Beck	Mid West York	Mud bank in limestone stream
473		2	Malham Beck	Mid West York	Small rivulet
506	E	6	Hopedale	Stafford	Muddy pond rich in humus
507		5	Esher Common	Surrey*	
Total		56			

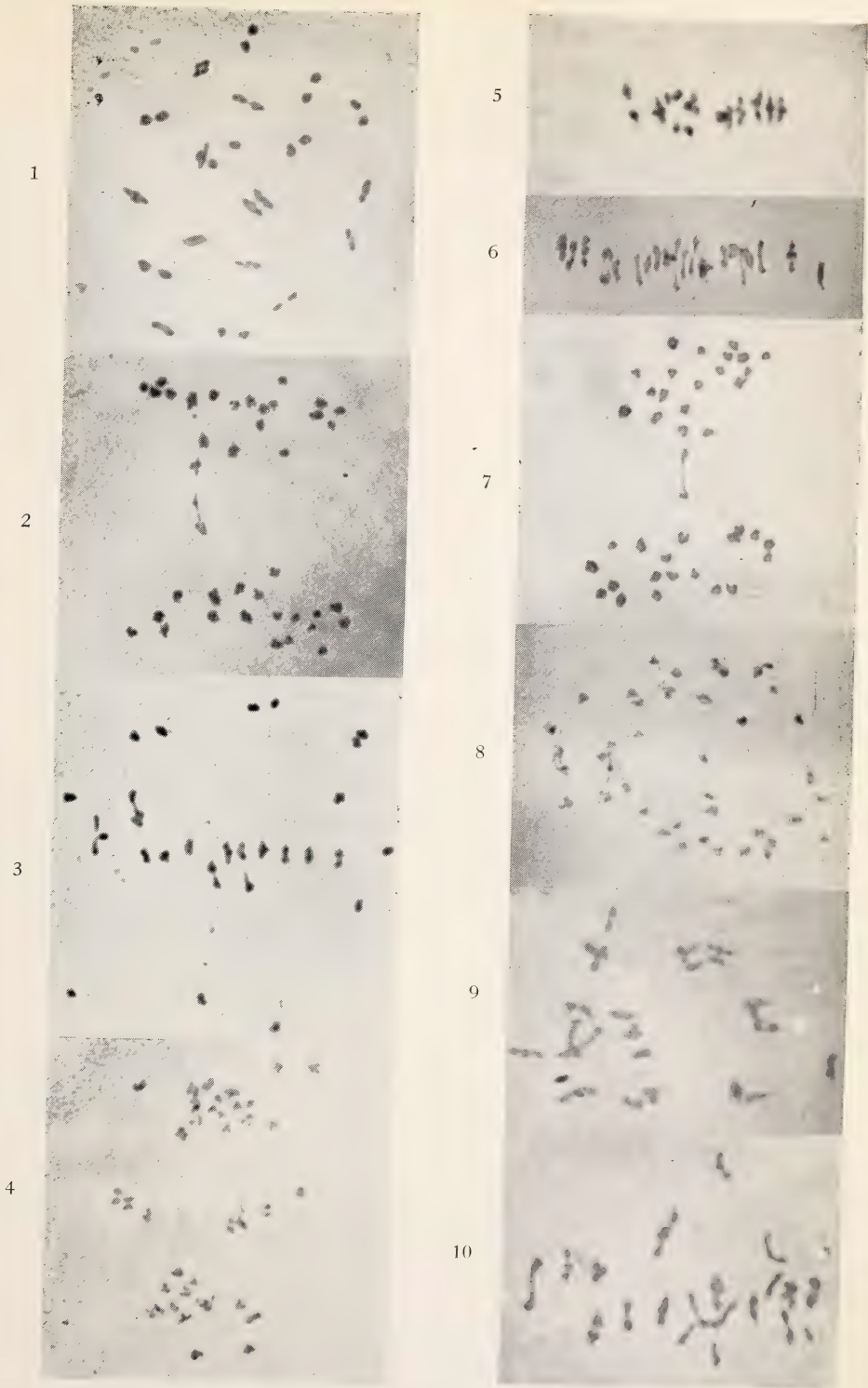
† Part of a thesis for the degree of Ph.D. of the University of London.

† The experimental work for this investigation was carried out in the Botany Department at the University College of Leicester.

* Plants raised from seed supplied by Dr. J. M. Lambert.

TABLE 1 (continued)

Herb. No.	Race	Plants counted	Location	Vice-County	Habitat
<i>G. plicata</i>					
400	F	7	Fulbourn	Cambridge	Chalk soil on stream bank
414		3	Ulverscroft	Leicester	Stream near priory
418		10	Botcheston	Leicester	Wet place in field
423	J	7	Wittering	Northampton	Small spring on limestone
426		1	Empingham	(Rutland)	Small marsh by river
430		4	Grimley	Worcester	In muddy pond
444	H	2	Wistow	Leicester	Pond edge in marl pit
466	I	1	Malham	Mid West York	Freshet on limestone
472		2	Malham	Mid West York	Runnel by beck
491		1	Weybridge Marshes	East Norfolk	Trampled ground near dyke
—	G	7	Breedon	Leicester	Gravel bed of small stream
	Total	45			
<i>G. fluitans</i>					
405		1	Botcheston	Leicester	In turf near pond
408		4	Kilby	Leicester	In ditch
409		2	Narborough Bog	Leicester	Very wet ground soil rich in humus
411		1	Ulverscroft	Leicester	Stream in priory field
422		4	Wittering	Northampton	Rill on limestone
431		1	Grimley Pond	Worcester	Mud by swampy place
435		1	Grimley Pond	Worcester	Mud by swampy place
437	M	5	Loddington	Leicester	Wet place in field at Loddington Reddish
439		4	Botcheston	Leicester	Small runnel in the bog
449		1	Roecliffe	Leicester	Stony stream bed
452		2	Lough Yganavan	North Kerry	In several inches of water
454	L	4	Ulverscroft	Leicester	Muddy ditch
457		1	Malham	Mid West York	Edge of tarn near Great Close Mire
460		4	Malham	Mid West York	Swampy place on Great Close Mire
475	O	3	Acle	East Norfolk	About 30 cm. of water in dyke
490	N	3	Acle	East Norfolk	Trodden ground by dyke
495		2	Brandon	West Norfolk	Dried up place in field by river
498		1	Hopedale	Derby	Muddy pond
526		1	Broad Oak	Monmouth	Partly dried up muddy pool
—	K	4	Breedon	Leicester	Canal bed rich in humus
	Total	49			
<i>G. × pedicellata</i>					
410		10	Narborough Bog	Leicester	Swampy ground
415		1	Botcheston Pond	Leicester	Trampled ground by pond
425		1	Empingham	(Rutland)	Wet ground by stream
428		1	Keyham	Leicester	In small stream
429		6	Grimley	Worcester	Mud in shallow water
438		10	Kilby	Leicester	Ditch near river Sence
453		10	Dovedale	Derby	Limestone stream
459		1	Malham	Mid West York	Great Close Mire
	Total	40			



Pollen mother cell meiosis at first division in species of section *Glyceria* ($\times 1,000$).

1-2. Late metaphase and anaphase in *G. fluitans* (H439) $2n = 40$. 3. Metaphase in *G. pedicellata* (H429) $2n = 40$ showing: 10 bivalents; 2 trivalents; 14 univalents. 4. Anaphase in *G. pedicellata* (H429) $2n = 40$ showing: 7 lagging and dividing univalents. 5. Metaphase in *G. declinata* (H413) $2n = 20$. 6-7. Metaphase and anaphase in *G. plicata* (H423) $2n = 40$. 8. Anaphase in *G. plicata* (H444) showing: 1 quadrivalent. 9. Metaphase in sterile *G. plicata* (H426) $2n = 40$, showing: 1 6-valent; 17 bivalents. 10. Metaphase in sterile *G. plicata* (H426) showing: 1 6-valent; 1 4-valent; 15 bivalents.

METHODS

The method adopted for fixing and staining was based on the procedure developed by Thomas (1940), using acetocarmine for small chromosome fruit material. In 1952 Carnoy's fluid (Darlington & La Cour 1947) was used alone; in 1953 the material was premordanted by the addition of a few drops of ferric chloride to the fixative, which gave improved staining of *G. declinata* and *G. plicata*.

Tubes of fixed material were stored without deterioration, in a deep freeze refrigerator at -15°C until required for use (Davies 1952). The preparations were made permanent by infiltration using triacetin, an oily liquid of low volatility completely miscible with acetic acid.

The preparations were irrigated at 30°C on a hot plate by means of a drop of triacetin placed at the edge of the cover glass; this was drawn through the preparation by the evaporation of the acetic acid and carmine, giving clear mounts in 24 hours; the cover glasses were then ringed with Canada balsam. To minimise any evaporation due to imperfect ringing the slides were stored at 5°C , and showed little or no deterioration after eighteen months.

Meiosis was found to occur when the inflorescences were young, soft and entirely enclosed within the leaf-sheaths. One floret per spikelet in a few of the spikelets in each panicle showed the stages diakinesis, metaphase, anaphase. When a floret contained anthers at first metaphase, the one above showed prophase and the one below, second division. Stages before diakinesis were not sufficiently stained for study. In *G. declinata* the number of pollen mother cells was small, about ten per loculus.

CHROMOSOME NUMBERS

The chromosome numbers reported in this and previous studies are shown in Table 2. All the counts made subsequent to 1939 verify the basic number $x = 10$ given by Maude. The basic number $x = 7$ given by Stählin (1929), which apparently is erroneous, has been discussed fully by Fitzpatrick (1946). No intraspecific chromosomal races have been found and since in this study meiosis has been examined in many plants it is possible that such races do not occur, supporting the view put forward in a previous paper (Borrill, 1956).

TABLE 2.
Chromosome numbers of Section *Glyceria*

Species	Stählin (1929)	Maude (1939-40) Britain	Church (1942) N. Amer.	Fitzpatrick (1946) Britain	Church (1949) N. Amer.	Knaben (1950) Norway	Löve (1951) Iceland	Jovet (1952) France	Litardière (1951-55) France and Corsica	Present Study Britain
<i>G. declinata</i>	—	20	20*	20	20	20	—	20	20	20
<i>G. plicata</i>	28	40	—	40	—	—	—	—	—	40
<i>G. fluitans</i>	28	40	40	40	40	—	40	—	—	40
<i>G. × pedicellata</i>	—	—	—	40	—	—	—	—	—	40

* This plant was originally identified as a form of *G. fluitans* and named *G. cookii* by Swallen (1941).

MEIOSIS (See Plate 21)

G. declinata and *G. fluitans*

In these species pairing occurred as bivalents only, ten pairs in *G. declinata* and twenty

pairs in *G. fluitans* (Figs. 1, 5). Metaphse plates of *G. fluitans* could generally be distinguished from those of the other species by the more compact appearance of the bivalents.

G. plicata

In this species, plants from eight populations were studied in detail. In two of these (H.414 and H.423) pairing was regular with twenty bivalents at metaphase (Fig. 6). Anaphase stages were very clear and one bivalent was occasionally seen to disjoin later than the others, probably associated with an interstitial chiasma; the same behaviour occurs in *G. fluitans* (Figs. 2, 7). In the other six populations a variable number of pollen mother cells had one, occasionally two quadrivalents, the rest of the chromosomes pairing as bivalents (Fig. 8). The sporadic occurrence of quadrivalents is consistent with the view that occasional pairing takes place between homologous chromosomes from all four genomes in the tetraploid, and is not due to segmental interchange.

Considering all the populations, the percentage of cells with one or two quadrivalents ranged from 0 to 41; as follows:—

H.414	H.423	H.400	H.472	H.430	Race G	H.444	H.418
Nil	Nil	8	11	15	19	32	41

The majority of these quadrivalents were of alternate configuration and disjoined regularly; the pollen fertility approached 100 per cent.

In the plant represented by specimen H.418 from the population with the highest quadrivalent frequency, giant pollen mother cells were observed with twice the somatic chromosome number. These cells were scattered amongst normal cells and divided at the same time, and all showed features characteristic of first meiotic metaphase. It would appear therefore that these giant cells arise during a division preceding meiosis as a consequence of failure in cell wall formation.

Sterile *G. plicata* (H.426)

This sterile clone was discussed in a previous paper (Borrill, 1956), the conclusion being drawn that on morphological grounds it could be classified as *G. × pedicellata* or *G. plicata* forma. This material was therefore examined cytologically; at first metaphase most pollen mother cells displayed one or more multivalents, and the different types present in five panicles are classified in Table 3.

TABLE 3.
First Metaphase pairing in 5 panicles of sterile *G. plicata* (H.426).

Panicle Number	Number of Cells	Type of association per cell					
		I	II	III	IV	V	VI
1	14	0.07	15.7	0.07	1.20	—	0.57
2	8	0.13	12.1	0.13	1.25	—	0.50
3	10	0.01	15.2	—	0.90	0.01	1.00
4	10	0.02	13.5	0.01	1.00	0.01	1.00
5	10	—	16.3	—	1.10	—	0.50
Total	52	—	—	—	—	—	—
Average per cell	—	0.046	14.6	0.04	1.09	0.004	0.71

Most cells had one quadrivalent, and about half had one 6-valent as well, the remaining chromosomes pairing as bivalents. Associations with odd numbers were rare, probably representing stages in the disjunction of more complex multivalents (Figs. 9, 10).

Numerical unbalance occurs at first anaphase since in a few cells odd numbers of chromosomes, usually 19 : 21, were seen; 18 : 22 were observed in one cell of panicle No. 4. Most 6-valents, and several of the quadrivalents, were non-disjunctional in type, which would lead to genetical unbalance in the genomes of the pollen grains. Second division proceeds regularly and tetrads are formed, the contents of the pollen then degenerate rapidly. The plants were also female sterile since no seed was produced. The genetical and numerical unbalance does not seem to be extensive enough for its effects to account for the complete sterility of this clone, which suggests that some further genetic and physiological disturbances are present.

G. × pedicellata

Pairing at first metaphase was studied in plants from 4 stands of *G. × pedicellata*. In all the cells analysed pairing was at its zenith, and the number of bivalents recorded represents the maximum amount of pairing in the cell. The frequency of chromosome pairing is shown in Table 4.

TABLE 4.

G. × pedicellata all fixations $2n = 40$

Herb. No.	No. of Plants	No. of Cells	Mean metaphase pairing per cell			
			I	II	III	IV
410	10	30	16.9	10.7	0.83	—
429	6	30	15.7	10.9	0.91	0.03
438	10	30	15.6	11.2	0.74	—
453	10	30	16.6	10.3	1.10	0.06
Total	36	120	—	—	—	—
Average per cell	—	—	16.2	10.7	0.89	0.05

The frequency of chromosome pairing is low, the number of bivalents ranging from six to fifteen per cell, (Fig. 3) trivalents were infrequent, less than one per cell, and only two quadrivalents were observed in all the cells studied. Anaphase was very irregular, the univalents either being distributed precociously and at random to the poles or lagging and dividing at the equator (Fig. 4), and were lost at second division. Considerable numerical unbalance occurred in the pollen, as a result of first metaphase behaviour, since the number of chromosomes at the poles at the end of first anaphase varied widely from 14 to 25, plus, in some cases, one or more divided univalents. Lagging univalents often persisted at telophase and were lost; consequently the number of chromosomes at each pole cannot often be counted.

It appears that the complete sterility of this hybrid is accounted for by numerical and genetical unbalance in the pollen mother cells and ovules.

CHIASMA FREQUENCIES

Chiasma frequencies were determined in plants from several populations, the mean per bivalent being 1.33 for *G. declinata* 1.34 for *G. fluitans* and 1.13 for *G. plicata*; hence *G. plicata* has a lower chiasma frequency than the other species. The detailed results are given in Table 5.

TABLE 5.
Chiasma frequency in species of section Glyceria

Herb. No.	No. of Cells	Chiasma Frequency Bivalents per cell with			Mean per Bivalent
		1 x ta	2 x ta	3 x ta	
<i>G. declinata</i>					
1B	10	6.3	3.3	0.4	1.45
413	9	6.6	3.0	0.4	1.37
427	12	6.3	3.3	0.3	1.40
436	9	7.4	2.3	0.2	1.27
446	10	6.7	3.0	0.3	1.36
448	8	7.7	2.2	—	1.22
458	10	7.4	2.4	0.2	1.30
464	12	7.8	2.1	0.1	1.21
468	10	6.8	3.2	—	1.32
506	10	6.6	3.1	0.3	1.37
Total	100	—	—	—	—
Average	—	6.96	2.86	0.21	1.33
<i>G. fluitans</i>					
408	10	11.7	8.0	0.3	1.43
409	10	13.9	6.0	0.1	1.35
422	10	14.0	6.0	—	1.31
431	10	11.9	7.9	0.2	1.41
435	10	13.2	6.9	—	1.41
437	10	14.4	5.5	—	1.28
439	10	10.9	8.7	0.4	1.47
452	10	12.6	6.7	0.1	1.34
454	10	15.0	5.0	—	1.27
460	10	14.9	5.0	0.2	1.26
475	10	13.0	7.0	—	1.30
490	10	14.7	5.2	0.1	1.32
498	10	12.1	7.6	0.3	1.41
Race K	10	13.8	6.2	—	1.31
Total	140	—	—	—	—
Average	—	13.2	6.5	0.12	1.34
<i>G. plicata</i>					
400	10	18.2	1.8	—	1.09
414	10	19.1	0.9	—	1.04
418	10	15.9	4.0	—	1.20
423	10	18.0	2.0	—	1.10
430	10	18.0	2.0	—	1.10
444	10	16.8	3.2	—	1.16
472	10	16.9	3.1	—	1.15
Race G	10	13.5	4.5	—	1.22
Total	80	—	—	—	—
Average	—	17.0	2.7	—	1.13

DISCUSSION

The origin of G. × pedicellata

The high univalent frequency at meiosis in this species fully accounts for the complete sterility observed, and confirms the view, generally accepted on grounds of morphological intermediacy, that *G. × pedicellata* is a hybrid between *G. fluitans* and *G. plicata*.

G. × pedicellata is a perfect example of a successful vegetatively propagated hybrid which spreads extensively by means of stolons, forming large stands which often occur in swift flowing streams. Under these circumstances, dispersal can take place by detached ramets carried by the moving water. The vegetative efficiency of this plant is such that it is often found in places from which one or both parental species are absent.

The status of sterile G. plicata. H.426

Meiotic pairing in panicles from various parts of this sterile clone was entirely different from that observed in *G. × pedicellata*. The majority of the chromosomes paired as bivalents but in addition 6-valents occurred involving associations of unlike-sized and therefore presumably non-homologous chromosomes (Fig. 9). This is consistent with the view that a segmental interchange has taken place between non-homologous chromosomes (Darlington 1937). This meiotic irregularity does not seem sufficient in itself to account for the complete sterility observed, which suggests that some further genetic and physiological disturbances are present. This plant should be regarded as a sterile form of *G. plicata*.

Interspecific Relationships

In section *Glyceria* there are two types of plant in which a study of metaphase pairing should provide evidence of the relationships between the genomes involved. These are the hybrids between *G. declinata* and the two tetraploids, and the hybrid between the tetraploids. Attempts to synthesize these hybrids have not proved successful and no spontaneous triploids have been found. This will be described in a subsequent paper. Discussion is therefore confined to the naturally occurring hybrid *G. × pedicellata* and its parents.

A detailed analysis of pairing in *G. × pedicellata* reveals some affinity between the parents, since on average 10.7 bivalents per cell occurred, and hence there appears to be some homology between one genome from each parent. The maximum number of bivalents per cell observed was fifteen, however, and this implies either that intragenomal pairing occurs, or, more probably, that there is some homology between chromosomes from all four genomes. The occurrence of about one trivalent per cell and the rare occurrence of a quadrivalent support the latter view.

A study of pairing in the parents may assist in understanding the nature of pairing in the hybrid. The low chiasma frequency per bivalent, 1.13 in *G. plicata* and 1.34 in *G. fluitans*, shows that in many chromosomes a chiasma is formed in one arm only, this may be associated with the small size of the chromosomes, and would permit little multivalent formation to occur; nevertheless, quadrivalent formation occurs sporadically in some populations of *G. plicata* although this species has the lower chiasma frequency, and it is therefore possible that *G. plicata* is an autopolyploid or segmental allopolyploid (Stebbins, 1947). In *G. fluitans*, with a higher chiasma frequency, bivalent pairing is the rule, suggesting that this species may be allopolyploid.

The evidence suggests that in *G. × pedicellata* there is homology between one genome from each parent, some homology between these genomes and the second genome of *G. plicata*, and slight homology between some chromosomes from one or more of these

three genomes and chromosomes of the remaining genome of *G. fluitans*. Pairing would thus be primarily allosyndetic between one genome from each parent, and occasionally autosyndetic, between chromosomes of the *plicata* genomes. Occasional pairing would also take place between chromosomes of these three genomes and slightly homologous chromosomes of the fourth genome.

It appears that *G. fluitans* and *G. plicata* have a common ancestor, which may be *G. declinata*, since this species is closely related morphologically (Borrill, 1956).

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STUDIES ON *ONONIS* IN BRITAIN

1. *Hybridity in the Durham Coast Colonies of Ononis* ,

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The two common species of *Ononis* in the British Isles, *O. repens* L. and *O. spinosa* L., are normally readily distinguishable. Plants with apparently intermediate characters have occasionally been reported, but in most localities the species are quite distinct and usually grow in different habitats. Such, however, is not the case on the Durham coast, where both species intermingle on the Magnesian Limestone cliffs, and where the identity of many individuals is indeterminate. The present paper is concerned with assessing the degree to which the characters of these two species overlap in this region and determining whether this is due primarily to hybridity or to intraspecific variation. *O. repens* in Britain has a diploid chromosome number of 64, and *O. spinosa* of 32. The existence of hybrid plants with an intermediate chromosome number has recently been established in these Durham coast colonies. Further work on the cytology of these, and other, plants is in progress and a report on this will appear in due course.

LOCATION OF THE COLONIES

Two colonies were studied on the Durham coast; one in the north, at Marsden, and the other in the south, at the Blackhall Rocks. These two colonies are isolated from each other, being separated by many miles of cliff on which only normal *O. repens* occurs, and also by the large area of low-lying land at the mouth of the River Wear. The Marsden colony is considerably smaller than the Blackhall Rocks colony and is confined to a narrow belt of land, only a few feet wide, at the top of the Magnesian Limestone cliffs. The cliffs here differ from those at the Blackhall Rocks in not having a well-developed grassy slope at the top. For the most part they fall sheer, almost from the top, and hence the area in which these plants can grow is very narrow, being limited at the back by the cliff path, behind which is cultivated and waste land. At the Blackhall Rocks there are broad, steep, grassy slopes above the cliffs, and on these *Ononis* grows in profusion. The enormous number of individuals in this colony made it impossible to examine them all. The position of the colony, also, on a steep slope over the cliffs, made it difficult to use random sampling methods. These slopes are, however, divided into a series of hollows, and in one of these every plant of *Ononis* was examined and scored. At Marsden, the smaller size of the colony made it possible to examine and score every plant (with the exception of a few on inaccessible cliff ledges) growing on the cliffs from the miners' cottages at the south end of the bay to the promontory at the north end.

For purposes of comparison, pure colonies of both *O. repens* and *O. spinosa*, growing in other localities, have been scored by the same methods as the Durham coast colonies. Pure colonies of *O. repens*, on the coast at Whitburn, and of *O. spinosa*, in the Quarrington Hill area, were selected because of their close proximity to the mixed colonies at Marsden and Blackhall Rocks. Two other colonies, from much further afield, were also studied – the *O. spinosa* colony from the coast on the east side of Eastbourne, Sussex, and the *O. repens* colony from nearby on Beachy Head.

METHOD

In the first place an indication of the nature of the colonies at Marsden and Blackhall Rocks was obtained by recording each plant under the following categories :— *O. spinosa*, *O. repens*, intermediate plants approaching *O. spinosa*, intermediate plants approaching *O. repens*, and completely intermediate plants. The results of this estimation are shown in Table 1 below.

TABLE 1.

	Marsden	Blackhall
	%	%
<i>O. repens</i>	31	27.3
Intermediate plants approaching <i>O. repens</i>	5	0.7
Completely intermediate plants	11.5	12
Intermediate plants approaching <i>O. spinosa</i>	34.5	32
<i>O. spinosa</i>	18	28
<i>Apparent composition of the colonies based on visual characterisation of individual plants</i>		

Later, a more precise method was used, in which the various characters of the individual plants were each given a numerical value, the *character index*. The sum of the character indices for each plant gives the *character sum index*. This is highest in plants approaching most closely to *O. spinosa* and lowest in those approaching most closely to *O. repens*. The following are the characters which were scored and the method used in their assessment :—

- (a) *Leaf Index*. This was obtained by dividing the length of the terminal leaflet by the greatest breadth. An index of from 0 to 1.8 was scored as 1, from 1.9 to 2.1 as 2, and 2.2 upwards as 3. There is considerable overlap between the two species in respect of this character, and the dividing points in the method of scoring were selected as being the most realistic, after examination of colonies, belonging to both species, from many parts of the country.

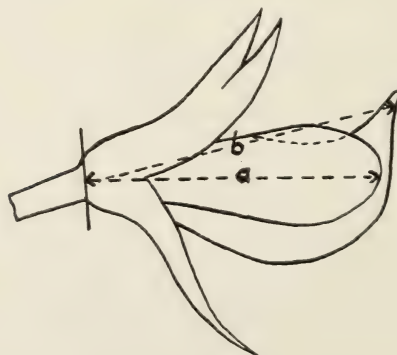


Fig. 1. Diagram of *Ononis* Flower (with standard removed) to show the method of measuring the lengths of wing (a) and keel (b).

- (b) *Flower Index*. This was obtained by dividing the length of the wings by the length of the keel, the measurements being taken along the axes shown in Fig. 1. An index of 0 to 0.96 was scored as 3, 0.97 to 1.03 as 2, and 1.04 upwards as 1.

- (c) *Occurrence of spines.* A spinous condition such as is normal to *O. spinosa* was scored as 3, absence of spines as 1, and an intermediate condition as 2.



Fig. 2. Stem pubescence in *Ononis*.

Left : uniform pubescence in *O. repens*. Right : band of hairs in *O. spinosa*. $\times 2$.

- (d) *Occurrence of a band of hairs on the stem.* A distinct band of hairs, such as is normal to *O. spinosa*, was scored at 3, uniform pubescence as 1, and an intermediate condition as 2. (See Fig. 2).
- (e) *Stem colour.* *O. spinosa* normally has a very dark red stem, a condition which was scored as 3. *O. repens* usually has a green stem sometimes tinged with red. Such stems were scored as 1, and an intermediate condition as 2.
- (f) *Habit.* *O. repens* has long underground rhizomes and straggling aerial shoots. *O. spinosa* has an erect bushy habit and no rhizome. The *O. repens* condition was scored as 1, the *O. spinosa* as 3, and intermediates as 2.

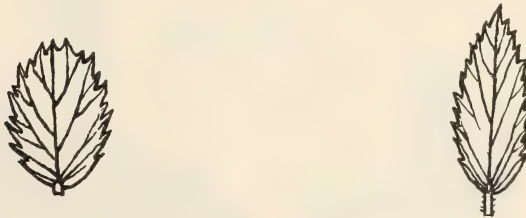


Fig. 3. Typical terminal leaflets of *O. repens* (left) and *O. spinosa* (right). $\times 2$.

- (g) *Leaflet Tip.* The leaflet tip of *O. spinosa* normally has an acute point, whilst that of *O. repens* is obtuse and rounded, or even emarginate. The former condition was scored as 3, the latter as 1 and intermediates as 2. (See Fig. 3).

Thus the character sum index of a plant with all *O. repens* characters would be 7 and one with all *O. spinosa* characters, 21.

THE STRUCTURE OF THE COLONIES

The normal range of variation, even in pure colonies, produces individual plants of *O. repens* with slightly higher scores, and of *O. spinosa* with slightly lower scores, but this variation is by no means sufficient to cause any overlap in the character sum indices. This is clearly shown by the histograms in Figs. 4A to D in which two pure colonies of each species are scored, and in which the histograms for each species are separated by at least 5 units. This is in contrast to the position in the hybrid colonies at Marsden and the Blackhall Rocks, where the histograms (Figs. 4E and F respectively) show an unbroken,

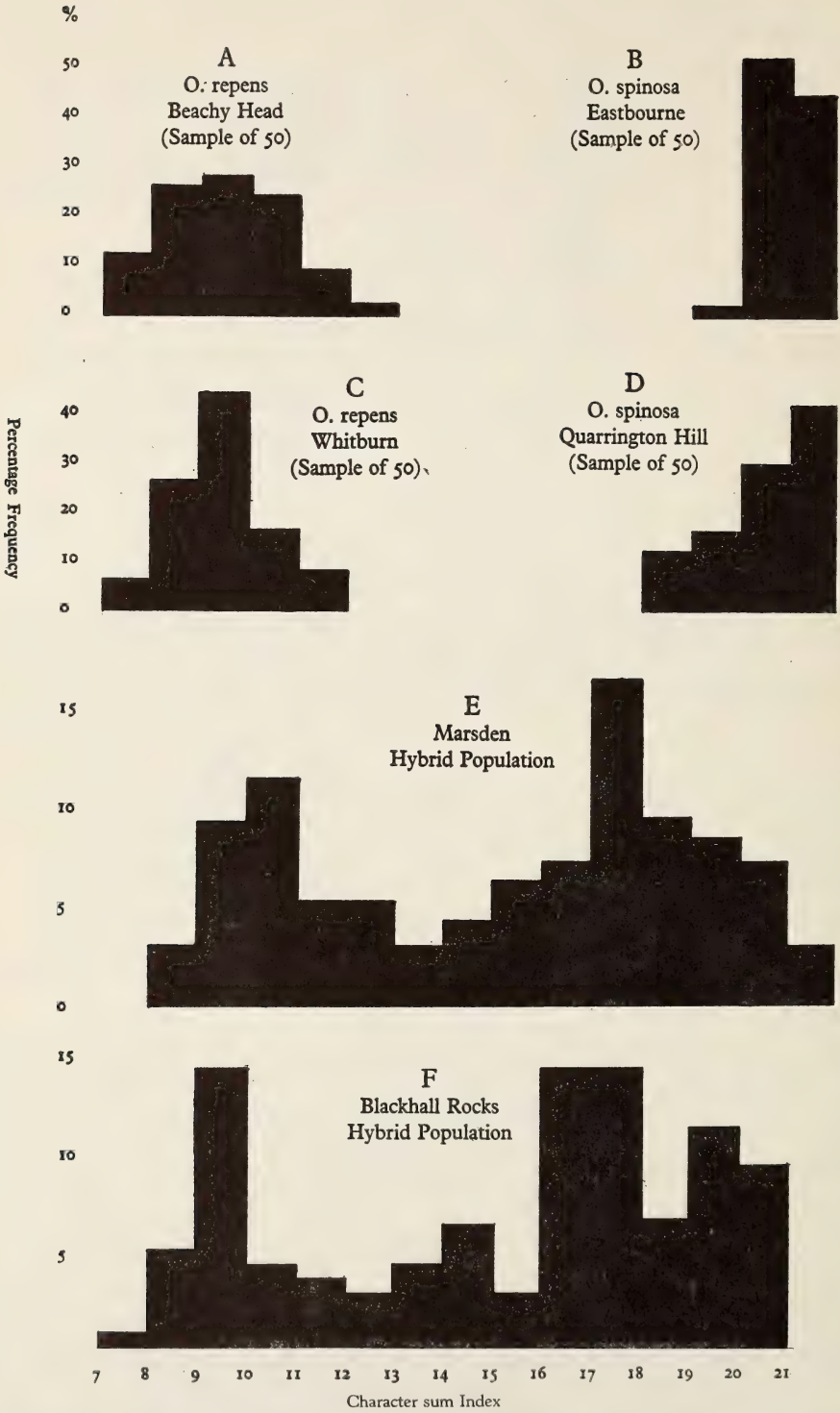


Fig. 4. Character sum index frequency distribution histograms in pure populations of *O. repens* (A and C) and *O. spinosa* (B and D), and in hybrid populations (E and F).

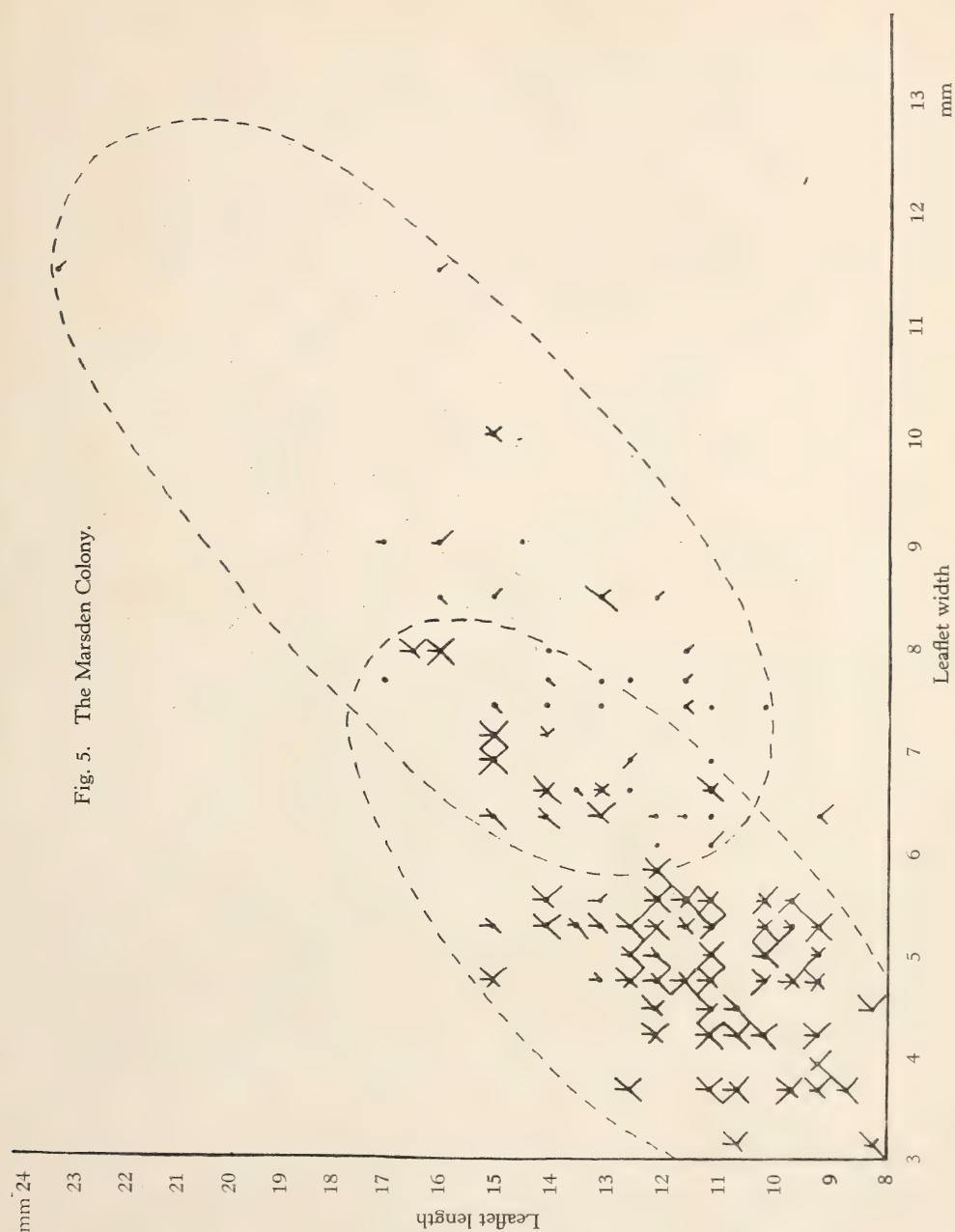
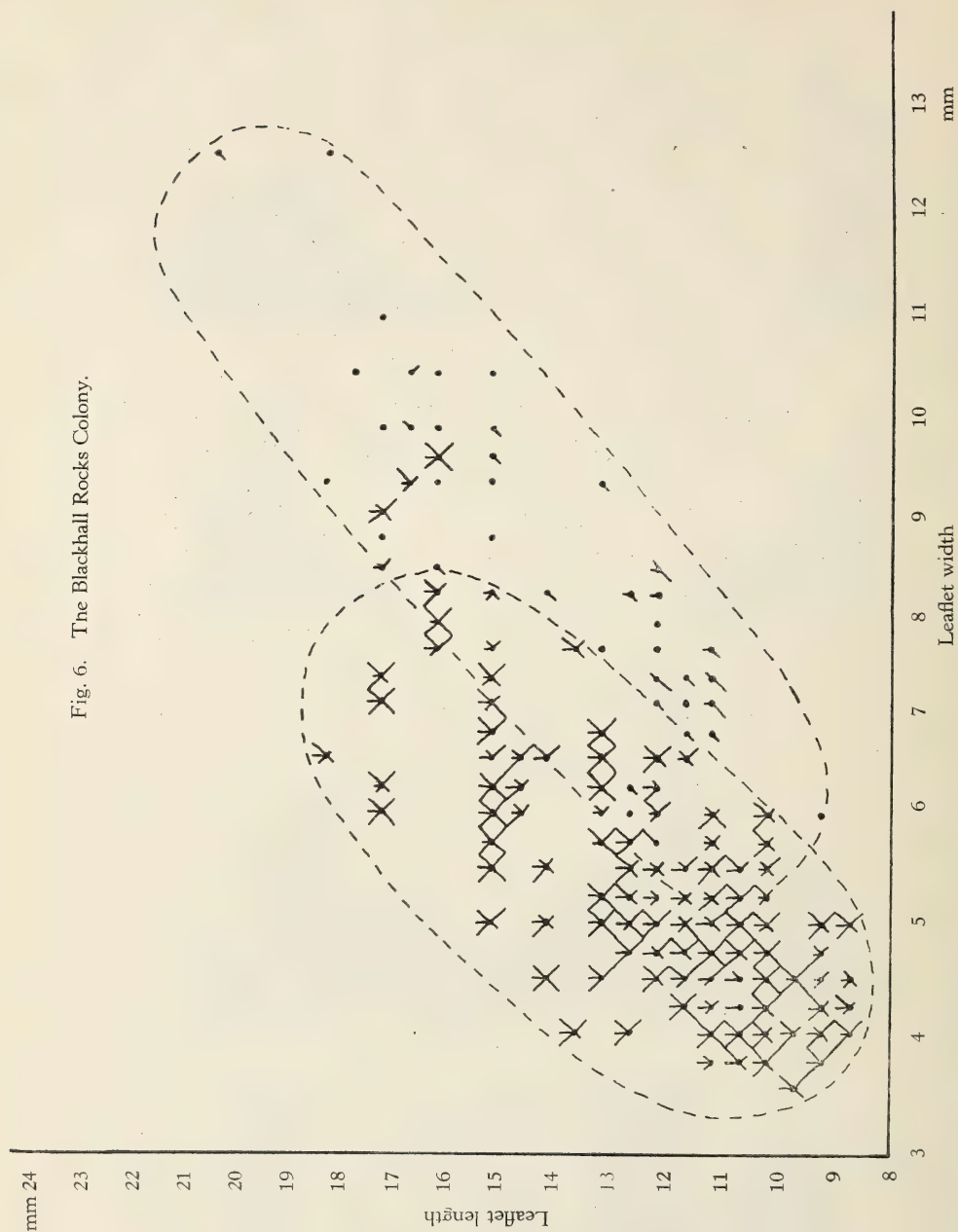


Fig. 5. The Marsden Colony.

if uneven, transition from *O. repens* to *O. spinosa*. There is an obvious mode coinciding with that shown in the pure *O. repens* colonies, and in both these localities this species abounds, a fact which is clearly shown in Table 1. At the other end of the histograms there is no mode coinciding exactly with that to be expected from normal *O. spinosa*, through the histogram for the Blackhall Rocks colony (Fig. 4F) has a secondary mode in approximately this position. This again is in general agreement with the visual assessment of these colonies as shown in Table 1.

Fig. 6. The Blackhall Rocks Colony.



From these results it is clear that interbreeding is taking place between the two species in these populations. At the Blackhall Rocks, in particular, the structure of the colony is as would be expected if a proportion of F_1 hybrids (mode at 14-15) occurred, together with a large number of back-crosses with *O. spinosa* (mode at 16-18). The structure of the Marsden colony is less variable, and may represent a more advanced state of introgression in which *O. spinosa* has been largely eliminated, though a high proportion of plants belonging to the other parent still remain. A clearer indication of the degree of interbreeding can be gained from the pictorial scatter diagrams in Figs. 5 and 6.

ANALYSIS OF INDIVIDUAL CHARACTERS.

The way in which intermediate characters tend to occur in the same plants is not displayed to full advantage by the pictorial scatter diagrams, owing to the unreliability of leaf measurements as an indication of hybridity. These were the only quantitative characters, amongst those scored, which were sufficiently variable to serve, as the axes in the diagrams. A clearer indication of this tendency for intermediate characters to be associated with each other can be obtained from an analysis of the individual characters which were used in compiling the character sum index, and also from the additional

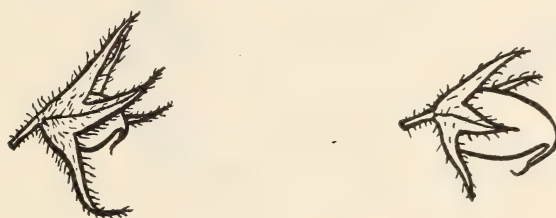


Fig. 7. Mature legume and calyx of *O. repens* (left) and *O. spinosa* (right). $\times 2$.

character of fruit index*. The same pure populations were again used for purposes of comparison. The results for each character, in the hybrid populations, were separated into three groups on the basis of the character sum index, (a) plants scoring under 13 (i.e. resembling *O. repens*), (b) plants scoring 13 to 17 (i.e. intermediate), and (c) plants scoring 18 and over (i.e. resembling *O. spinosa*). The results for leaflet and fruit index are expressed in Fig. 8, and for the remaining characters, with the exception of flower index†, in Table 2. They show an obvious correlation between each character and the character sum index. In all cases (except in the spinous condition at Marsden) intermediate characters are predominantly associated with intermediate plants, and are not distributed throughout most of the individuals in the colony. The occurrence of non-spiny plants of *O. spinosa* (var. *mitis*) at Marsden is shown in Table 2 in which 22.5% of the plants with a character sum index of 18 and over have no spines. This condition is not entirely due to hybridity, for similar plants have been noted in apparently pure populations of this species (e.g. in the Quarrington area – cf. Table 2 in which 2% of the plants which were scored had no spines).

CONCLUSIONS

Two conclusions may be drawn from these results; one relating to the method used in analysing the colonies, and the other to the colonies themselves. In so far as the method is concerned, the results obtained from the analysis of the pure colonies give a clear indication that the characters, when used together, provide a reliable means of separating these two species. The value of the individual characters varies considerably and it is probable that no single character would give a satisfactory separation. Separation of the two species should be equally effective in a mixed colony provided that the species

* A fruit index was obtained by dividing the calyx length by the legume length (see Fig. 7). As mature fruits cannot always be obtained at the same time as well-developed flowers, this character could not be included in the character sum index, which was prepared at the time of flowering. For this reason the analysis of this character was based on the appearance of the plants, whether identifiable as *O. repens*, *O. spinosa*, or intermediate, and not on the character sum index.

† Flower index was omitted because, on analysis, it was found that the relative lengths of the wing and keel showed no significant differences between the two species, in the colonies which were studied. It would therefore appear probable that this character is of no value in separating these two species, though it is sometimes used in floras.

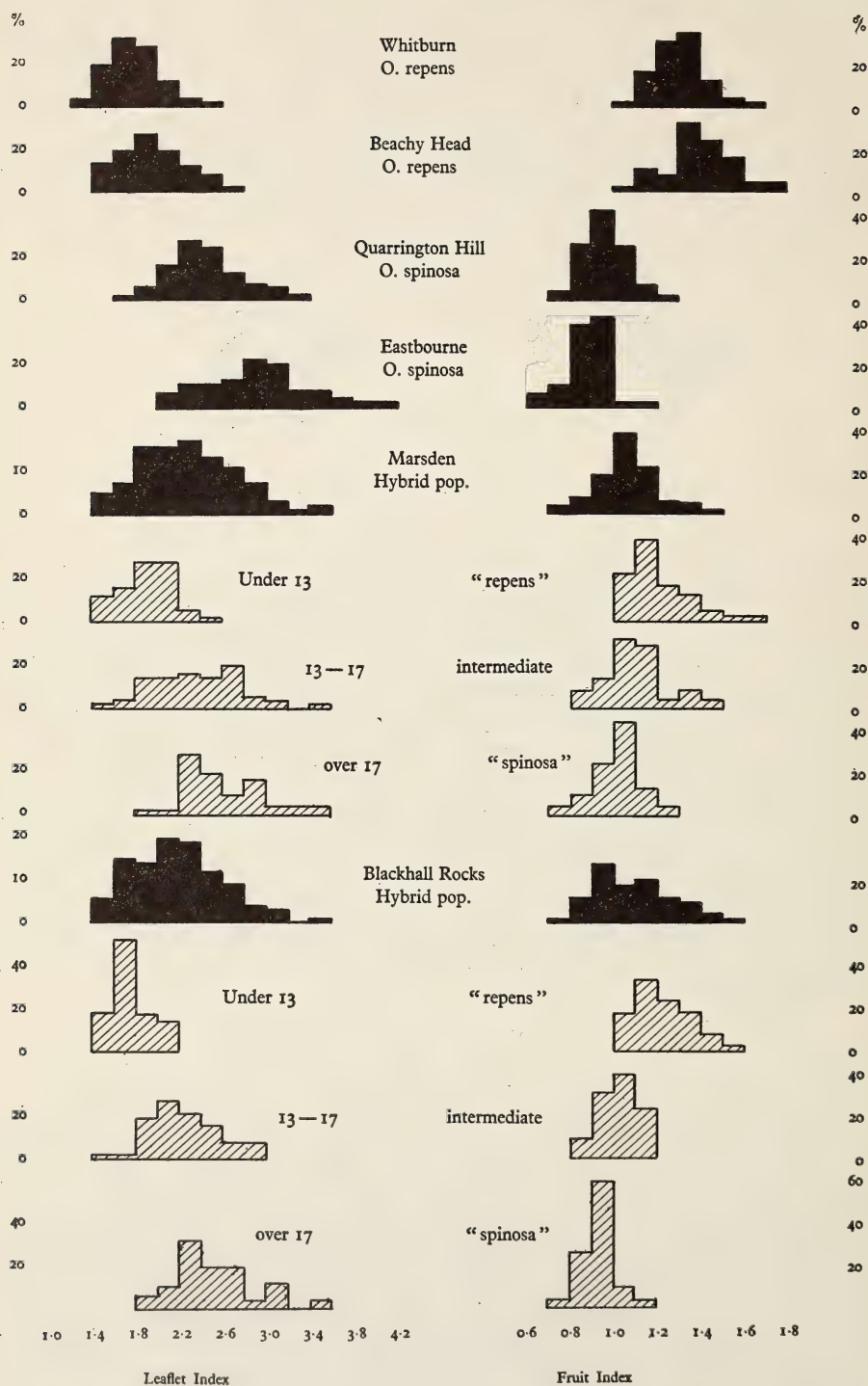


Fig. 8. Frequency distribution histograms for *Leaf Index* and *Fruit Index* in *Ononis*. The position in each of the colonies is portrayed by the black histograms. An analysis of the hybrid colonies (see text) to show association of intermediate characters is portrayed by the shaded histograms.

TABLE 2.

Analysis of characters used in the character sum index. In the case of the hybrid colonies the results are divided, on the basis of the character sum index, into plants resembling *O. repens* (i.e. scoring under 13), intermediate plants (i.e. scoring 13 to 17) and plants resembling *O. spinosa* (i.e. scoring 18 and over).

	Ononis repens		Ononis spinosa		Marsden Colony			Blackhall Rocks Colony					
	Whitburn	Beachy Hd.	Quarrington	Eastbourne	Under 13	13-17	18 & over	Tot. %	Under 13	13-17	18 & over	Tot. %	
Spines	Full	0	0	90	100	0	16.7	59	25	0	40	95	43
	Mid	0	0	8	0	3	13.9	18.5	11	5	32.5	5	17
	0	100	100	2	0	97	69.4	22.5	64	95	27.5	0	40
Line of Hairs	Full	0	0	70	100	0	38	70	34	7.3	46.6	61	21.8
	Mid	16	24	28	0	15.6	43	22.5	28	31	29	29	36.3
	0	84	76	2	0	84.4	19	7.5	38	61.7	45.4	10	41.9
Stem Colour	Red	0	0	98	100	9	38.5	85	41.5	0	45.4	95	45
	Mid	22	12	0	0	30	36	15	28	7.3	45.4	5	23.3
	Green	78	88	2	0	61	25.5	0	30.5	92.7	9.2	0	31.7
Habit	Erect	0	0	98	100	0	52.8	85	44	2.4	51.6	97.5	49
	Mid	0	0	2	0	3	41.5	15	21	9.6	46.6	2.5	23.6
	Repent	100	100	0	0	97	5.7	0	35	88	1.8	0	27.4
Leaf Tip	Acute	0	0	96	100	0	52.8	89	44.5	2.4	67.5	87	53.4
	Mid	2	4	4	0	18	41.5	11	25	16.6	32.5	13	23
	Obtuse	98	96	0	0	82	5.7	0	30.5	81	0	0	23.6

Figures expressed as a percentage

do not hybridise. The results obtained, from both the Marsden and the Blackhall Rocks colonies, show that the two species cannot be clearly separated here, and that a high proportion of intermediate plants occurs in both localities. Further, the analysis of each character shows that characters of an intermediate nature tend to be associated in the same plant, and do not occur at random throughout most of the individuals in the colony. Thus it may be concluded that the range of variability, in the two populations studied, is due mainly to hybridity between the two species, and is not due to variation within the species themselves.

ACKNOWLEDGMENTS

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Key to Symbols Used in the Pictorial Scatter Diagrams

Vertical axis = leaflet length (in mm.). Horizontal axis = leaflet width (in mm.). Each plant is represented by a dot. Characters are denoted by arms ; presence of a character by a full length arm, an intermediate condition by an arm of half the length, and absence of a character by omission of the arm.

! - leaflet tip

! - habit

q - stem colour

/ - line of hairs

\ - spines.

Thus a plant in which all the characters are present will appear as — X and one in which all the characters are absent as — ●

GENERIC CRITERIA IN FLOWERING PLANTS*

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The genus, like the species and the family, is in origin a rather ill-defined concept based on morphological features. It is, and, in spite of the efforts of geneticists, cytologists and orthodox taxonomists, seems likely to remain, to a considerable degree subjective. In consequence genera and generic criteria in different families are by no means comparable; characters which in one family are used for separating genera may appear trifling in comparison with those used for defining sections or even species in another family. In the Ranunculaceae for instance the genera mostly differ from one another in what are usually considered major morphological characters. There are two apparently basically different types of ovary, actinomorphic and zygomorphic flowers occur, and the homologies of the perianth differ in different genera. In the Compositae on the other hand *Carduus* and *Cirsium* are distinguished mainly by the nature of the pappus hairs while *Hypochoeris* and *Leontodon*, so similar in all other respects, are separated by the occurrence of scales on the receptacle in the former. Doubt is thrown on the validity of the latter character by the fact that Babcock & Cave (1938) found that *Rodigia commutata*, distinguished from *Crepis* by the presence of scales on the receptacle, could interchange genes freely with *Crepis foetida*. The inference is that these two plants, far from being genetically distinct, are in fact more closely related than many of the species traditionally included in the genus *Crepis*. It would seem therefore that re-investigation of the validity of the pairs of genera *Hypochoeris* and *Leontodon*, and *Anthemis* and *Matricaria* is desirable. I would venture to suggest that apparently trivial floral characters should be used for distinguishing genera only when the taxa thus circumscribed also differ in several other, perhaps less easily definable, features.

Indeed I believe that many of the older taxonomists regularly adopted this practice. The best of them spent many years studying the external features of plants with great patience and skill, untroubled by thoughts of cytology, genetics, ecology or physiology. They formed the opinion, probably based more or less subconsciously on a host of vegetative as well as floral characters, that certain species belonged together in one genus. They knew from experience that reproductive parts vary much less than vegetative ones so that, having mentally formed their genus largely on general 'look,' they searched for some reproductive character to define it.

This procedure worked well on the whole, but from time to time the rigid application of a minor floral feature has led to the inclusion of occasional species in the wrong genus. A case of this kind seems to me to have arisen in *Lathyrus*, which in its reproductive parts closely resembles *Vicia*.

The genera are separated technically by the staminal tube being obliquely truncate and the style either downy all round, glabrous, or bearded below the stigma in *Vicia*. In *Lathyrus* on the other hand the staminal tube is transversely truncate and the style bearded on its upper side. Incidentally, in the 3rd edition of Hooker's *Students' Flora* (1884) these characters are mixed up, the obliquely truncate staminal tube of *Vicia* being attributed to *Lathyrus* and *vice versa*, a good indication of how little attention working taxonomists pay to such characters.

As Corner (1954) has pointed out, *Lathyrus* and *Vicia* differ in the nature of their

* This paper was read at a meeting of the Systematics Association at Edinburgh.

leaflets. In *Lathyrus* these are basipetal with the result that they commonly have three prominent vascular bundles, the lateral ones arising near the base and running almost the whole length of the leaflet, while in *Vicia* the venation is of the normal pinnate type. This is a character of developmental as well as morphological significance and one which in my opinion should be taken into account in defining the genera. An additional vegetative character, possibly associated with the tendency to reduction in the leaf surface, is the development of wings of tissue from the angles of the stem in *Lathyrus*. *Lathyrus niger* is an example of one of the few species in which floral and vegetative characters do not agree. Here the flowers are those of a *Lathyrus* but the leaflets and unwinged stems suggest a *Vicia*. Perhaps the happiest solution is to put it, as has been done in the past, in a separate genus, *Orobus*.

The satisfactory recognition of genera by the traditional method of using macroscopic morphological characters of the reproductive parts becomes difficult or impossible in families where there is extreme reduction or great uniformity of pattern in these parts.

A good indication of this difficulty is obtained by comparing the number of genera recognised in certain families in the 18th century and at the present time. To simplify the comparison and to make it more exact it will be confined to British genera. In the Ranunculaceae, where generic differences are large and obvious, the numbers are the same, if we exclude *Nigella*, as even now scarcely naturalised, and *Eranthis*, a recent introduction.

In the Papilionaceae, where the floral pattern is more uniform but the fruit still varied, if we make the same allowances the number of genera is also the same.

In the Umbelliferae with small and very uniform flowers and somewhat inconspicuous fruit characters there is a considerable difference. In the 18th century 32 genera were recognised as British, while excluding, once more, recent introductions, 40 genera are now listed. The change has in fact been greater than these figures suggest as the British representatives of *Anethum* and *Athamanta* are now separated from those genera and *Imperatoria* and *Phellandrium* are no longer recognised as distinct. This change, while in part due to more careful study along traditional lines, no doubt owes something to the improvement in lenses and the increased use of the dissecting microscope.

Taking the Gramineae as an example of a family with small and very reduced flowers, fruits showing little variety superficially, and vegetative parts which appear to conform to a common pattern, we find, as would be expected, an even greater difference.

Withering (1796) gives 24 genera which include most of the species (and in some genera several more) and nearly all the genera which are today regarded as forming the 56 genera recognised as British. The change has once again been due to more detailed examination, and to some extent to the use of the compound microscope, combined with the recognition of the fact that resemblances in the inflorescence and even in the gross morphology of the spikelet are not necessarily criteria for making a satisfactory classification of plants with inflorescences as reduced as these.

An excellent example of this is the genus *Parapholis*. The British species were originally put in *Rottboellia*, together with tropical species now included in the tribe Andropogoneae. This genus was defined by characters of the inflorescence and was in reality a highly heterogeneous one. Later the British species were transferred to *Lepturus*, which after many vicissitudes was eventually shown by Hubbard (1946) to be only slightly less heterogeneous than the original *Rottboellia*. Using all the available characters, including microscopic ones such as starch-grains, silica cells and chromosome number and sizes, he showed that the species included in *Lepturus* and the comparatively recently but unsatisfactorily distinguished genera *Pholiurus* and *Monerma* should in fact be placed in five genera and no fewer than three tribes.

It is interesting to note that Hubbard started on this investigation because *Lepturus*, as then delimited, contained a mixture of temperate and lowland tropical species, so that phytogeography in this instance gave a clue to an unsatisfactory taxonomic situation.

The Gramineae, on account of their economic importance as well as their intrinsic interest, have been studied in more detail than most families of flowering plants. For the reasons just indicated, taxonomists have been driven to search for generic criteria which can be used in addition to the customary reproductive ones. This search has been remarkably successful and, since there is no reason to believe that the family is unique in this respect, it seems worth mentioning the kind of characters which have been found useful. There is in fact every reason to suppose that vegetative characters can be profitably used, with due caution, in most if not all families.

Duval Jouve and later Prat were the first to make a thorough study of the systematic value of epidermal characters and other anatomical features in the Gramineae, and so to provide a number of new generic and specific criteria which have since been used to good effect. The shape and orientation of silica cells, the type of hair or papilla, the shape of the stomata, and the general pattern of the epidermis all help in characterising not only genera but tribes and subfamilies. The distribution of green tissues in the leaves and the occurrence of simple or compound starch grains in the endosperm are also characters of major taxonomic importance. In groups where the vegetative as well as the reproductive parts are extremely reduced and all conform to a single pattern in their gross morphology microscopic characters of the epidermis and internal tissues may prove of great value.

Salicornia, which is said to be cosmopolitan on coastal and inland saline soils, may well be like one of the form genera of palaeobotanists. A preliminary examination of the epidermis of *S. dolichostachya*, *S. perennis* and the Mediterranean species, *S. macrostachya*, shows differences which may be significant.

The value of cytology in helping to define the limits of genera and subgenera and sometimes, as in Ranunculaceae (Gregory, 1941), in grouping genera into tribes, is well known. The value of the basic number as a generic criterion varies considerably in different families. In the Cruciferae, Manton (1932) has shown that cytology on the whole confirms the classification of traditional taxonomy, a conclusion which must greatly strengthen our faith in the reality of genera, at least in this family. She was also able to provide guidance about the separation or union of six pairs of genera about which varied views had been held by taxonomists and to point out a number of other genera in which systematic revision or further cytological work was desirable.

A point of particular interest is that the taxonomic changes made by Schulz in his revision of the family in *Das Pflanzenreich* are supported by the cytological evidence. The changes that Schulz made were mainly the result of his use of the number and orientation of the nectaries and the presence or absence of branched hairs as generic criteria, and it is striking that criteria as diverse as these comparatively trivial ones and the basic chromosome numbers should be in such good agreement.

In the Chenopodiaceae on the other hand the basic number 9 appears to be of universal occurrence, except for *Spinacia* with $x = 6$, and is therefore of no help in settling generic limits. In the Gramineae there is a variety of basic numbers which help mainly in the delimitation of tribes or subfamilies. Chromosome numbers have however confirmed the correctness of the separation of *Puccinellia* from *Glyceria*, the basic number being 7 in the former and 10 in the latter, and have led to a more thorough morphological examination of these genera with the result that they are now placed in different tribes. The occurrence of the basic number 10 in *Catabrosa*, another genus until now classified in the tribe Festuceae has stimulated a re-investigation of its morphology which, as might be expected, has revealed a close similarity to *Glyceria*.

In using cytological criteria it is of course a great help if information is available about the kind of relationship between the different basic numbers which sometimes occur within a genus, as this may enable a decision to be made about their taxonomic significance.

Chromosome size is generally of more value as a guide to larger classificatory units such as tribes, subfamilies or families, than as a generic criterion, though it may indicate genera which require investigation anew. For instance *Brachypodium* is reported to contain species with large chromosomes and others with small ones, and has three different basic numbers, 7, 9 and 15; it is therefore highly probable that once again superficial similarities mask fundamental differences.

It seems desirable, though possibly unnecessary, to point out once again that taxonomists using cytological data should do so with great caution. Many of the earlier chromosome counts are quite misleading: for instance the first counts made on *Glyceria* (Stählin, 1920) included the numbers 28 and 56 for *G. maxima*, while the true number is without doubt $2n = 60$. Some of the apparent discrepancies in chromosome number are almost certainly due to mistakes in identification of the plants on which the counts were made, mistakes which cannot now be rectified as cytologists rarely keep specimens.

In some families, for example Orchidaceae and Gramineae, a number of naturally occurring intergeneric hybrids are known and others have been made artificially. This situation seems to be regarded by most taxonomists as just one of those things which sometimes happen, but which do not invalidate the genera concerned. Geneticists on the other hand quite naturally regard the possibility of gene-exchange as of far greater importance than any number of morphological dissimilarities. Failure of two plants to cross may be due to a single gene or may, at the other extreme, be due to a totally different genetical make-up. The sterility barrier, from whatever cause it arises, obviously has an evolutionary significance, and it is with this that the geneticist is concerned. Unless, however, sterility is accompanied by some perceptible degree of differentiation the taxonomist, who is concerned with classifying organisms as they exist today, cannot be expected to take note of it.

The question of the treatment of genera between which some hybridisation is possible is bound up with the fundamental assumptions on which our scheme of classification is based. This scheme is basically a morphological one, on to which varying amounts of phylogenetic speculation (it cannot be called fact) have been grafted by different workers. At the species level solid facts about phylogeny are sometimes available. For genera and higher taxa definite unambiguous information about evolutionary relationships is rarely obtainable and there seems no great prospect of getting it in the future.

It seems impossible to make a firmly based phylogenetic classification, and even if we could do so it would probably prove highly inconvenient, though interesting. In view of this I think that, while we should pay due attention to what genetical evidence is available, we should not utterly disrupt parts of our classification to incorporate it, while the major portion has to remain on a morphological basis.

Turning once more to the Gramineae for examples, in the tribe Hordeae Stebbins and his co-workers have made a series of intergeneric hybrids connecting up all or nearly all the genera so that, from the genetical point of view, the numerous and diverse species included in this tribe should be regarded as forming a single genus. This seems to me to be an unjustifiable conclusion. What Stebbins has shown is that the plants included by taxonomists in the Hordeae form a natural group related phylogenetically to one another. During the course of evolution changes have occurred which have produced a considerable degree of morphological and ecological diversity but which do not happen to have given rise to sterility barriers. The absence of these barriers is of significance from the point of

view of genetics and evolution but, by itself, is no argument for demolishing genera. It is as if we said that unless one particular type of morphological change occurred in the course of evolution we would not regard any other differences, however great, as justifying the recognition of genera.

The taxonomist can and should make use of genetical evidence to improve his classification, bearing in mind that it is a general purpose one and not primarily a geneticist's one. Hybridisation experiments in the *Hordeae* support the separation of *Hordelymus* and throw light on the genus *Agropyron*, to take two examples of interest to British botanists. *Agropyron*, as represented in this country includes two non-rhizomatous species and three or perhaps four rhizomatous species. These two groups of species have been placed in separate genera, *Roegneria* and *Elytrigia*, the latter differing from the former in having spikelets which fall entire at maturity, instead of the glumes remaining attached to the rachis, larger anthers, deeply grooved caryopses and long rhizomes. Interspecific hybrids though usually, if not invariably, sterile occur commonly within these genera, and species of *Elytrigia* are known to cross with *Elymus* and *Hordeum*. There appear, however, to be no records of hybrids between the British species of *Roegneria* and *Elytrigia*. These facts suggest that the relationships between the two genera, though they are morphologically similar, may not be particularly close. In this particular group inter-generic sterility appears to be a character of positive value and brings the number of correlated characters available for separating *Roegneria* and *Elytrigia* up to at least five.

On the other hand when the intergeneric hybrid between *Festuca pratensis* and *Lolium perenne* (known as $\times$ *Festulolium loliaceum*) and its parents are re-examined it is found that the generic characters are all associated with the form of the inflorescence. In *Festuca* this is a more or less branched panicle and the spikelets have two glumes. In *Lolium* the inflorescence is typically a spike and, except in the terminal spikelet, one glume is suppressed; however forms of *L. perenne* with branched inflorescences occur not infrequently, and here the spikelets have two glumes. Such plants are difficult to distinguish from *Festuca* except by the rather more strongly compressed spikelets. Here the genetical evidence for a close relationship between *Festuca pratensis* and *Lolium perenne* is supported by the morphological evidence, and the probability is that the generic limits have been wrongly drawn. There seems to me to be no doubt that *Lolium perenne* should be included in *Festuca*, leaving *Lolium temulentum* and allied annual species in *Lolium*, though the whole problem requires a thorough re-investigation.

The case of *Ammophila* and *Calamagrostis* is even clearer. Though the two genera look different, the difference is due to the fact that *Ammophila* has short panicle branches and large spikelets while *Calamagrostis* has long panicle branches and small spikelets; the details of spikelet structure are extraordinarily alike in both. There is nothing but a well-established tradition to prevent us from following the genetical indications and returning *Ammophila* to its old place as a species of *Calamagrostis*, and it is time we broke from tradition here.

To sum up, I would suggest that genera should be delimited by as many different but correlated characters as possible and that careful consideration should be given to the validity of genera where the number of characters involved is small, even though these be reproductive and therefore traditionally respectable ones. In fact genera should be recognisable at sight, at least in the great majority of cases.

The characters which can be used in addition to those of the flower and fruit are cytological, genetical and anatomical ones: geographical distribution and the duration of the plant may also be useful in certain groups. These criteria are not of equal importance in different families and an attempt should be made to assess their validity for the genera being investigated.

However much time one may waste in trying to define a genus or to standardise generic criteria, the personal opinion of individual taxonomists is bound to come in. It is in fact remarkable that so large a measure of agreement about generic limits exists. I, personally, like fairly "small" genera for two reasons: first there is a greater chance of them representing natural, that is to say phylogenetic units, and, second if they are reasonably homogeneous they are more easily recognisable and therefore more convenient. I have not talked about convenience before but, in the absence of a reliable phylogenetic system, convenience is perhaps the most important thing to aim at in a general purposes classification.

A consideration of some of the British representatives of the tribe Scirpeae of the Cyperaceae may help to illustrate the use of a number of these criteria and also demonstrate the importance of the personal factor.

Hooker (1884), and more recently Hutchinson (1934), group the British species of this tribe in three genera, *Eleocharis*, characterised by the persistent style-base, *Eriophorum*, with generally numerous bristles which elongate and become silky in fruit, and *Scirpus*, with neither of these characters. The flowers are closely similar in all the species, apart from the bristles, which vary from none to many and from long to short, and the occurrence of the swollen style-base in some species. On the other hand the inflorescence and more especially the vegetative parts show a considerable range of structure.

If one adopts the broad Hooker view of *Scirpus*, covering plants as different vegetatively as *S. setaceus*, *S. lacustris*, and *S. sylvaticus* and others, such as *S. pauciflorus*, which only differ from *Eleocharis* in the absence of the swollen style-base, it is logically impossible to separate *Eleocharis* and very difficult to maintain the distinctness of *Eriophorum*. Thus Lid in *Norsk Flora* (1952) recognises only *Eriophorum* and *Scirpus*. If on the other hand the nature of the inflorescence and vegetative and anatomical characters are used, *Scirpus* sensu Lid can be divided into eight genera each of which can be recognised at sight.

The cytological evidence is less complete than could be desired and some counts are open to doubt, largely owing to the technical difficulties of the group, but using what appear to be reliable figures we find the basic number 29 for *Eriophorum* and for *Scirpus* (sensu Lid) 10, 11, 13, 21, 29, 31 and 43. The following table shows the haploid chromosome numbers of seven of the eight genera into which *Scirpus* is divided, using vegetative and inflorescence characters, in the *Flora of the British Isles* (1952):

TABLE 1

Genus	Basic chromosome number
<i>Trichophorum</i>	13, 29
<i>Eleocharis</i>	8, 10, 19, 23 (perhaps aneuploid)
<i>Scirpus</i>	31, 43, 55 (perhaps aneuploid)
<i>Holoschoenus</i>	—
<i>Blysmus</i>	11
<i>Schoenoplectus</i>	21
<i>Isolepis</i>	13
<i>Eleogiton</i>	10

It will be seen that the cytology, as far as it goes, supports the genera based on non-floral characters on the whole, though the present classification is not altogether satisfactory. The haploid number 29 in *Trichophorum* refers to *T. alpinum* which has been put in *Eriophorum*, to which genus it would seem properly to belong. The size of

the chromosomes will probably help to settle some points, and there seems no doubt that the classification of the Scirpeae could be put on a sound basis, following the general lines indicated, by further cytological and anatomical investigation.

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TAXONOMIC STUDIES IN THE GENUS *CERASTIUM*

II. *CERASTIUM SUBTETRANDRUM* (LANGE) MURB.

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This species was first described from Scandinavian material and is generally regarded as having a predominantly S. Swedish distribution. It has, however, been reported from time to time as occurring in the British Isles. An examination of material in the Druce Herbarium, Oxford University, showed that the determination of specimens labelled with this name was doubtful. For example, one sheet has specimens which Druce sent to Murbeck for verification and which he returned with his opinion that they belonged to *C. atrovirens* Bab. Nevertheless, these were labelled as *C. subtetrandrum* by Druce and included in his herbarium under this name. Doubt has also been thrown in the past on the correctness of the determination of material included under his name in other herbaria. A close examination of material collected in Sweden and determined by Murbeck, who first described the species, showed that there exist a number of differences between it and British material determined as *C. subtetrandrum*. The seed size of the Swedish material appeared to be smaller whilst the pollen size was larger. The petals also were much broader in relation to their length in the Swedish material. Other characters, said to be of diagnostic value, were also examined but were found not to be correlated. These latter characters were seed colour, the ratio sepal-length petal-length and plant colour. The seeds of *C. subtetrandrum* are said to be light in colour whilst those of *C. atrovirens* are dark brown (Murbeck, 1898). Fresh Swedish material of *C. subtetrandrum* was examined and found to have pale yellow-brown seeds; herbarium material, often of some age, of plants from similar habitats usually was found to have similar coloured seeds. Some specimens, however, had seeds of a much darker colour, but it was noticed that these specimens had become damp and that decay had set in at some time subsequent to their collection. The darker colour of these seeds may be due to this decay. The colour of freshly gathered *C. atrovirens* seeds is usually dark reddish brown but some plants have paler seeds. These latter plants are usually from the north of the British Isles.

The sepals of the Swedish material were found to be much longer than the petals and usually more pointed than the sepals of most plants of *C. atrovirens*. However, some plants of *C. atrovirens* were also found to have sepals much larger than the petals and this character was found to be scattered throughout the British *C. atrovirens* population.

A personal communication from Bengt Pettersson stated that *C. subtetrandrum* is always a paler and more yellow green than *C. atrovirens*. Plants were grown from seed taken from plants determined by him and also checked by the discriminant analysis which follows. These plants were found to vary in colour and growth form in relation to light intensity as did other *Cerastia* (Whitehead, 1956) – the higher the light intensity the more anthocyanin, etc. Since *C. subtetrandrum* is usually found growing amongst grasses on the edges of dunes rather than in the exposed situations more common for *C. atrovirens* this may account for the observation that *C. subtetrandrum* is usually of a paler and more yellow shade of green.

A discriminant analysis, as described in the previous paper (Whitehead, 1955), has

been calculated in order to distinguish between *C. atrovirens* and *C. subtetrandrum* and the results are given below. The specimens of *C. subtetrandrum* used in this analysis were all from Scandinavian localities and many of them were originally determined by Murbeck himself. The *C. atrovirens* were determined by the preceding discriminant analysis. The characters used were :-

- (1) Seed size as defined before (x) Table 2 (Whitehead 1955)
- (2) Pollen size as defined before (y) Table 1 (Whitehead 1955)
- (3) Length/Breadth ratio of petals (h) (see Table 1).

TABLE 1
Critical values of the ratio petal-length/petal-breadth

01	2.518	21	2.878	41	3.238	61	3.598	81	3.958
02	2.536	22	2.896	42	3.256	62	3.616	82	3.976
03	2.554	23	2.914	43	3.274	63	3.634	83	3.994
04	2.572	24	2.932	44	3.292	64	3.652	84	4.012
05	2.590	25	2.950	45	3.310	65	3.670	85	4.030
06	2.608	26	2.968	46	3.328	66	3.688	86	4.048
07	2.626	27	2.986	47	3.346	67	3.706	87	4.066
08	2.644	28	3.004	48	3.364	68	3.724	88	4.084
09	2.662	29	3.022	49	3.382	69	3.742	89	4.102
10	2.680	30	3.040	50	3.400	70	3.760	90	4.120
11	2.698	31	3.058	51	3.418	71	3.778	91	4.138
12	2.716	32	3.076	52	3.436	72	3.796	92	4.156
13	2.734	33	3.094	53	3.454	73	3.814	93	4.174
14	2.752	34	3.112	54	3.472	74	3.832	94	4.192
15	2.770	35	3.130	55	3.490	75	3.850	95	4.210
16	2.788	36	3.148	56	3.508	76	3.868	96	4.228
17	2.806	37	3.166	57	3.526	77	3.886	97	4.246
18	2.824	38	3.184	58	3.544	78	3.904	98	4.264
19	2.842	39	3.202	59	3.562	79	3.922	99	4.282
20	2.860	40	3.220	60	3.580	80	3.940	100	4.300

From this analysis the values of λ were found to be :-

$$\lambda_1 = + 32.9449$$

$$\lambda_2 = - 84.5845$$

$$\lambda_3 = + 25.8831$$

The mean values of F were as follows :-

$$\bar{F} \text{ } C. \text{ atrovirens} = - 41.8732$$

$$\bar{F} \text{ } C. \text{ subtetrandrum} = - 2280.2617$$

It follows therefore that specimens for which a value of F greater than -1.161 should be allocated to *C. atrovirens* and those for which the F value is less than -1.161 should be allocated to *C. subtetrandrum*. The distribution of the values of F for the specimens used is shown in Fig. 1. It was found that complete separation was obtained and that there is complete bimodality in the distribution of F values.

An examination of the values of F for the specimens of *C. atrovirens* is of interest since it is found that those with the lowest values, i.e. those specimens which in respect of the characters used are most like *C. subtetrandrum*, are from localities in the North of Britain, where *C. subtetrandrum* has been from time to time reported as occurring. An examination, however, of British material determined as *C. subtetrandrum* showed that

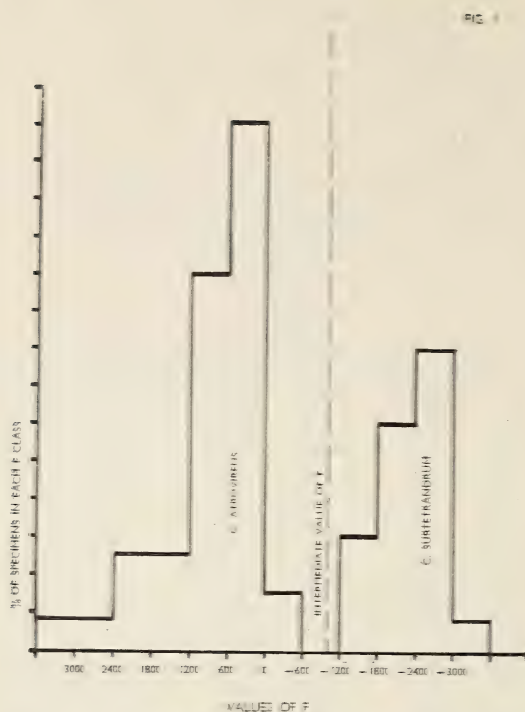


Figure 1. Histogram showing distribution of F values for *C. atrovirens* and *C. subtetrandrum*.

these specimens should be, on the basis of this analysis, allocated to *C. atrovirens*. No specimens from the British Isles, so far examined, can be regarded, on this basis, as belonging to *C. subtetrandrum*. It is considered that *C. subtetrandrum* has not, so far, been shown to occur in Britain.

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REVIEWS

Grasses. A Guide to their Structure, Identification, Uses, and Distribution in the British Isles. C. E. Hubbard. Pp. xii + 428 with 159 full-page line drawings. Pelican Book series. Penguin Books Ltd., Harmondsworth, Middlesex, 1954 ; 3s. 6d. (with paper cover) or 8s. 6d. (bound).

Grasses are the most important members of the world flora, possessing a wide distribution and being of the greatest economic value to man. Numerous papers have been devoted to the study of them from different aspects and many books have been written in the past about their identification, uses, etc. For a long time, however, there has been a need for a modern popular book on British grasses which incorporates the results of the latest studies and which could be used also for their identification.

The desideratum has been fulfilled by C. E. Hubbard, one of the world's leading grass experts, who is in charge of the grass collection at the Kew Herbarium. He has produced the most comprehensive work ever published on British grasses, which is rich in contents, masterly written, easy to read and to understand.

This book deals with nearly all species of grasses, including hybrids and well-established aliens, in the British Isles. In all, 152 grasses are fully described and illustrated in full-page plates, each of which shows the habit of the plant, a ligule, a spikelet and parts of the spikelet. All drawings are original, accurate from the scientific point of view, and of high artistic standard. The drawings of the ligules and spikelets and the detailed analyses of the structure of the spikelets have been most precisely reproduced by Miss Joan Sampson from the author's excellent pencil drawings and they are of sufficient magnification to show the structure quite distinctly. She has depicted also the habits of grasses with great skill. There is no doubt that these drawings will be of great benefit to students who are interested in the structure of floral organs in grasses. They will be also of great assistance to beginners who may identify specimens by comparing them with drawings, especially as the drawing of each species is on the opposite page to the description.

The drawings are accompanied by comprehensive and extremely good descriptions of individual grasses, which are supplemented by accurate measurements of the vegetative and floral organs. Since the descriptions are set out in a uniform manner, comparison of the plants with them is simple. The descriptions end with the diploid chromosome number, if it is known. It would have been useful if the author had pointed out which of the chromosome numbers refer to British material. The chromosome numbers of British material may differ from those of specimens elsewhere, e.g. *Sieglingia decumbens* $2n = 124$ (in British material), 18, 36 (foreign); *Puccinellia maritima* $2n = 63$ (in British material), 56, 70 (foreign); *Hierochloë odorata* $2n = 28$ (in British material), 42, 56 (foreign). Such an indication might have stimulated somebody to undertake cytological investigations of particular grasses. It should be noted that the majority of the British grasses have not yet been studied cytologically.

The descriptions are followed by short notes on habitat, distribution in the British Isles and abroad, time of flowering, variation, relationships, etc. They often also include details of the most important subspecies and varieties, as well as closely related rare aliens, with their essential characters.

For students, who wish to identify rapidly an unknown grass, several keys for identification are given. Before proceeding to use them, the student should fully understand the structure of the different organs and some technical terms. The technical terms, which the author was unable to avoid in descriptions and keys, are explained in the text and by line drawings in the chapter "The structure of grasses" and in the glossary at the end of the book. Great care has obviously been taken by the author in the construction of the keys, in which the most striking and contrasting characters are used. The main key can be used for identification when the specimen is complete and mature. For naming incomplete material of the common grasses two other keys are provided: for immature specimens – based on vegetative characters, and for fruiting specimens – on "seed" characters. The use of these keys is explained in separate chapters: "Vegetative characters of grasses" and "The 'seeds' of grasses."

A special chapter includes the classification of grasses under habitats. This classification, combined with the brief notes at the foot of the plates, indicating the degree of frequency and the type of habitat, will be of great assistance to all who wish to study grasses from an ecological point of view.

Another chapter deals with the uses of grasses and it includes "Cereals in Britain" (with a key), "Herbage grasses," "Lawn grasses" (with a key) and "Ornamental grasses." This chapter will be of special interest to agriculturists and horticulturists.

In addition, the author has given a short introduction to the classification of grasses, and has demonstrated how grasses can be distinguished from rushes and sedges.

The book concludes with a classified and well-selected bibliography and indexes to both common and botanical names, including synonyms.

The botanical nomenclature is up-to-date in this treatment. It is, with a few exceptions, in agreement with that used in Clapham, Tutin and Warburg, *Flora of the British Isles*, 1952.

A few of the botanical names given will be new to most botanists. These changes are due either to compliance with the international rules of botanical nomenclature, e.g. *Calamagrostis stricta* instead of *C. neglecta* and *Bromus diandrus* instead of *Bromus gussonii*, or to a new generic position, as in *Catapodium marinum* and *C. rigidum* (cf. Dony, *Flora of Bedfordshire*, 1953). In some instances the author has considered some grasses, treated as subspecies in the *Flora of the British Isles*, as separate species, e.g. *Festuca tenuifolia*, *Poa angustifolia* and *P. subcaerulea*. He has included *Koeleria albescens* under *K. gracilis* and *Poa irrigata* (*P. pratensis* subsp. *irrigata*) under *P. subcaerulea*. All these changes are well-grounded. It should be mentioned that the author has not followed Tutin in the splitting of the genus *Bromus*.

Special attention has been paid to the sterile inter- and intra-generic hybrids recorded from the British Isles. There are mentioned 8 intergeneric hybrids, viz. *Agrostis* x *Polypogon* (1), *Ammophila* x *Calamagrostis* (1), *Festuca* x *Lolium* (5) and *Festuca* x *Vulpia* (1); the latter is a new addition to the British flora. Since the publication of this book, Hubbard and Sandwith (cf. *Proc. B.S.B.I.*, 1, 387, 1954) have added to them another intergeneric hybrid, *Agropyron* x *Hordeum* (the putative parents of which are *Agropyron repens* and *Hordeum secalinum*). Hubbard discusses also about 24 interspecific hybrids, between species of the genera *Agropyron*, *Agrostis*, *Alopecurus*, *Bromus*, *Festuca*, *Glyceria*, *Poa* and *Puccinellia*.

The list of species treated in this book is nearly complete. Of native species, only *Bromus benekenii*, which has been neglected in all recent British works, may be added to it.

The author is to be congratulated on this contribution to our knowledge of British grasses which deserves the greatest admiration. It is a standard work which will never lose its importance to students either in Britain or abroad. It is very cheap, but its scientific value is very high. This book can be unreservedly recommended for use not only to botanists, but also to agriculturists, horticulturists, teachers, students and to all beginners who wish to learn this group of plants.

A. MELDERIS

Origin and distribution of the British flora. J. R. Matthews. Pp. vi + 167, 6 maps in text. Hutchinson's University Library, London, 1955. 8s. 6d.

Professor Matthews has presented in a very convenient form an excellent summary of the work carried out during the last fifty years by quaternary geologists, plant geographers, and the workers in that relatively new, but by now well-known, field of pollen analysis to which Godwin and his students have contributed so much. This book gives a brief survey of the British flora of pre-glacial times, and then deals with the effects of the Ice Age with its glacial and inter-glacial periods, the re-establishment of the flora in late- and post-glacial times as seen chiefly by the study of macroscopic sub-fossils and pollen grains in peat, the changes in distribution which have taken place in historical times, and the study of the present flora as geographical elements which may be related to their continental distribution.

A word of caution should perhaps have been offered so that the reader does not assume that the remains in the Cromer Forest Bed were necessarily preserved in situ, for geologists are by no means unanimous on this point, as some of the wood in the deposits shows signs of being considerably water-worn, and it may, therefore, have been carried with some of the fruits from what is now continental Europe and deposited in one of the quiet backwaters near the mouth of the original Rhine, to become preserved with some genuine members of the British flora.

According to Tutin and Warburg (*J. Bot.*, 1932) the species of *Sibthorpia* in the Azores is *S. africana* and not *S. europaea* as stated in Chapter III. It is to be regretted that the recent paper by Pigott and Walters on discontinuous distributions of species of open habitats in the *Journal of Ecology* did not receive more than a bare mention in connection with the possibly more widespread distribution in Britain of the members of the continental southern element.

This book has been well produced within the limits set by a low-priced edition, with the exception of Map 1 which was poorly reproduced in several copies which were examined, and it would have been a great help to have had the titles of the papers in the list of references.

P. J. WANSTALL

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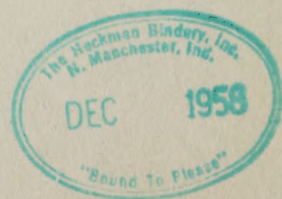
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